Title

The Foraging Ecology and Ecomorphology of Extant and Extinct Pinnipeds

Author

Valenzuela Toro, Ana Margarita

Publication Date

2022

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

THE FORAGING ECOLOGY AND ECOMORPHOLOGY OF EXTANT AND EXTINCT PINNIPEDS

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

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Ana M. Valenzuela Toro

June 2022

The Dissertation of
Ana M. Valenzuela Toro is approved:

Professor Paul L. Koch, Chair

Professor Daniel P. Costa

Professor Rita Mehta

Nicholas D. Pyenson, Ph.D.

Peter Biehl
Vice Provost and Dean of Graduate Studies

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

THE FORAGING ECOLOGY AND ECOMORPHOLOGY OF EXTANT AND EXTINCT PINNIPEDS

Ana M. Valenzuela Toro

ABSTRACT

As large-bodied predators, pinnipeds (seals, fur seals, sea lions, and walruses) play essential roles in the structure and function of marine ecosystems through consumer-prey interactions. Solid knowledge of their foraging ecology and trophic niche is critical to investigating changes in the structure of ecosystems over time. Diverse studies have shown that extant pinnipeds display divergent foraging strategies and habitat preferences. However, it is not well understood what mechanisms underlie these different strategies, nor how they have evolved and affected community structure. In this dissertation, I use stable isotope and morphometric analyses on museum specimens to examine the foraging ecology, niche segregation, and ecomorphology of extant pinnipeds and to uncover how extinct pinnipeds partitioned their ancient communities and how these dynamics compare to modern ones.

In this dissertation, I show that sympatric otariids across the North Pacific and the Southern Hemisphere display distinct foraging modes, consistent with energetic tradeoffs associated with their body size disparities. Fur seals predominantly feed offshore and on pelagic food webs, whereas sympatric sea lions rely on nearshore and benthic resources, resulting in comparable niche segregation patterns across regions and stressing the driving role of body size in otariids' foraging behavior and niche

partitioning. I also conducted an exhaustive examination of sympatric otariids from the eastern North Pacific, the most diverse otariid community in the world. I demonstrate that California sea lions (*Zalophus californianus*), Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*), and Guadalupe fur seals (*Arctocephalus townsendi*) display significant differences in their size, feeding morphology, and foraging. Body size and feeding morphology are not related to foraging at the intraspecific level in a consistent way. However, when species and sex identity are excluded, foraging is significantly related to body size and feeding morphology emphasizing their underlying role in niche segregation at the community level.

In a closer examination of California sea lions, I show that male sea lions from the North Pacific have significantly increased rather than decreased their body size over the last five decades of population recovery. These surprising results demonstrate that body size decrease is not a general response to increased resource competition during the recovery of marine mammals and reveal how density-dependent sexual and natural selection might affect body size, feeding morphology, and in turn the foraging ecology of marine predators.

Little is known about how pinniped foraging ecology and niche partitioning have evolved over geologic time, and additional quantitative and comparative studies are needed to test palaeoecological hypothesis based on comparative morphology. Before addressing this subject, I first examined the modes and trends of the pinniped fossil record. My co-authored work demonstrates that the pinniped fossil record is adequate and does not show significant biases, validating its suitability for paleoecological investigations. Then, by conducting stable isotope analysis on fossil tooth enamel of fossil pinnipeds from Southern California and western North Atlantic, I reveal that fossil

pinniped assemblages had foraging patterns analogous to those described in modern communities (i.e., with nearshore and offshore foraging modes). These results suggest that these foraging modes were acquired in pinniped communities early in their evolutionary history, hinting that niche partitioning has contributed to the structure of pinniped communities over time.

DEDICATION

A mis padres, por su constante apoyo y

darme las herramientas para emprender mi propia aventura

ACKNOWLEDGEMENTS

I would like to start by extending my deepest gratitude to my advisors, Drs. Paul Koch and Daniel Costa for their endless support and mentoring over the last six years. Learning from you has been an extraordinary experience, and nothing that I have accomplished here would it be possible without your insightful guidance. Paul, your encouragement to think hard, pay attention to details, learn from mistakes, and tackle questions in creative ways have been transformative. I do not doubt that I will continue to benefit from this experience for the rest of my career. Likewise, Dan, thank you for accepting me to your lab and sharing your enthusiasm and wisdom for marine mammals. I have truly enjoyed learning the wonders of marine mammals' ecology and physiology from you. I hope someday we will be able to describe new fossil elephant seals together.

I want to thank my committee members, Drs. Rita Mehta and Nicholas Pyenson for their support and enthusiasm for my research and professional development. Rita, thank you for being a fantastic researcher, instructor, mentor, and human being. I have enjoyed all and each of our conversations, and I sincerely value your encouragement to trust in my judgment and advocate for myself. I hope that this dissertation is just the beginning, and that new research will allow me to continue learning from you. Nick, there are not enough words for me to express my gratitude for your endless support and generosity over the last ten years. You are an incredible scientist, writer, leader, and mentor. Thank you for opening doors to research opportunities, helping me navigate academia's visible (and invisible) complexities, cheering me up when things were rough, and always encouraging me to do better. I will strive to share everything I have learned from you with my future students, and I am looking forward to seeing what new adventures will come and what new papers we will write.

I am extremely grateful for the financial support I received from several organizations and programs. Especially, I would like to thank the Agencia Nacional de Investigación y Desarrollo Programa de capital humano Avanzado Becas Chile for funding me for four and half years of my graduate program allowing me to pursue a Ph.D. in the first place. I am also highly appreciative of the support provided by the Peter Buck Predoctoral Fellowship of the National Museum of Natural History, Smithsonian Institution, and the UCSC Dissertation Year Fellowship Chancellor's Award, which funded my research during the last year and a half of my program. Additional research funding was also provided by the Society for Marine Mammalogy Grants in Aid of Research, UC Natural Reserves Mildred E. Mathias Graduate Student Research Grant, UCSC Rebecca and Steve Sooy Graduate Fellowship in Marine Mammals, UCSC Graduate Student Association, UCSC Division of Physical and Biological Sciences, and the UCSC Ecology and Evolutionary Biology Summer Fellowship.

This work would not have been possible without the support of several museum curators, collection managers, and other specialists who allowed me to collect data and samples from collections under their care: M. McGowen, D. Lunde, J. Ososky, J. Nakano, A. Millhouse, K. Klim, K. Behrensmeyer, D. Bohaska, and H. Little from the National Museum of Natural History; N. Duncan, S. Ketelsen, and E. Hoeger at the American Museum of Natural History; C. Lay and A. Krohn from the Kenneth S. Norris Center for Natural History at UC Santa Cruz; R. Baldwin at the Department of Anthropology at UC Santa Cruz; and J. Velez-Juarbe, and S. McLeod from Los Angeles County Museum. I am also incredibly thankful to M. Flannery and M. Velez at the California Academy of

Sciences for their support and trust and for welcoming me over the last five years, enabling me to collect a unique dataset that I never even dreamed I could have someday.

During the last six years at UCSC, I have had the privilege to work and learn from outstanding researchers, staff, and students. I am incredibly thankful to my comprehensive exam committee, Drs. Giacomo Bernardi, Dan Costa, James Estes, and Paul Koch for making this exam one of the most gratifying experiences I had in my graduate program. I am highly appreciative to Dr. Diane Gifford Gonzalez for encouraging me and allowing me to learn from her the marvels of the pinniped taphonomy. I want to acknowledge Dr. Judy Straub for her continuous support and always caring for my interests and wellness. I am also extremely grateful to Colin Carney for his support in running and helping me understand the many intricacies of the stable isotope analyses. In addition, I am appreciative of the undergraduate research assistants, Brittany Burrows, Aaron Rosenfield, Kevin Salladay, and Alexander Yuen, for their commitment and enthusiasm for my research. Especially, I thank Sarah Gutierrez for sharing her artistic talent with me and transforming my research into extraordinary pieces of art.

Thank you to the past and present Koch, Costa and Beltran labs' members for your friendship, expertise, and support. From the Koch lab: Renee Boucher, Dr. Emily Brault, Anirudh Chaudhary, Isabella Chiaravalloti, Max Pearson, Adrienne Ricker, and Pedro Valencia. It has been a pleasure to work with you all. From the Costa and Beltran labs: Salma Abdel-Raheem, Stephanie Adamczak, Dr. Roxanne Beltran, Dr. Caroline Casey, Arina Favilla, Dr. Morgan Gilmour, Dr. Chandra Goetsch, Dr. Keith Hernandez, Dr. Rachel Holser, Dr. Luis Hückstadt, Dr. Joeffry Jouma, Theresa Keates, Kelly Keen, Dr. Sarah Kienle, Jessica Kendall-Bar, Dr. Caitlin Kroeger, Dr. Elizabeth McHuron, Michelle

Modest, Clare Nasr, Daniel Palance, Logan Pallin, Haley Robb, Dr. Patrick Robinson, Theresa Tatom-Naecker, Florencia Vilches, Dr. Stella Villegas-Amtmann, and Jordann Young. It has been such a delight to work with such brilliant group of scientists. Particularly, I would like to extend my most profound appreciation to Drs. Patrick Robinson and Rachel Holser. Patrick, thank you so much for always believing in me and my research, even when it involved dragging dead and stinking animals through the beach or sampling rotten animals. Rachel, your exceptional research, enthusiasm for learning, leadership, and willingness to help and empower others are inspiring and very appreciated. I am sure many good things will come for you!

Among my friends at UCSC, I would like to extend my deepest gratitude to Adrienne Ricker. Adrienne, your passion for making things better and amplifying the voice and needs of others has been inspiring. You are one of the most assertive, determined, and heartfelt human beings I have ever met. I am incredibly grateful for your friendship and for sharing our adventures and misadventures as graduate students. Likewise, I am extremely thankful to Dr. Luis Hückstadt for his continuous and generous advice and support throughout the graduate program. Thank you for always keeping your office (and chatbox) open for my endless inquiries.

I also thank the members of the Pyenson lab at the Smithsonian Institution: Katie Klim, Dr. Lene Liebe Delsett, Dr. Clare Fieseler, and Dr. Kumiko Matsui. I am thrilled to have connected my academic path with you. You are such an incredible group of brilliant and fearless scientists. I admire each of you so much. I'm looking forward to continuing collaborating and moving forward in our several endeavors and paving the way for many to come.

Science is a collective endeavor; I would like to acknowledge all the early career paleontologists with whom I have been lucky to collaborate, share ideas, and start new projects over the last years. Much of this work has been inspired and nurtured by you, Dr. James Rule, Dr. Leonard Dewaele, Dr. Carlos Peredo, Aldo Benitez Palomino, Dr. Monica Buono, Dr. Carolina Loch, Dr. Yuri Kimura, Dr. Matt McCurry, Alex Boersma, Dr. Judith Pardo, and many others. I have been fortunate to be surrounded by amazing friends and collaborators. Thank you to my Los Angeles family, Drs. James Parham, Sarah Rieboldt, Jorge Velez-Juarbe, and Tania Pineda. I will always be immensely grateful for your friendship, advice, and encouragement to pursue my research. Thank you for opening the doors of your families and making me always feel at home. I treasure every one of our experiences together and the many laughs we have shared. For my family on the East coast, Holly Little, Doug Zywiol, Max, and Mason, thank you for your friendship (I am not sure about Mason, though) and always welcoming and making their home my home. I am also grateful to my master's advisor and friend, Dr. Carolina Gutstein, for her uninterrupted mentoring and encouragement to face new challenges. Dr. Mariana Viglino, I am thankful that our paths crossed again. You have been such an essential part of my life during the last few years. Your professionalism, unconditional support, dedication, and friendship are precious to me. What we started last year is just the beginning, and I'm sure many new things will come.

I am also very grateful to Dr. Karen Barad. Karen, your friendship has been a delight for me. Your research, perspective and insights have transformed how I see the world (I mean that!) and have inspired me to become a better scientist, thinker, and human being.

My other friends, whose unconditional support has for keeping me sane when everything looked insane – Carolina Martínez, Carolina Cuadros, Noelia Segovia, Nicole Gutiérrez, Constanza Figueroa, Rodrigo Otero, Fernanda Parada, Ariel Valdéz, Andrea Aceituno, Camila Martínez, Emilia Valenzuela, and Martín Ordoñez – thank you for always being there for me and offering advice and perspective when I needed them the most.

Oh, one more thing! I had the incredible fortune to meet Christy, Ian, and Rosa during my first days in Santa Cruz almost six years ago, and since then, they have become my extended family. Thank you so much for believing in me since time zero, cheering for my work, and always being there when the going got tough. Over the last few years, your friendship has been priceless and has made this whole adventure extraordinary. Rosa, I will be forever grateful for bringing Dobby to our lives. Also, I want to thank Dana, Loren, Bronwyn, Craig, and many others for their friendship and memorable laughs and stories. You have made my life in Santa Cruz such a joy!

I want to express my deepest gratitude to my family. My father and grandmother in law, Raúl and Adriana; thank you so much for accepting me as a daughter and granddaughter in your family and always sheering for my success and happiness! I am infinitely grateful to my parents Ana and Juan for always giving me the freedom to make my own decisions and learn from my mistakes, and for giving me the means and encouragement to follow my own path. Finally, I owe all this work to Andrés, my life partner. He is my biggest cheerleader, the person who understands me the most and brings the greatest happiness. In addition to being the most committed research assistant, the best field photographer, the most thriving pinniped seeker, and the most skilled cooker, he is the most caring person I have ever met. Without your dedicated support, which included starting from zero in a new country, nothing of this would be possible. Thank you for believing in my dreams and making them come true.

The text of this dissertation includes reprints of the following previously published material:

CHAPTER 4

Valenzuela-Toro, A. and Pyenson, N.D., 2019. What do we know about the fossil record of pinnipeds? A historiographical investigation. *Royal Society Open Science*, *6*(11), p.191394.

For this chapter, I was responsible for the study design, data curation, data analysis, manuscript preparation, and manuscript submission. The second co-author in this publication, Nicholas D. Pyenson, assisted with study design, and manuscript revisions.

INTRODUCTION

Among marine mammals, pinnipeds (seals, fur seals, sea lions, and walruses) play essential roles in the structure and function of marine ecosystems through consumer-prey interactions (Estes et al., 2016). Pinnipeds have evolved and maintained a semiaquatic lifestyle – breeding on land but foraging in the water – over the past ~30 million years (Berta et al., 2018). Over this time, drastic climatic, oceanographic, and, more recently, anthropogenic disturbances have affected marine ecosystems, likely influencing pinnipeds' ecological dynamics. Understanding if and how pinnipeds' ecological dynamics and community structure have been affected by these long-term environmental shifts is essential to developing effective conservation strategies moving forward.

The foraging ecology of living pinnipeds has been intensively investigated throughout content, scat, fatty-acid, and stable isotope analyses, as well as animal-borne telemetry (e.g., Zeppelin and Orr, 2010; Robinson et al., 2012; Goetsch et al., 2018; Brault et al., 2019; Chilvers, 2019; Horning et al., 2019; Steingass et al., 2019). These studies have shown that co-occurring species display divergent foraging and habitat preferences with variable niche partitioning. For instance, female northern elephant seals (*Mirounga angustirostris*) are highly pelagic and offshore foragers that feed on small sized mesopelagic fishes, where California sea lions, which breed in the same region, are comparatively nearshore feeders that consume benthic and pelagic prey. Still, it is not well understood what mechanisms underlie these different strategies, or how they have evolved (Berta et al., 2018; Berta and Lanzetti, 2020).

Pinnipeds have a globally distributed fossil record, and their study has revealed several aspects of their evolutionary history (e.g., Valenzuela-Toro et al., 2013; Churchill et al., 2014; Rule et al., 2022). However, the macroecological transformations associated with their land-to-sea-transition, including when and how modern foraging strategies and community structure originated, remain unclear (Berta et al., 2018). Our knowledge of pinniped paleoecology is primarily sourced from the comparative morphology of fossils. Yet, an inconsistent relationship between morphological traits and foraging ecology has been detected in living species, raising uncertainty on the validity of paleoecological interpretations. Novel ecological and ecomorphological studies in living and fossil pinnipeds are necessary to test these paleoecological interpretations and advance the understanding of the emergence of modern foraging strategies and how they have been affected by environmental transformations.

In this dissertation, I contribute to bridging this gap by conducting stable isotope and ecomorphological analyses on museum specimens to examine the foraging ecology, niche partitioning, and ecomorphology of living and fossil pinnipeds. I explore the ecological and ecomorphological attributes of extant members of this group, from individuals to communities, and investigate how those attributes compare to extinct ones.

Chapter 1 examines how co-occurring extant otariids partition their niche across their geographic distribution. I evaluate habitat and resource partitioning in sympatric fur seals and sea lions and explore whether (or not) body size disparities among co-occurring species might contribute to their segregation, shedding light on the mechanisms underlying their coexistence. I use original and published carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values, proxies of the foraging habitat and trophic level, respectively, and morphometric data to contrast the foraging and habitat preferences of co-occurring otariids from the North Pacific and the Southern Hemisphere.

Chapter 2 is an exhaustive community-wide examination of the foraging ecology, resource partitioning, and ecomorphology of otariids from the eastern North Pacific, the most diverse otariid community in the world. I use original morphological and stable isotope data to test the association between body size, feeding morphology, and foraging in four sympatric otariid species: California sea lions (*Z. californianus*), Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*), and Guadalupe fur seals (*Arctocephalus townsendi*). Using museum specimens, I quantify the relationship between individuals' skull length (as a proxy for body length), morphological indices accounting for the relative ability to generate bite force, the relative size of the oral cavity, and the $\delta^{13}C$ and $\delta^{15}N$ values of co-occurring otariids at an intra- and interspecific and community-wide levels.

Chapter 3 is a decadal-scale exploration of California sea lions' body size, feeding morphology, and foraging ecology from the eastern North Pacific. I use skeletal measurements and $\delta^{13}C$ and $\delta^{15}N$ values from museum specimens collected from central and northern California to evaluate if and how resource competition influenced the growth and foraging of females and males (over a 24- and 46-year period, respectively) as their population increased. I investigate how density-dependent ecological pressures can affect sea lions' morphology and foraging ecology and how these dynamics might, ultimately, influence their population recovery.

Chapter 4 is a historiographic review of the published pinniped fossil record. I ground my study on the information available in the Paleobiology Database and describe and evaluate the modes and trends in sampling, geographic and temporal origin, and preservation of the pinniped fossil record. I assess how these factors might bias our understanding of the evolutionary history of this group and affect paleoecological interpretations based on their fossil record, which are explored in the final chapter.

Chapter 5 is a paleoecological investigation of extinct pinnipeds' foraging ecology from the Miocene and Pliocene of the eastern North Pacific and western North Atlantic, respectively. I conduct $\delta^{13}C$ and oxygen stable isotope ($\delta^{18}O$) analyses on fossil tooth enamel to assess extinct taxa's foraging and habitat preferences, unraveling the foraging ecology of extinct pinnipeds and how these dynamics compare to modern ones.

REFERENCES

Berta, A., Churchill, M. and Boessenecker, R.W., 2018. The origin and evolutionary biology of pinnipeds: seals, sea lions, and walruses. *Annual Review of Earth and Planetary Sciences*, *46*, pp.203-228.

Berta, A. and Lanzetti, A., 2020. Feeding in marine mammals: an integration of evolution and ecology through time. *Palaeontologia Electronica*, *23*, p.a40.

Brault, E.K., Koch, P.L., Costa, D.P., McCarthy, M.D., Hückstädt, L.A., Goetz, K.T., McMahon, K.W., Goebel, M.E., Karlsson, O., Teilmann, J. and Harkonen, T., 2019. Trophic position and foraging ecology of Ross, Weddell, and crabeater seals revealed by compound-specific isotope analysis. *Marine Ecology Progress Series*, *611*, pp.1-18.

Chilvers, B.L., 2019. Whisker stable isotope values indicate long-term foraging strategies for female New Zealand sea lions. *Endangered Species Research*, *38*, pp.55-66.

Churchill, M., Boessenecker, R.W. and Clementz, M.T., 2014. Colonization of the Southern Hemisphere by fur seals and sea lions (Carnivora: Otariidae) revealed by combined evidence phylogenetic and Bayesian biogeographical analysis. *Zoological Journal of the Linnean Society*, *172*(1), pp.200-225.

Estes, J.A., Heithaus, M., McCauley, D.J., Rasher, D.B. and Worm, B., 2016. Megafaunal impacts on structure and function of ocean ecosystems. *Annual Review of Environment and Resources*, *41*, pp.83-116.

Goetsch, C., Conners, M.G., Budge, S.M., Mitani, Y., Walker, W.A., Bromaghin, J.F., Simmons, S.E., Reichmuth, C.J. and Costa, D.P., 2018. Energy-Rich Mesopelagic Fishes Revealed as a Critical Prey Resource for a Deep-Diving Predator Using Quantitative Fatty Acid Signature Analysis. *Frontiers in Marine Science*, *5*, p.430.

Horning, M., Andrews, R.D., Bishop, A.M., Boveng, P.L., Costa, D.P., Crocker, D.E., Haulena, M., Hindell, M., Hindle, A.G., Holser, R.R. and Hooker, S.K., 2019. Best practice recommendations for the use of external telemetry devices on pinnipeds. *Animal Biotelemetry*, *7*(1), pp.1-17.

Robinson, P.W., Costa, D.P., Crocker, D.E., Gallo-Reynoso, J.P., Champagne, C.D., Fowler, M.A., Goetsch, C., Goetz, K.T., Hassrick, J.L., Hückstädt, L.A. and Kuhn, C.E., 2012. Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PloS one*, *7*(5), p.e36728.

Rule, J.P., Marx, F.G., Evans, A.R., Fitzgerald, E.M. and Adams, J.W., 2022. True seals achieved global distribution by breaking Bergmann's rule. *Evolution*.

Steingass, S., Horning, M. and Bishop, A.M., 2019. Space use of Pacific harbor seals (*Phoca vitulina richardii*) from two haulout locations along the Oregon coast. *PloS one*, *14*(7), p.e0219484.

Valenzuela-Toro, A.M., Gutstein, C.S., Varas-Malca, R.M., Suarez, M.E. and Pyenson, N.D., 2013. Pinniped turnover in the South Pacific Ocean: new evidence from the Plio-Pleistocene of the Atacama Desert, Chile. *Journal of Vertebrate Paleontology*, *33*(1), pp.216-223.

Van Valkenburgh, BV., 1994. Ecomorphological analysis of fossil vertebrates and their paleocommunities. In: Wainwright PC, Riley SM, editors. Ecological morphology: integrative organismal biology. Chicago (IL): University of Chicago Press. pp. 140 – 66.

Zeppelin, T.K. and Orr, A.J., 2010. Stable isotope and scat analyses indicate diet and habitat partitioning in northern fur seals *Callorhinus ursinus* across the eastern Pacific. *Marine Ecology Progress Series*, *409*, pp.241-253.

CHAPTER 1

DISTINCT SIZE-DRIVEN FORAGING MODES LEAD TO NICHE PARTITIONING PATTERNS IN SYMPATRIC FUR SEALS AND SEA LIONS

1.1 ABSTRACT

Based on their morphological and physiological attributes, eared seals are traditionally classified as fur seals and sea lions. Fur seals have smaller body sizes and preferentially utilize offshore and pelagic resources. Sea lions, instead, have larger sizes and generally feed in nearshore and benthic food webs. Notably, fur seals and sea lions co-occur (i.e., breed in the same region) throughout the North Pacific and Southern Hemisphere, exhibiting variable foraging and niche partitioning. Whether these foraging distinctions are globally prevalent, leading to similar niche partitioning patterns across communities, remains uncertain. We gathered published and original skull length (a proxy for body length) and $\delta^{13}C$ and $\delta^{15}N$ (indicators of habitat, and trophic preferences, respectively) measurements for nine otariid species from six communities and examined their foraging and niche partitioning patterns. We found that co-occurring fur seals and sea lions had consistently distinct foraging modes compatible with the energetic and ecological trade-offs emerging from their body size disparities. Sea lions had predominantly nearshore and benthic foraging, whereas co-occurring fur seals preferentially exploited offshore pelagic food webs. Although some species departed from this pattern, distinct foraging modes still prevailed in their respective communities, mirroring the niche partitioning patterns described elsewhere. Cumulative, this study reveals that resource partitioning underlies the structure of otariid communities.

1.2 INTRODUCTION

Otariids (eared seals) are semiaquatic marine predators that inhabit productive upwelling zones throughout the North Pacific and the Southern Hemisphere (Figure 1.1A; Berta et al., 2018). They have been traditionally classified in fur seals and sea lions based on morphological, ecological, and physiological attributes (Arnould and Costa, 2006; Liwanag et al., 2012a, b; Marshall et al., 2015; Costa and Valenzuela-Toro, 2021; Hooker et al., 2021). Sea lions have a larger body size, they depend on a thick blubber layer for insulation, lactating females undertake relatively short foraging trips, and maternal milk has relatively low-lipid content. Fur seals, instead, have generally smaller body sizes, insulation is provided by a dense underfur coat, females conduct comparatively longer foraging trips, and maternal milk is lipid enriched. Nevertheless, fur seals and sea lions are not monophyletic (Figure 1.1B), denoting repeated evolution of these modes of life. Species of fur seals and sea lions commonly co-occur throughout their distribution range, breeding in shared geographical regions (Figure 1.1A). The duration of these sympatric interactions is not well known. Nevertheless, the archaeological record has proved that these interactions might have extended, at least, through part of the Holocene (e.g., Erlandson and Rick, 2010; Zangrando et al., 2014; Drago et al., 2017), implying long-established mechanisms underlying their coexistence.

Otariids are central place foragers. However, different foraging modes have been described in fur seals and sea lions, likely leading to reduced interspecific competition between sympatric species and facilitating their coexistence. Sea lions preferentially exploit nearshore and benthic food webs, whereas fur seals feed mainly on pelagic prey (e.g., Páez-Rosas et al., 2012; Waite et al., 2012; Jeglinski et al., 2013; Villegas-Amtmann et al., 2013). Still, some exceptions have been documented, eclipsing generalizations of sympatric fur seals and sea lions' foraging behavior (Arnould and Costa, 2006), and confounding our understanding of the ecological mechanisms enabling their widespread coexistence.

Body size affects foraging in otariids (Marshall et al., 2015; Kienle et al., 2022). Sea lions have larger oxygen stores and relatively lower metabolic rates than smaller fur seals (Williams, 1999; Rosen and Trites, 2002). Because of this, sea lions have lower energetic expenditure per unit of mass during diving, maximizing their net energy intake during foraging compared to fur seals (Fish, 2000; Williams et al., 2001). Larger predators also have larger feeding morphology, allowing the consumption of a greater prey size range than smaller ones (Cohen et al., 1993; Segura et al., 2015). Moreover, the different insulation mechanisms employed by otariids can further affect their diving performance and, by implication, their foraging. Blubber in sea lions is relatively incompressible, maintaining its insulative properties irrespective of diving depth (Liwanag et al., 2012a). Conversely, the insulating capacity of fur is reduced at depth because of the compression of the trapped air layer within the coat as pressure increases (Liwanag et al., 2012b), restricting fur seals from diving and foraging as deep as sea lions (Arnould and Costa, 2006).

Benthic and pelagic foraging – the principal foraging strategies in otariids – also involve distinct energetic trade-offs in marine predators. While there are notable exceptions represented by extremely deep pelagic divers like northern elephant seals, benthic diving generally involves greater depths and higher time spent at sea than pelagic diving, characterized by shallower and shorter events (Costa et al., 2004; Laads et al., 2020). As a result, benthic foraging is more energetically expensive than pelagic foraging (Costa and Gales, 2000; Costa et al., 2004). Still, benthic ecosystems have higher species richness with a comparatively homogenous spatial distribution at the benthos (Cury et al., 2000). Pelagic ecosystems, instead, have lower species diversity but have more sporadic, abundant, and energy-dense prey aggregations throughout the water column (Eder and Lewis, 2005; Machovsky-Capuska and Raubenheimer, 2020; Anthony et al., 2000). Therefore, exploiting benthic and pelagic food webs can lead to distinct energetic trade-offs that are interdependent with those derived from the predator's body size. Because of their relatively lower transport cost, more efficient insulation at depth, and capacity of consuming a more comprehensive prey size range, larger sea lions can offset the higher energetic costs of benthic diving more efficiently than fur seals, favoring their feeding in benthic food webs. Conversely, fur seals have less efficient insulation at depth and smaller feeding morphology, limiting their diving depth and range of prey sizes, favoring the exploitation of shallower, smaller, less predictable, but more abundant energy-dense prey in pelagic food webs.

Whether these ecological- and size-driven energetic compensations lead to consistently distinct foraging modes and niche partitioning patterns in sympatric fur seals and sea lions across regions is unknown. Here we illuminate this subject by examining the foraging strategies of sympatric otariids in the eastern North Pacific and the Southern Hemisphere by using bulk stable carbon (and nitrogen isotopes values ($\delta^{13}C$ and $\delta^{15}N$) as proxies of habitat and trophic preferences, respectively. We test whether co-occurring fur seals and sea lions have consistently divergent foraging modes associated with their body size disparities, rendering comparable niche segregation patterns across communities.

1.3 METHODOLOGY

1.3.1 Bibliographic review

We gathered $\delta^{13}C$ and $\delta^{15}N$ data on fur seal and sea lion species from the literature. We collected data for nine otariid species (five fur seals and four sea lions) from the Gulf of Alaska and the Bering Sea: male northern fur seals (*Callorhinus ursinus*) and Steller sea lions (*Eumetopias jubatus*); the California Current: male Guadalupe fur seals (*Arctocephalus townsendi*); the Galapagos Islands: Galapagos fur seals (*Arctocephalus galapagoensis*), and Galapagos sea lions (*Zalophus wollebaeki*); southern Australia: female New Zealand fur seals (*Arctocephalus forsteri*) and female and male Australian sea lions (*Neophoca cinerea*); Río de la Plata and adjoining areas: female and male South American fur seals (*Arctocephalus australis*) and South American sea lions (*Otaria flavescens*); and northern Patagonia: male South American fur seals and female and male South American sea lions. We chose these communities and regions based on data availability and because they capture the phylogenetic, ecological, and biogeographical diversity of fur seals and sea lions across the world.

We only included data from specimens whose geographical provenance and collection year were specified in the original publication. We compiled data from a single tissue for each region to avoid the confounding issue of different discrimination factors among tissues (Hobson et al., 1996). Bone and dentine of adult individuals were selected for species from the Gulf of Alaska and the Bering Sea (Hobson and Sease, 1998; Newsome et al., 2007), California Current (this work), Río de la Plata (Vales et al., 2014; Zenteno et al., 2015; Drago et al., 2017), and northern Patagonia (Drago et al., 2009a,b; Vales et al., 2020). Pup fur and whiskers of adult females were used for otariids from the Galapagos Islands (Páez-Rosas et al., 2014) and southern Australia (Lowther and Goldsworthy, 2011; Foo et al., 2019), respectively. We only used published stable isotope data of individuals, except for adult female Australian sea lions, for which the average $\delta^{13}C$ and $\delta^{15}N$ values of up to three individuals from a single breeding site were included. The published average of successive $\delta^{13}C$ and $\delta^{15}N$ values of dental collagen and whiskers of single individuals were also considered for individuals male Steller sea lions of the Gulf of Alaska and otariids from southern Australia, respectively. We manually extracted the stable isotope data from Galapagos fur seals and sea lions' fur from graphed data in Figure 4 of Páez-Rosas et al. (2014) by using WebPlotDigitizer, a free web-based plot digitizing tool (Rohatgi, 2020), which has proved to be a reliable and valid tool for extracting data from graphs (Drevon et al., 2016).

1.3.2 Stable isotope analysis of otariids from eastern North Pacific

We complemented our bibliographic review by analyzing the bulk $\delta^{13}C$ and $\delta^{15}N$ values of sympatric otariids from the eastern North Pacific Ocean, the most diverse otariid community in the world. We collected bone collagen of 226 physically mature skulls from the following sympatric species: Guadalupe fur seals (*A. townsendi*; four females), northern fur seals (*C. ursinus*; 12 females, four males), California sea lions (*Zalophus californianus*; 57 females, 104 males), and Steller sea lions (*E. jubatus*; 24 females, 11 males) collected from skeletal remains of individuals stranded in central and northern California. Samples containing ~20 mg of bone were cleaned and demineralized by soaking for 48 h in 0.5N HCl at 4°C (Newsome et al., 2006). Lipids were extracted by repetitive soaking cycles and agitation in a petroleum ether solution followed by several rinses with deionized water. Samples were freeze-dried for 24 h with a Labconco Freeze Dry System prior to isotope analysis. We weighed ~ 0.6 mg into tin capsules (Costech; 5x9 mm) for analysis.

The carbon and nitrogen isotope compositions and C and N concentrations were determined at the University of California Santa Cruz Stable Isotope Laboratory using a CE Instruments NC2500 elemental analyzer coupled to a Thermo Scientific DELTAplus XP isotope ratio mass spectrometer via a Thermo-Scientific Conflo III. Isotopic data are expressed in delta (δ) notation which for $\delta^{13}C$ and $\delta^{15}N$ (‰) = $[(R_{sample} / R_{standard}) - 1] \times 1000$, where R_{sample} or $R_{standard}$ are the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in the sample or standard for carbon and nitrogen, respectively. Measurements were standardized relative to VPDB (Vienna PeeDee Belemnite) for $\delta^{13}C$ and AIR for $\delta^{15}N$ against an in-house gelatin standard reference material (PUGel) which is extensively calibrated against international standard reference materials. Measurements were corrected for size effects, blank-mixing effects, and drift effects. An externally calibrated Acetanilide #1 standard reference material purchased from Dr. Arndt Schimmelmann of Indiana University is measured as a sample for independent quality control. In this set of sample measurements, 22 replicates of Acetanilide #1 had reproducibility (1σ) of 0.06‰ and 0.1‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, and 0.13 for the C:N ratio. The 47 replicates of PUGel had reproducibility of 0.05‰ and 0.09‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, and 0.03 for the C:N ratio. Typical reproducibility is significantly better than 0.1‰ for $\delta^{13}C$ and significantly better than 0.2‰ for $\delta^{15}N$. The atomic C:N ratio of bone samples was determined and varied between 3.1 and 3.6, which is within the range for well-preserved collagen (DeNiro, 1985).

1.3.3 *Body size estimations*

The skull length of adult otariid species was obtained from Churchill et al. (2014a). It consisted of the basal length, which is the straight distance between the most anterior tip of the premaxilla to the posterior-most margin of the basion. Additionally, one of us (AVT) recorded the condylobasal length (CBL; distance between the most anterior tip of the premaxilla to the posterior-most margin of the occipital condyles) of female Guadalupe fur seals (n = 4) using a digital caliper with an accuracy of 0.01 mm. The CBL of female Australian sea lions was obtained from Tedman (2003). Both measures (i.e., basal and condylobasal lengths) are representative of the cranial length; however, the condylobasal length is approximately 2 cm greater than the former. Yet, this difference is within the variation range observed among fur seal populations and does not bias comparisons between them (see Figure 1.1C).

1.3.4 *Data analysis*

Data analyses were performed in R statistical software version 4.0.3 (R Development Core Team 2020) with RStudio 1.3.1093 interface. Prior to statistical analysis or graphing, $\delta^{13}C$ values were corrected for the Suess effect using a time-dependent correction factor following Szteren et al. (2018) as follows:

$$(1)\ \delta^{13}C_{\text{corrected}} = \delta^{13}C - (\text{Number of years to 1960}) \times 0.005 - (a \times 0.022)$$

$$(2)\ \delta^{13}C_{\text{corrected}} = \delta^{13}C - (\text{Number of years to } a) \times 0.022$$

The correction factors used were 0.005‰ for data before 1959 (1) and 0.022‰ for data from 1960 to the present (2). *a* corresponds to the difference between 1960 and the reference year, which is variable for the otariid assemblages and corresponds to the most recent year in which a specimen was collected in the field. Previous studies in northern elephant seals (*Mirounga angustirostris*) have revealed that bone collagen integrates the stable nitrogen isotope composition for approximately the last five years of the life of the individuals (Riofrío-Lazo and Aurioles-Gamboa, 2013). The precise bone turnover in adult otariids is unknown, but it likely ranges between 1 and 5 years, as suggested in studies on juvenile otariids and elephant seals (Newsome et al., 2006; Riofrío-Lazo and Aurioles-Gamboa, 2013). Consequently, the use of the year in which the specimens were collected in the field will likely result in a slight overestimation of the Suess effect (<0.1‰), which will not significantly affect ecological interpretations and comparisons between species.

The stable isotope data of Steller sea lions from the Gulf of Alaska and the Bering Sea were derived from dentine. Yet, their $\delta^{13}C$ and $\delta^{15}N$ values were obtained from different tissue components. The $\delta^{13}C$ values were measured from the inorganic (i.e., carbonate bearing hydroxyapatite or bioapatite) fraction, whereas the $\delta^{15}N$ values were obtained from the organic (i.e., collagen) phase (Hobson and Sease, 1998). Bioapatite is ^{13}C-enriched relative to collagen due to different diet-to-tissue fractionation factors (Lee-Thorp et al., 1989; Clementz et al., 2009). The difference in $\delta^{13}C$ value between of bioapatite and collagen ($\Delta^{13}C_{\text{bioapatite-collagen}}$) varies among taxa and trophic levels. While the specific $\Delta^{13}C_{\text{bioapatite-collagen}}$ is not available for pinnipeds, we estimated it to be equivalent to 2.1‰, which corresponds to the average spacing by some medium-sized odontocete cetaceans (value calculated from published data by Clementz et al., 2009). We adjusted the $\delta^{13}C$ values of Steller sea lions from the Gulf of Alaska and the Bering Sea by subtracting 2.1‰, allowing subsequent comparisons with collagen $\delta^{13}C$ values.

Otariids are highly sexually dimorphic and polygynous species with sex-specific life-history strategies, including distinct energetic and foraging constraints (McKnight and Boyd, 2018). To account for these distinctions, females, and males were analyzed as separate populations when available for each species. Stable isotope data for male Guadalupe fur seals was originally obtained from skeletal remains at the Magdalena Island in Baja California (26º N) (Aurioles-Gamboa and Szteren, 2020). For our analysis, male Guadalupe fur seals data were separated into two ecologically distinct populations following the original publication. These two populations were based on differences in their $\delta^{13}C$ values and corresponded to "coastal" and "oceanic" populations that hadhad nearshore and offshore foraging preferences, respectively (Aurioles-Gamboa and Szteren, 2020).

Carbon and nitrogen isotope baselines (i.e., values in primary producers at the base of the food chain) vary spatially across marine regions (e.g., Bowen et al., 2010; McMahon et al., 2013); therefore, we did not attempt to compare the isotopic composition of individuals across regions. Instead, we assessed the foraging preferences of co-occurring fur seal and sea lion populations by calculating their relative position (expressed in percentages) over the $\delta^{13}C$ and $\delta^{15}N$ ranges for each community following Drago et al. (2021). For the $\delta^{13}C$ range, 100% represented nearshore/benthic foraging preferences while 0% represented offshore/pelagic foraging. For the $\delta^{15}N$ range, 100% indicated populations with the highest trophic level, and 0% indicated populations with the lowest trophic level. We estimated the relative position over an isotopic range by calculating the difference between the average isotopic composition of an otariid population and the minimum average isotopic value for the isotopic system within a community (e.g., -15.2‰ for female Guadalupe fur seals from the California Current).

The maximum difference within a community (e.g., 2.8‰ for a subpopulation of Guadalupe fur seals from the California Current) was equivalent to 100%, which was used to calculate the relative position of co-occurring populations. The same process was conducted for calculating the relative position over the $\delta^{13}C$ and $\delta^{15}N$ range for each otariid community.

We compared the $\delta^{13}C$ and $\delta^{15}N$ values among co-occurring species within communities using the Mann-Whitney-U test or the Kruskal-Wallis test followed by a Dunn test with Bonferroni correction for multiple comparisons. We contrasted the calculated relative position over the $\delta^{13}C$ and $\delta^{15}N$ ranges among fur seals and sea lions' populations across regions using the non-parametric Mann-Whitney test. All statistical comparisons were conducted using the package ggbetweenstats (Patil, 2021).

1.4 RESULTS

There was a positive and significant relationship between the calculated relative positions over the $\delta^{13}C$ and the $\delta^{15}N$ ranges (Spearman's $\rho = 0.44$, $p = 0.036$) when all regions and populations are considered, indicating that nearshore otariids (with higher relative positions over the $\delta^{13}C$ range) tend to have higher trophic levels (with higher relative positions over the $\delta^{15}N$ range). Broadly, sea lions had significantly higher relative positions over the $\delta^{13}C$ (Mann-Whitney test: $W = 18.00$, $p = 0.0029$) and $\delta^{15}N$ (Mann-Whitney test: $W = 14.50$, $p = 0.0014$) ranges than fur seals. Otariids from the California Current displayed the largest average $\delta^{13}C$ difference (2.8‰), whereas populations from the Gulf of Alaska showed the largest average $\delta^{15}N$ difference (2.4‰) (Figure 1.2B, C).

Populations of fur seals and sea lions from the Gulf of Alaska and the Bering Sea, the Galapagos Islands, Río de la Plata, and northern Patagonia had distinct distributions in their corresponding isospaces (biplots of $\delta^{13}C$ versus $\delta^{15}N$) (Figure 1.2), indicating that they had comparably distinct foraging and habitat partitioning patterns. Fur seal and sea lion populations from the California Current and southern Australia showed more variable and largely overlapping $\delta^{13}C$ and the $\delta^{15}N$ values, suggesting more intricate foraging and niche partitioning dynamics.

In the California Current, the stable isotope composition of male northern fur seals largely overlapped that of female California sea lions. Moreover, the "oceanic" male Guadalupe fur seal population (Aurioles-Gamboa and Szteren, 2020) had equivalent values with those of female Guadalupe fur seals but they were ~3‰ ^{13}C-depleted relative to those classified as "coastal" male Guadalupe fur seals, which in turn had higher average $\delta^{13}C$ values than California and Steller sea lions from this region. Likewise, in southern Australia, the $\delta^{13}C$ and the $\delta^{15}N$ values of female New Zealand fur seals and Australian sea lions largely overlapped.

Driven by these differences in their isospaces, sea lions from the Gulf of Alaska and Bering Sea, the Galapagos Islands, the Río de la Plata, and northern Patagonia had higher relative positions over the $\delta^{13}C$ and $\delta^{15}N$ ranges than co-occurring fur seals (Figure 1.3B, C). Variations of the average $\delta^{13}C$ and $\delta^{15}N$ values driving these results ranged from 0.6‰ (Galapagos Islands) to 2.8‰ (California Current) for $\delta^{13}C$, and from 1.0‰ (Galapagos Islands) to 2.4‰ (Gulf of Alaska and the Bering Sea) for $\delta^{15}N$.

Otariid populations from the California Current and southern Australia departed from this pattern (Figure 1.3). Among otariids inhabiting the California Current, "coastal" male Guadalupe fur seals (population 7 in Figure 1.3B) had the highest position over the $\delta^{13}C$ range relative to coexisting populations. Male northern fur seals (population 4 in Figure 1.3B) also had slightly higher relative position over the $\delta^{13}C$ range compared to female California sea lions, and lower than those of male California sea lions. Female Guadalupe fur seals (population 5 in Figure 1.3C) had high relative position over the $\delta^{15}N$ range, exceeding those of female and male California sea lions. Moreover, female California sea lions (population 8 in Figure 1.3C) had a lower position over the $\delta^{15}N$ range than male northern fur seals and Guadalupe fur seals.

Male Australian sea lions (population 16 in Figure 1.3B, C) had the lowest relative position over the $\delta^{13}C$ compared to concurrent otariids, although the variation of the average $\delta^{13}C$ values underlying these results was barely above measurement error (0.2‰). Moreover, female Australian sea lions (population 15 in Figure 1.3C) had the lowest relative position over the $\delta^{15}N$ range.

1.5 DISCUSSION

We showed that sympatric populations of fur seals and sea lions from the Gulf of Alaska and the Bering Sea, Galapagos Islands, Río de la Plata, and northern Patagonia had distinct foraging modes (Figure 2,3). Sea lions had predominantly nearshore and benthic foraging (as indicated by their significantly higher $\delta^{13}C$ values and relative positions over the $\delta^{13}C$ range). In contrast, co-occurring fur seals preferentially exploited offshore pelagic food webs (as suggested by their lower $\delta^{13}C$ values and relative positions over the $\delta^{13}C$ range). Sea lions also had higher $\delta^{15}N$ values (and relative positions over the $\delta^{15}N$ range) than concurrent fur seals. However, these differences were variable in magnitude across communities (ranging from 1.0‰ to

2.4‰), indicating that foraging partitioning might not predetermine the consumption of distinct trophic-level prey by sympatric fur seals and sea lions in a predictable way.

These findings are consistent with previous, complementary examinations of otariid foraging ecology. Biochemical dietary analyses and satellite telemetry have shown that Steller sea lions from eastern Russia feed nearshore and benthically at a higher trophic level than co-occurring fur seals, which fed primarily offshore and pelagically (Hobson et al., 1997; Waite et al., 2011, 2012; Olivier et al., 2022). Likewise, Galapagos fur seals are offshore predators whose diet primarily consists of squids and some vertically migrating pelagic fish (Páez-Rosas et al., 2012, 2014). Galapagos sea lions, in contrast, are nearshore benthic foragers, although they can be behaviorally and dietary flexible, consuming benthic and pelagic fish (Dellinger and Trillmich 1999; Páez-Rosas and Aurioles-Gamboa, 2010; Páez-Rosas et al., 2012, 2014). Previous studies have shown that South American fur seals and sea lions inhabiting the western South Atlantic have significantly different foraging modes. Sea lions are predominantly benthic and coastal foragers, contrasting with the co-occurring fur seals, which preferentially feed on small pelagic fish and squid available across the water column (Vales et al., 2013; Zenteno et al., 2015; Sepulveda et al., 2017; Guerrero et al., 2020). These observations support the conclusion that sympatric fur seals, and sea lions display different foraging modes, following predictions derived from ecological- and size-driven energetic compensations.

Two remarkable differences arise when comparing the ecological attributes of otariid communities inhabiting the California Current to others. First, this is the most diverse otariid community globally, encompassing two fur seal and two sea lion species. Second, some of these species had weak distinctions in their $\delta^{13}C$ and $\delta^{15}N$ values, denoting foraging overlap and potential departures from the foraging partitioning patterns described in other regions. In this region, we found isotopic evidence Steller sea lions were predominantly nearshore and benthic foraging. Populations of Guadalupe fur seals and northern fur seals had mean isotopic data consistent with preferential offshore and pelagic foraging, but they showed considerable intraspecific isotopic variability. Still, the extensive overlap in the isospace occupied by California sea lions and co-occurring fur seals suggests more intricate foraging and niche partitioning dynamics.

Before interpreting the foraging and niche partitioning of California sea lions and co-occurring fur seals, it is necessary to assess the potential effect of foraging locations on their stable isotope composition. The $\delta^{13}C$ and $\delta^{15}N$ values of phytoplankton and particulate organic matter are negatively correlated with latitude in the eastern Pacific Ocean, and these baseline differences affect the $\delta^{13}C$ and $\delta^{15}N$ values of predators (Burton and Koch 1999; Aurioles-Gamboa et al. 2006). Except for male Guadalupe fur seals, which were collected at the Magdalena Island in Baja California (26º N) (Aurioles-Gamboa and Szteren, 2020), otariid remains were from individuals that stranded in central and northern California (36º - 42º N). That said, the precise location of the foraging grounds used by individuals included in this study is unknown. Male Guadalupe fur seals likely circumscribed their foraging to areas near their breeding sites at the Guadalupe Island and the San Benito Islands (Aurioles-Gamboa and Szteren, 2020), substantially further south than the waters exploited by co-occurring otariids along the central California coast (e.g., McHuron et al., 2016; Figure 1.1A). Because of these baseline differences, 'the $\delta^{13}C$ and $\delta^{15}N$ values of Guadalupe fur seals would be ~1.5‰ higher than predators feeding at higher latitudes (e.g., southern and central

California; Burton and Koch, 1999; Aurioles et al., 2006). After accounting for these baseline differences, the $\delta^{13}C$ and $\delta^{15}N$ values of female California sea lions and co-occurring northern and Guadalupe fur seals substantially overlap, indicating (1) foraging convergence between these populations and (2) the prevalence of offshore pelagic foraging in female sea lions.

California sea lions are generalist marine predators that usually forage on seasonally abundant prey in nearshore and nearby offshore habitats (Weise and Harvey, 2008; McHuron et al., 2016). In contrast to other sea lions, California sea lions have been characterized as primarily shallow and epipelagic divers (Arnould and Costa, 2006), although substantial foraging variability has been described, with some individuals performing benthic and mixed foraging (e.g., Feldkamp et al., 1989; Melin et al., 2008; Weise et al., 2010; Kuhn and Costa, 2014; McHuron et al., 2016; Rosas-Hernández et al., 2019). Little is known about how foraging behavior of California sea lions affects resource partitioning among other co-occurring otariid species. Yet, studies have revealed varying spatial and dietary overlap with co-occurring northern and Guadalupe fur seals (e.g., Antonelis et al., 1990; Aurioles-Gamboa and Camacho-Ríos 2007, Zeppeling and Orr, 2010), indicating variable levels of interspecific competition.

The mechanisms underlying the predominantly pelagic foraging of California sea lions are undetermined. However, the body size disparities observed between this and co-occurring otariid species might provide some clues. California sea lions are smaller than co-occurring Steller sea lions, matching the size range of Guadalupe and northern fur seals (Figure 1.1C). Accordingly, their relatively small body size may induce different energetic compensations than those of (larger) Steller sea lions, favoring pelagic foraging. The historical population dynamics in the eastern North Pacific might further contribute to unusual foraging behavior of California sea lions. Although the precise extent of their decline due to commercial hunting during the 18th and 19th centuries is not available (Cass, 1985), it was less severe than that experienced by the fur seals, which were nearly exterminated (Cass, 1985; Zavala-Gonzalez and Mellink, 2000). If so, it is possible that the regional extirpation of pelagic fur seals promoted the passive diversification of California sea lions into the vacant niches left by fur seals in the pelagic food webs. Future stable isotope analyses on museum specimens of California sea lions from before and after Guadalupe and northern fur seals persecution might provide ways to test a progressive shift from exploiting nearshore and benthic to offshore and pelagic food webs.

In sum, our results show that co-occurring otariids with different body sizes from the California Current (i.e., Steller sea lions and fur seals) have strongly different foraging modes. When the body size contrast is smaller, as between fur seals and California sea lions, those foraging distinctions are much weaker. The highly productive nature of the California Current (Kudela et al., 2008; McClatchie et al., 2009; Brady et al., 2017), combined with the differential decrease in population sizes due to hunting between sea lions and fur seals, might lead to lessened selection for niche partitioning among these species, explaining their foraging convergence.

Co-occurring otariids from southern Australia exhibited apparent departures from expected stable isotope patterns. New Zealand fur seals and Australian sea lions showed non-significant differences in their $\delta^{13}C$ and $\delta^{15}N$ compositions, suggesting no prominent resource partitioning. However, these results are not consistent with prior telemetry, diving, and dietary studies denoting significant differences in their foraging ecology (McIntosh and Pitcher, 2021). Indeed, Australian sea lions have been characterized as non-migratory and predominantly benthic predators, feeding almost exclusively at or near the benthos in continental shelf areas (Costa and Gales, 2003). Conversely, New Zealand fur seals are epipelagic foragers that exploit diverse foraging grounds, ranging from the continental shelf to deeper oceanic waters (Page et al., 2006; Baylis and Nichols, 2009; Baylis et al., 2008, 2012). Why then do we not see significant differences in the stable isotope composition of these species? Local biological and oceanographic dynamics may explain these results. In southern Australia, a considerable mixture of differently sourced water masses (with distinct $\delta^{13}C$ and $\delta^{15}N$ values) occurs, which, combined with broad latitudinal gradients of $\delta^{13}C$ values, can confound distinctions between nearshore and offshore, hindering ecological interpretations (Lowther et al., 2013; Foo et al., 2019). The future performance of compound specific stable isotopes might help to disentangle the occurrence of variable isotope baselines vs. foraging differences in these populations. Grounded on previous behavioral and dietary analyses, it is manifest that Australian sea lions and New Zealand fur seals indeed exhibit divergent foraging modes, resembling the niche partitioning observed in other otariid communities elsewhere.

Populations of Australian fur seals (*Arctocephalus pusillus doriferus*) and New Zealand fur seals also co-occur along the coastlines of the Bass Strait in southeastern Australia, constituting one of the few otariid communities composed exclusively of fur seal species (other colonies of Antarctic and subantarctic fur seals co-occur at the Marion and Macquarie Islands in the Southern Ocean; Lancaster et al., 2006). Unfortunately, no comparable stable isotope data for Australian and New Zealand fur seals were available for this study. Nevertheless, several studies have emphasized the distinct foraging strategies of these populations. Australian fur seals have been described as primarily benthic foragers, preying on diverse benthic and demersal prey within the shallow continental shelf in the Bass Strait (Gales et al., 1993; Arnould and Hindell, 2001; Arnould and Kirkwood et al., 2008; Deagle et al., 2008; Hoskins et al., 2015; Knox et al. 2017). New Zealand fur seals, in contrast, are predominantly pelagic foragers (Page et al., 2005). Remarkably, the distinct foraging modes portrayed by these species resemble those described for sympatric fur seals and sea lions elsewhere. Moreover, body size differences between Australian and New Zealand fur seals are similar to those reported in fur seals and sea lions' pairs (Figure 1.1C). Together, these observations emphasize the pervasiveness of different foraging and ecological modes in sympatric otariids across their geographical range.

The unusual foraging behavior of Australian fur seals deserves further consideration. Australian fur seals are a subspecies of the Cape fur seal (*Arctocephalus pusillus pusillus*), from which they separated ~18,000 years ago (Kirkman and Arnould, 2018). Noticeably, Australian fur seals are the largest body-sized fur seals, with adult females and males reaching masses up to 120 kg and nearly 350 kg, respectively (Warneke and Shaughnessy, 1985; Arnould and Warneke, 2002; Kirkwood and Goldworthy, 2013). Together, Australian fur seals' enlarged body size, benthic foraging, vocalization, and thigmotaxis correspondwith sea lion traits (Kirkwood and Goldworthy, 2013; Costa and Valenzuela-Toro, 2021). The drivers of this unusual sea lion-like morphology and foraging behavior in Australian fur seals is unknown. Phylogenetic analyses have concluded that Australian and Cape fur seals are sister taxa of Subantarctic fur seals (*Arctocephalus tropicalis*) and, in turn, are closely related to other fur seals from the Southern Hemisphere (Churchill et al., 2014b). These results hint that shared evolutionary history with sea lions might not be the most likely driver of Australian fur seals' exceptional traits, emphasizing alternative drivers. Although additional studies are required to support or reject potential hypotheses, Australian fur seals' unusual foraging behavior and morphology might reflect an evolutionary response to sympatry, as demonstrated by other vertebrate fauna (e.g., Anderson and Weir, 2021).

Remarkably, regional variability in the foraging behavior of South American sea lions has been described between populations inhabiting the Atlantic and Pacific coasts of South America (Hückstädt et al., 2007, 2016). As described above, South American sea lions' populations inhabiting the Atlantic coast are predominantly nearshore and benthic foragers (Riet-Sapriza et al., 2013; Drago et al., 2017; Denuncio et al., 2021). Conversely, populations from the Pacific coast exhibit mainly epipelagic foraging, likely associated with the deeper and narrower extension of the continental shelf in this region (Soto et al., 2006; Hückstädt et al., 2007, 2014, 2016; Sarmiento-Devia et al., 2020). While we could not examine the foraging ecology of sympatric sea lions and fur seals inhabiting the Pacific coast, recent studies in populations inhabiting the Peruvian coast have shown significant differences in their diet. South American fur seals primarily consume pelagic and demersal-pelagic prey, whereas sea lions feed on demersal-pelagic prey (Cárdenes-Alayza et al., 2022). Together, these results indicate that foraging and resource partitioning between these two species occur even under different environmental conditions, stressing the ubiquity of distinct foraging modes in sympatric fur seals and sea lions.

In summary, we detected broad-scale patterns of foraging and resource partitioning among co-occurring otariids compatible with the energetic and ecological trade-offs emerging from their body size disparities. Together, our work highlights the critical role biotic interactions (i.e., interspecific competition) play in populations, structuring modern communities, and likely, driving macroecological change.

1.6 Acknowledgments.

We thank M. Flannery and M. Velez at the Ornithology and Mammalogy Department of the California Academy of Sciences provided access to the pinnipeds osteological collection. B. Sellers and A. Yuen helped with sample preparation. C. Carney provided assistance and guidance during stable isotope analyses. L. Hückstadt and M. Carr offered comments and advice during the performance of this study. Funding was provided by the University of California Santa Cruz Division of Physical and Biological Sciences and the Graduate Student Association, the Peter Buck Predoctoral Fellowship of the National Museum of Natural History, Smithsonian Institution, the Society for Marine Mammalogy, and ANID PCHA/Becas Chile, Doctoral Fellowship, Grant No. 2016-72170286 to A.V.T.

1.7 REFERENCES

Aguirre, M.L., Donato, M., Richiano, S. and Farinati, E.A., 2011. Pleistocene and Holocene interglacial molluscan assemblages from Patagonian and Bonaerensian littoral (Argentina, SW Atlantic): palaeobiodiversity and palaeobiogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *308*(3-4), pp.277-292.

Akin, S. and Winemiller, K.O., 2008. Body size and trophic position in a temperate estuarine food web. *Acta Oecologica*, *33*(2), pp.144-153.

Amador-Capitanachi, M.J., Moreno-Sánchez, X.G., Juárez-Ruiz, A., Ferretto, G. and Elorriaga-Verplancken, F.R., 2017. Trophic variation between the two existing Guadalupe fur seal colonies on Guadalupe Island and the San Benito Archipelago, Mexico. *Aquatic mammals*, *43*(1).

Anderson, S.A. and Weir, J.T., 2021. Character displacement drives trait divergence in a continental fauna. *Proceedings of the National Academy of Sciences*, *118*(20).

Anthony, J.A., Roby, D.D. and Turco, K.R., 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology*, *248*(1), pp.53-78.

Antonelis, G.A., Stewart, B.S. and Perryman, W.F., 1990. Foraging characteristics of female northern fur seals (Callorhinus ursinus) and California sea lions (Zalophus californianus). *Canadian Journal of Zoology*, *68*(1), pp.150-158.

Arnould, J.P. and Hindell, M.A., 2001. Dive behaviour, foraging locations, and maternal-attendance patterns of Australian fur seals (Arctocephalus pusillus doriferus). *Canadian Journal of Zoology*, *79*(1), pp.35-48.

Arnould, J.P.Y. and Costa, D.P., 2006. Sea lions in drag, fur seals incognito: insights from the otariid deviants. *Sea Lions of the World. Fairbanks: Alaska Sea Grant College Program*, pp.309-323.

Kirkwood, R. and Arnould, J.P., 2008. Australian fur seal. *The mammals of Australia*, pp.723-725.

Arnould, J.P.Y. and Warneke, R.M., 2002. Growth and condition in Australian fur seals (*Arctocephalus pusillus doriferus*)(Carnivora: Pinnipedia). *Australian Journal of Zoology*, *50*(1), pp.53-66.

Aurioles, D., Koch, P.L. and Le Boeuf, B.J., 2006. Differences in foraging location of Mexican and California elephant seals: evidence from stable isotopes in pups. *Marine Mammal Science*, *22*(2), pp.326-338.

Aurioles-Gamboa, D. and Camacho-Ríos, F.J., 2007. Diet and feeding overlap of two otariids, *Zalophus californianus* and *Arctocephalus townsendi*: Implications to survive environmental uncertainty. *Aquatic Mammals*, *33*(3), p.315.

Aurioles-Gamboa, D. and Szteren, D., 2020. Lifetime coastal and oceanic foraging patterns of male Guadalupe fur seals and California sea lions. *Marine Mammal Science*, *36*(1), pp.246-259.

Baylis, A.M. and Nichols, P.D., 2009. Milk fatty acids predict the foraging locations of the New Zealand fur seal: continental shelf versus oceanic waters. *Marine Ecology Progress Series*, *380*, pp.271-286.

Baylis, A.M.M., Page, B. and Goldsworthy, S.D., 2008. Effect of seasonal changes in upwelling activity on the foraging locations of a wide-ranging central-place forager, the New Zealand fur seal. *Canadian Journal of Zoology*, *86*(8), pp.774-789.

Baylis, A.M., Page, B., McKenzie, J. and Goldsworthy, S.D., 2012. Individual foraging site fidelity in lactating New Zealand fur seals: Continental shelf vs. oceanic habitats. *Marine Mammal Science*, *28*(2), pp.276-294.

Berta, A., Churchill, M. and Boessenecker, R.W., 2018. The origin and evolutionary biology of pinnipeds: seals, sea lions, and walruses. *Annual Review of Earth and Planetary Sciences*, *46*, pp.203-228.

Blakeway, J.A., Arnould, J.P., Hoskins, A.J., Martin-Cabrera, P., Sutton, G.J., Huckstadt, L.A., Costa, D.P., Páez-Rosas, D. and Villegas-Amtmann, S., 2021. Influence of hunting strategy on foraging efficiency in Galapagos sea lions. *PeerJ*, *9*, p.e11206.

Bowen, G.J., 2010. Isoscapes: spatial pattern in isotopic biogeochemistry. *Annual review of earth and planetary sciences*, *38*, pp.161-187.

Brady, R.X., Alexander, M.A., Lovenduski, N.S. and Rykaczewski, R.R., 2017. Emergent anthropogenic trends in California Current upwelling. *Geophysical Research Letters*, *44*(10), pp.5044-5052.

Burton, R.K. and Koch, P.L., 1999. Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds. *Oecologia*, *119*(4), pp.578-585.

Cárdenas-Alayza, S., Torres, D.A., Gutiérrez, D. and Tremblay, Y., 2022. Resource partitioning as a mechanism for trophic segregation in sympatric otariids from the productive upwelling Peruvian Humboldt Current System. *Austral Ecology*.

Cass, V.L., 1985. Exploitation of California sea lions, Zalophus californianus, prior to 1972. *Marine Fisheries Review*, *47*(1), pp.36-38.

Churchill, M., Clementz, M.T. and Kohno, N., 2014a. Predictive equations for the estimation of body size in seals and sea lions (Carnivora: Pinnipedia). *Journal of Anatomy*, *225*(2), pp.232-245.

Churchill, M., Boessenecker, R.W. and Clementz, M.T., 2014b. Colonization of the Southern Hemisphere by fur seals and sea lions (Carnivora: Otariidae) revealed by combined evidence phylogenetic and Bayesian biogeographical analysis. *Zoological Journal of the Linnean Society*, *172*(1), pp.200-225.

Clementz, M.T., Fox-Dobbs, K., Wheatley, P.V., Koch, P.L. and Doak, D.F., 2009. Revisiting old bones: coupled carbon isotope analysis of bioapatite and collagen as an ecological and palaeoecological tool. *Geological Journal*, *44*(5), pp.605-620.

Cohen, J.E., Pimm, S.L., Yodzis, P. and Saldaña, J., 1993. Body sizes of animal predators and animal prey in food webs. *Journal of animal ecology*, pp.67-78.

Cohen, J.E., Jonsson, T. and Carpenter, S.R., 2003. Ecological community description using the food web, species abundance, and body size. *Proceedings of the national academy of sciences*, *100*(4), pp.1781-1786.

Codignotto, J.O. and Aguirre, M.L., 1993. Coastal evolution, changes in sea level and molluscan fauna in northeastern Argentina during the Late Quaternary. *Marine Geology*, *110*(1-2), pp.163-175.

Costa, D.P., Kuhn, C.E., Weise, M.J., Shaffer, S.A. and Arnould, J.P., 2004, December. When does physiology limit the foraging behaviour of freely diving mammals?. In *International congress series* (Vol. 1275, pp. 359-366). Elsevier.

Costa, D.P. and Gales, N.J., 2000. Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri*. *Journal of Experimental Biology*, *203*(23), pp.3655-3665.

Costa, D.P. and Gales, N.J., 2003. Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecological Monographs*, *73*(1), pp.27-43.

Costa, D.P. and Valenzuela-Toro, A.M., 2021. When Physiology and Ecology Meet: The Interdependency Between Foraging Ecology and Reproduction in Otariids. In *Ethology and Behavioral Ecology of Otariids and the Odobenid* (pp. 21-50). Springer, Cham.

Costa, G.C., 2009. Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology*, *90*(7), pp.2014-2019.

Cury, P., Bakun, A., Crawford, R.J., Jarre, A., Quinones, R.A., Shannon, L.J. and Verheye, H.M., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, *57*(3), pp.603-618.

Deagle, B.E., Kirkwood, R. and Jarman, S.N., 2009. Analysis of Australian fur seal diet by pyrosequencing prey DNA in faeces. *Molecular ecology*, *18*(9), pp.2022-2038.

DeNiro, M.J., 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. *Nature*, *317*(6040), pp.806-809.

Dellinger, T. and Trillmich, F., 1999. Fish prey of the sympatric Galapagos fur seals and sea lions: seasonal variation and niche separation. *Canadian Journal of Zoology*, *77*(8), pp.1204-1216.

Denuncio, P., Gana, J.C., Giardino, G.V., Rodríguez, D.H. and Machovsky-Capuska, G.E., 2021. Prey composition and nutritional strategies in two sympatric pinnipeds. *Journal of Experimental Marine Biology and Ecology*, *545*, p.151629.

Drago, M., Crespo, E.A., Aguilar, A., Cardona, L., García, N., Dans, S.L. and Goodall, N., 2009a. Historic diet change of the South American sea lion in Patagonia as revealed by isotopic analysis. *Marine Ecology Progress Series*, *384*, pp.273-286.

Drago, M., Cardona, L., Crespo, E.A. and Aguilar, A., 2009b. Ontogenic dietary changes in South American sea lions. *Journal of Zoology*, *279*(3), pp.251-261.

Drago, M., Cardona, L., Franco-Trecu, V., Crespo, E.A., Vales, D.G., Borella, F., Zenteno, L., Gonzáles, E.M. and Inchausti, P., 2017. Isotopic niche partitioning between two apex predators over time. *Journal of Animal Ecology*, *86*(4), pp.766-780.

Drago, M., Signaroli, M., Valdivia, M., González, E.M., Borrell, A., Aguilar, A. and Cardona, L., 2021. The isotopic niche of Atlantic, biting marine mammals and its relationship to skull morphology and body size. *Scientific Reports*, *11*(1), pp.1-14.

Drevon, D., Fursa, S.R. and Malcolm, A.L., 2017. Intercoder reliability and validity of WebPlotDigitizer in extracting graphed data. *Behavior modification*, *41*(2), pp.323-339.

Eder, E.B. and Lewis, M.N., 2005. Proximate composition and energetic value of demersal and pelagic prey species from the SW Atlantic Ocean. *Marine Ecology Progress Series*, *291*, pp.43-52.

Erlandson, J.M. and Rick, T.C., 2010. Archaeology meets marine ecology: the antiquity of maritime cultures and human impacts on marine fisheries and ecosystems. *Annual Review of Marine Science*, 2: 231-251.

Feldkamp, S.D., DeLong, R.L. and Antonelis, G.A., 1989. Diving patterns of California sea lions, Zalophus californianus. *Canadian Journal of Zoology*, *67*(4), pp.872-883.

Fish, F.E., 2000. Biomechanics and energetics in aquatic and semiaquatic mammals: platypus to whale. *Physiological and Biochemical Zoology*, *73*(6), pp.683-698.

Foo, D., McMahon, C., Hindell, M., Goldsworthy, S. and Bailleul, F., 2019. Influence of shelf oceanographic variability on alternate foraging strategies in long-nosed fur seals. *Marine Ecology Progress Series*, *615*, pp.189-204.

Franco-Trecu, V., Aurioles-Gamboa, D. and Inchausti, P., 2014. Individual trophic specialisation and niche segregation explain the contrasting population trends of two sympatric otariids. *Marine Biology*, *161*(3), pp.609-618.

Gales, R., Pemberton, D., Lu, C.C. and Clarke, M.R., 1993. Cephalopod diet of the Australian fur seal: variation due to location, season and sample type. *Marine and Freshwater Research*, *44*(5), pp.657-671.

Gallo-Reynoso, J.P., Figueroa-Carranza, A.L. and Le Boeuf, B.J., 2008. Foraging behavior of lactating Guadalupe fur seal females. *Avances en el Estudio de los Mamíferos de México, C. Lorenzo, E. Espinoza and J. Ortega (eds.). Publicaciones Especiales*, *2*, pp.595-614.

Gallo-Reynoso, J.P. and Esperón-Rodríguez, M., 2013. Diet composition of the Guadalupe fur seal (*Arctocephalus townsendi*). Where and what do they eat?. *Marine and Freshwater Behaviour and Physiology*, *46*(6), pp.455-467.

Guerrero, A.I., Pavez, G., Santos-Carvallo, M., Rogers, T.L. and Sepúlveda, M., 2020. Foraging behaviour of the South American sea lion (*Otaria byronia*) in two disparate ecosystems assessed through blubber fatty acid analysis. *Scientific Reports*, *10*(1), pp.1-13.

Hobson, K.A., Schell, D.M., Renouf, D. and Noseworthy, E., 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(3), pp.528-533.

Hobson, K.A., Sease, J.L., Merrick, R.L. and Piatt, J.F., 1997. Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. *Marine Mammal Science*, *13*(1), pp.114-132.

Hobson, K.A. and Sease, J.L., 1998. Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using Steller sea lions. *Marine Mammal Science*, *14*(1), pp.116-129.

Hooker, S.K., Andrews, R.D., Arnould, J.P., Bester, M.N., Davis, R.W., Insley, S.J., Gales, N.J., Goldsworthy, S.D. and McKnight, J.C., 2021. Fur seals do, but sea lions don't—cross taxa insights into exhalation during ascent from dives. *Philosophical Transactions of the Royal Society B*, *376*(1830), p.20200219.

Hoskins, A.J., Costa, D.P. and Arnould, J.P., 2015. Utilisation of intensive foraging zones by female Australian fur seals. *PLoS One*, *10*(2), p.e0117997.

Hückstädt, L.A., Rojas, C.P. and Antezana, T., 2007. Stable isotope analysis reveals pelagic foraging by the Southern sea lion in central Chile. *Journal of Experimental Marine Biology and Ecology*, *347*(1-2), pp.123-133.

Hückstädt, L.A., Quiñones, R.A., Sepúlveda, M. and Costa, D.P., 2014. Movement and diving patterns of juvenile male South American sea lions off the coast of central Chile. *Marine Mammal Science*, *30*(3), pp.1175-1183.

Hückstädt, L.A., Tift, M.S., Riet-Sapriza, F., Franco-Trecu, V., Baylis, A.M., Orben, R.A., Arnould, J.P., Sepulveda, M., Santos-Carvallo, M., Burns, J.M. and Costa, D.P., 2016. Regional variability in diving physiology and behavior in a widely distributed air-breathing marine predator, the South American sea lion (*Otaria byronia*). *Journal of Experimental Biology*, *219*(15), pp.2320-2330.

Jeglinski, J.W., Goetz, K.T., Werner, C., Costa, D.P. and Trillmich, F., 2013. Same size–same niche? Foraging niche separation between sympatric juvenile Galapagos sea lions and adult Galapagos fur seals. *Journal of Animal Ecology*, *82*(3), pp.694-706.

Jennings, S., Pinnegar, J.K., Polunin, N.V. and Boon, T.W., 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, pp.934-944.

Juárez-Ruiz, A., Elorriaga-Verplancken, F.R., Moreno-Sánchez, X.G., Aguíniga-García, S., Amador-Capitanachi, M.J. and Gálvez, C., 2018. Diversification of foraging habits among Guadalupe fur seals from their only well-established breeding colony, Guadalupe Island, Mexico. Marine biology, 165(5), pp.1-12.

Kienle, S.S., Cuthbertson, R.D. and Reidenberg, J.S., 2022. Comparative examination of pinniped craniofacial musculature and its role in aquatic feeding. *Journal of anatomy*, *240*(2), pp.226-252.

Kirkman, S.P. and Arnould, J.P., 2018. Cape and Australian fur seals: *Arctocephalus pusillus pusillus* and *A. p. doriferus*. In Encyclopedia of Marine Mammals (pp. 158-161). Academic Press.

Kirkwood, R. and Goldsworthy, S., 2013. Fur seals and sea lions. Csiro publishing.

Kirkwood, R., Warneke, R.M. and Arnould, J.P., 2009. Recolonization of Bass Strait, Australia, by the New Zealand fur seal, *Arctocephalus forsteri*. Marine Mammal Science, 25(2), pp.441-449.

Knox, T.C., Baylis, A.M. and Arnould, J.P., 2017. Habitat use and diving behaviour of male Australian fur seals. *Marine Ecology Progress Series*, 566, pp.243-256.

Kopf, R.K., Yen, J.D., Nimmo, D.G., Brosse, S. and Villéger, S., 2021. Global patterns and predictors of trophic position, body size and jaw size in fishes. *Global Ecology and Biogeography*, *30*(2), pp.414-428.

Kudela, R.M., Banas, N.S., Barth, J.A., Frame, E.R., Jay, D.A., Largier, J.L., Lessard, E.J., Peterson, T.D. and Vander Woude, A.J., 2008. New insights into the controls and mechanisms of plankton productivity in coastal upwelling waters of the northern California Current System. *Oceanography*, *21*(4), pp.46-59.

Kuhn, C.E. and Costa, D.P., 2014. Interannual variation in the at-sea behavior of California sea lions (*Zalophus californianus*). *Marine Mammal Science*, *30*(4), pp.1297-1319.

Ladds, M., Rosen, D., Gerlinsky, C., Slip, D. and Harcourt, R., 2020. Diving deep into trouble: the role of foraging strategy and morphology in adapting to a changing environment. *Conservation Physiology*, *8*(1), p.coaa111.

Lancaster, M.L., Gemmell, N.J., Negro, S., Goldsworthy, S. and Sunnucks, P., 2006. Ménage à trois on Macquarie Island: hybridization among three species of fur seal (*Arctocephalus* spp.) following historical population extinction. *Molecular Ecology*, *15*(12), pp.3681-3692.

Layman, C.A., Winemiller, K.O., Arrington, D.A. and Jepsen, D.B., 2005. Body size and trophic position in a diverse tropical food web. *Ecology*, 86(9), pp.2530-2535.

Lee-Thorp, J.A., Sealy, J.C. and Van Der Merwe, N.J., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of archaeological science*, *16*(6), pp.585-599.

Ling, J., 1999. Exploitation of fur seals and sea lions from Australian, New Zealand and adjacent subantarctic islands during the eighteenth, nineteenth and twentieth centuries. *Australian Zoologist*, *31*(2), pp.323-350.

Liwanag, H.E., Berta, A., Costa, D.P., Budge, S.M. and Williams, T.M., 2012a. Morphological and thermal properties of mammalian insulation: the evolutionary transition to blubber in pinnipeds. *Biological Journal of the Linnean Society*, *107*(4), pp.774-787.

Liwanag, H.E., Berta, A., Costa, D.P., Abney, M. and Williams, T.M., 2012. Morphological and thermal properties of mammalian insulation: the evolution of fur for aquatic living. *Biological Journal of the Linnean Society*, *106*(4), pp.926-939.

Lowther, A.D. and Goldsworthy, S.D., 2011. Detecting alternate foraging ecotypes in Australian sea lion (*Neophoca cinerea*) colonies using stable isotope analysis. *Marine Mammal Science*, *27*(3), pp.567-586.

Lowther, A.D., Harcourt, R.G., Page, B. and Goldsworthy, S.D., 2013. Steady as he goes: at-sea movement of adult male Australian sea lions in a dynamic marine environment. *PLoS One*, *8*(9), p.e74348.

Machovsky-Capuska, G.E. and Raubenheimer, D., 2020. The nutritional ecology of marine apex predators. *Annual review of marine science*, *12*, pp.361-387.

Madigan, D.J., Carlisle, A.B., Dewar, H., Snodgrass, O.E., Litvin, S.Y., Micheli, F. and Block, B.A., 2012. Stable isotope analysis challenges wasp-waist food web assumptions in an upwelling pelagic ecosystem. *Scientific reports*, *2*(1), pp.1-10.

McClatchie, S., Charter, R., Watson, W., Lo, N., Hill, K., Manzano-Sarabia, M., Goerlicke, R., Collins, C., Bjorkstedt, E., Schwing, F.B. and Bograd, S.J., 2009. State of the California Current, Spring 2008-2009: cold conditions drive regional differences in coastal production.

McHuron, E.A., Robinson, P.W., Simmons, S.E., Kuhn, C.E., Fowler, M. and Costa, D.P., 2016. Foraging strategies of a generalist marine predator inhabiting a dynamic environment. *Oecologia*, *182*(4), pp.995-1005.

McIntosh, R.R. and Pitcher, B.J., 2021. The Enigmatic Life History of the Australian Sea Lion. In *Ethology and Behavioral Ecology of Otariids and the Odobenid* (pp. 557-585). Springer, Cham.

McKnight, J.C. and Boyd, I.L., 2018. Pinniped life history. In *Encyclopedia of marine mammals* (pp. 722-726). Academic Press.

McMahon, K.W., Hamady, L.L. and Thorrold, S.R., 2013. A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnology and oceanography*, *58*(2), pp.697-714.

Marshall, C.D., Rosen, D.A. and Trites, A.W., 2015. Feeding kinematics and performance of basal otariid pinnipeds, Steller sea lions and northern fur seals: implications for the evolution of mammalian feeding. *Journal of Experimental Biology*, *218*(20), pp.3229-3240.

Melin, S.R., DeLong, R.L. and Siniff, D.B., 2008. The effects of El Niño on the foraging behavior of lactating California sea lions (*Zalophus californianus californianus*) during the nonbreeding season. *Canadian Journal of Zoology*, *86*(3), pp.192-206.

Mori, Y., 2002. Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology*, *15*(2), pp.269-276.

Nagai, R.H., Sousa, S.H.D.M., Lourenço, R.A., Bícego, M.C. and Mahiques, M.M.D., 2010. Paleoproductivity changes during the Late Quaternary in the Southeastern Brazilian upper continental margin of the Southwestern Atlantic. *Brazilian Journal of Oceanography*, *58*, pp.31-41.

Newsome, S.D., Koch, P.L., Etnier, M.A. and Aurioles-Gamboa, D., 2006. Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. *Marine Mammal Science*, *22*(3), pp.556-572.

Newsome, S.D., Etnier, M.A., Kurle, C.M., Waldbauer, J.R., Chamberlain, C.P. and Koch, P.L., 2007. Historic decline in primary productivity in western Gulf of Alaska and eastern Bering Sea: isotopic analysis of northern fur seal teeth. *Marine Ecology Progress Series*, *332*, pp.211-224.

Olivier, P.A., Andrews, R., Burkanov, V. and Davis, R.W., 2022. Diving behavior, foraging strategies, and energetics of female Steller sea lions during early lactation. *Journal of Experimental Marine Biology and Ecology*, *550*, p.151707.

Páez-Rosas, D. and Aurioles-Gamboa, D., 2010. Alimentary niche partitioning in the Galapagos sea lion, *Zalophus wollebaeki*. *Marine Biology*, *157*(12), pp.2769-2781.

Páez-Rosas, D., Aurioles-Gamboa, D., Alava, J.J. and Palacios, D.M., 2012. Stable isotopes indicate differing foraging strategies in two sympatric otariids of the Galapagos Islands. *Journal of Experimental Marine Biology and Ecology*, *424*, pp.44-52.

Páez-Rosas, D., Riofrío-Lazo, M. and Aurioles-Gamboa, D., 2014. Flexibility in the foraging strategies of the Galapagos sea lion inferred from a multiple approach analysis. In *The Galapagos Marine Reserve* (pp. 71-80). Springer, Cham.

Páez-Rosas, D. and Aurioles-Gamboa, D., 2014. Spatial variation in the foraging behaviour of the Galapagos sea lions (*Zalophus wollebaeki*) assessed using scat collections and stable isotope analysis. *Journal of the Marine Biological Association of the United Kingdom*, *94*(6), pp.1099-1107.

Páez-Rosas, D., Villegas-Amtmann, S. and Costa, D., 2017. Intraspecific variation in feeding strategies of Galapagos sea lions: A case of trophic specialization. *PLoS One*, 12(10), p.e0185165.

Page, B., McKenzie, J. and Goldsworthy, S.D., 2005. Dietary resource partitioning among sympatric New Zealand and Australian fur seals. *Marine Ecology Progress Series*, *293*, pp.283-302.

Page, B., McKenzie, J., Sumner, M.D., Coyne, M. and Goldsworthy, S.D., 2006. Spatial separation of foraging habitats among New Zealand fur seals. Marine Ecology Progress Series, 323, pp.263-279.

Patil, I., 2021. Visualizations with statistical details: The 'ggstatsplot' approach. *Journal of Open Source Software*, *6*(61), p.3167.

Pivel, M.A.G., Santarosa, A.C.A., Toledo, F.A.L. and Costa, K.B., 2013. The Holocene onset in the southwestern South Atlantic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *374*, pp.164-172.

Ponce, J.F., Rabassa, J., Coronato, A. and Borromei, A.M., 2011. Palaeogeographical evolution of the Atlantic coast of Pampa and Patagonia from the last glacial maximum to the Middle Holocene. *Biological Journal of the Linnean Society*, *103*(2), pp.363-379.

Riet-Sapriza, F.G., Costa, D.P., Franco-Trecu, V., Marín, Y., Chocca, J., González, B., Beathyate, G., Chilvers, B.L. and Hückstadt, L.A., 2013. Foraging behavior of lactating South American sea lions (*Otaria flavescens*) and spatial–temporal resource overlap with the Uruguayan fisheries. *Deep Sea Research Part II: Topical Studies in Oceanography*, *88*, pp.106-119.

Riofrío-Lazo, M. and Aurioles-Gamboa, D., 2013. Timing of isotopic integration in marine mammal skull: comparative study between calcified tissues. *Rapid Communications in Mass Spectrometry*, *27*(9), pp.1076-1082.

Rohatgi, A., 2020. Webplotdigitizer: Version 4.4. *URL https://automeris. io/WebPlotDigitizer*.

Romanuk, T.N., Hayward, A. and Hutchings, J.A., 2011. Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography*, *20*(2), pp.231-240.

Rosas-Hernández, M.P., Aurioles-Gamboa, D. and Hernández-Camacho, C.J., 2019. Specialized foraging habits of adult female California sea lions *Zalophus californianus*. *Marine Mammal Science*, *35*(4), pp.1463-1488.

Rosen, D.A. and Trites, A.W., 2002. Cost of transport in Steller sea lions, *Eumetopias jubatus*. *Marine Mammal Science*, *18*(2), pp.513-524.

Saporiti, F., Bearhop, S., Silva, L., Vales, D.G., Zenteno, L., Crespo, E.A., Aguilar, A. and Cardona, L., 2014. Longer and less overlapping food webs in anthropogenically disturbed marine ecosystems: confirmations from the past. *PLoS One*, *9*(7), p.e103132.

Saporiti, F., Bearhop, S., Vales, D.G., Silva, L., Zenteno, L., Tavares, M., Crespo, E.A. and Cardona, L., 2016. Resource partitioning among air-breathing marine predators: are body size and mouth diameter the major determinants?. *Marine Ecology*, *37*(5), pp.957-969.

Sarmiento-Devia, R., Sepúlveda, M., Pavez, G., Valdés, J., Canto, A., Orellana, M. and Oliva, D., 2020. Diet composition of an opportunistic predator from an upwelling area in the Southeastern Pacific. *Austral Ecology*, *45*(8), pp.1145-1155.

Segura, A.M., Franco-Trecu, V., Franco-Fraguas, P. and Arim, M., 2015. Gape and energy limitation determine a humped relationship between trophic position and body size. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(2), pp.198-205.

Sepúlveda, M., Pavez, G., Santos-Carvallo, M., Balbontín, C., Pequeño, G. and Newsome, S.D., 2017. Spatial, temporal, age, and sex related variation in the diet of South American sea lions in southern Chile. *Marine Mammal Science*, *33*(2), pp.480-495.

Soto, K.H., Trites, A.W. and Arias-Schreiber, M., 2006. Changes in diet and maternal attendance of South American sea lions indicate changes in the marine environment and prey abundance. *Marine ecology progress series*, *312*, pp.277-290.

Szteren, D., Aurioles-Gamboa, D., Labrada-Martagón, V., Hernández-Camacho, C.J. and De María, M., 2018. Historical age-class diet changes in South American fur seals and sea lions in Uruguay. *Marine Biology*, *165*(4), pp.1-17.

Tedman, R., 2003. Sex-and age-related variations in cranial measurements and suture closure in the Australian sea lion, *Neophoca cinerea* (Peron, 1816). *Australian journal of zoology*, *51*(5), pp.463-484.

Toledo, F.A., Costa, K.B., Pivel, M.A. and Campos, E.J., 2008. Tracing past circulation changes in the western South Atlantic based on planktonic foraminifera. *Revista Brasileira de Paleontologia*, *11*(3), pp.169-178.

Tucker, M.A. and Rogers, T.L., 2014. Examining predator–prey body size, trophic level and body mass across marine and terrestrial mammals. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797), p.20142103.

Vales, D.G., Saporiti, F., Cardona, L., De Oliveira, L.R., Dos Santos, R.A., Secchi, E.R., Aguilar, A. and Crespo, E.A., 2014. Intensive fishing has not forced dietary change in the South American fur seal *Arctophoca* (= *Arctocephalus*) australis off Río de la Plata and adjoining areas. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(6), pp.745-759.

Vales, D.G., Cardona, L., Loizaga, R., García, N.A. and Crespo, E.A., 2020. Long-term stability in the trophic ecology of a pelagic forager living in a changing marine ecosystem. *Frontiers in Marine Science*, *7*, p.87.

Villegas-Amtmann, S., Costa, D.P., Tremblay, Y., Salazar, S. and Aurioles-Gamboa, D., 2008. Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus wollebaeki*. *Marine Ecology Progress Series*, *363*, pp.299-309.

Villegas-Amtmann, S., Jeglinski, J.W., Costa, D.P., Robinson, P.W. and Trillmich, F., 2013. Individual foraging strategies reveal niche overlap between endangered Galapagos pinnipeds. *Plos one*, *8*(8), p.e70748.

Waite, J.N., Trumble, S.J., Burkanov, V.N. and Andrews, R.D., 2012. Resource partitioning by sympatric Steller sea lions and northern fur seals as revealed by biochemical dietary analyses and satellite telemetry. *Journal of Experimental Marine Biology and Ecology*, *416*, pp.41-54.

Warneke, R.M. and Shaughnessy, P.D., 1985. Arctocephalus pusillus, the South African and Australian fur seal: taxonomy, evolution, biogeography, and life history. *Studies of sea mammals in south latitudes*, pp.53-77.

Weise, M.J. and Harvey, J.T., 2008. Temporal variability in ocean climate and California sea lion diet and biomass consumption: implications for fisheries management. *Marine Ecology Progress Series*, *373*, pp.157-172.

Weise, M.J., Harvey, J.T. and Costa, D.P., 2010. The role of body size in individual-based foraging strategies of a top marine predator. *Ecology*, *91*(4), pp.1004-1015.

Williams, T.M., 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *354*(1380), pp.193-201.

Williams, T.M., Haun, J., Davis, R.W., Fuiman, L.A. and Kohin, S., 2001. A killer appetite: metabolic consequences of carnivory in marine mammals. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *129*(4), pp.785-796.

Zangrando, A.F., Panarello, H. and Piana, E.L., 2014. Zooarchaeological and stable isotopic assessments on pinniped–human relations in the Beagle Channel (Tierra del Fuego, southern South America). *International Journal of Osteoarchaeology*, *24*(2), pp.231-244.

Zavala-Gonzalez, A. and Mellink, E., 2000. Historical exploitation of the California sea lion, Zalophus californianus, in Mexico. *Marine Fisheries Review 62*(1)

Zenteno, L., Crespo, E., Vales, D., Silva, L., Saporiti, F., Oliveira, L.R., Secchi, E.R., Drago, M., Aguilar, A. and Cardona, L., 2015. Dietary consistency of male South American sea lions (*Otaria flavescens*) in southern Brazil during three decades inferred from stable isotope analysis. *Marine Biology*, *162*(2), pp.275-289.

Zeppelin, T.K. and Orr, A.J., 2010. Stable isotope and scat analyses indicate diet and habitat partitioning in northern fur seals *Callorhinus ursinus* across the eastern Pacific. *Marine Ecology Progress Series*, *409*, pp.241-253.

FIGURES

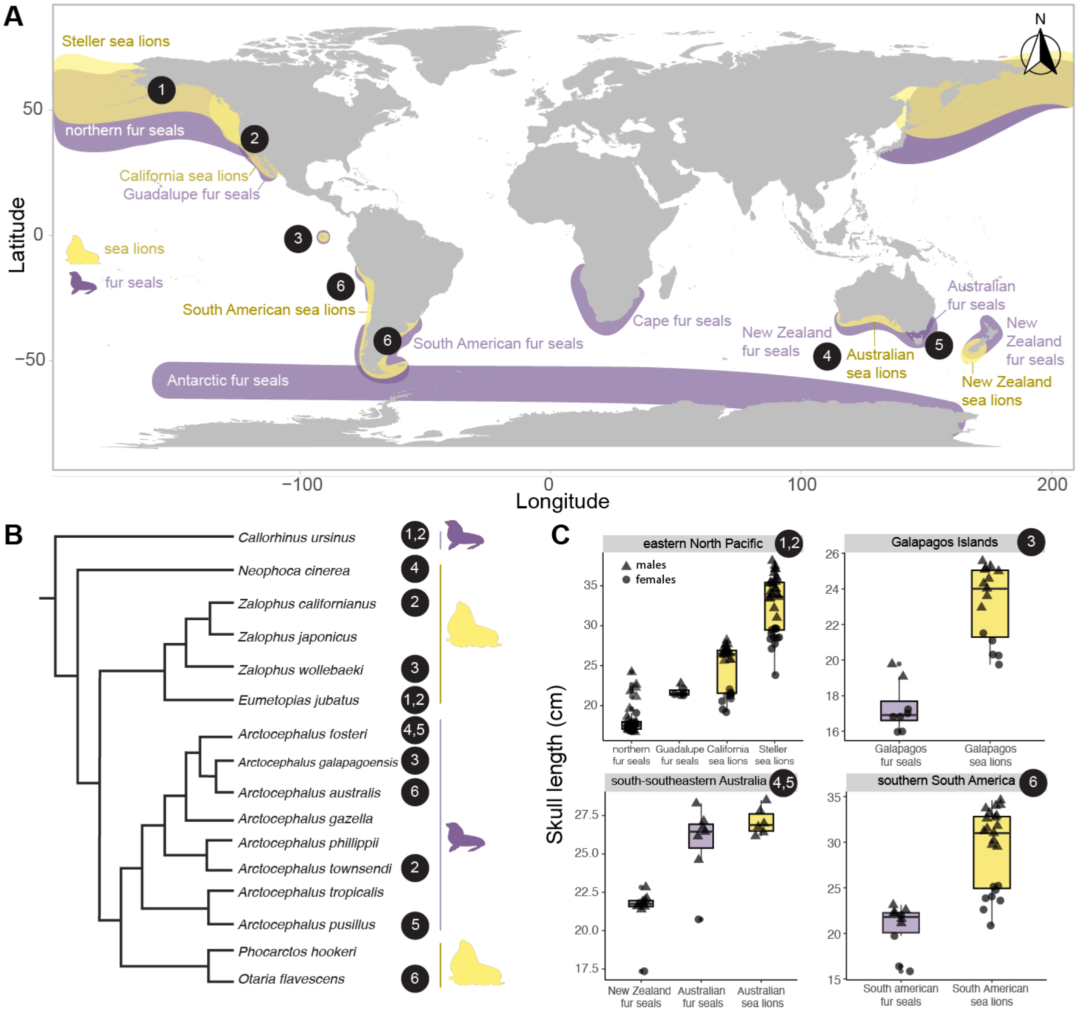

Figure 1.1. (A) Map showing the distribution of fur seals (purple) and sea lions (sea lions). Numbers within black circles indicate the otariid communities discussed in the text. The distribution of subantarctic fur seals (*Arctocephalus tropicalis*) is not depicted. (B) Phylogeny of eared seals based on combined morphological and molecular evidence. Cladogram was modified from Churchill et al. (2014b). Numbers in black circles refer to the otariid communities to which each species belongs and correspond to those described in part (A). (C) Box plots depicting the skull length (as a proxy of body length) of female (circles), and male (triangle) fur seals (purple) and sea lions (yellow) discussed in this study. Skull length data from Churchill et al. (2014a). Boxplots represent the median (horizontal line), inter-quartile range (rectangle), 95% range (vertical lines), and outliers (black dots). Letters on top represent significant differences between groups.

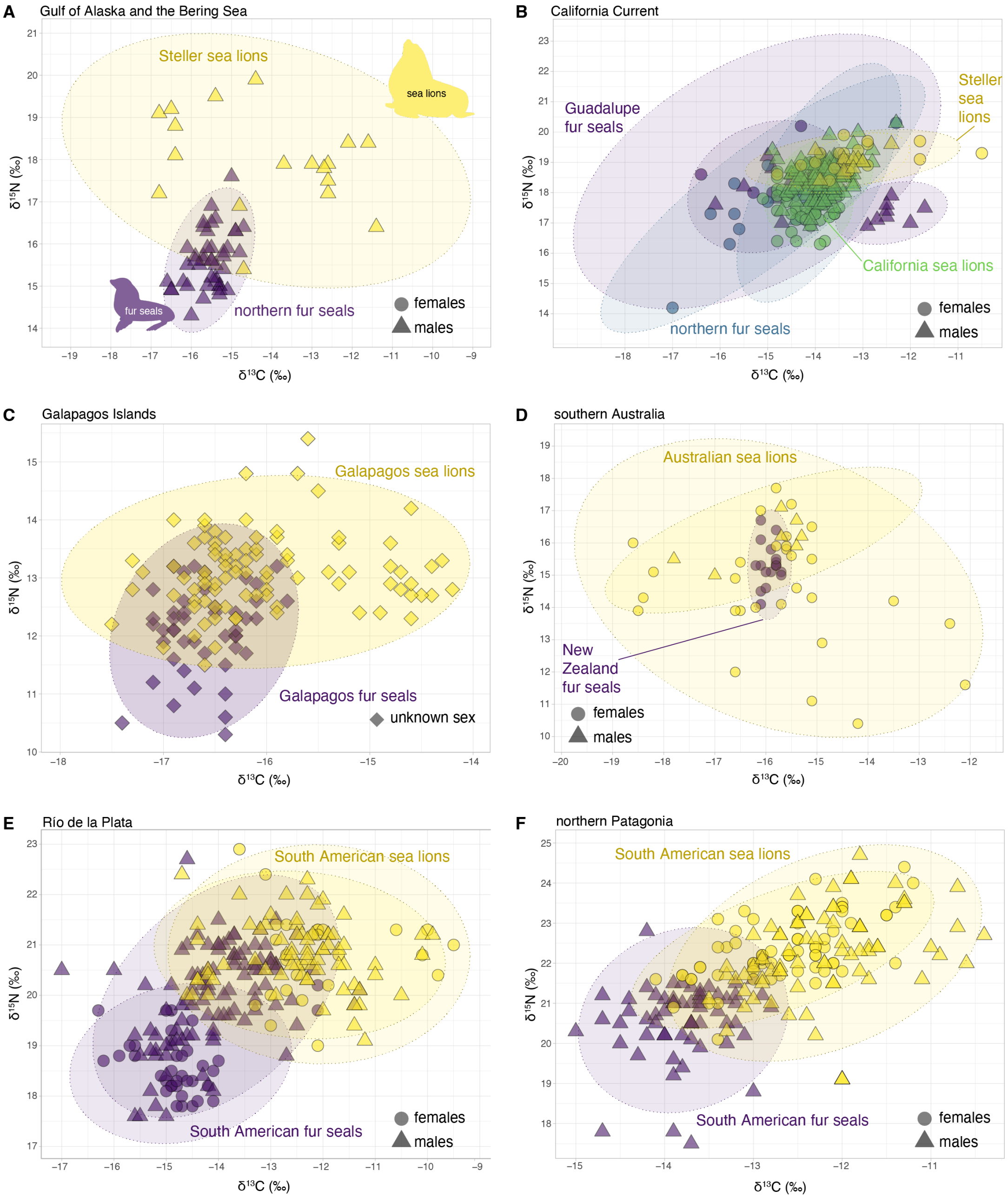

Figure 1.2. Biplots of the $\delta^{13}C$ and $\delta^{15}N$ values of co-occurring fur seals (deep purple) and sea lions (yellow) in the Gulf of Alaska (A), the California Current (B), the Galapagos Islands (C), southern Australia (D), Río de la Plata (E), and northern Patagonia (F). Additional colors were used for otariids from the California Current (B). Blue represents northern fur seals, and green California sea lions. Females are indicated by circles, males by triangles and unknown sex by diamonds. Ellipses represent the size-corrected standard ellipse area (SEA_C), including 95% of the data.

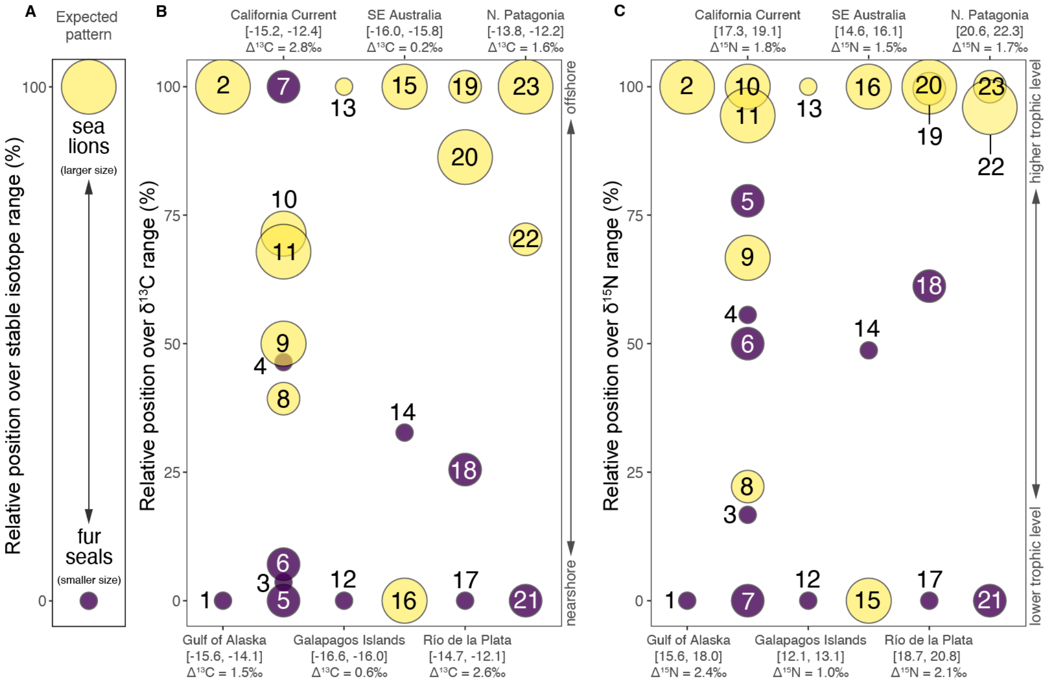

Figure 1.3. Bubble plot depicting the relative position over the $\delta^{13}C$ and $\delta^{15}N$ range of sympatric fur seals (deep purple) and sea lions (yellow) across regions. (A) Expected pattern with small body-sized fur seals having lower relative position over the stable isotope ranges than large body-sized sea lions. (B) Relative position over the $\delta^{13}C$ range, and (C) Relative position over the $\delta^{15}N$ range. Brackets indicate the lowest and the highest average stable isotope value at each region and Δ represents the isotopic range at each region. Circles' size is scaled to skull length. Numbers in bubbles indicate populations as follows: 1. Male northern fur seals; 2. Male Steller sea lions; 3. Female northern fur seals; 4. Male northern fur seals; 5. Female Guadalupe fur seals; 6. Male Guadalupe fur seals (offshore population); 7. Male Guadalupe fur seals (nearshore population); 8. Female California sea lions; 9. Male California sea lions; 10. Female Steller sea lions; 11. Male Steller sea lions; 12. Galapagos fur seals (unknown sex); 13. Galapagos fur seals (unknown sex); 14. Female New Zealand fur seals; 15. Female Australian sea lions; 16. Male Australian sea lions; 17. Females South American fur seals; 18. Male South American fur seals; 19. Female South American sea lions; 20. Male South American sea lions; 21. Male South American fur seals; 22. Female South American sea lions; 23. Male South American sea lions.

CHAPTER 2

FORAGING IN EARED SEAL COMMUNITY IS STRUCTURED BY BODY SIZE AND FEEDING MORPHOLOGY

2.1 ABSTRACT

Body size and feeding morphology influence foraging and resource partitioning within communities. To what degree these factors contribute to the structure of marine mammal communities remains unknown. Here we test the association between size, feeding morphology, and foraging in sympatric otariids (eared seals) from the eastern North Pacific Ocean, the most diverse otariid community in the world. We recorded skull measurements and stable carbon and nitrogen isotope values from museum specimens to estimate foraging ecology in four sympatric otariid species: California sea lions (*Zalophus californianus*), Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*), and Guadalupe fur seals (*Arctocephalus townsendi*). We found significant differences in size, feeding morphology, and foraging between species and sexes. Sea lions have larger body sizes and preferentially forage in coastal regions compared to fur seals. Yet, both groups consume prey at a similar trophic level. Moreover, there is a significant correlation between skull size, feeding morphology, and foraging when species and sex identity is excluded. Larger individuals have stronger bite forces and are preferentially coastal, benthic, and consume slightly higher trophic level prey than smaller individuals. Our study reveals that body size and feeding morphology contribute to community structure and resource partitioning.

2.2 INTRODUCTION

Body size and morphological differences in body traits play a major role in resource partitioning among sympatric species (i.e., species co-occurring in geographic areas), influencing the structure of ecological communities (Wilson, 1975; Dayan and Simberloff, 2005). Among marine tetrapods, body size and feeding morphology affect foraging dynamics (Kelley and Motani, 2015; McCurry et al., 2017a,b). Larger taxa can dive deeper and longer, display lower relative metabolic rates than smaller ones (Kooyman et al., 1981; Kooyman, 1989; Williams, 1999; Mori, 2002; Weise et al., 2010), and can exploit a greater diversity of prey by reaching greater depths. Skull traits can limit prey size and processing efficiency (Jones et al., 2013; Kienle and Berta, 2016; McCurry et al., 2017a; Franco-Moreno et al., 2021; Kienle et al., 2021), further influencing foraging dynamics and resource partitioning (Verwaijen et al., 2002; Futuyma and Moreno, 1988; DeVries, 2017; Žagar et al., 2017; Jones and Law, 2018). Few studies have quantified the relationship between body size, feeding morphology, and the foraging ecology in co-occurring marine tetrapods (e.g., Liu et al., 2015; Segura et al., 2015; Saporiti et al., 2016; Drago et al., 2021). While these studies have revealed general associations between size, feeding morphology, and trophic level, they do not follow a consistent trend among species. These studies included taxa (e.g., cetaceans, penguins, seals) with body sizes ranging over several orders of magnitude, and with disparate life histories, and it is possible that taxon-specific evolutionary trade-offs may be confounding these results. Consequently, additional studies are required to test ecomorphological relationships in closely related sympatric species that shed light on the factors influencing the structure of marine communities.

Pinnipeds (true seals, eared seals, and walruses) are a group of marine mammals that breed on land and forage in the water. Eared seals (otariids) are polygynous breeders that inhabit upwelling zones throughout the North Pacific and the Southern Hemisphere (Costa and Valenzuela-Toro, 2021; Figure 2.1). Otariids have been traditionally grouped in fur seals and sea lions based on morphological and foraging differences (Brunner, 2004; Liwanag et al., 2012; Villegas-Amtmann et al., 2013; Marshall et al., 2015; Favilla and Costa, 2020; Hooker et al., 2021). Sea lions have a larger body size, their insulation relies on a thick blubber layer, and their lactating females undertake short foraging trips. Fur seals, instead, have smaller sizes, a dense underfur coat that provides insulation, and females that conduct long foraging trips. Nevertheless, fur seals and sea lions are not monophyletic (Figure. S2.1), indicating repeated evolutionary convergence on these modes of life. Fur seals and sea lions commonly co-occur throughout their geographic range (Figure 2.1), and variable levels of interspecific competition and resource partitioning have been described between them (e.g., Dellinger and Trillmich, 1999; Páez-Rosas et al., 2012, 2014; Jeglinski et al., 2013). Studies have suggested that size and feeding morphology affect foraging performance in otariids (e.g., Marshall et al., 2015; Kienle et al., 2021), shaping these sympatric associations. However, the explicit association between body size, feeding morphology, and foraging in sympatric otariids has not been explored, and their role in structuring otariid communities remains unknown.

We examined the association between body size, feeding morphology, and stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes, which are proxies of the foraging habitat and trophic level, respectively (Newsome et al., 2006) in sympatric fur seals and sea lions from the eastern North Pacific Ocean. In this region, four species co-occur:

California sea lions (*Zalophus californianus*), Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*), and Guadalupe fur seals (*Arctocephalus townsendi*), constituting the most diverse eared seal community in the world.

2.3 METHODOLOGY

2.3.1 Skull measurements and functional indices

We measured 216 physically mature skulls from the following sympatric species: Guadalupe fur seals (4 females), northern fur seals (12 females, 4 males), California sea lions (57 females, 104 males), and Steller sea lions (24 females, 11 males) collected from central and northern California. We recorded 9 linear measurements accounting for the size of the skull (Table S2.1) using a digital caliper with an accuracy of 0.01 mm. We recorded the standard body length (SL) of a subset of 161 specimens and used it to evaluate its relationship with skull length (condylobasal length; CBL). SL was recorded by the original collectors in the field and consisted of the straight-line distance from the snout to the tip of the tail. We calculated three morphological indices accounting for feeding morphology. Mechanical Advantage (MA) and Skull Shape Index (SSI) served as proxies for the relative ability to generate bite force in the mandible and cranium, respectively, whereas the Relative Palatal Length (RPL) indicated the relative size of the oral cavity.

2.3.2 Foraging ecology and stable isotope analysis

We analyzed the bulk $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen of 226 specimens (those indicated above plus ten adult female California sea lions). Samples consistent in 20 mg of bone were cleaned and then demineralized (Newsome et al., 2006). Lipids were extracted by repetitive cycles of soaking and agitation in a petroleum ether solution followed by several rinses with deionized water in glass scintillation vials. Samples were freeze-dried for 24 h and then weighed (~0.6mg) into tin capsules (Costech; 5x9 mm) for analysis. The carbon and nitrogen isotopic compositions and C and N amounts were determined by the University of California Santa Cruz Stable Isotope Laboratory using a CE Instruments NC2500 elemental analyzer coupled to a Thermo Scientific DELTAplus XP isotope ratio mass spectrometer via a Thermo-Scientific Conflo III. Isotope data are expressed in delta (δ) notation which for $\delta^{13}C$ and $\delta^{15}N$ (‰) = $[(R_{sample} / R_{standard}) - 1] \times 1000$, where R_{sample} or $R_{standard}$ are the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in the sample or standard for carbon and nitrogen, respectively. Measurements are corrected to VPDB (Vienna PeeDee Belemnite) for $\delta^{13}C$ and AIR for $\delta^{15}N$ against an in-house gelatin standard reference material (PUGel) which is extensively calibrated against international standard reference materials. Measurements are corrected for size effects, blank-mixing effects, and drift effects. An externally calibrated Acetanilide #1 standard reference material purchased from Dr. Arndt Schimmelmann of Indiana University is measured as a sample for independent quality control. In this set of sample measurements, 22 replicates of Acetanilide #1 had reproducibility (1σ) of 0.06‰ and 0.1‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, and 0.13 for the C:N ratio. The 47 replicates of PUGel had reproducibility of 0.05‰ and 0.09‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, and 0.03 for the C:N ratio. Typical reproducibility is significantly better than 0.1‰ for $\delta^{13}C$ and significantly better than 0.2‰ for $\delta^{15}N$. The atomic C:N ratio of bone samples was determined and varied between 3.1 and 3.6, which is within the range for well-preserved collagen (DeNiro, 1985).

2.3.3 Statistical analysis

Data analyses were performed in R statistical software version 4.0.3 (R Development Core Team, 2008). We compared skull length, morphological indices, the $\delta^{13}C$ and $\delta^{15}N$ values between fur seals and sea lions using Mann–Whitney *U* test using the package ggstatsplot (Patil, 2021). The relationship between skull length, morphological indices, and $\delta^{13}C$ and $\delta^{15}N$ values was examined using the non-parametric Spearman's ρ correlation coefficients. Linear regressions were used to test skull length as a significant predictor of standard length. Two-way analysis of variance (two-way ANOVA) was conducted using species and sex as fixed variables and skull length and morphological indices as dependent variables. We performed separate one-way ANOVA to determine which species and sex pairs differed in their size and feeding morphology, followed by Tukey post hoc tests. We used a non-parametric multivariate analysis of variance (PERMANOVA) (Anderson, 2001) to compare the $\delta^{13}C$ and $\delta^{15}N$ among species, sexes, and the interaction between them, considering Euclidean distance measure and 10,000 permutations using the package vegan (Oksanen et al., 2020). Univariate nonparametric Kruskal-Wallis one-way analysis of variance, followed by pairwise Dunn tests were used to test the effects of species and sex pairs on the $\delta^{15}N$ and $\delta^{13}C$ values using the package FSA (Ogle et al., 2020).

2.4 RESULTS

2.4.1 Body size

Skull length and standard length were strongly correlated ($\rho = 0.88$, $p < 0.00001$; Figure S2.2), indicating that skull length is a valid proxy of body size (Churchill et al., 2014). There were significant differences in the skull length between species (F =

1041.28.8, $p < 0.0001$), sexes ($F = 1957.33$, $p < 0.0001$), and their interaction ($F = 4.14$, $p = 0.017$). Sea lions have significantly larger skull length than co-occurring fur seals ($U = 144.00$, $p < 0.\ 0001$) and males are larger than females, resulting in a body size continuum from the smallest female northern fur seals (184.7 ± 9.0 mm) to the largest male Steller sea lions (371.2 ± 20.6 mm). Only male northern fur seals and female California sea lions did not significantly differ in skull length (Table S2.3).

2.4.2 Feeding morphology

Sea lions had significantly higher MA ($U = 756$, $p < 0.\ 0001$) but lower SSI ($U = 3275$, $p < 0.\ 0001$) than fur seals. Although feeding morphology differed between species and sexes (Table S2.2, Figure S2.3), no consistent significant differences were detected (Table S4-6), except for California sea lions, in which males had higher MA, RPL, and SSI than females (Figure S2.3; Table S2.4-6).

2.4.3 Foraging ecology

We obtained a significant community-wide correlation between the $\delta^{13}C$ and $\delta^{15}N$ values ($\rho = 0.46$, $p < 0.00001$; Figure 2.2A). The PERMANOVA showed that $\delta^{13}C$ and $\delta^{15}N$ values were significantly different between species ($F = 36.48$; $p < 0.0001$), sexes ($F = 45.03$; $p < 0.0001$), and the interaction between them ($F = 6.98$; $p < 0.001$). Species and sexes pairs significantly differed in their $\delta^{13}C$ ($H(6) = 98.41$, $p < 0.001$) and $\delta^{15}N$ ($H(6) = 95.94$, $p < 0.001$) values (Figure S2.4). Sea lions had significantly higher $\delta^{13}C$ values than fur seals ($U = 475$, $p < 0.\ 0001$; Table S2.7) but variable differences in the $\delta^{13}C$ were found between species and sexes (Table S2.8). The $\delta^{15}N$ values did not differ between fur seals and sea lions (p = 0.18), but we detected significant and variable differences among species and sexes pairs (Table S2.9).

2.4.4 Relationship between size, feeding morphology, and foraging ecology

When species and sex is excluded, we found that larger individuals had higher $\delta^{13}C$ and $\delta^{15}N$, occupying a higher position in the isotopic space (Figure 2.2A). The Spearman correlation revealed that the $\delta^{13}C$ and $\delta^{15}N$ values were significantly correlated with the skull length ($\delta^{13}C$: $\rho = 0.61$, $p < 0.00001$; $\delta^{15}N$: $\rho = 0.54$, $p < 0.00001$; Figure 2.2B, C) and the RPL ($\delta^{13}C$: $\rho = 0.44$, $p < 0.00001$; $\delta^{15}N$: $\rho = 0.49$, $p < 0.00001$). The MA is only significantly correlated with $\delta^{13}C$ values ($\delta^{13}C$: $\rho = 0.22$, $p = 0.0020$; $\delta^{15}N$: p = 0.12), whereas the SSI was correlated with $\delta^{15}N$ but not $\delta^{13}C$ values ($\delta^{13}C$: p = 0.27; $\delta^{15}N$: $\rho = 0.35$, $p < 0.00001$). No consistent relationship between $\delta^{13}C$ (Table S2.10) and $\delta^{15}N$ (Table S2.11) values and skull length or feeding morphology was found between species and sexes.

2.5 DISCUSSION

Sympatric otariid species from the northeastern Pacific display significant differences in their size, feeding morphology, and foraging ecology. While sea lions have larger body sizes than sympatric fur seals, no consistent differences in their feeding morphology were detected (Figure S2.3. Sea lions are 1.2‰ ^{13}C- and 0.3‰ ^{15}N-enriched relative to fur seals, hinting at foraging habitat differences (Figure S2.4, Table S2.7). Previous studies have shown a stepwise trophic-level enrichment of ~1‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$ in marine predators (Burton and Koch, 1999). If due solely to differences in trophic level, the 0.3‰ difference in the $\delta^{15}N$ values found here is too small to account for the 1.2‰ difference in the $\delta^{13}C$ values between fur seals and sea lions. Instead, our results are consistent with an offshore to nearshore ^{13}C-enrichment gradient due to baseline differences linked with higher coastal primary productivity. This evidence hints that fur seals and sea lions forage in different habitats (sea lions exploiting nearshore habitats with higher $\delta^{13}C$ values vs. fur seals feeding in offshore habitats with lower $\delta^{13}C$ values), but on similar trophic level prey as is inferred from the minimal $\delta^{15}N$ differences (0.3‰) between them, which is consistent with animal-borne telemetry and dietary analyses (e.g., Antonelis et al., 1990; Aurioles-Gamboa and Camacho-Ríos, 2007; Zeppelin and Orr, 2010; Orr et al., 2011; Waite et al., 2012; Elorriaga-Verplancken et al., 2021). Compound-specific stable isotopes of these groups are required to test this interpretation and exclude other explanations, including spatial $\delta^{15}N$ differences.

Our study did not find a consistent association between size, feeding morphology, and foraging ecology across species and sexes. While the low sample size can partially explain these results for some groups (e.g., Guadalupe fur seals), the lack of pattern in California and Steller sea lions (with a larger sample size) suggest that, at the intraspecific level, body size and feeding morphology do not explain differences in foraging and resource partitioning. Although some studies have found that body size influences foraging behavior at the intraspecific level in some pinniped species (e.g., Thompson et al., 1998; Cronin et al., 2013; Hoskins et al., 2015; Kienle et al., 2021), other studies have found no relationship (e.g., Kernaléguen et al., 2016; Kirkman et al., 2019). Recent research has emphasized how individual specialization emerging from physiological, behavioral, and environmental trade-offs within populations can influence ecological dynamics, including small-scale resource competition (Bolnick et al., 2003; Codron et al., 2008; Vander Zanden et al., 2010; Araújo et al., 2011; Bolnick et al., 2011; Bison et al., 2015; Maldonado et al., 2017; Pansu et al., 2019). Indeed, otariids display large individual behavioral variability independent from body size or physical condition (e.g., Villegas-Amtmann et al., 2008; Cherel et al., 2009; McHuron et al., 2016; Riverón et al., 2021), suggesting that additional factors might account for foraging dynamics at the intraspecific level.

The community-wide association between body size, feeding morphology, and $\delta^{13}C$ and $\delta^{15}N$ values shows that when species and sex identity are excluded, larger individuals with stronger bite forces forage closer to shore at a slightly higher or equivalent trophic level. This relationship can be explained by energetic trade-offs originating from benthic versus pelagic foraging (the predominant foraging strategies among otariids). Benthic diving entails longer durations and thus longer time spent at sea than pelagic foraging (Costa et al., 2004; Ladds et al., 2020), making it more energetically costly (Costa and Gales, 2003; Costa et al., 2004). Benthic and pelagic food webs are functionally and structurally different, which influences the energetic compromises associated with their exploitation. Benthic food webs have higher species richness with a relatively homogenous and predictable spatial distribution (Cury et al., 2000). Pelagic food webs have lower species diversity but more abundant and energy-dense in highly sporadic prey aggregations (Anthony et al., 2000; Eder and Lewis, 2005; Machovsky-Capuska and Raubenheimer, 2020). Larger individuals have a lower relative metabolic rate and cost of transport than smaller individuals (e.g., Weise et al., 2010), which combined with the consumption of larger prey (enabled by larger sizes and stronger bite capacities) in the benthos might offset the higher energetic costs of benthic diving. Smaller individuals have a smaller feeding apparatus, limiting their range of prey sizes, favoring the exploitation of schooling energy-rich but smaller pelagic fish (Anthony et al., 2000; Eder and Lewis, 2005; Machovsky-Capuska and Raubenheimer, 2020).

While we focused on otariids from the eastern North Pacific, the community-wide ecomorphological relationships found here may be prevalent in other geographic areas. Otariid communities throughout the Southern Hemisphere have lower taxonomic richness than those from the eastern North Pacific (Figure 2.1); however, comparable body size, morphological, and foraging disparities occur among sympatric species (Costa and Valenzuela-Toro, 2021). Future work comparing the ecomorphological attributes of these sympatric communities will shed light on this matter. The fossil record also reveals that pinniped assemblages were taxonomically diverse and had body size and morphological differences analogous to modern otariid and other pinniped communities (Valenzuela-Toro et al., 2016; Velez-Juarbe, 2017). These observations suggest that differences in body size and feeding morphology among co-occurring otariids (and other pinnipeds) have repeatedly evolved independently, contributing to foraging and resource segregation, as has been suggested for some marine herbivore and terrestrial carnivore communities (e.g., Van Valkenburgh, 1988, 2007; Radloff and Du Toit, 2004; Velez-Juarbe et al., 2012)

2.6 ACKNOWLEDGMENTS

We thank R. Bandar for collecting the osteological remains used in this study. M. Flannery and M. Velez of the California Academy of Sciences provided access to the osteological collection. A. Guzmán assisted in sample collection. B. Sellers and A. Yuen assisted with sample preparation. C. Carney carried out the stable isotope analyses.

Funding was provided by the University of California Santa Cruz Division of Physical and Biological Sciences and the Graduate Student Association; the Peter Buck Predoctoral Fellowship of the National Museum of Natural History, Smithsonian Institution; the Society for Marine Mammalogy; the Rebecca and Steve Sooy Graduate Fellowship, and ANID PCHA/Becas Chile, Doctoral Fellowship, Grant No. 2016-72170286.

2.7 REFERENCES

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral ecology*, *26*(1), pp.32-46.

Antonelis, G.A., Stewart, B.S. and Perryman, W.F., 1990. Foraging characteristics of female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*). *Canadian Journal of Zoology*, *68*(1), pp.150-158.

Anthony, J.A., Roby, D.D. and Turco, K.R., 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology*, *248*(1), pp.53-78.

Araújo, M.S., Bolnick, D.I. and Layman, C.A., 2011. The ecological causes of individual specialisation. *Ecology letters*, *14*(9), pp.948-958.

Aurioles-Gamboa, D. and Camacho-Ríos, F.J., 2007. Diet and feeding overlap of two otariids, *Zalophus californianus* and *Arctocephalus townsendi*: Implications to survive environmental uncertainty. *Aquatic Mammals*, *33*(3), p.315.

Bison, M., Ibanez, S., Redjadj, C. *et al.* Upscaling the niche variation hypothesis from the intra- to the inter-specific level. *Oecologia* **179,** 835–842 (2015). https://doi.org/10.1007/s00442-015-3390-7

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. and Forister, M.L., 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, *161*(1), pp.1-28.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H., Schreiber, S.J., Urban, M.C. and Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution*, *26*(4), pp.183-192.

Brunner, S., 2004. Fur seals and sea lions (Otariidae): identification of species and taxonomic review. *Systematics and Biodiversity*, *1*(3), pp.339-439.

Burton, R.K. and Koch, P.L., 1999. Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds. *Oecologia*, *119*(4), pp.578-585.

Cherel, Y., Kernaléguen, L., Richard, P. and Guinet, C., 2009. Whisker isotopic signature depicts migration patterns and multi-year intra-and inter-individual foraging strategies in fur seals. *Biology letters*, *5*(6), pp.830-832.

Churchill, M., Clementz, M.T. and Kohno, N., 2014. Predictive equations for the estimation of body size in seals and sea lions (Carnivora: Pinnipedia). *Journal of Anatomy*, *225*(2), pp.232-245.

Codron, D., Brink, J.S., Rossouw, L., Clauss, M., Codron, J., Lee-Thorp, J.A. and Sponheimer, M., 2008. Functional differentiation of African grazing ruminants: an example of specialized adaptations to very small changes in diet. *Biological Journal of the Linnean Society*, *94*(4), pp.755-764.

Costa, D.P. and Gales, N.J., 2003. Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecological Monographs*, *73*(1), pp.27-43.

Costa, D.P., Kuhn, C.E., Weise, M.J., Shaffer, S.A. and Arnould, J.P., 2004, December. When does physiology limit the foraging behaviour of freely diving mammals?. In *International congress series* (Vol. 1275, pp. 359-366). Elsevier.

Costa, D.P. and Valenzuela-Toro, A.M., 2021. When Physiology and Ecology Meet: The Interdependency Between Foraging Ecology and Reproduction in Otariids. In *Ethology and Behavioral Ecology of Otariids and the Odobenid* (pp. 21-50). Springer, Cham.

Cronin, M., Pomeroy, P. and Jessopp, M., 2013. Size and seasonal influences on the foraging range of female grey seals in the northeast Atlantic. *Marine biology*, *160*(3), pp.531-539.

Cury, P., Bakun, A., Crawford, R.J., Jarre, A., Quinones, R.A., Shannon, L.J. and Verheye, H.M., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, *57*(3), pp.603-618.

Dayan, T. and Simberloff, D., 2005. Ecological and community-wide character displacement: the next generation. *Ecology letters*, *8*(8), pp.875-894.

Dellinger, T. and Trillmich, F., 1999. Fish prey of the sympatric Galapagos fur seals and sea lions: seasonal variation and niche separation. *Canadian Journal of Zoology*, *77*(8), pp.1204-1216.

DeNiro, M.J., 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. *Nature*, *317*(6040), pp.806-809.

deVries, M.S., 2017. The role of feeding morphology and competition in governing the diet breadth of sympatric stomatopod crustaceans. *Biology letters*, *13*(4), p.20170055.

Drago, M., Signaroli, M., Valdivia, M., González, E.M., Borrell, A., Aguilar, A. and Cardona, L., 2021. The isotopic niche of Atlantic, biting marine mammals and its relationship to skull morphology and body size. *Scientific Reports*, *11*(1), pp.1-14.

Eder, E.B. and Lewis, M.N., 2005. Proximate composition and energetic value of demersal and pelagic prey species from the SW Atlantic Ocean. *Marine Ecology Progress Series*, *291*, pp.43-52.

Elorriaga-Verplancken, F.R., Acevedo-Whitehouse, K., Norris, T., Gutiérrez-Gutiérrez, A., Amador-Capitanachi, M.J., Juárez-Ruiz, A., Sandoval-Sierra, J., Gálvez, C. and Moreno-Sánchez, X.G., 2021. Guadalupe Fur Seals and California Sea Lions: Two Sympatric Otariids from the California Current Ecosystem. In *Ethology and Behavioral Ecology of Otariids and the Odobenid* (pp. 621-634). Springer, Cham.

Favilla, A.B. and Costa, D.P., 2020. Thermoregulatory Strategies of Diving Air-Breathing Marine Vertebrates: A Review. *Frontiers in Ecology and Evolution*, *8*, p.292.

Franco-Moreno, R.A., Polly, P.D., Toro-Ibacache, V., Hernández-Carmona, G., Aguilar-Medrano, R., Marín-Enríquez, E. and Cruz-Escalona, V.H., 2021. Bite force in four pinniped species from the west coast of Baja California, Mexico, in relation to diet, feeding strategy, and niche differentiation. *Journal of Mammalian Evolution*, *28*(2), pp.307-321.

Futuyma, D.J. and Moreno, G., 1988. The evolution of ecological specialization. *Annual review of Ecology and Systematics*, *19*(1), pp.207-233.

Hooker, S.K., Andrews, R.D., Arnould, J.P., Bester, M.N., Davis, R.W., Insley, S.J., Gales, N.J., Goldsworthy, S.D. and McKnight, J.C., 2021. Fur seals do, but sea lions don't—cross taxa insights into exhalation during ascent from dives. *Philosophical Transactions of the Royal Society B*, *376*(1830), p.20200219.

Hoskins, A.J., Costa, D.P., Wheatley, K.E., Gibbens, J.R. and Arnould, J.P., 2015. Influence of intrinsic variation on foraging behaviour of adult female Australian fur seals. *Marine Ecology Progress Series*, *526*, pp.227-239.

Jeglinski, J.W., Goetz, K.T., Werner, C., Costa, D.P. and Trillmich, F., 2013. Same size–same niche? Foraging niche separation between sympatric juvenile Galapagos sea lions and adult Galapagos fur seals. *Journal of Animal Ecology*, *82*(3), pp.694-706.

Jones, K.E., Ruff, C.B. and Goswami, A., 2013. Morphology and biomechanics of the pinniped jaw: mandibular evolution without mastication. *The Anatomical Record*, *296*(7), pp.1049-1063.

Jones, K. and Law, C.J., 2018. Differentiation of craniomandibular morphology in two sympatric *Peromyscus* mice (Cricetidae: Rodentia). *Mammal Research*, *63*(3), pp.277-283.

Kelley, N.P. and Motani, R., 2015. Trophic convergence drives morphological convergence in marine tetrapods. *Biology Letters*, *11*(1), p.20140709.

Kernaléguen, L., Cherel, Y., Guinet, C. and Arnould, J.P.Y., 2016. Mating success and body condition not related to foraging specializations in male fur seals. *Royal Society open science*, *3*(7), p.160143.

Kienle, S.S., Cuthbertson, R.D. and Reidenberg, J.S., 2022. Comparative examination of pinniped craniofacial musculature and its role in aquatic feeding. *Journal of anatomy*, *240*(2), pp.226-252.

Kienle, S.S. and Berta, A., 2016. The better to eat you with: the comparative feeding morphology of phocid seals (Pinnipedia, Phocidae). *Journal of Anatomy*, *228*(3), pp.396-413.

Kirkman, S.P., Costa, D.P., Harrison, A.L., Kotze, P.G.H., Oosthuizen, W.H., Weise, M., Botha, J.A. and Arnould, J.P.Y., 2019. Dive behaviour and foraging effort of female Cape fur seals *Arctocephalus pusillus pusillus*. *Royal Society open science*, *6*(10), p.191369.

Kooyman, G.L., 2012. *Diverse divers: physiology and behavior* (Vol. 23). Springer Science & Business Media.

Kooyman, G.L., Castellini, M.A. and Davis, R.W., 1981. Physiology of diving in marine mammals. *Annual review of physiology*, *43*(1), pp.343-356.

Ladds, M., Rosen, D., Gerlinsky, C., Slip, D. and Harcourt, R., 2020. Diving deep into trouble: the role of foraging strategy and morphology in adapting to a changing environment. *Conservation Physiology*, *8*(1), p.coaa111.

Liwanag, H.E., Berta, A., Costa, D.P., Budge, S.M. and Williams, T.M., 2012. Morphological and thermal properties of mammalian insulation: the evolutionary transition to blubber in pinnipeds. *Biological Journal of the Linnean Society*, *107*(4), pp.774-787.

Liu, J.Y., Chou, L.S. and Chen, M.H., 2015. Investigation of trophic level and niche partitioning of 7 cetacean species by stable isotopes, and cadmium and arsenic tissue concentrations in the western Pacific Ocean. *Marine pollution bulletin*, *93*(1-2), pp.270-277.

Machovsky-Capuska, G.E. and Raubenheimer, D., 2020. The nutritional ecology of marine apex predators. *Annual review of marine science*, *12*, pp.361-387.

Maldonado, K., Bozinovic, F., Newsome, S.D. and Sabat, P., 2017. Testing the niche variation hypothesis in a community of passerine birds. Ecology, 98(4), 2017, pp. 903–908.

Marshall, C.D., Rosen, D.A. and Trites, A.W., 2015. Feeding kinematics and performance of basal otariid pinnipeds, Steller sea lions and northern fur seals: implications for the evolution of mammalian feeding. *Journal of Experimental Biology*, *218*(20), pp.3229-3240.

McCurry, M.R., Fitzgerald, E.M., Evans, A.R., Adams, J.W. and Mchenry, C.R., 2017a. Skull shape reflects prey size niche in toothed whales. *Biological Journal of the Linnean Society*, *121*(4), pp.936-946.

McCurry, M.R., Evans, A.R., Fitzgerald, E.M., Adams, J.W., Clausen, P.D. and McHenry, C.R., 2017b. The remarkable convergence of skull shape in crocodilians and toothed whales. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1850), p.20162348.

McHuron, E.A., Robinson, P.W., Simmons, S.E., Kuhn, C.E., Fowler, M. and Costa, D.P., 2016. Foraging strategies of a generalist marine predator inhabiting a dynamic environment. *Oecologia*, *182*(4), pp.995-1005.

Misarti, N., Finney, B., Maschner, H. and Wooller, M.J., 2009. Changes in northeast Pacific marine ecosystems over the last 4500 years: evidence from stable isotope analysis of bone collagen from archeological middens. *The Holocene*, *19*(8), pp.1139-1151.

Mori, Y., 2002. Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology*, *15*(2), pp.269-276.

Newsome, S.D., Koch, P.L., Etnier, M.A. and Aurioles-Gamboa, D., 2006. Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. *Marine Mammal Science*, *22*(3), pp.556-572.

Ogle, D.H., Wheeler, P. and Dinno, A., 2020. FSA: fisheries stock analysis. R package version 0.8. 30.9000.

Oksanen, F. Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R. B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., and Wagner, H. 2020. vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Orr, A.J., VanBlaricom, G.R., DeLong, R.L., Cruz-Escalona, V.H. and Newsome, S.D., 2011. Intraspecific comparison of diet of California sea lions (*Zalophus californianus*) assessed using fecal and stable isotope analyses. *Canadian Journal of Zoology*, *89*(2), pp.109-122.

Páez-Rosas, D., Aurioles-Gamboa, D., Alava, J.J. and Palacios, D.M., 2012. Stable isotopes indicate differing foraging strategies in two sympatric otariids of the Galapagos Islands. *Journal of Experimental Marine Biology and Ecology*, *424*, pp.44-52.

Páez-Rosas, D., Rodríguez-Pérez, M. and Riofrío-Lazo, M., 2014. Competition influence in the segregation of the trophic niche of otariids: a case study using isotopic bayesian mixing models in Galapagos pinnipeds. *Rapid Communications in Mass Spectrometry*, *28*(23), pp.2550-2558.

Pansu, J., Guyton, J.A., Potter, A.B., Atkins, J.L., Daskin, J.H., Wursten, B., Kartzinel, T.R. and Pringle, R.M., 2019. Trophic ecology of large herbivores in a reassembling African ecosystem. *Journal of Ecology*, *107*(3), pp.1355-1376.

Patil, I., 2021. Visualizations with statistical details: The 'ggstatsplot' approach. *Journal of Open Source Software*, *6*(61), p.3167.

R Development Core Team, 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing. ISBN 3-900051-07-0, Vienna, Austria. Available at: http://www.R-project.org

Radloff, F.G. and Du Toit, J.T., 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology*, *73*(3), pp.410-423.

Riverón, S., Raoult, V., Baylis, A.M., Jones, K.A., Slip, D.J. and Harcourt, R.G., 2021. Pelagic and benthic ecosystems drive differences in population and individual specializations in marine predators. *Oecologia*, *196*(3), pp.891-904.

Saporiti, F., Bearhop, S., Vales, D.G., Silva, L., Zenteno, L., Tavares, M., Crespo, E.A. and Cardona, L., 2016. Resource partitioning among air‐breathing marine predators: are body size and mouth diameter the major determinants?. *Marine Ecology*, *37*(5), pp.957-969.

Segura, A.M., Franco-Trecu, V., Franco-Fraguas, P. and Arim, M., 2015. Gape and energy limitation determine a humped relationship between trophic position and body size. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(2), pp.198-205.

Thompson, P.M., Mackay, A., Tollit, D.J., Enderby, S. and Hammond, P.S., 1998. The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology*, *76*(6), pp.1044-1053.

Valenzuela‐Toro, A.M., Pyenson, N.D., Gutstein, C.S. and Suárez, M.E., 2016. A new dwarf seal from the late Neogene of South America and the evolution of pinnipeds in the southern hemisphere. *Papers in Palaeontology*, *2*(1), pp.101-115.

Van Valkenburgh, B., 1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology*, *14*(2), pp.155-173.

Van Valkenburgh, B., 2007. Déjà vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology*, *47*(1), pp.147-163.

Vander Zanden, H.B., Bjorndal, K.A., Reich, K.J. and Bolten, A.B., 2010. Individual specialists in a generalist population: results from a long-term stable isotope series. *Biology letters*, *6*(5), pp.711-714.

Velez-Juarbe, J., Domning, D.P. and Pyenson, N.D., 2012. Iterative evolution of sympatric seacow (Dugongidae, Sirenia) assemblages during the past~ 26 million years. PLoS One, 7(2), p.e31294.

Velez-Juarbe, J., 2017. *Eotaria citrica*, sp. nov., a new stem otariid from the "Topanga" formation of Southern California. *PeerJ*, *5*, p.e3022.

Verwaijen, D., Van Damme, R. and Herrel, A., 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology*, *16*(6), pp.842-850.

Villegas-Amtmann, S., Jeglinski, J.W., Costa, D.P., Robinson, P.W. and Trillmich, F., 2013. Individual foraging strategies reveal niche overlap between endangered Galapagos pinnipeds. *Plos one*, *8*(8), p.e70748.

Villegas-Amtmann, S., Costa, D.P., Tremblay, Y., Salazar, S. and Aurioles-Gamboa, D., 2008. Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus wollebaeki*. *Marine Ecology Progress Series*, *363*, pp.299-309.

Waite, J.N., Trumble, S.J., Burkanov, V.N. and Andrews, R.D., 2012. Resource partitioning by sympatric Steller sea lions and northern fur seals as revealed by biochemical dietary analyses and satellite telemetry. *Journal of Experimental Marine Biology and Ecology*, *416*, pp.41-54.

Weise, M.J., Harvey, J.T. and Costa, D.P., 2010. The role of body size in individual-based foraging strategies of a top marine predator. *Ecology*, *91*(4), pp.1004-1015.

Williams, T.M., 1999. The evolution of cost-efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *354*(1380), pp.193-201.

Wilson, D.S., 1975. The adequacy of body size as a niche difference. *The American Naturalist*, *109*(970), pp.769-784.

Žagar, A., Carretero, M.A., Vrezec, A., Drašler, K. and Kaliontzopoulou, A., 2017. Towards a functional understanding of species coexistence: ecomorphological variation in relation to whole-organism performance in two sympatric lizards. *Functional Ecology*, *31*(9), pp.1780-1791.

Zeppelin, T.K. and Orr, A.J., 2010. Stable isotope and scat analyses indicate diet and habitat partitioning in northern fur seals *Callorhinus ursinus* across the eastern Pacific. *Marine Ecology Progress Series*, *409*, pp.241-253.

FIGURES

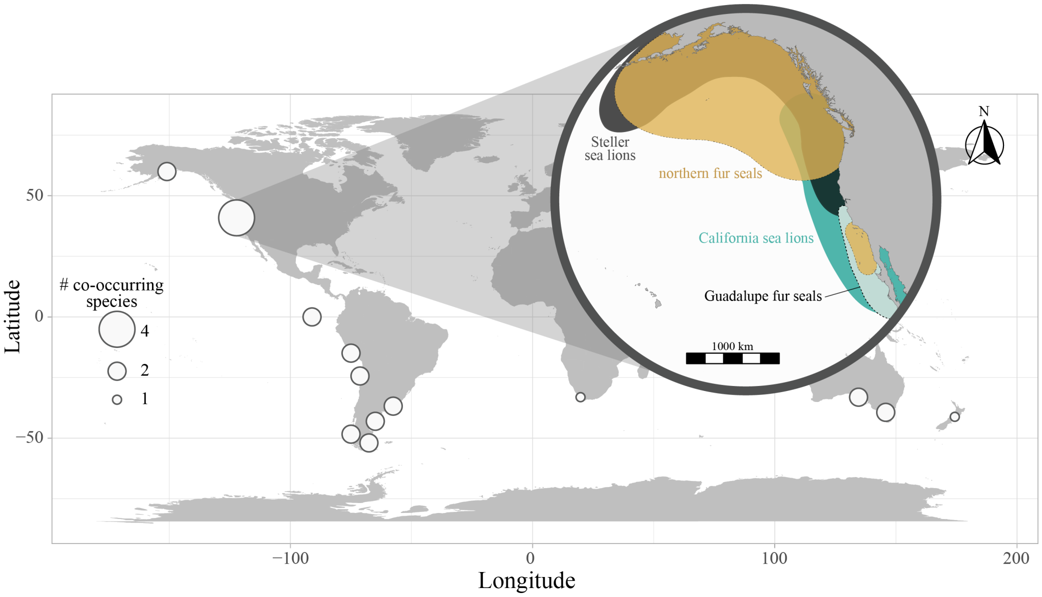

Figure 2.1. Distribution of otariids. Circles represent the location of breeding colonies and their size the number of co-existing otariid species in each region. Inset depicts the distribution range of species inhabiting the eastern North Pacific Ocean.

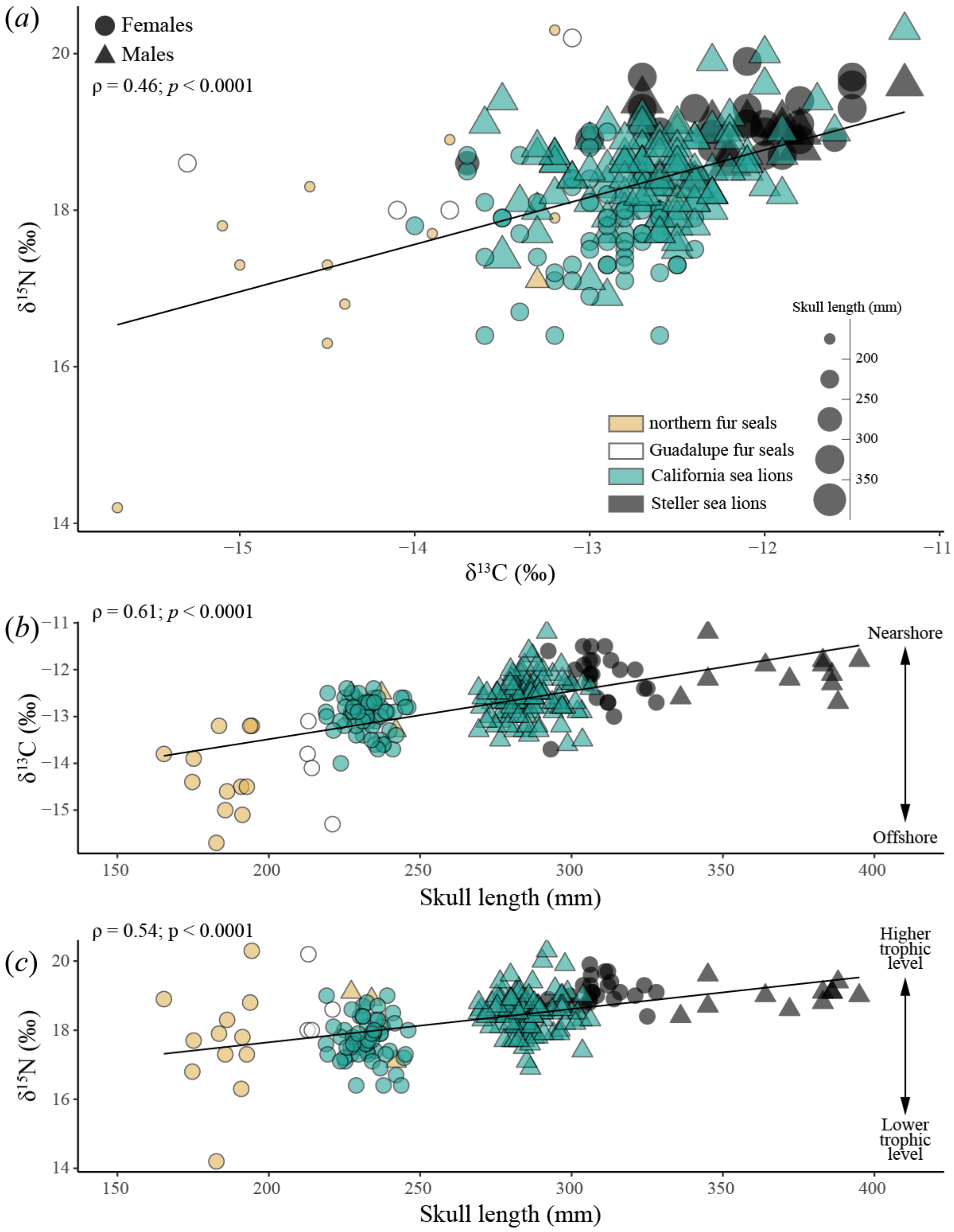

Figure 2.2. A) Community-wide relationship between $\delta^{13}C$ and $\delta^{15}N$ values showing an enrichment in larger skull sizes. Correlation between the skull length and $\delta^{13}C$ (B) and $\delta^{15}N$ values (C). Spearman's ρ correlations are displayed. Black lines represent the linear correlation model.

CHAPTER 2

2.8 SUPPLEMENTARY INFORMATION

Table S 2.1. Description and interpretation of skull measurements and morphological indices taken for specimens of co-occurring otariids.

Anatomical measurements (abbreviation)	**Definition and description**
Standard length (SL)	Straight-line distance from the snout to the tip of the tail.
Condylobasal length (CBL)	The most anterior tip of the premaxilla to the posteriormost margin of the occipital condyles.
Mechanical Advantage (MA)	Length of the insertion area for the masseter muscle relative to the mandible length. Higher values indicate higher bite force capacity (Timm-Davis et al., 2015).
Relative Palatal Length (RPL)	Measured as the length of the palate from the anteriormost to the posteriormost margin divided by the skull length. Higher values indicate a relatively longer rostrum.
Skull Shape Index (SSI)	Skull width at the level of the zygomatic arches relative to the total skull length (skull width/skull length). Indicates relative ability to generate bite force, given that a broader cranium is associated with larger jaw-closing muscles and a shorter cranium increases the mechanical advantage of the jaw-closing muscles (Biknevicius et al., 1996).

Table S 2.2. Results of two-way ANOVA for differences in the skull length and feeding morphology among species and sexes. d.f. = degrees of freedom.

Variable	source of variation	d.f.	sums of squares	mean squares	F-value	*p*-value
Skull length (CBL)	Species	3	218720	72907	917.52	**< 0.0001**
	Sex	1	140654	140654	1770.11	**< 0.0001**
	Species:Sex	2	517	258	3.25	**0.041**
	Residuals	209	16607	79		
Mechanical Advantage (MA)	Species	3	0.031	0.010	16.55	**< 0.0001**
	Sex	1	0.039	0.039	62.16	**< 0.0001**
	Species:Sex	2	0.0055	0.0027	4.35	**0.014**
	Residuals	190	0.12	0.00063		
Relative Palatal Length (RPL)	Species	3	0.27	0.090	331.15	**< 0.0001**
	Sex	1	0.021	0.021	78.66	**< 0.0001**
	Species:Sex	2	0.0015	0.00076	2.79	0.064
	Residuals	191	0.052	0.00027		
Skull Shape Index (SSI)	Species	3	0.031	0.010	21.26	**< 0.0001**
	Sex	1	0.076	0.076	156.45	**< 0.0001**
	Species:Sex	2	0.0044	0.0022	4.56	**0.012**
	Residuals	205	0.10	0.00049		

Table S 2.3. Tukey *post hoc* pairwise comparisons of the Skull Length among female and male sympatric otariids included in this study. Significant results are bold.

	female Guadalupe fur seals	female Northern fur seals	male Northern fur seals	female California sea lions	male California sea lions	female Steller sea lions
female Guadalupe fur seals	-					
female Northern fur seals	**< 0.001**	-				
male Northern fur seals	**0.0031**	**< 0.001**	-			
female California sea lions	**0.0048**	**< 0.001**	0.99	-		
male California sea lions	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	-	
female Steller sea lions	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	-
male Steller sea lions	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**

Table S 2.4. Tukey *post hoc* pairwise comparisons of the Mechanical Advantage among female and male sympatric otariids included in this study. Significant results are bold.

	female Guadalupe fur seals	female Northern fur seals	male Northern fur seals	female California sea lions	male California sea lions	female Steller sea lions
female Guadalupe fur seals	-					
female Northern fur seals	0.69	-				
male Northern fur seals	**0.0065**	0.077	-			
female California sea lions	**0.021**	0.23	0.63	-		
male California sea lions	**< 0.001**	**< 0.001**	0.96	**< 0.001**	-	
female Steller sea lions	**0.023**	0.26	0.75	1.00	**< 0.001**	-
male Steller sea lions	**0.015**	0.18	0.95	0.98	**0.015**	1.00

Table S 2.5. Tukey *post hoc* pairwise comparisons of the Relative Palatal Length among female and male sympatric otariids included in this study. Significant results are bold.

	female Guadalupe fur seals	female Northern fur seals	male Northern fur seals	female California sea lions	male California sea lions	female Steller sea lions
female Guadalupe fur seals	-					
female Northern fur seals	**< 0.001**	-				
male Northern fur seals	**< 0.001**	0.72	-			
female California sea lions	**< 0.001**	0.83	0.97	-		
male California sea lions	**< 0.001**	**< 0.001**	0.77	**< 0.001**	-	
female Steller sea lions	0.76	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	-
male Steller sea lions	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**

Table S 2.6. Tukey *post hoc* pairwise comparisons of the Skull Shape Index among female and male sympatric otariids included in this study. Significant results are bold.

	female Guadalupe fur seals	female Northern fur seals	male Northern fur seals	female California sea lions	male California sea lions	female Steller sea lions
female Guadalupe fur seals	-					
female Northern fur seals	0.53	-				
male Northern fur seals	0.42	1.00	-			
female California sea lions	**< 0.001**	**< 0.001**	**< 0.001**	-		
male California sea lions	1.00	**0.0011**	**0.030**	**< 0.001**	-	
female Steller sea lions	0.38	**< 0.001**	**< 0.001**	**< 0.001**	**0.0016**	-
male Steller sea lions	1.00	0.64	0.56	**< 0.001**	0.57	**0.0014**

Table S 2.7. Mean and standard deviation of $\delta^{13}C$ and $\delta^{15}N$ isotope values (‰) of fur seal and sea lions included in this study.

Variable	Sea lions n = 206	Fur seals n = 20
Mean $\delta^{13}C$ ± SD (min, max)	-12.7 ± 0.5 (-14.0, -11.2)	-13.9 ± 0.9 (-15.7, -12.5)
Mean $\delta^{15}N$ ± SD (min, max)	18.3 ± 0.7 (16.3, 20.3)	18.0 ± 1.4 (14.2, 20.3)

Table S 2.8. Dunn *post hoc* pairwise comparisons of the δ^{13}C values among female and male sympatric otariids included in this study. Significant differences are bolded.

	female Guadalupe fur seals	female Northern fur seals	male Northern fur seals	female California sea lions	male California sea lions	female Steller sea lions
female Guadalupe fur seals	-					
female Northern fur seals	0.93	-				
male Northern fur seals	0.092	**0.034**	-			
female California sea lions	0.10	**0.0049**	0.50	-		
male California sea lions	**0.0023**	**< 0.001**	0.51	**< 0.001**	-	
female Steller sea lions	**< 0.001**	**< 0.001**	0.054	**< 0.001**	**0.0031**	-
male Steller sea lions	**< 0.001**	**< 0.001**	**0.033**	**< 0.001**	**0.0055**	**0.58**

Table S 2.9. Dunn *post hoc* pairwise comparisons of the δ15N values among female and male sympatric otariids included in this study. Significant differences in bold.

	female Guadalupe fur seals	female Northern fur seals	male Northern fur seals	female California sea lions	male California sea lions	female Steller sea lions
female Guadalupe fur seals	-					
female Northern fur seals	0.23	-				
male Northern fur seals	0.97	0.28	-			
female California sea lions	**0.10**	0.63	0.14	-		
male California sea lions	0.95	**0.027**	0.93	**< 0.001**	-	
female Steller sea lions	0.14	**< 0.001**	0.11	**< 0.001**	**< 0.001**	-
male Steller sea lions	0.24	**< 0.001**	0.20	**< 0.001**	**0.024**	0.81

Table S 2.10. Spearman's ρ correlation between morphological variables and $\delta^{13}C$ and $\delta^{15}N$ Significant correlations are in bold.

$\delta^{13}C$	CBL		MA		RPL		SSI	
	ρ	*p*	ρ	*p*	ρ	*p*	ρ	*p*
Guadalupe fur seals	-0.80	0.33	0.80	0.33	0.20	0.92	0.80	0.33
Northern fur seals	0.54	**0.03**	0.56	**0.03**	0.22	0.41	0.13	0.64
California sea lions	0.38	**< 0.001**	0.26	**0.00**	0.26	**0.00**	0.31	**< 0.001**
Steller sea lions	-0.10	0.59	-0.01	0.95	0.02	0.92	-0.05	0.75

$\delta^{15}N$	CBL		MA		RPL		SSI	
	ρ	*p*	ρ	*p*	ρ	*p*	ρ	*p*
Guadalupe fur seals	0.21	0.79	-0.21	0.79	-0.74	0.26	0.63	0.37
Northern fur seals	0.32	0.23	0.23	0.41	0.16	0.56	0.34	0.20
California sea lions	0.42	**< 0.001**	0.29	**< 0.001**	0.30	**< 0.001**	0.53	**< 0.001**
Steller sea lions	0.04	0.81	0.08	0.67	-0.06	0.74	0.22	0.20

Table S 2.11. Spearman's ρ correlation between morphological variables and $\delta^{13}C$ and $\delta^{15}N$ values among species and sexes. Significant correlations are in bold.

$\delta^{13}C$

		CBL		MA		RPL		SSI	
	Sex	ρ	*p*	ρ	*p*	ρ	*p*	ρ	*p*
Guadalupe fur seals	F	-0.80	0.33	0.80	0.33	0.20	0.92	0.80	0.33
Northern fur seals	F	0.11	0.74	0.18	0.59	0.17	0.61	0.17	0.60
Northern fur seals	M	-0.63	0.37	0.95	0.05	-0.32	0.68	0.63	0.37
California sea lions	F	-0.10	0.45	0.08	0.56	-0.22	0.11	0.07	0.59
California sea lions	M	0.13	0.20	0.00	0.99	0.09	0.40	0.01	0.89
Steller sea lions	F	-0.30	0.16	-0.07	0.74	0.06	0.81	-0.39	0.06
Steller sea lions	M	-0.06	0.97	0.12	0.98	0.21	0.48	0.50	0.11

$\delta^{15}N$

		CBL		MA		RPL		SSI	
	Sex	ρ	*p*	ρ	*p*	ρ	*p*	ρ	*p*
Guadalupe fur seals	F	0.21	0.79	-0.21	0.79	-0.74	0.26	0.63	0.37
Northern fur seals	F	0.28	0.38	-0.19	0.57	0.30	0.34	0.43	0.16
Northern fur seals	M	-1.00	0.08	0.80	0.33	-0.40	0.75	0.20	0.92
California sea lions	F	0.01	0.97	0.01	0.93	-0.05	0.74	0.48	**< 0.001**
California sea lions	M	-0.03	0.74	0.01	0.91	0.04	0.73	0.19	0.06
Steller sea lions	F	0.26	0.22	-0.07	0.74	-0.01	0.98	0.15	0.49
Steller sea lions	M	0.30	0.19	0.29	0.13	0.37	0.33	0.72	0.01

SUPPLEMENTARY FIGURES

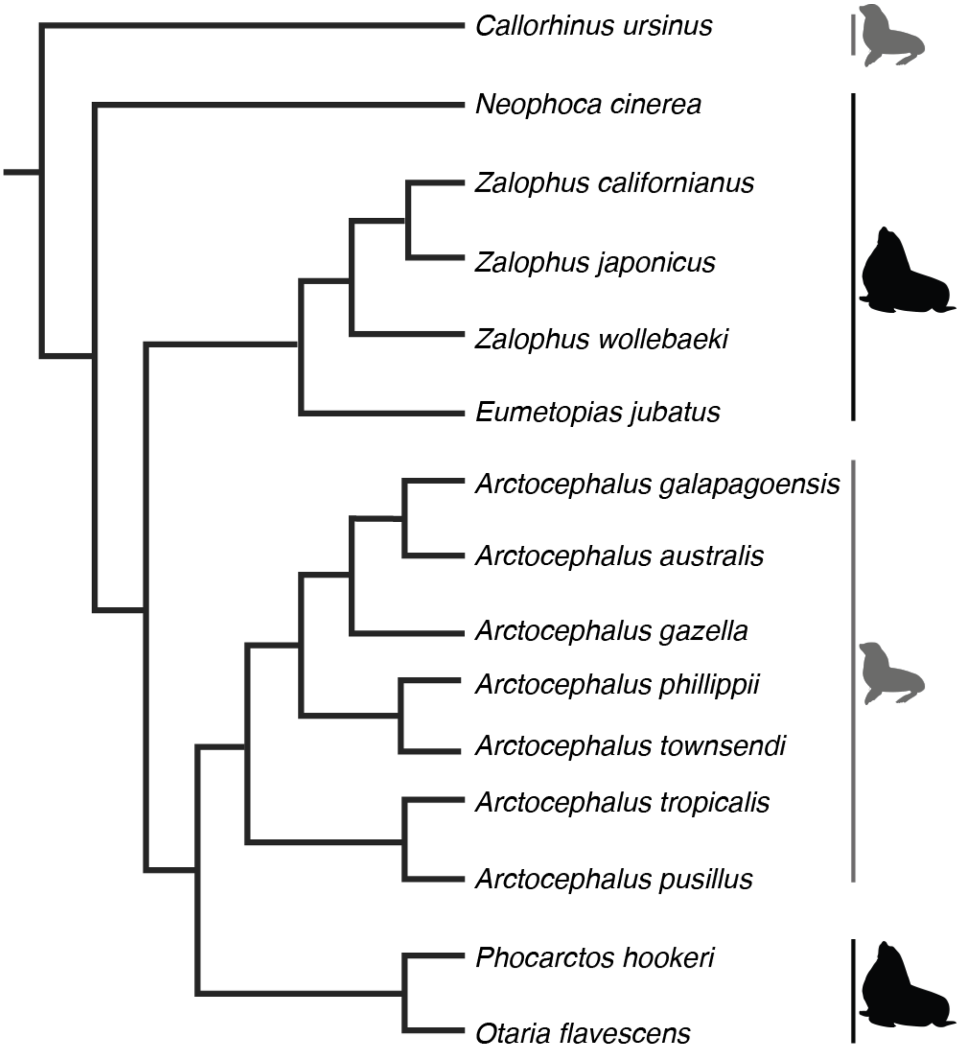

Figure S 2.1. Phylogeny of eared seals based on combined morphological and molecular evidence. Modified from Churchill et al. (2014). Grey icons represent fur seals, and black icons represent sea lions.

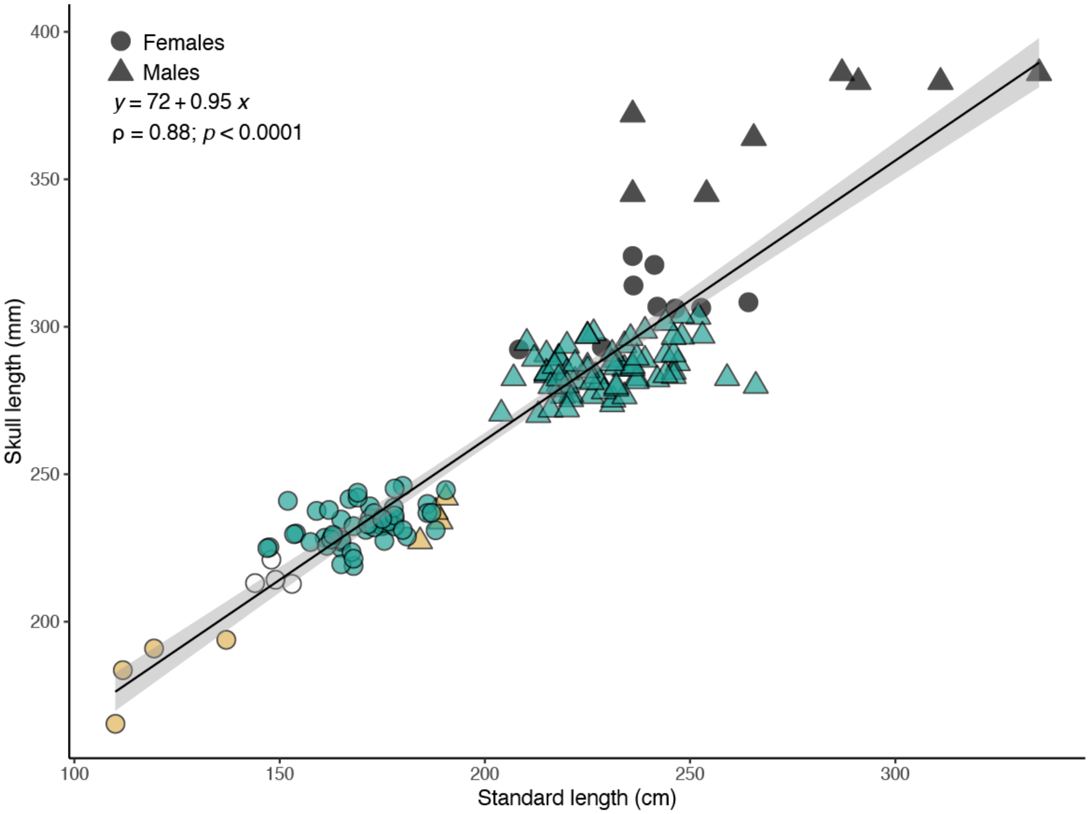

Figure S 2.2. Relationship between skull length (CBL) and the standard length (SL) of otariids from the eastern North Pacific. Species colors are the same as Figure 2.2: yellow represents northern fur seals (n = 8), white represents Guadalupe fur seals (n = 4); turquoise represents California sea lions (n = 122), and black represents Steller sea lions (n = 17). Black line indicates the significant linear regression at the community-wide level ($R^2 = 0.86$, F(1, 149) = 927.5, $p < 0.0001$) and the gray shadow represent their 95% confidence interval. Regression equation is provided in the plot. The Spearman correlation between CBL and SL is ρ = 0.88, $p < 0.0001$.

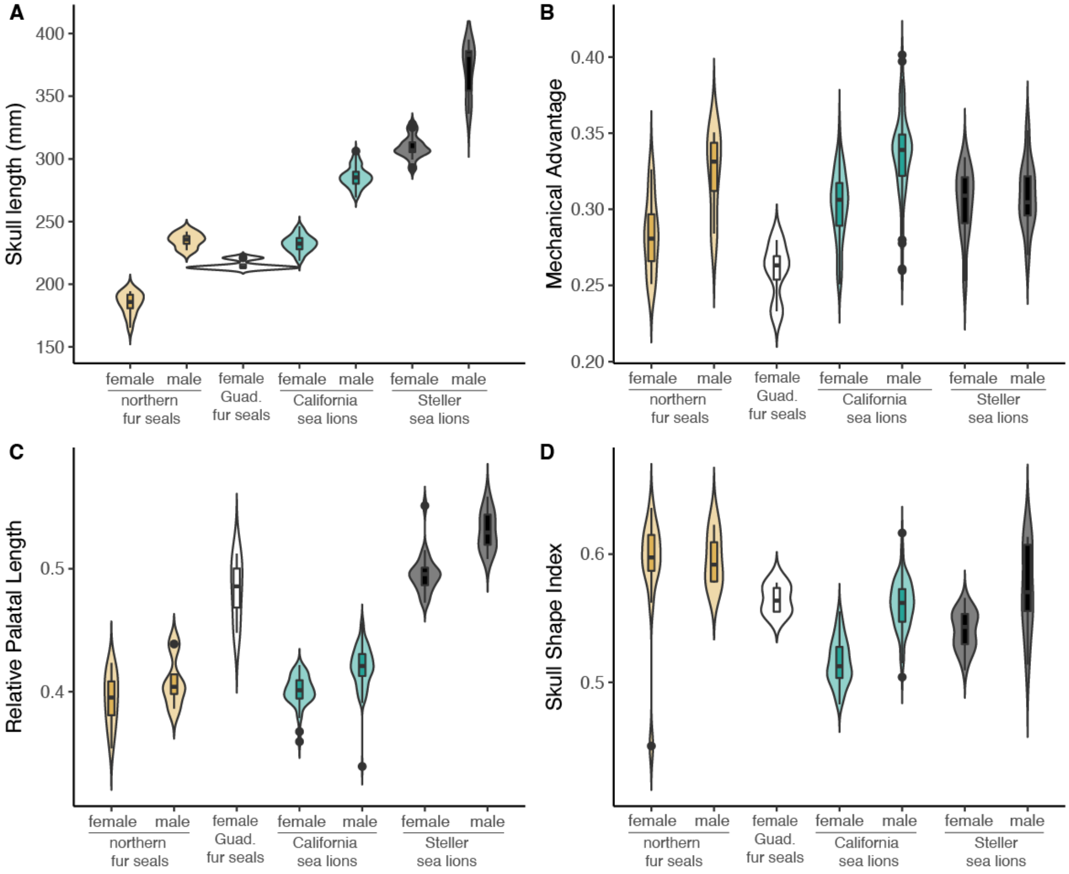

FIGURE S2.3. Skull length (CBL) (A), Mechanical Advantage (B), Relative Palatal Length (C), Skull Shape Index (D) of female and male northern fur seals, Guadalupe fur seals, California sea lions, and Steller sea lions.

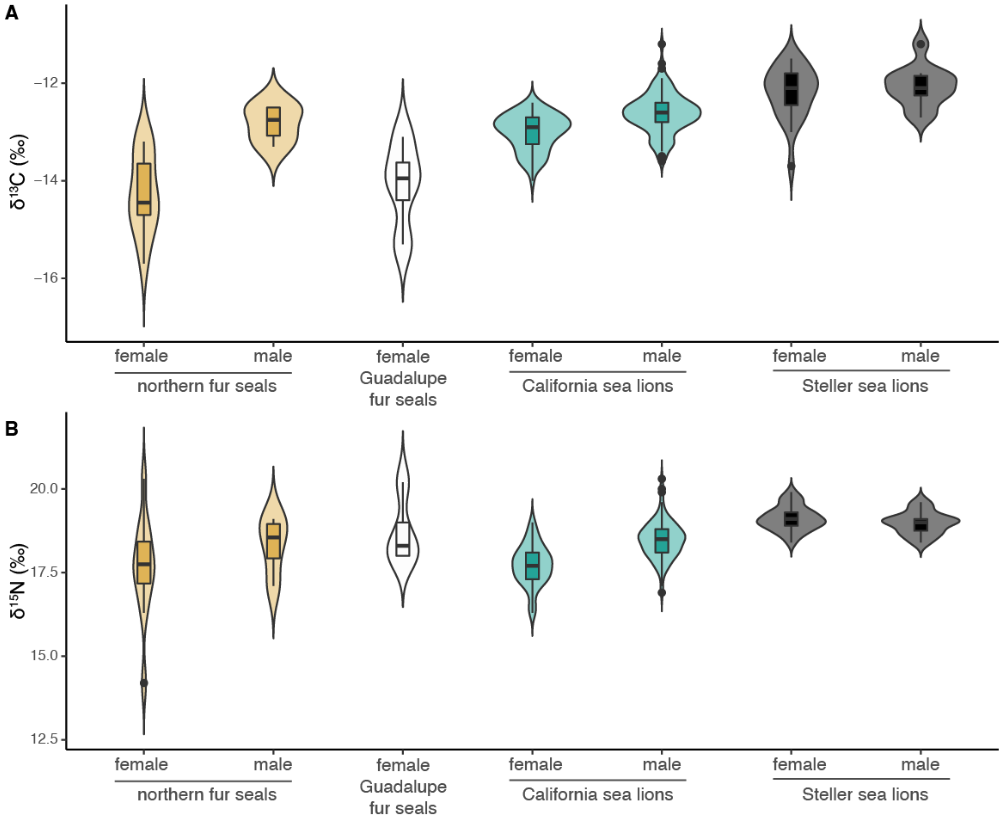

FIGURE S2.4. $\delta^{13}C$ (A) and $\delta^{15}N$ (B) values of females and males co-occurring otariids in the northeastern North Pacific Ocean.

SUPPLEMENTARY REFERENCES

Biknevicius, A.R., Van Valkenburgh, B. and Walker, J., 1996. Incisor size and shape: implications for feeding behaviors in saber-toothed “cats”. *Journal of Vertebrate Paleontology*, *16*(3), pp.510-521.

Churchill, M., Boessenecker, R.W. and Clementz, M.T., 2014. Colonization of the Southern Hemisphere by fur seals and sea lions (Carnivora: Otariidae) revealed by combined evidence phylogenetic and Bayesian biogeographical analysis. *Zoological Journal of the Linnean Society*, *172*(1), pp.200-225.

Timm-Davis, L.L., DeWitt, T.J. and Marshall, C.D., 2015. Divergent skull morphology supports two trophic specializations in otters (Lutrinae). *PloS one*, *10*(12), p.e0143236.

CHAPTER 3

UNEXPECTED DECADAL DENSITY-DEPENDENT SHIFTS IN CALIFORNIA SEA LION SIZE, MORPHOLOGY, AND FORAGING NICHE

3.1 ABSTRACT

Many marine mammal populations are recovering after long eras of exploitation. To what degree density-dependent body size decline in some recovering marine mammal species reflects a response to increased competition for food resources is unknown. Using museum collections, we show that, contrary to predictions, male California sea lions (*Zalophus californianus*) increased rather than decreased their average body size over a 46-year (1962-2008) population recovery. Larger males had proportionally longer oral cavities, more powerful bite strength, and expanded foraging niche. Females' size between 1983-2007 remained stable, but their isotopic niche was larger than contemporary males. We demonstrate that body size decrease is not a general response to increased resource competition during recovery and uncover how sexual and natural selection tradeoffs contributed to population recovery but are likely unattainable under climate change.

3.2 INTRODUCTION

Legal protections over the past 50 years have facilitated the recovery of many marine mammal populations after decades to centuries of human exploitation (Rossi et al., 2021). Several populations of pinnipeds (seals, fur seals, sea lions, and walruses) have shown a marked recovery, reaching, and even surpassing historical baselines and becoming iconic emblems of conservation success (Magera et al., 2013). While population recovery for many marine mammal species has been a long-term conservation goal, marine predator recoveries can affect the structure and function of food webs by exerting top-down pressure on prey, sometimes producing new conservation challenges (e.g., Marshall et al., 2016). Predicting the long-term effects of marine mammal recovery on food webs and how those webs will respond to climate change requires a mechanistic understanding of the ecological dynamics experienced as populations increase over time.

As marine mammal populations increase and approach their carrying capacities, density-dependent limiting factors such as intraspecific competition for resources will intensify, affecting traits such as body size. In marine mammals, body size increases with food availability during growth (Scheffer, 1955). During population recovery, increased competition for resources is thought to drive declines in adult body size, as observed in northern fur seals, South American sea lions, and harbor seals (Scheffer, 1955; Fowler, 1990; Etnier, 2004; Drago et al., 2010; Harding et al., 2018; Sosa Drouville et al., 2021). These examples suggest that density-dependent body size reduction is a general response to pinniped population growth. Yet, pinnipeds display distinctive species and sex-specific life-history strategies that influence the response to density-dependent pressures. The extent to which body size reduction is a stereotyped response to population growth, and how shifting body size might relate to other fundamental traits of individuals, such as their foraging ecology and reproduction, remains unknown.

Body size influences diving and foraging abilities in marine mammals, and thus density-dependent body size shifts could exert cascading effects on foraging performance: larger individuals, for example, dive more efficiently and can fast longer than smaller ones (Williams, 1999; Moori, 2002; Costa and Valenzuela-Toro, 2021). These benefits, however, are offset by higher absolute energy requirements, causing larger individuals to consume more abundant or larger prey, resulting in increased foraging effort (Peters, 1986). Moreover, density-dependent body size dynamics can affect the reproductive dynamics of polygynous species like pinnipeds via sexual selection (Bartholomew, 1970). As populations recover and density at colonies rise, male confrontations to establish and maintain territory and monopolize mates during reproductive seasons should intensify. Consequently, density-dependent sexual selection of more competitive phenotypes (e.g., enlarged body size and stronger bite strength; Kokko and Rankin, 2006; Fitzpatrick et al., 2012; Izuriera-Benitez et al., 2022) may rise, confounding predictions of density-dependent body size shifts.

Here we test whether density-dependent body size reduction is the general response to population recovery. California sea lions (*Zalophus californianus*) are the most abundant and rapidly growing marine mammal species in the eastern North Pacific, so body size declines are anticipated. While variable population dynamics have been recorded in the Gulf of California (Adame et al., 2020), California sea lions' population has steadily increased in the Channel Islands (Southern California) during the last five decades, with recent expansions of rookery sites to central California, which are currently experiencing exponential growth (Lowry et al., 2017, 2021; Laake et al., 2018; Figure 3.1A; Figure. S3.1-5). California sea lions are polygynous breeders and sexually dimorphic in size, shape, and behavior. Every year, males congregate at sites occupied by females and engage in aggressive male-male interactions for territorial control. Body size and physical display are determinants for their reproductive success (Pörschmann et al., 2010; Bohorquez-Herrera et al., 2014). Males undergo long post-breeding foraging trips, whereas females remain at their breeding sites, alternating short foraging trips near their rookery with nursing on land (Melin et al., 2000; McHuron et al., 2016; Figure 3.1B), experiencing, in theory, higher levels of intraspecific competition. Consequently, as California sea lions' population recovers, individuals have experienced varying density-dependent selection pressures. Disentangling how California sea lions' body size, morphology, and foraging have shifted during their recovery is vital for designing appropriate conservation strategies moving forward.

We conduct the first decadal-scale study of density-dependent morphological and ecological shifts in a top marine predator inhabiting the eastern North Pacific coastline. We recorded skeletal and isotopic measurements from museum specimens from central and northern California to test the prediction that during recovery, California sea lions underwent a density-dependent reduction in body size. We examined if and how resource competition influenced the growth and foraging of females and males (over a 24- and 46-year period, respectively) as the population increased.

3.3 MATERIALS AND METHODS

3.3.1 Specimens

We measured skeletal material from specimens at the Ornithology and Mammalogy Collection at the California Academy of Sciences. In total, we surveyed 340 skulls of adult California sea lions collected between 1962 and 2008 for males (n = 274) and between 1983 and 2007 for females (n = 66). We selected specimens based on the preservation of skull morphology, geographic origin, year of collection, and relative age. Sex was determined when collected and confirmed by the presence of the baculum when available. We only included skeletal materials collected from central and northern California (encompassing the coastline between Del Norte to Monterey counties, but mainly (> 85%) from Año Nuevo State Park, the San Francisco area, and Point Reyes National Seashore to avoid the confounding effect of geographical variation among populations (Brunner, 1998; Bohórquez-Herrera et al., 2017).

Because of their sexually dimorphic life history and variable population dynamics across their geographic range (see Supplementary Text), the accumulation of female and male California sea lion skeletal remains in central California may reflect the interplay of distinctive ecological processes. During the study period (1962-2008), the male California sea lion population was dominated by individuals breeding on the Channel Islands (Supplementary Text). From the early 1960s to the late 1970s, male skeletal remains found in central and northern California would correspond predominantly to transient individuals stranded during their post-breeding foraging trip from or toward their reproductive sites in Southern California. As new breeding colonies were established on Año Nuevo and the Farallon Islands in the late 1970s to early 1980s (Keith et al. 1984), an increasing number of resident individuals (i.e., breeding in central California) might have contributed to the local death assemblage (and our dataset), though the scale of breeding in the region was dramatically smaller than on the Channel Islands for much of our study interval (compare Figure S3.3 and S3.4). Thus, male skeletal remains chronicle population and ecological dynamics experienced by sea lions in the Channel Islands and, more recently, in central California. Although no population surveys before the 2000s are available for females, intermittent records of newborn pups in central California since the 1980s (Figure S3.4) demonstrate that females have consistently (but in low density) inhabited Año Nuevo and the Farallon Islands during the study period (1983-2007). These observations, combined with the fact that females do not conduct long-distance foraging trips and remain in their breeding rookeries all-year-round, indicate that female' skeletal remains collected in central California primarily corresponded to resident individuals, registering the population and ecological dynamics prevailing in these new breeding sites.

3.3.2 Age estimation

Various methods have been used to age pinniped skulls. The count of annual growth layer groups in sectioned canine teeth is one of the most reliable (Laws, 1961; Hohn, 2009), but this method is destructive. Relative age measures, such as the cranial suture age or Suture Index (SI), have been developed (Sivertsen, 1954; Brunner 1998). SI is based on the observed degree of fusion of nine cranial sutures (occipito-parietal, squamosoparietal, interparietal, interfrontal, coronal, basioccipito-basisphenoid, maxillary, basisphenoid-presphenoid, and premaxilla-maxillary; Sivertsen, 1954), which ranges from 1 (unfused suture) to 4 (completely fused suture). The SI is calculated as the sum of the degree of fusion, with physically adult skulls ranging between 19 and 36 (Sivertsen, 1954; Brunner et al., 2004).

Previous studies of cranial sutures in California sea lions have shown a correlation of chronological age and SI, with 15-year-old males having all cranial sutures fully closed (SI > 30; Orr et al., 1970). However, extensive variability in the cranial suture pattern across carnivorans suggests a strong influence of feeding ecology (Goswami et al., 2013). Furthermore, male otariids, including California sea lions, display biphasic development with secondary growth in structures associated with male-male combat (and territorial dominance) well after physical maturity is reached (Brunner et al., 2004). Despite being physically and reproductively mature, males that fail to maintain territories do not develop the complete secondary sexual characteristics, including the complete suture fusion of the facial skeleton (Brunner et al., 2004; Stewardson et al., 2008). Moreover, the fusion of premaxilla-maxillary suture is delayed in otariids, resulting in underestimating the SI relative to counts of the annual growth layer groups (Audibert et al., 2017).

Male California sea lions reach their maximum skull length, zygomatic breadth, mastoid breadth, and sagittal crest when ten years old, corresponding to an SI of 20 (Orr, 1970; Brunner et al., 2004). Similarly, females reach their maximum skull length at SI equal to 17-19 (Brunner et al., 2004). For this study, we included male specimens whose SI was equal to or greater than 20. Likewise, we included female skulls whose SI was equal to or greater than 19. In addition, other qualitative features were evaluated to confirm the physical maturity of the specimens, including the absence of deciduous teeth, the display of dental wear, the prominence of the sagittal crest, and the relative ossification of the tympanic bulla and the dentaries (Vasquez-Cuevas et al., 2000; Sinai et al., 2014).

3.3.3 Standard length, skull measurements, and morphological indices

Standard body length (SL) was available for a subset of specimens (187 males and 59 females). SL was recorded by the original collectors in the field and consisted of the straight distance from the snout to the tip of the tail, representing the length of the axial skeleton (McLaren, 1993). To develop a proxy for overall body size, we evaluate the relationship between SL and skull length (condylobasal length, CBL). We recorded 7 linear measurements of the cranium and dentary (Figure S3.6 and Table S3.1) using a digital caliper with an accuracy of 0.01 mm. To minimize error, all specimens were measured by one of the authors (AVT) using a manual caliper. The measurements were selected based on previous studies evaluating morphological variability in otariid species, including California sea lions (Drago et al., 2010; Franco-Moreno et al., 2015). We calculated four functional indices (Mechanical Advantage, Relative Mastoid Width, Relative Palatal Length, and the Skull Shape Index) from the morphological measurements (see Table S3.2).

3.3.4 Stable isotope analysis

We subsampled 166 specimens of those included in the morphometric assessment to perform stable carbon and nitrogen isotope analysis on bone collagen. Specifically, we analyzed 66 females (ranging from 1983 to 2007), and 104 males (ranging from 1962 to 2006) for carbon and nitrogen stable isotopes. Two of the female specimens were not included in the morphometric study. We collected ~20 mg of ethmoid turbinals or cranium using tweezers and stored and transported them in 5 ml Eppendorf tubes. Samples were cleaned and then demineralized by soaking for 48 h in 0.5N HCl at 4°C (Newsome et al., 2006). Lipids were extracted by repetitive soaking cycles and agitation in a petroleum ether solution followed by several rinses with deionized water in glass scintillation vials. Samples were freeze-dried for 24 h with a Labconco Freeze Dry System prior to isotope analysis. We weighed ~ 0.6 mg into tin capsules (Costech; 5x9 mm). The carbon and nitrogen isotopic compositions and C and N amounts were determined by the University of California Santa Cruz Stable Isotope Laboratory using a CE Instruments NC2500 elemental analyzer coupled to a Thermo Scientific DELTAplus XP isotope ratio mass spectrometer via a Thermo-Scientific Conflo III. Isotope data are expressed in delta (δ) notation which for $\delta^{13}C$ and $\delta^{15}N$ (‰) = $[(R_{sample} / R_{standard}) - 1] \times 1000$, where R_{sample} or $R_{standard}$ are the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in the sample or standard for carbon and nitrogen, respectively. Measurements are corrected to VPDB (Vienna PeeDee Belemnite) for $\delta^{13}C$ and AIR for $\delta^{15}N$ against an in-house gelatin standard reference material (PUGel) which is extensively calibrated against international standard reference materials. Measurements are corrected for size effects, blank-mixing effects, and drift effects. An externally calibrated Acetanilide #1 standard reference material purchased from Dr. Arndt Schimmelmann of Indiana University is measured as a sample for independent quality control. In this set of sample measurements, 19 replicates of Acetanilide #1 had reproducibility (1σ) of 0.06‰ and 0.11‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, and 0.13 for the C:N ratio. The 40 replicates of PUGel had reproducibility of 0.06‰ and 0.09‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, and 0.03 for the C:N ratio. Typical reproducibility is significantly better than 0.1‰ for $\delta^{13}C$ and significantly better than 0.2‰ for $\delta^{15}N$. The atomic C:N ratio of bone samples was determined and varied between 3.1 and 3.6, which is within the range for well-preserved collagen (DeNiro, 1985).

3.3.5 Correction for anthropogenic changes to δ^{13}C values

Carbon isotope values were corrected for the global decrease in the ^{13}C concentration of atmospheric carbon dioxide, largely due to fossil fuel burning over the last 150 years, a phenomenon named the Suess effect. A time-dependent correction factor was applied to the δ^{13}C values following Misarti et al. (2009) as follows:

$$\text{Suess effect correction factor} = d * e^{0.027*(t-1850)}$$

d is the maximum annual rate of δ^{13}C decrease specific to the North Pacific (-0.014 from Quay et al., 1992) and *t* is the year represented by the year of specimen collection. Notably, the magnitude of the Suess effect exhibits a broad range of spatial variability (Tagliabue and Bopp, 2008). Therefore, we used a specific parametrization for the northeastern Pacific Ocean. The corrected δ^{13}C values were used for all the subsequent analyses.

3.3.6 Data analysis

All data analyses were performed in R statistical software version 4.0.3 (R Core Team 2020). Males and females were analyzed separately because of the sexual dimorphism displayed by California sea lions.

3.3.6.1 Analysis of body size, skull measurements, and functional indices through time

We analyzed females and males separately to avoid biases because of the extreme sexual dimorphism in California sea lions**.** We assessed the relationship between standard length (SL) and skull length (CBL) using a linear regression model. We tested the stability of the ratio between the SL and CBL through time for each sex by performing linear regression analysis with the year when the specimen was collected as the independent variable and CBL as the dependent variable. We evaluated the relationship between skull measurements and functional indices and year of collection of the skeletal remains using the Spearman nonparametric correlation test.

3.3.6.2 Changes in the isotopic niche through time

The population of California sea lions has sustained growth over, at least, the last six decades (Figure 3.1, Figure S3.3, S3.4). To investigate the relationship between population increase, foraging, and habitat preferences of California sea lions through time, we categorized individuals analyzed for stable isotopes values into groups depending on their sex and the year they were collected. We defined three groups: (1) males collected between 1962 and 1982, (2) males collected between 1983 and 2006 (note that this group's upper temporal limit is lower than those included in the morphometric analysis), and (3) females collected between 1983 and 2007. Based on their sex-specific life history and population dynamics across their range, these groups would chronicle distinct density-dependent ecological pressures. Males belonging to groups (1) and (2) would largely correspond to transient individuals stranded during their post-breeding foraging trips from breeding sites in the Channel Islands. Group (2) might also include a small number of individuals breeding at Año Nuevo and the

Farallon Islands in central California (Figure S3.4,5). These differences imply that individuals from group (1) would chronicle the effects of increasing density-dependent ecological pressures resulting from California sea lions' steady population increase in the Channel Islands (Figure S3.3). Individuals from group (2) would document the effects of intensified density-dependent competition resulting from the accelerated population increase observed in the Channel Island between the 1980s and the late 2000s (period during which they approached and presumably reached their carrying capacity) (Figure S3.3) strengthened by the consistent population expansion of males residing in central California (Figure S3.4,5). Conversely, females (group 3) would primarily represent residents from central California, which remained in low density during their study period, experiencing, therefore, potentially low levels of intraspecific competition.

To estimate isotopic niche width (a proxy for an ecological niche) between groups in the population, we used Bayesian multivariate ellipse-based metrics implemented in the packages SIBER and rjags (Jackson et al., 2011). We calculated the standard ellipse areas considering the 95% of the data corrected for small sample size (SEA_C) and Bayesian standard ellipses (SEA_B) for each group. We estimated SEA_B using 5 chains of 10,000 iterations, a burning of 1,000, and a thinning of 10. We compared the posterior probabilities of SEA_B of each group by using a Kruskal-Wallis analysis of the variance, followed by a Dunn test with Bonferroni correction for multiple comparisons using the package ggbetweenstats (Patil, 2021) in R.

3.4 RESULTS

3.4.1 Shifts in adult body size and functional skull traits over time

We recorded 7 linear measurements of the skulls of adult female (n = 66) and male (n = 273) California sea lions skeletons collected from the coastlines of central and northern California (Figure S3.6, Table S3.1; see the Methods for details). Females remain near the breeding colony and are considered resident to the small central California rookeries, based on this species' life history and historical population dynamics. In contrast, males are considered transient and likely stranded during their lengthy post-breeding foraging trip from much larger breeding sites on the Channel Islands (see Supplementary Text). We calculated four morphological indices (Table S3.2) associated with feeding and physical display performance. We found that skull length (condylobasal length) and standard body length were significantly correlated for females (Pearson's r = 0.43, $p = 0.00061$) and males (Spearman's $\rho = 0.39$, $p < 0.00001$) (Figure S7). We can, therefore, use skull length as a proxy for body size (Churchill et al., 2014).

We hypothesized that as their population increased, an increase in intraspecific competition would lead to a decline in adult body size for both female and male California sea lions, as observed in other pinniped species. Contrary to this prediction, we found that skull dimensions (including our body size proxy, skull length) of male adult California sea lions significantly increased between 1962 and 2008 (Table 3.1, Figure 3.2A, Figure S3.8). Likewise, metrics of skull function such as the Skull Shape Index (indicator of the masticatory muscle insertion area), and Relative Mastoid Width (indicator of neck muscle insertion area) significantly increased over this 46-year interval (Table 3.1). These results are consistent with adult male California sea lions evolving more robust skulls with enhanced abilities to engage in physical encounters.

The temporal record for females in our dataset was shorter (1983 to 2007) and restricted to resident animals from central California. Females did not show a change in skull dimensions or functional traits during this period. Of course, while the number of females at central California breeding sites increased at the end of this interval (in the early 2000s), there is no evidence that they were at carrying capacity by 2007 (Figure S3.4). In contrast, males stranding on the central California coast during this time interval (1983 to 2008) significantly increased their skull length and the dimensions of their mouth as well as their mechanical advantage (indicator of bite force) and their relative palatal length (size corrected length of the oral cavity) (Table 3.1). These changes occurred contemporaneous to the regional increase of California sea lions population, approaching their carrying capacity (Figure S3.4).

3.4.2 Decadal shift in foraging ecology

We tested whether California sea lions shifted their foraging and habitat preferences during this period of population recovery by measuring the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of bone collagen for a subset of adult females (n = 67) and males (n = 104), encompassing a period between 1983 and 2007, and between 1962 and 2006, respectively. Note that the time frame record for males analyzed for stable isotopes was briefer than for the morphometric analysis. We found significant differences between the Standard Ellipse Area of females and males (χ^2 (2) = 1010.2, $p <$ 0.00001). Pairwise comparisons indicated that males collected between 1962 and 1982 had significantly smaller isotopic niches than males collected between 1983 and 2006 (*p* < 0.00001) and than females (*p* < 0.00001). We could not evaluate long-term variation in the female isotopic niche due to the shorter time frame of our female data set (1983-2007). Yet, the isotopic niche breadth of females is significantly larger than that of contemporary males (*p* < 0.00001, Figure 3.2C), indicating that females have greater foraging variability than contemporaneous males.

3.5 DISCUSSION

Contrary to our predictions, we found that over a 46-year (1962-2008) period, during which male California sea lions' population was growing and approaching carrying capacity (Figure 3.1A, Figure S3.2, 3), adult males significantly increased rather than decreased their average body size, as deduced from increases in skull length (and other skull dimensions). Male sea lions collected between 1983 and 2008 had larger and broader skulls, enhanced bite force, and an expanded isotopic niche width. Our sample of females from central California were not at carrying capacity, and female skull dimensions remained stable, but their isotopic niche was conspicuously larger than that of contemporaneous males. These results indicate that body size decrease is not the universal response to increased competition associated with population recovery in marine predators. Moreover, we show that male California sea lions have expanded their foraging niche over recent decades and that females display unexpectedly high foraging variability.

The morphometric response of females and males suggests that food limitation did not adversely affect sea lions' body size growth during decades over which their population increased. This shouldn't be surprising for females, as their increased density did not approach carrying capacity, but it is surprising for males, whose population numbers had plateaued. This unexpected increase in the body size and change in the functional traits (i.e., Mechanical Advantage, Relative Mastoid Width, Relative Palatal Length, and Skull Shape Index) of male sea lions suggest that other density-dependent factors may have influenced their morphological and ecological dynamics. California sea lions are polygynous breeders that annually congregate at reproductive sites. As their population recovered, the density of males at breeding sites increased (Figure S3.2), and male-male confrontations for territorial control presumably also intensified (Young and Gerber, 2008; Gerber et al., 2010). While body size influences male competitiveness through aggressive displays (Schusterman and Dawson, 1968; Bartholomew, 1970), it also influences attendance patterns during the breeding season. Larger individuals can endure extended fasting spans, allowing them to stay and defend territories for longer periods, increasing their reproductive success (Pörschmann et al., 2010; Meise et al., 2014). Consequently, as the population recovers, larger and more competitive individuals with higher fasting ability would be favored by increased sexual selection on the breeding colonies.

Bite force and neck mobility are also relevant to male-male confrontations and reproductive success (Jones et al., 2013; Bohórquez-Herrera et al., 2014). Therefore, if sexual selection intensified, a positive selection of biting force and neck mobility would be anticipated. Indeed, adult male California sea lions have developed broader insertion areas for the muscles associated with biting (e.g., the temporalis muscle as indicated by an increased Skull Shape Index) and in neck lateral flexion and rotation (e.g., sternocleidomastoid muscle as indicated from Relative Mastoid Width) between 1962 and 2008 (Table 3.1). Long-term assessments of sexual selection are not available for this species; however, future decadal-scale studies on relative baculum size (e.g., Fitzpatrick et al., 2012), reproductive steroid hormones (e.g., Chaparrata et al., 2021), or genetic paternity (e.g., Harcourt et al., 2007) in museum specimens might provide ways to test and quantify the occurrence of density-dependent sexual selection in adult male California sea lions associated with population recovery.

Larger individuals could, in theory, forage further, longer, and deeper with proportionally lower energy expenditure than smaller individuals (Costa 1993; Mori, 2002; Weise et al., 2010; Costa and Valenzuela-Toro, 2021). Therefore, positive selection for more efficient foraging may have reinforced the trend toward larger size. While increased body size results in higher absolute energy requirements (Peters, 1986), adult males have expanded their isotopic niche, hinting at the exploitation of more diverse resources during their post-breeding foraging trips (Figure 3.1B). Some individuals from 1983 to 2006 had lower δ^{15}N values than earlier males, which is consistent with a northward extension of their foraging trips and the consumption of higher latitude (with lower isotope baseline) prey (Aurioles et al., 2006). This is consistent with sightings of male California sea lions in southeastern Alaska in recent decades (Maniscalco et al., 2004). Moreover, the increase in oral cavity length of adult males would enhance their ability to capture and handle larger prey (e.g., Franco-Moreno et al., 2021). This is further supported by some contemporary adult males displaying higher maximum δ^{15}N values, which would indicate the preferential consumption of higher trophic level prey.

While other studies have documented the occurrence of significant body size reductions of female sea lions during population recovery (Drago et al., 2010; Sosa Drouville et al., 2020), adult female California sea lions' size remained stable. The spatial distribution of our sample coupled with the distinct population dynamics observed in sea lions' breeding rookeries along the Californian coast is likely influencing these results. Unlike males, which have occupied haulout sites along central California for several decades (Bartholomew 1965; Gearin et al., 2017), female California sea lions were relatively rare until the mid-2010s, when new breeding sites were established at Año Nuevo and the Farallon Islands (Lowry et al., 2017, Figure S3.4). Information on the feeding ecology of females inhabiting these sites is not available. However, female California sea lions are central place foragers and conduct short foraging trips near their breeding sites, although exceptional sightings of females from the Channel Islands foraging in Monterey Bay in central California have been documented (Kuhn and Costa, 2014). The degree of foraging overlap between females and males in this area is unknown; yet, some spatial segregation is expected to be associated with body size differences (Weise and Costa 2007). These observations suggest that, during the study period (1983-2007), female sea lions inhabiting central California were rare, experiencing low density-dependent intraspecific competition for resources, which contributes to their body size stability.

We found that adult females have greater variability in their foraging and dietary preferences (as characterized by the isotopic niche) than contemporary adult males. The high foraging variability among females aligns with studies showing that they are highly efficient foragers (Weise and Costa, 2007) with varying foraging strategies (McHuron et al., 2016). The mechanisms underlying these observations are unclear; however, the association between functional traits and the $\delta^{15}N$ values (Figure S3.8, Table S3.3) hints that skull morphology might contribute to niche breadth by favoring foraging specialization that lessens intraspecific competition among females. Additional decadal-scale studies of females breeding rookeries in the Channel Islands

(Figure S3.1), which have presumably reached their carrying capacity (Figure S3.2,3), are required to test the occurrence (or not) of density-dependent shifts in body size and to further explore the effect of skull morphology on foraging dynamics.

Although dietary data are not available for our entire study period (1962-2008), reports from the 1980s to the early 2000s show that California sea lions' diet was diverse but consistently dominated by energy-rich pelagic species such as Pacific sardines (*Sardinops sagax*) and northern anchovies (*Engraulis morda*x; Lowry et al., 1991; Weise and Harvey, 2008), mirroring fluctuations in their regional abundance (Figure 3.1C). Following the collapse of these fisheries in the 2010s (Zwolinski and Demer, 2012; MacCall et al., 2016), however, California sea lions' diet shifted towards a higher contribution of less energy-dense prey (Robinson et al., 2018; Figure 3.1C), coinciding with lower pup recruitment (McClatchie et al. 2016; Figure 3.1A). Likewise, depletions of pelagic fish during El Niño events (Figure 3.1) have negatively affected California sea lions' energy budget, reproduction, and even their immune response (e.g., Costa et al., 1991; Melin et al., 2008; DeRango et al., 2019; Figure 3.1B). Together, these observations demonstrate that pelagic prey are critical for California sea lions' population dynamics, sustaining their recovery and their decade-scale, density-dependent shifts in body size, morphology, and foraging niche.

It is uncertain how the recovery of marine mammals will be affected as changes in prey abundance and distribution associated with climate further develop. Climate models predict widespread shifts for the California Current System because of global warming. Among other consequences, models forecast an increase in the frequency and intensity of El Niño-like warming conditions (Cai et al., 2014; Howard et al., 2020) as well as an overall reduction of body size and dispersal ability and poleward shift of pelagic fishes (Howard et al., 2020; Avaria-Llautureo et al., 2021; Fiechter et al., 2021). These new conditions are likely to impact marine predators, such as California sea lions, increasing their foraging effort and depressing their energy budget by decreasing foraging performance. Indeed, the energetic and ecological tradeoffs resulting from density-dependent selection pressures like those presented here may be unattainable, lowering their capability to overcome resource competition and reducing species' carrying capacity, leading to steep transformations in the structure and functioning of these populations of marine mammals.

3.6 ACKNOWLEDGMENTS

Our work would not have been possible without the tireless efforts of the late R. Bandar, whose long-term fieldwork produced an unprecedented osteological time series. M. Flannery at the Ornithology and Mammalogy Department of the California Academy of Sciences provided access to the California sea lion osteological collection. A. Guzmán assisted in sample collection. B. Sellers and A. Yuen assisted with sample preparation. C. Carney aided the stable isotope analyses. S. Adamczak, R. Beltran, A. Favilla, C. Fieseler, K. Hernandez, R. Holser, T. Keates, K. Keen, J. Kendall-Bar, D. Palace, A. Ricker, T. Tatom-Naecker, and J. Young offered comments on early versions of this study. Funding was provided by the University of California Santa Cruz Division of Physical and Biological Sciences and the Graduate Student Association; the Peter Buck Predoctoral Fellowship of the National Museum of Natural History, Smithsonian Institution; the Society for Marine Mammalogy; and ANID PCHA/Becas Chile, Doctoral Fellowship, Grant No. 2016-72170286.

3.7 REFERENCES

Adame, K., Elorriaga-Verplancken, F.R., Beier, E., Acevedo-Whitehouse, K. and Pardo, M.A., 2020. The demographic decline of a sea lion population followed multi-decadal sea surface warming. *Scientific reports*, *10*(1), pp.1-15.

Audibert, P., Drehmer, C.J., Danilewicz, D. and De Oliveira, L.R., 2018. Do cranial suture age and growth layer groups correlate in South American pinnipeds? *Journal of the Marine Biological Association of the United Kingdom*, *98*(3), pp.635-644.

Aurioles, D., Koch, P.L. and Le Boeuf, B.J., 2006. Differences in foraging location of Mexican and California elephant seals: evidence from stable isotopes in pups. *Marine Mammal Science*, *22*(2), pp.326-338.

Avaria-Llautureo, J., Venditti, C., Rivadeneira, M.M., Inostroza-Michael, O., Rivera, R.J., Hernández, C.E. and Canales-Aguirre, C.B., 2021. Historical warming consistently decreased size, dispersal and speciation rate of fish. *Nature Climate Change*, *11*(9), pp.787-793.

Bartholomew, G.A., 1965. Seal and sea lion populations of the California Islands.

Bartholomew, G.A., 1970. A model for the evolution of pinniped polygyny. *Evolution*, pp.546-559.

Bohorquez-Herrera, J., Hernández-Camacho, C.J., Aurioles-Gamboa, D. and Cruz-Escalona, V.H., 2014. Plasticity in the agonistic behaviour of male California sea lions, *Zalophus californianus*. *Animal behaviour*, *89*, pp.31-38.

Bohórquez-Herrera, J., Aurioles-Gamboa, D., Hernández-Camacho, C. and Adams, D.C., 2017. Variability in the skull morphology of adult male California sea lions and Galapagos Sea lions. In *Tropical Pinnipeds: bio-ecology, threats and conservation*.

Brunner, S., 1998. Cranial morphometrics of the southern fur seals *Arctocephalus forsteri* and *A. pusillus* (Carnivora: Otariidae). *Australian Journal of Zoology*, *46*(1), pp.67-108.

Brunner, S., Bryden, M.M. and Shaughnessy, P.D., 2004. Cranial ontogeny of otariid seals. *Systematics and Biodiversity*, *2*(1), pp.83-110.

Cai, W., Borlace, S., Lengaigne, M., Van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M.J., Wu, L. and England, M.H., 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature climate change*, *4*(2), pp.111-116.

Charapata, P., Horstmann, L. and Misarti, N., 2021. Steroid hormones in Pacific walrus bones collected over three millennia indicate physiological responses to changes in estimated population size and the environment. *Conservation physiology*, *9*(1), p.coaa135.

Churchill, M., Clementz, M.T. and Kohno, N., 2014. Predictive equations for the estimation of body size in seals and sea lions (Carnivora: Pinnipedia). *Journal of Anatomy*, *225*(2), pp.232-245.

Costa, D.P., Antonelis, G.A. and DeLong, R.L., 1991. Effects of El Niño on the foraging energetics of the California sea lion. In *Pinnipeds and El Niño* (pp. 156-165). Springer, Berlin, Heidelberg.

Costa DP. 1993 The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. In Symp Zool Soc Lond. 66, 293–314.

Costa, D.P. and Valenzuela-Toro, A.M., 2021. When Physiology and Ecology Meet: The Interdependency Between Foraging Ecology and Reproduction in Otariids. In *Ethology and Behavioral Ecology of Otariids and the Odobenid* (pp. 21-50). Springer, Cham.

DeNiro, M.J., 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. *nature*, *317*(6040), pp.806-809.

DeRango, E.J., Prager, K.C., Greig, D.J., Hooper, A.W. and Crocker, D.E., 2019. Climate variability and life history impact stress, thyroid, and immune markers in California sea lions (*Zalophus californianus*) during El Niño conditions. *Conservation physiology*, *7*(1), p.coz010.

Drago, M., Cardona, L., Crespo, E.A., Grandi, M.F. and Aguilar, A., 2010. Reduction of skull size in South American sea lions reveals density-dependent growth during population recovery. *Marine Ecology Progress Series*, *420*, pp.253-261.

Etnier, M.A., 2004. Reevaluating evidence of density-dependent growth in northern fur seals (*Callorhinus ursinus*) based on measurements of archived skeletal specimens. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(9), pp.1616-1626.

Fiechter, J., Buil, M.P., Jacox, M.G., Alexander, M.A. and Rose, K.A., 2021. Projected Shifts in 21st Century Sardine Distribution and Catch in the California Current. *Frontiers in Marine Science*, *8*, p.874.

Fitzpatrick, J.L., Almbro, M., Gonzalez-Voyer, A., Kolm, N. and Simmons, L.W., 2012. Male contest competition and the coevolution of weaponry and testes in pinnipeds. *Evolution: International Journal of Organic Evolution*, *66*(11), pp.3595-3604.

Fowler, C.W., 1990. Density dependence in northern fur seals (*Callorhinus ursinus*). *Marine Mammal Science*, *6*(3), pp.171-195.

Franco-Moreno, R.A., Cruz-Escalona, V.H., Aurioles-Gamboa, D., Vera-Alfaro, P., Salas, J. and Ravela, S., 2015. Variability and sexual dimorphism in skull morphometry of California Sea Lions (*Zalophus californianus*) in Mexico. Mammalian Biology, 80(4), pp.316-327.

Franco-Moreno, R.A., Polly, P.D., Toro-Ibacache, V., Hernández-Carmona, G., Aguilar-Medrano, R., Marín-Enríquez, E. and Cruz-Escalona, V.H., 2021. Bite force in four pinniped species from the west coast of Baja California, Mexico, in relation to diet, feeding strategy, and niche differentiation. *Journal of Mammalian Evolution*, *28*(2), pp.307-321.

Gearin, P.J., Melin, S.R., DeLong, R.L., Gosho, M.E. and Jeffries, S., 2017. Migration patterns of adult male California sea lions (*Zalophus californianus*). U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-346, 29 p.

Gerber, L.R., Gonzalez-Suarez, M., Hernandez-Camacho, C.J., Young, J.K. and Sabo, J.L., 2010. The cost of male aggression and polygyny in California sea lions (*Zalophus californianus*). *PloS one*, *5*(8), p.e12230.

Goswami, A., Foley, L. and Weisbecker, V., 2013. Patterns and implications of extensive heterochrony in carnivoran cranial suture closure. *Journal of evolutionary biology*, *26*(6), pp.1294-1306.

Harcourt, R.G., Kingston, J.J., Cameron, M.F., Waas, J.R. and Hindell, M.A., 2007. Paternity analysis shows experience, not age, enhances mating success in an aquatically mating pinniped, the Weddell seal (*Leptonychotes weddellii*). *Behavioral Ecology and Sociobiology*, *61*(4), pp.643-652.

Harding, K.C., Salmon, M., Teilmann, J., Dietz, R. and Harkonen, T., 2018. Population wide decline in somatic growth in harbor seals—early signs of density dependence. *Frontiers in Ecology and Evolution*, *6*, p.59.

Howard, E.M., Frenzel, H., Kessouri, F., Renault, L., Bianchi, D., McWilliams, J.C. and Deutsch, C., 2020. Attributing causes of future climate change in the California Current system with multimodel downscaling. *Global Biogeochemical Cycles*, *34*(11), p.e2020GB006646.

Hohn, A.A., 2009. Age estimation. In *Encyclopedia of marine mammals* (pp. 11-17). Academic Press.

Jackson, A.L., Inger, R., Parnell, A.C. and Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*(3), pp.595-602.

Jones, K.E., Ruff, C.B. and Goswami, A., 2013. Morphology and biomechanics of the pinniped jaw: mandibular evolution without mastication. *The Anatomical Record*, *296*(7), pp.1049-1063.

Kokko, H. and Rankin, D.J., 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1466), pp.319-334.

Kuhn, C.E. and Costa, D.P., 2014. Interannual variation in the at-sea behavior of California sea lions (*Zalophus californianus*). *Marine Mammal Science*, *30*(4), pp.1297-1319.

Laake, J.L., Lowry, M.S., DeLong, R.L., Melin, S.R. and Carretta, J.V., 2018. Population growth and status of California sea lions. *The Journal of Wildlife Management*, *82*(3), pp.583-595.

Laws, R.M., Age determination of pinnipeds with special reference to growth.

Lowry, M.S. Stewart, B.S., Heath, C.B., Yochem, P.K., and Francis, M. 1991. Seasonal and annual variability in the diet of California sea lions, *Zalophus californianus*, at San Nicolas Island, California, 1981–86. *Fish. Bull*, *89*, pp.331-336.

Lowry, M.S., Melin, S.R. and Laake, J.L., 2017. Breeding season distribution and population growth of California sea lions, *Zalophus californianus*, in the United States during 1964-2014. NOAA Technical Memorandum 574.

Lowry, M.S., Jaime, E.M. and Moore, J.E., 2021. Abundance and distribution of pinnipeds at the Channel Islands in southern California, central and northern California, and southern Oregon during summer 2016–2019. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-656. https://doi.org/10.25923/6qhf-0z55

MacCall, A.D., Sydeman, W.J., Davison, P.C. and Thayer, J.A., 2016. Recent collapse of northern anchovy biomass off California. *Fisheries Research*, *175*, pp.87-94.

Magera, A.M., Mills Flemming, J.E., Kaschner, K., Christensen, L.B. and Lotze, H.K., 2013. Recovery trends in marine mammal populations. *PloS One*, *8*(10), p.e77908.

Maniscalco, J.M., Wynne, K., Pitcher, K.W., Hanson, M.B., Melin, S.R. and Atkinson, S., 2004. The occurrence of California sea lions (Zalophus californianus) in Alaska. *Aquatic Mammals*, *30*(3), pp.427-433.

Marshall, K.N., Stier, A.C., Samhouri, J.F., Kelly, R.P. and Ward, E.J., 2016. Conservation challenges of predator recovery. *Conservation Letters*, *9*(1), pp.70-78.

McClatchie, S., Field, J., Thompson, A.R., Gerrodette, T., Lowry, M., Fiedler, P.C., Watson, W., Nieto, K.M., and Vetter, R.D., 2016. Food limitation of sea lion pups and the decline of forage off central and southern California. *Royal Society Open Science*, *3*(3), p.150628.

McHuron, E.A., Robinson, P.W., Simmons, S.E., Kuhn, C.E., Fowler, M. and Costa, D.P., 2016. Foraging strategies of a generalist marine predator inhabiting a dynamic environment. *Oecologia*, *182*(4), pp.995-1005.

McLaren, I.A., 1993. Growth in pinnipeds. *Biological Reviews of the Cambridge Philosophical Society*, *68*(1), pp.1-79.

Meise, K., Piedrahita, P., Krüger, O. and Trillmich, F., 2014. Being on time: size-dependent attendance patterns affect male reproductive success. *Animal Behaviour*, *93*, pp.77-86.

Melin, S.R., Delong, R.L., Thomason, J.R. and Vanblaricom, G.R., 2000. Attendance patterns of California sea lion (Zalophus californianus) females and pups during the non-breeding season at San Miguel Island. *Marine Mammal Science*, *16*(1), pp.169-185.

Melin, S.R., DeLong, R.L. and Siniff, D.B., 2008. The effects of El Niño on the foraging behavior of lactating California sea lions (*Zalophus californianus californianus*) during the nonbreeding season. *Canadian Journal of Zoology*, *86*(3), pp.192-206.

Misarti, N., Finney, B., Maschner, H. and Wooller, M.J., 2009. Changes in northeast Pacific marine ecosystems over the last 4500 years: evidence from stable isotope analysis of bone collagen from archeological middens. *The Holocene*, *19*(8), pp.1139-1151.

Mori, Y., 2002. Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology*, *15*(2), pp.269-276.

Newsome, S.D., Koch, P.L., Etnier, M.A. and Aurioles-Gamboa, D., 2006. Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. *Marine Mammal Science*, *22*(3), pp.556-572.

Orr, R.T., Shonewald, J., Kenyon, K.W., 1970. The California sea lion: Skull comparison of two populations. Proc. California Acad. Sci. 37, 381–394.

Patil, I., 2021. Visualizations with statistical details: The'ggstatsplot'approach. *Journal of Open Source Software*, *6*(61), p.3167.

Peters, R.H., 1986. *The ecological implications of body size* (Vol. 2). Cambridge university press.

Pörschmann, U., Trillmich, F., Mueller, B. and Wolf, J.B., 2010. Male reproductive success and its behavioural correlates in a polygynous mammal, the Galapagos sea lion (*Zalophus wollebaeki*). *Molecular Ecology*, *19*(12), pp.2574-2586.

Quay, P.D., Tilbrook, B. and Wong, C.S., 1992. Oceanic uptake of fossil fuel CO_2: Carbon-13 evidence. *Science*, *256*(5053), pp.74-79.

Robinson, H., Thayer, J., Sydeman, W.J. and Weise, M., 2018. Changes in California sea lion diet during a period of substantial climate variability. *Marine Biology*, *165*(10), pp.1-12.

Rossi, S.P., Cox, S.P., Hammill, M.O., den Heyer, C.E., Swain, D.P., Mosnier, A. and Benoît, H.P., 2021. Forecasting the response of a recovered pinniped population to sustainable harvest strategies that reduce their impact as predators. *ICES Journal of Marine Science*.

Scheffer, V.B., 1955. Body size with relation to population density in mammals. *Journal of Mammalogy*, *36*(4), pp.493-515.

Schusterman, R.J. and Dawson, R.G., 1968. Barking, dominance, and territoriality in male sea lions. *Science*, *160*(3826), pp.434-436.

Sinai, N.L., Dadaian, R.H., Kass, P.H. and Verstraete, F.J.M., 2014. Dental pathology of the California sea lion (*Zalophus californianus*). *Journal of comparative pathology*, *151*(1), pp.113-121.

Sivertsen, E.,1954. A survey on the eared seals (family Otariidae) with remarks on the Antarctic seals collected by M/K "Norvegia" in 1928–1929. Scientific Results of the Norwegian Antarctic Expeditions, 36. Oslo: Det Norske Vidskaps Akademi I Oslo.

Sosa Drouville, A., Paschetta, C., Crespo, E.A. and Grandi, M.F., 2021. Do changes in skull size of South American sea lions reflect changes in population density? *Marine Mammal Science*.

Stewardson, C.L., Prvan, T., Meyer, M.A. and Ritchie, R.J., 2008, March. Age determination and growth in the male South African Fur Seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae) based upon skull material. In *Proceedings of the Linnean Society of New South Wales* (Vol. 129, pp. 207-252).

Tagliabue, A. and Bopp, L., 2008. Towards understanding global variability in ocean carbon-13. *Global biogeochemical cycles*, *22*(1).

Vázquez-Cuevas, M.J., Aguayo-Lobo, A. and Medrano-González, L., 2000. Skull development of the California sea lion (*Zalophus californianus californianus*). *Ciencias Marinas*, *26*(1), pp.145-176.

Weise, M.J. and Costa, D.P., 2007. Total body oxygen stores and physiological diving capacity of California sea lions as a function of sex and age. *Journal of Experimental Biology*, *210*(2), pp.278-289.

Weise, M.J. and Harvey, J.T., 2008. Temporal variability in ocean climate and California sea lion diet and biomass consumption: implications for fisheries management. *Marine Ecology Progress Series*, *373*, pp.157-172.

Weise, M.J., Harvey, J.T. and Costa, D.P., 2010. The role of body size in individual-based foraging strategies of a top marine predator. *Ecology*, *91*(4), pp.1004-1015.

Williams, T.M., 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *354*(1380), pp.193-201.

Young, J.K. and Gerber, L.R., 2008. The influence of social composition on reproductive behavior of territorial male California sea lions. *Aquatic Mammals*, *34*(1), p.102-108.

Zwolinski, J.P. and Demer, D.A., 2012. A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. *Proceedings of the National Academy of Sciences*, *109*(11), pp.4175-4180.

TABLES

Table 3.1. Descriptive statistics of morphological variables of female and male California sea lions over time. Non-parametric Spearman's correlation between year of collection and morphological variables is described in Figure S3.1 and Table S3.1, 2. Years between brackets indicate the temporal range of collection of the individuals analyzed; ρ (rho): Spearman's correlation coefficient; and *p*: significance level. Significant correlations in bold.

Morphological variable	Males [1962-2008] n = 273		Males [1983-2008] n = 171		Females [1983-2007] n = 66	
	ρ	*p*	ρ	*p*	ρ	*p*
Cranium						
Condylobasal length (CBL)	0.28	**< 0.0001**	0.15	**0.044**	-0.012	0.92
Mastoid width (MW)	0.27	**< 0.0001**	0.12	0.10	-0.029	0.81
Maximum skull width (MSW)	0.28	**< 0.0001**	0.12	0.13	0.030	0.81
Palatal length (PL)	0.32	**< 0.0001**	0.28	**0.00037**	0.0052	0.97
Total height (TH)	0.13	**0.038**	0.069	0.38	-0.19	0.14
Mandible						
Mandible length (ML)	0.32	**< 0.0001**	0.18	**0.030**	0.12	0.34
Masseteric fossa length (MFL)	0.24	**0.00010**	0.25	**0.0012**	0.052	0.68
Morphological indices						
Mechanical Advantage (MA)	0.11	0.10	0.18	**0.024**	0.074	0.56
Relative Mastoid Width (RMW)	0.13	**0.029**	0.039	0.61	-0.071	0.57
Relative Palatal Length (RPL)	0.21	**0.00098**	0.27	**0.00048**	0.042	0.74
Skull Shape Index (SSI)	0.13	**0.037**	0.014	0.86	-0.020	0.87

FIGURES

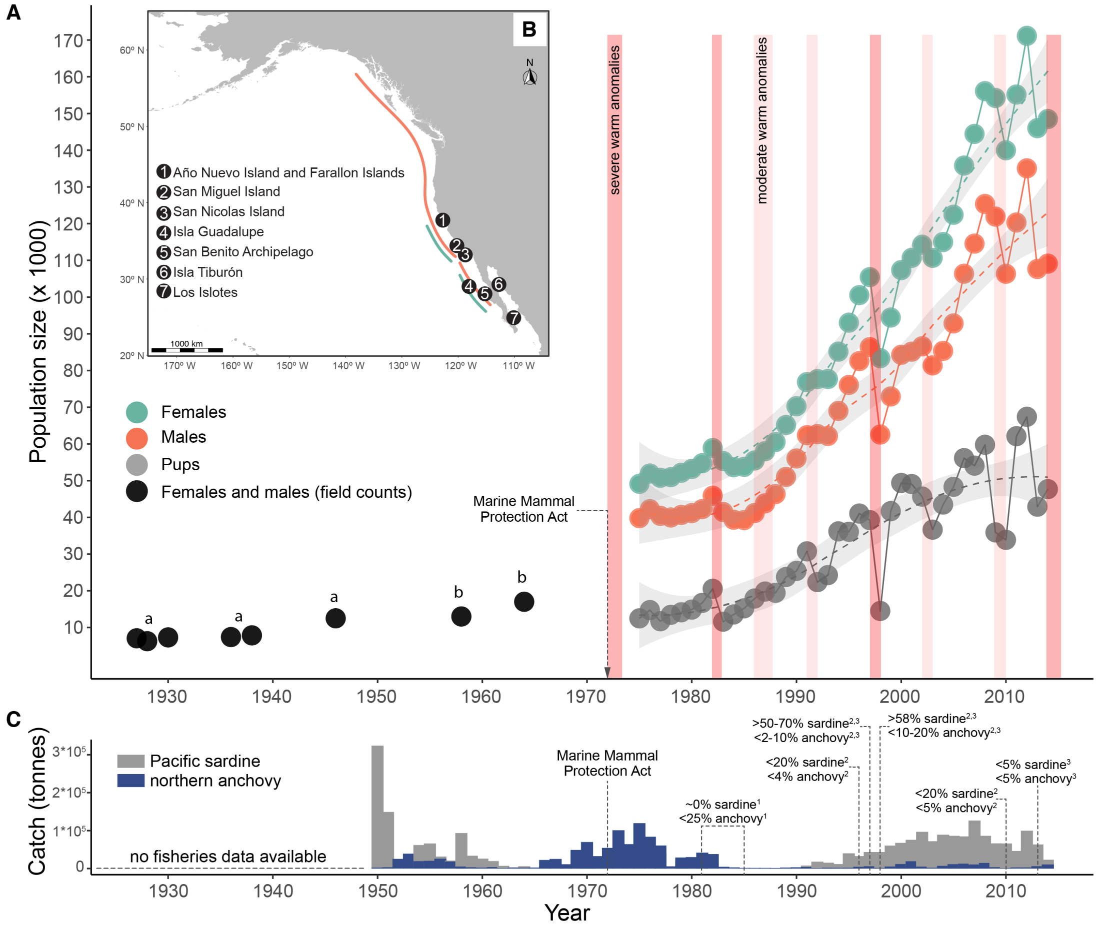

Figure 3.1. A) Estimated population of females (green), males (red), and pups (gray) from a population reconstruction model of California sea lions inhabiting the coastal waters off the west coast of the United States through time (data from Laake et al., 2018). Dashed lines indicate the local polynomial regression line, the gray shadows represent their 95% confidence intervals. Black dots represent the historical population of female and male California sea lions obtained from counts at rookeries and haulouts in southern California. Lower case letters next to points indicate the source: a. California Division of Fish and Game (1947); b. Bartholomew (1965). Vertical red rectangles represent moderate and strong warm anomalies in the eastern North Pacific (ONI index peaks > 1) after 1972. Data from NOAA (http: https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php). (B) Distribution of principal California sea lion rookeries along the North Pacific (circles 1-5) and the Gulf of California (circles 6 and 7). Colored lines represent the post-breeding foraging trips of females (green) and males (red) from the Channel Island rookeries, the only population that has been explored. (C) Reconstructed abundance of two of the historically preferred prey species of California sea lions, the Pacific sardine

and northern anchovy, along the western coast of the United States between 1950 and 2014 (data from Dunstan et al., 2020). Percentages indicate the proportion of these species in California sea lions' diet over time. Superscripts indicate the data source: [1]Lowry et al. (1991), [2]Weise and Harvey (2008), [3]Robinson et al. (2018).

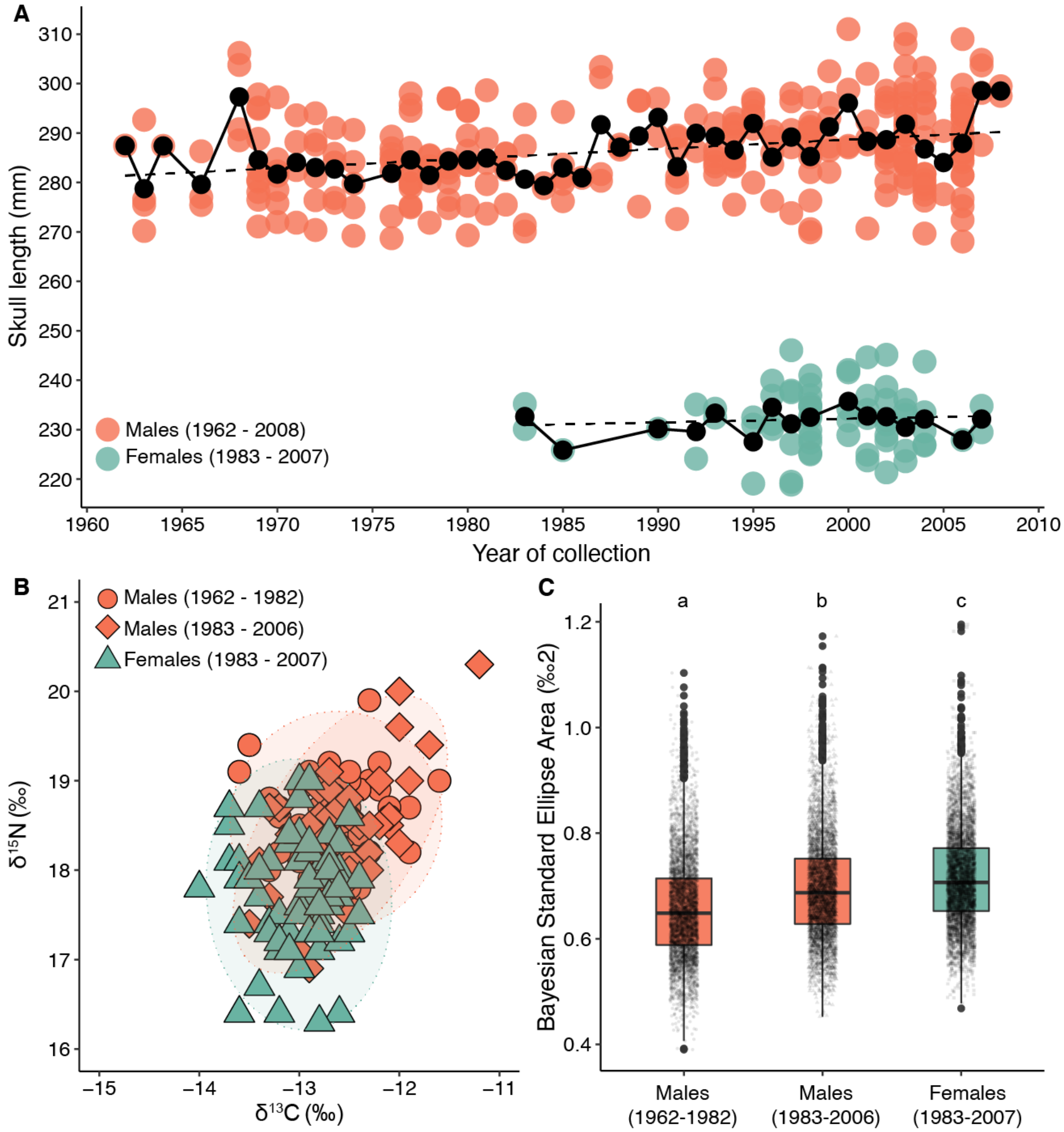

Figure 3.2. (A) Skull length (i.e., condylobasal length) of females (green) and males (red) over time. Black dots represent the mean value by year of collection. Dashed black lines represent the nonparametric Spearman's ρ correlation between the year of collection and the skull length. The correlation between the skull length and the year of collection was significant for males (Spearman's ρ = 0.28, p = 4.1e-06) and non-significant for females (Spearman's ρ = -0.012, p = 0.92). (B) Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of females (green triangles: 1983-2007) and males (red circles: 1962-1982; red diamonds: 1983-2006). Note that the upper temporal limit for the stable isotope analysis of males is shorter than for their morphometric analysis. Average values for each group are presented in Table S3.4. Ellipses represent the size-corrected standard ellipse area (SEA_C), including 95% of the data. Red dashed ellipse and continuous red ellipse represents the SEA_C of males collected between 1962-1982, and between 1983-

2006, respectively. Green ellipse represents SEA_C of females. (C) Isotopic niche space (Bayesian standard ellipse area) calculated for male and female California sea lions during the same periods indicated in (B). Boxplots represent the median (horizontal line), inter-quartile range (rectangle), 95% range (vertical lines), and outliers (black dots). Letters on top represent significant differences between groups.

CHAPTER 3

3.8 SUPPLEMENTARY INFORMATION

Supplementary Text

3.8.1.1 <u>Population size, carrying capacity, and resource competition of California sea lions over time</u>

Periodical surveys conducted between 1927 and 1946 (Bureau of Marine Fisheries, 1947) revealed that the sea lion population experienced a sustained increase in Southern and central California. Unfortunately, these surveys did not distinguish between California and Steller sea lions; therefore, no precise inferences on the California sea lion population can be obtained from these records.

Long-term monitoring has shown that the Channel Islands (Figure S3.1) harbor the more abundant and rapidly growing portion of the California sea lion population in the eastern North Pacific. Broadly, four islands, namely San Miguel, San Nicolas, San Clemente, and Santa Barbara, constitute the major breeding sites for the species on the Channel Islands, accounting for more than 99% of the pups and >77% of the non-pups counts during the breeding season in all California between the 2000s and the early 2010s (Lowry et al., 2017). Field surveys also reveal that two of these islands, San Miguel, and San Nicolas Islands, are the most extensive and productive California sea lion breeding rookeries, accounting, respectively, for ~90% and ~70% of this species population in the North Pacific Region (Lowry et al., 2017).

Field counts on the Channel Islands reveal that the California sea lion population, including all age classes and sexes, significantly increased between 1964 and 2019 (Lowry et al., 2021). However, conspicuous declines in pups in 1998, 2009, 2010, 2013, 2014, and 2016 occurred, likely associated with environmental variability, including severe El Niño events and the oceanic heatwave between 2013 and 2015 (Lowry and Maravilla-Chavez, 2005; McClatchie et al., 2016). Unlike pups, which have been consistently monitored on the Channel Islands since the 1960s, more varying information is available for other age classes. However, counts of juveniles and adult and subadult males between the ~1990s and 2019 show that they have unsteadily increased over time. While less consistent monitoring has been conducted for adult females on the Channel Islands, records between 2002 and 2019 reveal that their population remained relatively stable (Figure S3.2). However, conspicuous decreases between 2013 and 2018 occurred (Figure S3.3).

The recent declines in the number of California sea lion pups and, to some extent, females in the Channel Islands (Figure S3.3) indicate that this species might have substantially slowed down its population growth rate after the mid-2010s. Based on pup counts and survival estimates, it has been concluded that California sea lions remain within their optimum sustainable population range (i.e., population range between the populations' carrying capacity and the maximum productivity level) but have surpassed their maximum net productivity level (i.e., greatest net annual increment in population) approaching, therefore, their carrying capacity (Laake et al., 2018). Moreover, the consistent decline in the pup weight between 2004 and 2015 and the decay of the predicted daily weight growth rate between 2010 and 2015 on San Miguel Island (Melin et al., 2012; McClatchie et al., 2016) suggest that California sea lions have experienced a strengthening of adverse ecological conditions during recent decades, consistent with the intensification of density-dependent ecological pressures, as observed in other sea lions (e.g., Trites and Donnelly, 2003). Although a conspicuous population increase occurred on San Miguel and Nicolas Islands in 2019, reaching the population levels from the mid-2000s (Figure S3.2), it is unknown whether it represents a transient or a long-term trend, a critical issue to be resolved by future surveys.

Distinct population dynamics have been documented in central (Figure S3.2, 3) and northern California (Figure S3.4). Field surveys between the early 2000s and 2010s show that pups born in breeding sites in central California only represent the 0.3% of the California population (Lowry et al., 2017). Historical observations revealed that Año Nuevo and the Farallon Islands in central California constituted two major haul-out sites for males during their northward post-breeding foraging trips (Bartholomew 1965; Gearin et al., 2017). Unfortunately, censuses in these localities have been mainly conducted during the boreal summer (i.e., California sea lions' reproductive season), impeding more exhaustive assessments of their occupation by transient males during the non-breeding season. Nevertheless, these censuses have recorded the ubiquitous and relatively stable presence of adult and subadult males and juveniles during the 1990s and the 2000s (Figure S3.4,5). During the late 2010s, however, a notable increase of subadult and adult males occurred, coinciding with the establishment of new local reproduction in the area.

Females have been consistently monitored on Año Nuevo and the Farallon Islands only since the 2000s. Surveys indicate that except for conspicuous increases in 2003 and 2009, they remained at very low density until the 2010s when their population size boomed. Since then, their population has significantly expanded, reaching nearly 2000 individuals in 2019. Concurrently, intermittent newborn pups were observed on Año Nuevo and the Farallon Islands in past decades (e.g., Keith et al., 1984). Population surveys indicated the sporadic occurrence of newborn pups in central California since the 1980s, with notable boosts in 1998 and 2003 when near 50 were recorded. Since the late-2000s, the number of newborn pups on these islands has steadily increased, qualifying them as California sea lion breeding rookeries (Lowry et al., 2017; Figure S3.1-3). The number of newborn pups on these islands has continued to grow, reaching nearly 800 and 1000 individuals in 2019 in Año Nuevo and the Farallon Islands, respectively, becoming two small but rapidly growing breeding colonies (Lowry et al., 2021).

Considering the population dynamics in Southern and central California over time, stranded female and male sea lions in central and northern California (the region where skeletal remains including in this study were collected) between the 1960s and the late 2000s would chronicle different density-dependent dynamics, including intraspecific competition, as their population expanded.

As is inferred from the historical absence of sizeable reproductive colonies in central California until recently, male skeletal remains collected between 1962 and 2010s likely correspond to individuals breeding in the Channel Islands that temporally occupied haul-out sites in central and northern California during their post-breeding foraging trips. Moreover, as new breeding colonies on Año Nuevo and the Farallon Islands were established, some males residing during the breeding season may have contributed to the collection. Males presumably experienced rising density-dependent intraspecific competition for resources and space as their population in the Channel Islands expanded (Figure S3.2,3), which was likely intensified further as the number of resident males in central California began to rise.

California sea lions exhibit a resource-defense polygynous breeding system in which males secure their reproductive success by defending land territory and monopolizing female harems. Male sea lions frequently engage in aggressive male-male interactions in which body size and physical display are determinants for their reproductive success. As their population grew, larger congregations at their breeding sites on the Channel Islands occurred (Figure S3.3), likely leading to more frequent male-male aggressive encounters (Aurioles-Gamboa and Zavala-González, 1994; Kvarnemo and Ahnesjo, 1996; Weir et al., 2011), potentially intensifying levels of sexual selection in breeding colonies over time. Furthermore, as their population boosted, the number of adults and sub-adult males undertaking their northward post-breeding foraging trips rose as is suggested by increasing number of male California sea lions hauling out at the opening of the Columbia River estuary, one of the majors hauling out area for this species in the North Pacific (Schakner et al., 2017; Brown et al., 2020; Schakner and Blumstein, 2021).

Long-term monitoring indicates that females remained in very low densities in central California until the late 2000s when large scale breeding sites were established in this area (Figure S3.4,5). Therefore, skeletal remains collected between 1983 and 2007 in central California likely correspond to small scale resident breeders with a minor contribution of individuals from the Channel Islands. Limited information of the females now residing in central California is available, and critical aspects of their foraging ecology such as their preferred foraging locations and diet remain unknown. Yet, lactating females tend to be central place foragers, undertaking short foraging trips near their breeding colony (Melin et al., 2000; McHuron et al., 2016), which hints that resident female may be exploiting foraging grounds near Año Nuevo and the Farallon Islands. If so, resident females in central California likely encountered low density-dependent intraspecific competition for resources during the study period. While it is unknown to what extent foraging preferences between resident females and males might overlap, body size differences between them are significant, suggesting that some type of spatial foraging segregation occurred, including targeting different prey sizes or the exploitation of distinct depths in the water column, as has been observed in other pinniped species (e.g., Trites and Calkins, 2008).

Extended results

3.8.1.2 <u>Shifts of body size and functional morphology over time</u>

The ratio between the CBL and SL of both sexes did not change over the span (females: $p = 0.81$; males: $p = 0.41$); consequently, changes in the skull size over this period are expected to be associated with changes in the standard length. The average SL and CBL for females and males are presented in Table S3.5. The average CBL and the maximum and minimum CBL's for both sexes are within the range of the adult size reported by previous studies for this species (see Cruwys and Friday, 1995; Brunner et al., 2004). The residual plots for the linear model between skull length and year of collection show random patterns for males and females, indicating a good fit of the linear model. Similarly, we did not find a significantly correlation between residuals and the year of collection of the skeletal remains (Figure S3.8).

SUPPLEMENTARY TABLES

Table S 3.1. Description of skull measurements taken (and one calculated from measurements) of California sea lions included in this study. Measurements were modified from Drago et al. (2010) and Franco-Moreno et al. (2015).

Anatomical measurements (abbreviation)	**Definition and description**
Cranium	
Condylobasal length (CBL)	The most anterior tip of the premaxilla to the posterior-most margin of the occipital condyles
Mastoid width (MW)	Maximum breadth of the mastoid process
Maximum skull width (MSW)	Maximum breadth of the skull between the zygomatic arches
Palatal length (PL)	The maximum length of the palatal bone between the posterior edge of central incisor alveoli and the farthest posterior mid-point of the palate
Total height (TH)	Distance from the dorsal tip of the sagittal crest to the caudal end of the mastoid.
Mandible	
Mandible length (ML)	The most anterior tip of the dentary or tip of the anterior-most canine tooth to the lateral end of the condyle.
Masseteric fossa length (MFL)	Most anterior tip of the masseteric fossa on the lateral face of the mandible to posterior-most tip on the beginning of mandibular condyle.

Table S 3.2. Morphological indices, definitions, and their functional interpretations. These indices are calculated from skull measurements listed in Table S3.1.

Morphological indices	Description and functional interpretation
Mechanical Advantage (MA)	Length of the insertion area for the masseter muscle relative to the mandible length. This indicates the mechanical advantage of the masseter, with higher numbers indicating higher bite forces (Timm-Davies et al., 2015).
Relative Mastoid Width (RMW)	Calculated as the mastoid width (MW) divided by the total skull length (CBL). Higher values indicate a relatively larger area for muscle insertion.
Relative Palatal Length (RPL)	Measured as the length of the palate from the anterior-most to the posteriormost margin divided by the skull length. It relates to the size of the oral cavity.
Skull Shape Index (SSI)	Skull width at the level of the zygomatic arches relative to the total skull length (skull width/skull length). Indicates relative ability to generate bite force, given that a broader skull is associated with larger jaw-closing muscles and a shorter skull increases the mechanical advantage of the jaw-closing muscles (Biknevicius and Van Valkenburgh, 1996).

Table S 3.3. Relationship of morphological variables of female and male California sea lions and δ^{15}N values. [...]: Collection years of specimens; n: sample size; C.C.: correlation coefficient; r: Pearson's correlation coefficient; ρ: Spearman's correlation coefficient; and *p*: significance level. Variable abbreviations in Figure S3.1.

Variable	Males [1962-2006] n = 104		Males [1983-2006] n = 54		Females [1983-2007] n = 68	
	C.C.	*p*	C.C.	*p*	C.C.	*p*
Cranium						
CBL	0.000^{r}	1	0.03^{r}	0.84	-0.087^{r}	0.52
MW	0.063^{r}	0.53	0.10^{r}	0.47	0.27^{r}	**0.042**
MSW	0.095^{r}	0.34	0.084^{r}	0.55	0.35^{r}	**0.0076**
PL	0.038$^{\rho}$	0.72	-0.014^{r}	0.92	-0.086^{r}	0.53
TH	0.034^{r}	0.75	0.012^{r}	0.94	0.21^{r}	0.13
Mandible						
ML	0.037^{r}	0.73	-0.021^{r}	0.89	-0.042^{r}	0.76
MFL	-0.066^{r}	0.52	-0.23^{r}	0.12	-0.017^{r}	0.90
Morphological indices						
MA	-0.030$^{\rho}$	0.78	-0.22^{r}	0.14	-0.0063^{r}	0.96
RMW	0.076^{r}	0.45	0.12^{r}	0.40	0.40^{r}	**0.0022**
RPL	0.040$^{\rho}$	0.71	-0.051$^{\rho}$	0.73	-0.046	0.74
SSI	0.20$^{\rho}$	0.047	0.081^{r}	0.56	0.45^{r}	**0.00059**

Table S 3.4. Mean and standard deviation of $\delta^{13}C$ and $\delta^{15}N$ isotope values (‰), and isotopic standard ellipse areas for females and males California sea lions containing 95% of data. SEA_C is the standard ellipse area adjusted for small sample sizes, and SEA_B represents the average of the standard ellipse areas calculated from Bayesian approaches. Parentheses next to the Bayesian metrics indicate the 95% credibility intervals for each group.

Variable	Males [1962-1982] n = 50	Males [1983 – 2006] n = 54	Females [1983-2007] n = 67
Mean $\delta^{13}C$ ± SD (min, max)	-12.6 ± 0.4 (-13.6, -11.6)	-12.6 ± 0.4 (-13.5, -11.2)	-13.0 ± 0.4 (-14.0, -12.4)
Mean $\delta^{15}N$ ± SD (min, max)	18.6 ± 0.5 (17.6, 19.9)	18.4 ± 0.6 (16.9, 20.3)	17.7 ± 0.6 (16.3, 19.0)
SEA_C (‰^{2})	0.65	0.69	0.71
SEA_B (‰^{2})	0.63 (0.47 - 0.84)	0.67 (0.51 - 0.89)	0.70 (0.54 - 0.89)

Table S 3.5. Average standard length and skull length of California sea lions included in this study.

Morphological measurement	Females	Males
Average standard length (SL; cm)	169.03 ± 9.99	233.54 ± 12.79
Average condylobasal length (CBL, mm)	232.10 ± 6.28	286.60 ± 8.81
Minimum condylobasal length (mm)	218.88	268.05
Maximum condylobasal length (mm)	246.06	311.0

SUPPLEMENTARY FIGURES

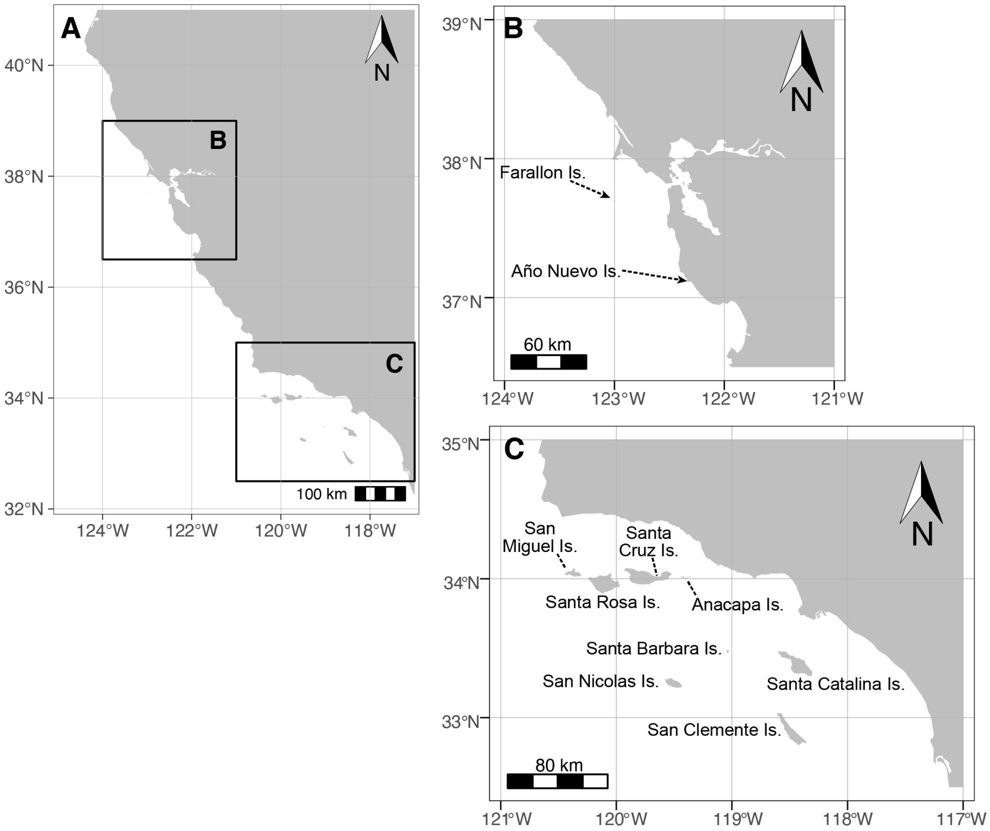

Figure S 3.1. Map of the California coast depicting the location of the principal California sea lion breeding colonies on central California (the Año Nuevo and the Farallon Islands) (B), and on the Channel Islands (Anacapa, San Clemente, San Miguel, San Nicolas, Santa Barbara, Santa Catalina, Santa Cruz, and Santa Rosa) in southern California (C). An additional breeding rookery is constituted by Richardson Rock, an islet located five and a half miles from the western point of San Miguel Island. Modified from Lowry et al. (2017).

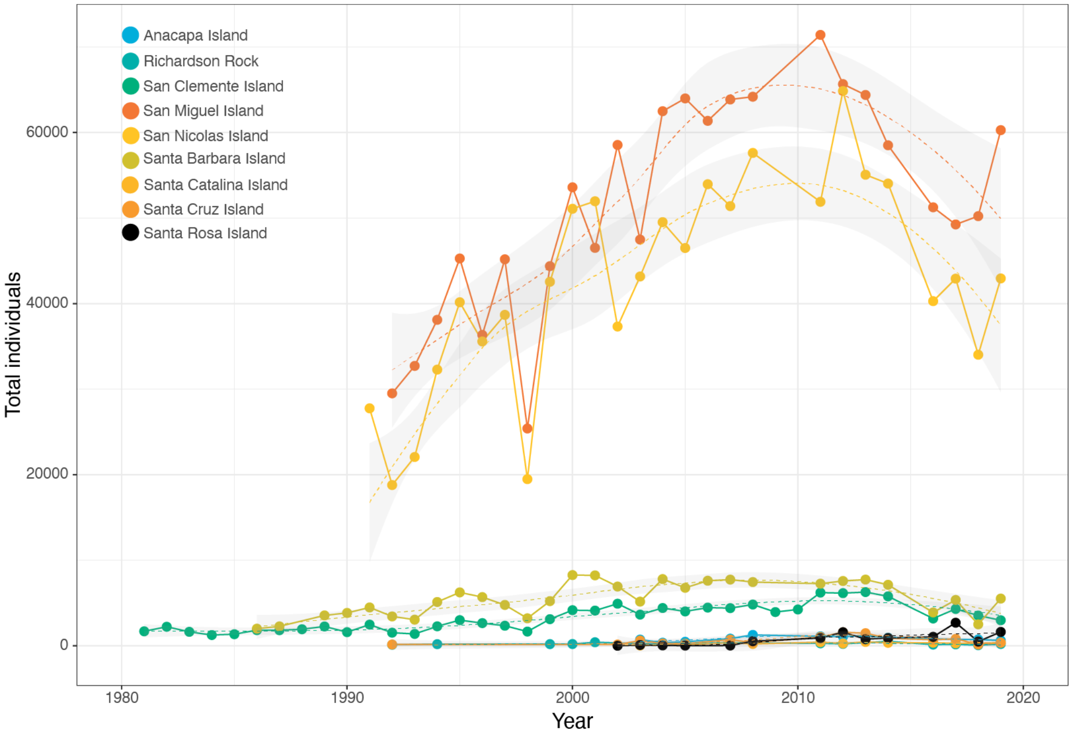

Figure S 3.2. Counts of California sea lions' individuals on the Channel Islands during the breeding season between 1981 and 2019. For each breeding sites, annual counts of pups, juveniles, adult females, young males, adult females or young adults, subadult males, and adult males were included when available. Only counts of more than one age class/sex category at each colony per year was included (therefore single pups counts at San Miguel and San Nicolas Island before ~1990s were not included; see Figure S3.3 for their visualization). Surveys were conducted using small boats, ground counts, and aerial photographs. Dashed lines indicate the local polynomial regression lines for counts at each rookery, and the grey segments represent the 95% confident interval. Data from Lowry et al. (2021).

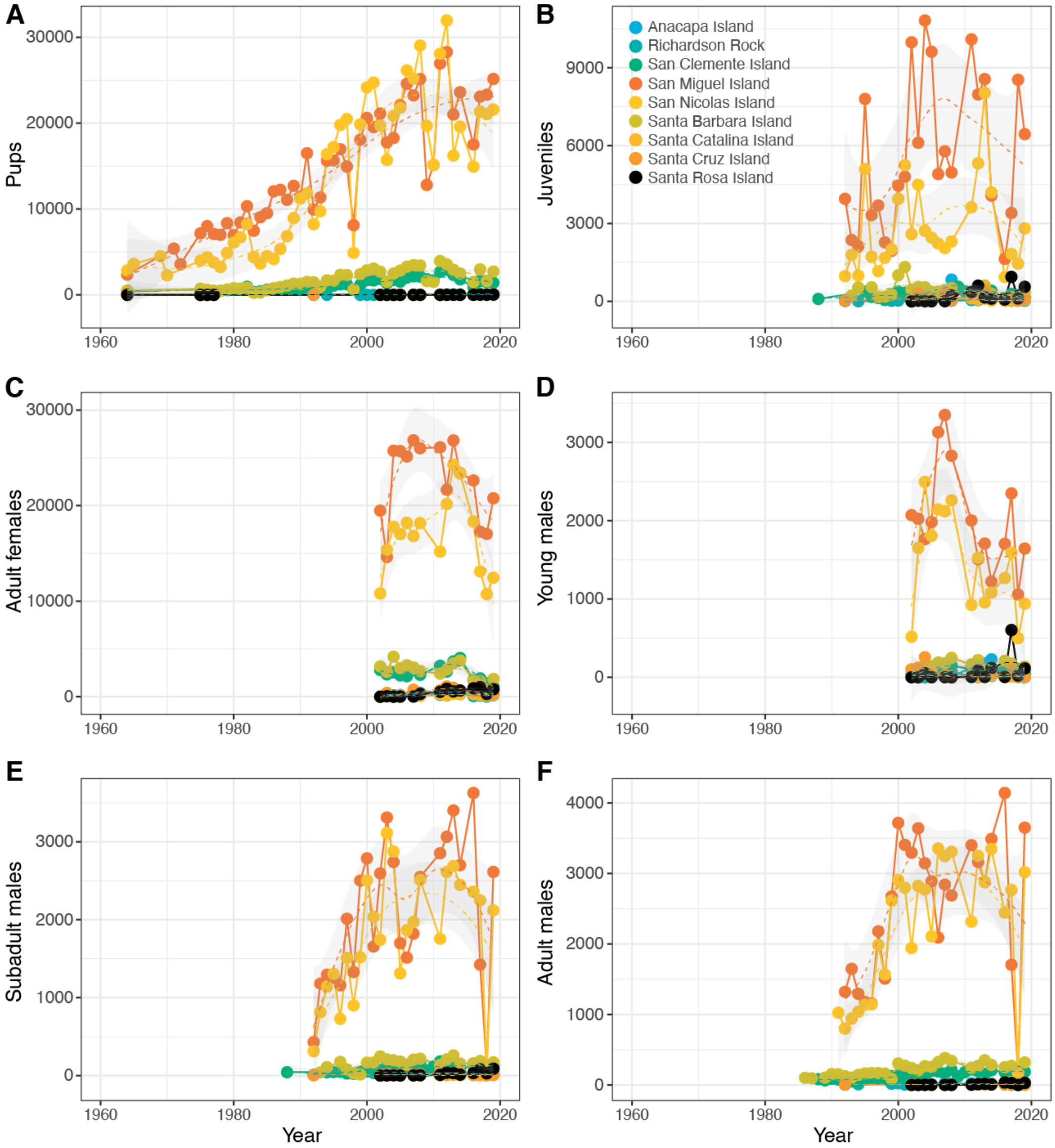

Figure S 3.3. Counts of California sea lion individuals on the Channel Islands during the breeding season between 1971 and 2019. Pups (A), juveniles (B), adult females (C), adult females or young males (D), subadult males (E), and adult males (F). Surveys were conducted using small boats, ground counts, and aerial photographs. Note that vertical axes have different scales. Dashed lines indicate the local polynomial regression lines for counts at each rookery, and the grey segments represent the 95% confident interval. Data from Lowry et al. (2017, 2021).

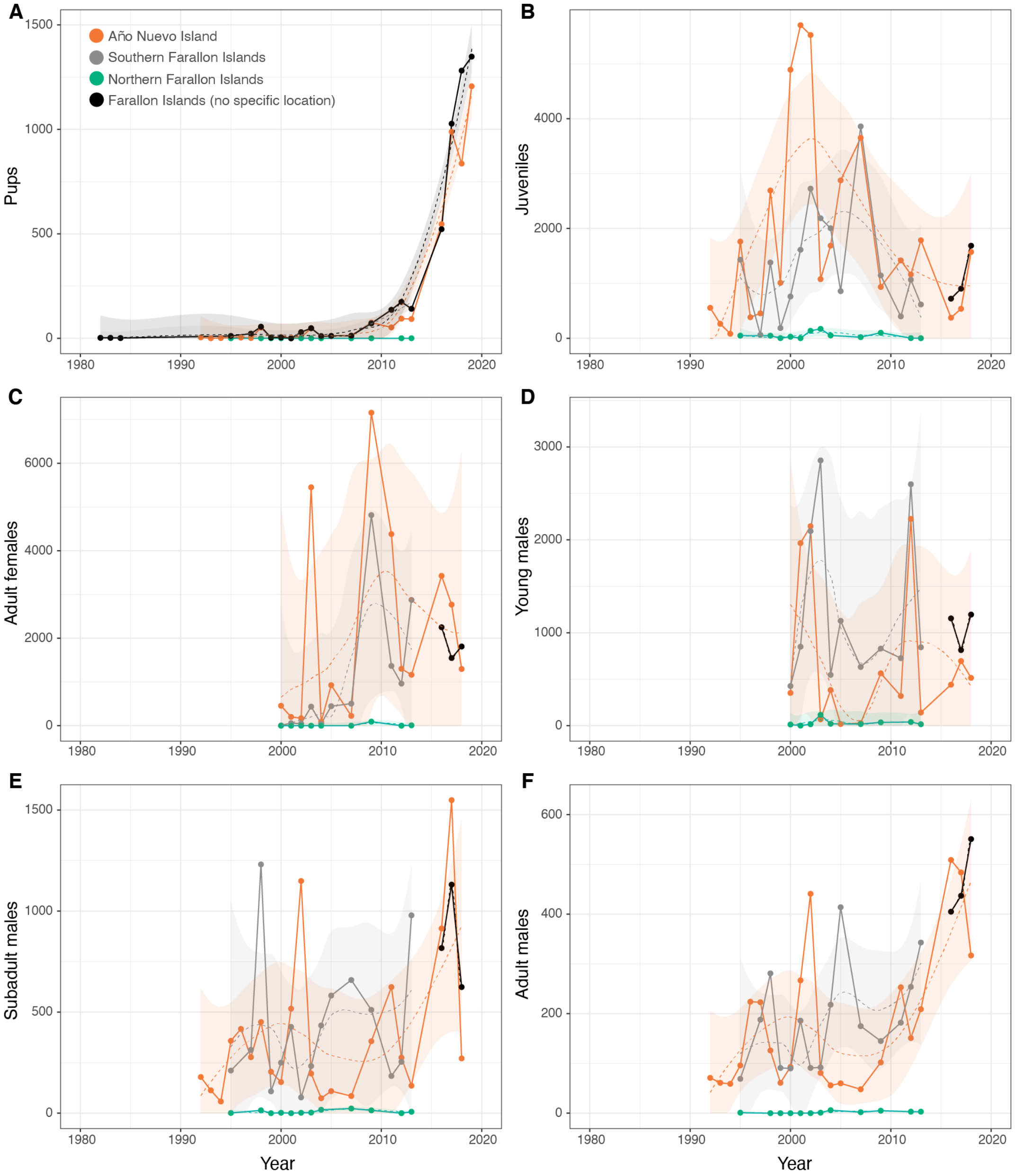

Figure S 3.4. Counts of California sea lion pups (A), juveniles (B), adult females (C), adult females or young males (D), subadult males (E), and adult males (F) using aerial photographs at Año Nuevo Island and the Farallon Islands (southern and northern islands, and undetermined location) in central California during the breeding seasons between 1982 and 2019. Dashed lines in plots indicate the local polynomial regression lines for counts at each rookery, and the colored segments represent the 95% confident interval for each site. Data from Lowry et al. (2017, 2021).

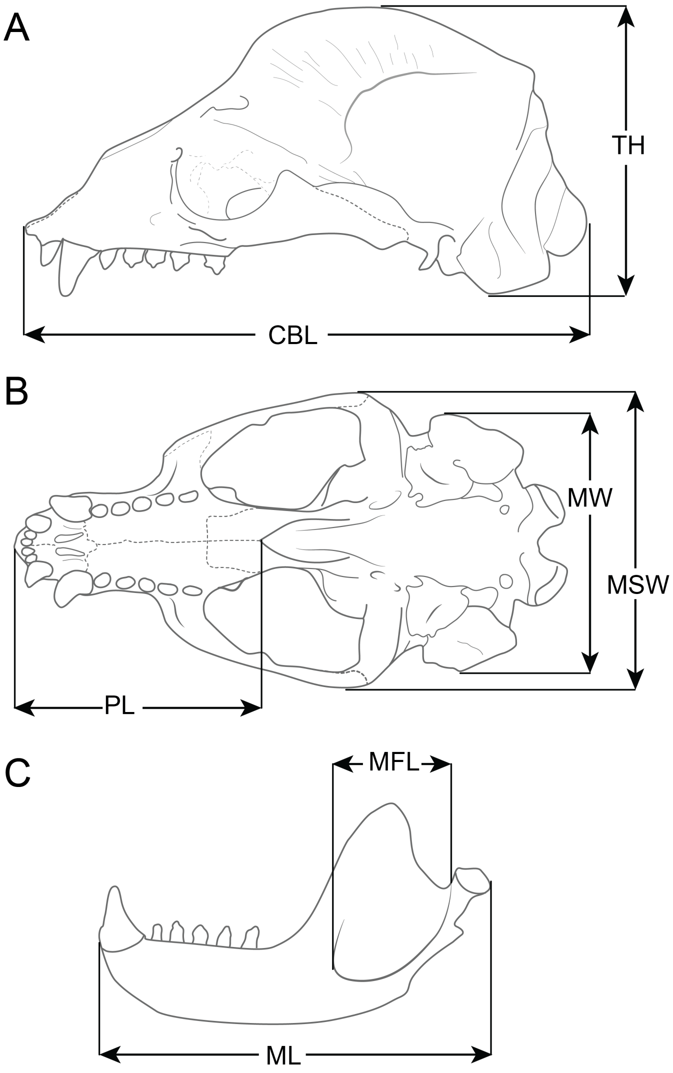

Figure S 3.5. Skull measurements taken for specimens of California sea lions in lateral (A) and ventral (B) views of the cranium, and lateral (C) view of the dentary. Abbreviations for cranium: Condylobasal length (CBL); Mastoid Width (MW); Maximum Skull Width (MSW); Palatal length (PL); Total height (CH). Abbreviations for mandible: Mandible length (ML); Masseteric fossa length (MFL).

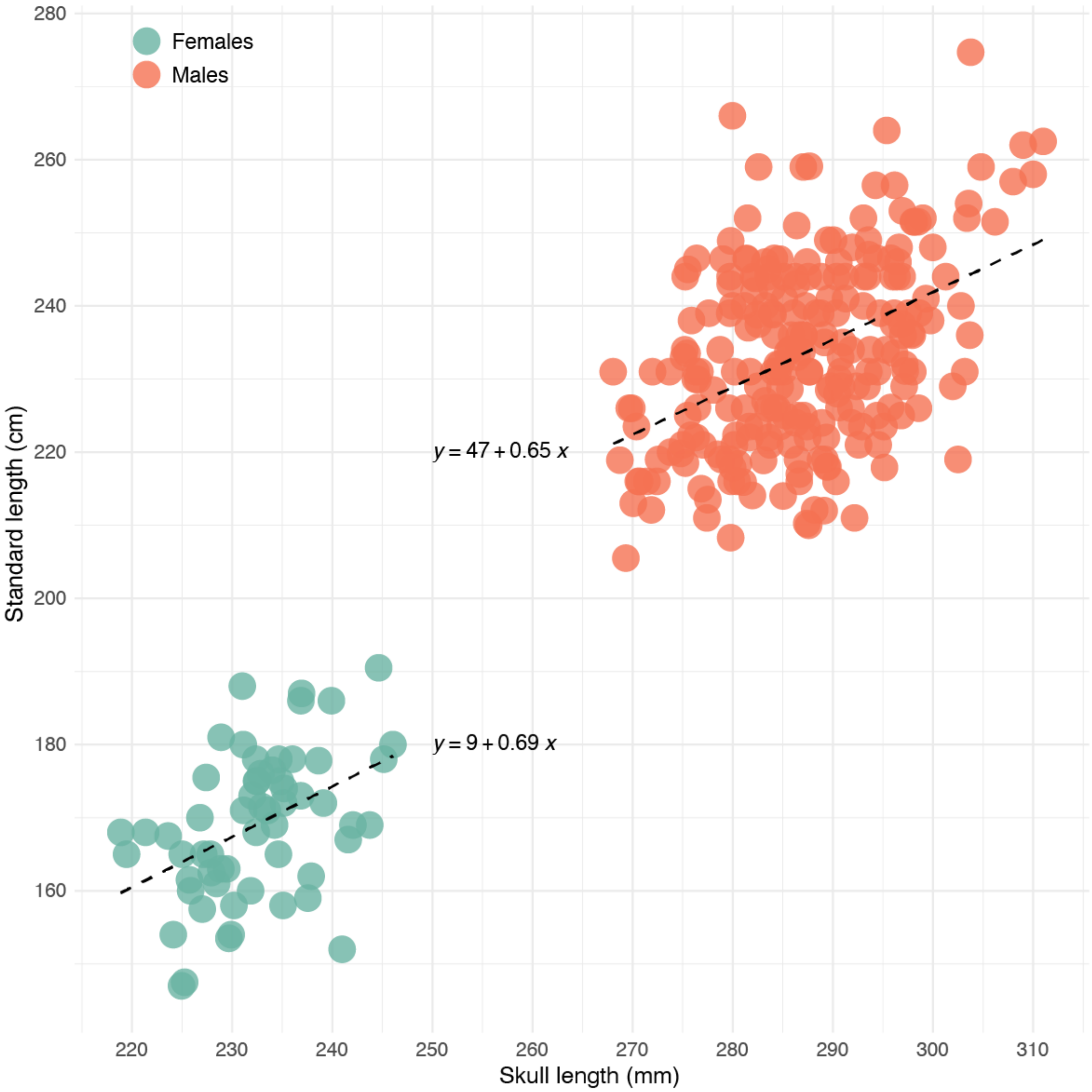

Figure S 3.6. Standard body length plotted against the skull length of a subset of female and male California sea lions included in the study. The correlation between the skull length (CBL) and the standard length was significant for females (Pearson's r = 0.43, *p* = 0.00061) and males (Spearman's ρ = 0.39, $p < 0.0001$). Dashed black lines represent the linear regression for each sex. The regression analysis between skull length and standard length was significant for males ($R^2 = 0.20$, F(1, 241) = 60.1, $p < 0.00001$) and females ($R^2 = 0.17$, F(1, 57) = 13.15, *p* = 0.00061).

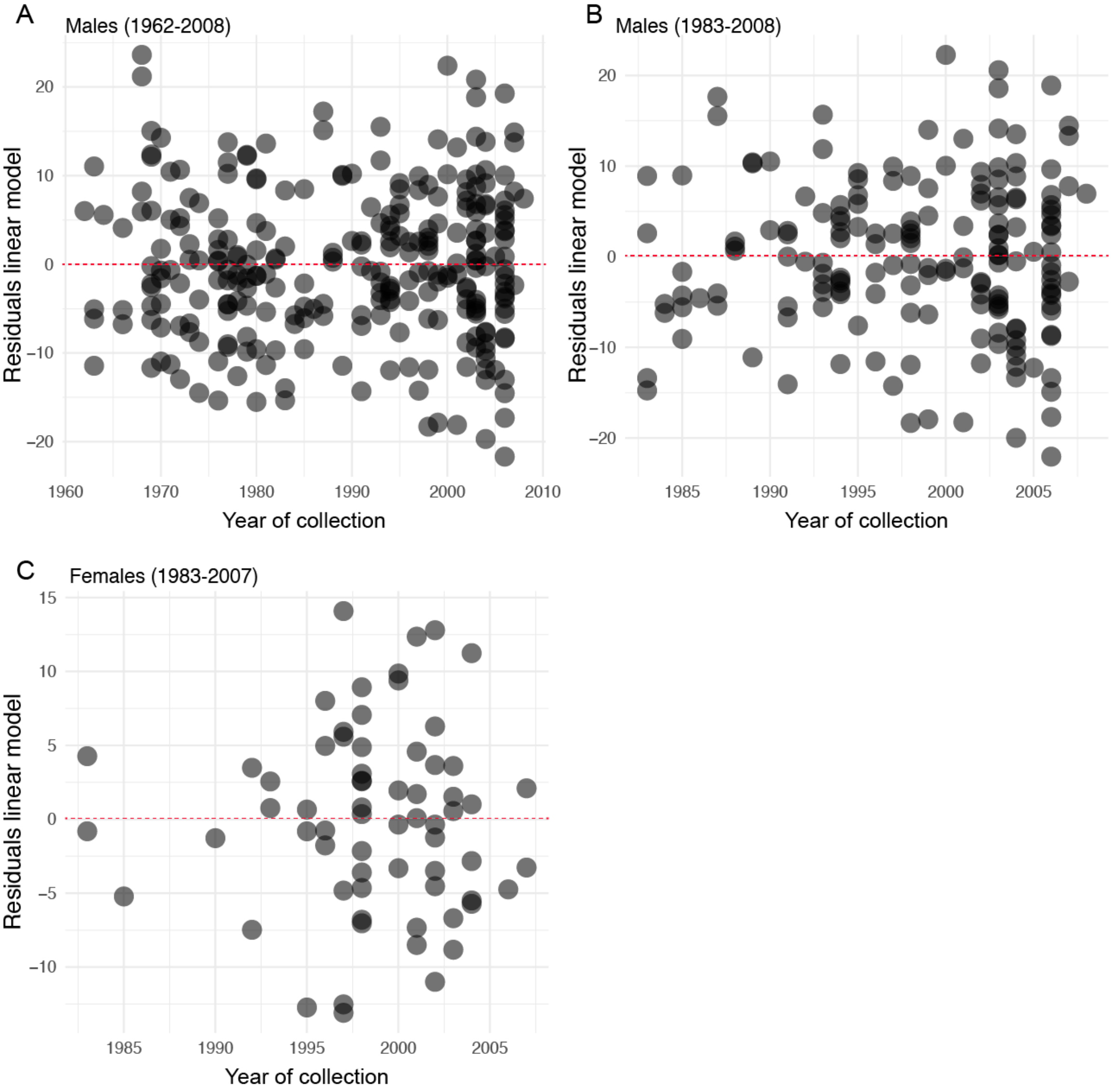

Figure S 3.7. Biplots between the residuals of the linear model between the skull length and the year versus the year of collection of the cranial remains for (A) males collected between 1962 and 2008 (B) males collected between 1983 and 2008 and (C) females collected between 1983 and 2007. The correlation between the residuals of the linear model and the year of collection was not significant for any of the cases (A: Spearman's ρ = 0.086, *p* = 0.16; B: Spearman's ρ = -0.0071, *p* = 0.93; C: Spearman's ρ = -0.041, *p* = 0.74).

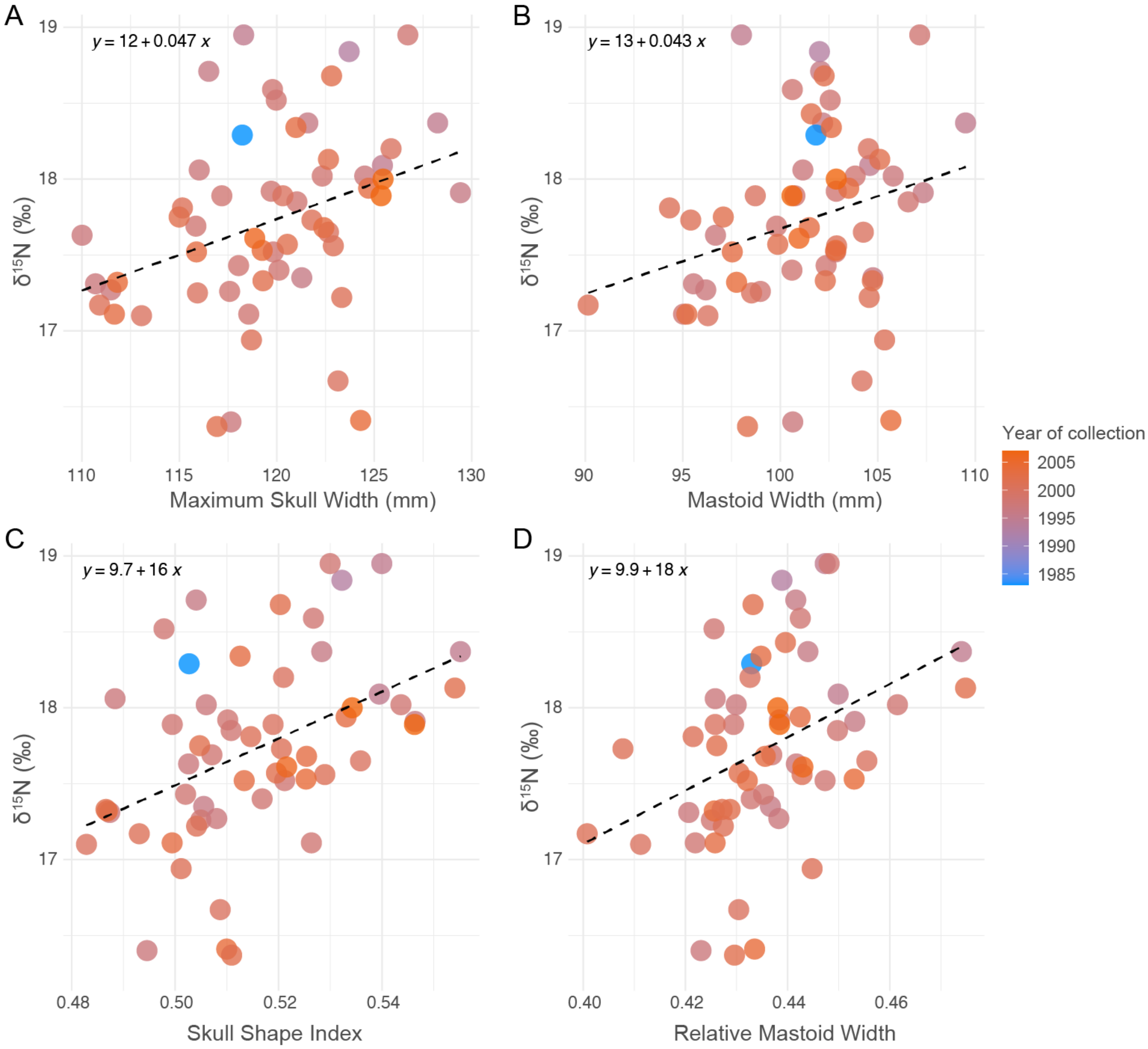

Figure S 3.8. Maximum skull width (A), mastoid width (B), Skull Shape Index (C), and Relative Mastoid Width (D) versus δ^{15}N values of female California sea lions collected between 1983 and 2007. Gradient of color indicates the year in which the specimens were collected in the field. Dashed black lines represent the linear regression between morphological indices and δ^{15}N values. The correlation morphological variables and the δ^{15}N values was significant for (A) maximum skull width (Pearson's r = 0.35, *p* = 0.0075); (B) mastoid width (Pearson's r = 0.27, *p* = 0.042); (C) Skull Shape Index (Pearson's r = 0.45, *p* = 0.00059); and (D) Relative Mastoid Width (Pearson's r = 0.40, *p* = 0.0022).

SUPPLEMENTARY REFERENCES

Aurioles-Gamboa, D.A. and Zavala-González, A.Z., 1994. Algunos factores ecológicos que determinan la distribución y abundancia del lobo marino *Zalophus californianus*, en el golfo de California. *Ciencias Marinas*, *20*(4), pp.535-553.

Bartholomew, G.A., 1965. Seal and sea lion populations of the California Islands.

Biknevicius, A.R., Van Valkenburgh, B. and Gittleman, J.L., 1996. Design for killing: craniodental adaptations of predators. *Carnivore behavior, ecology, and evolution*, *2*, pp.393-428.

Brown, R.F., Wright, B.E., Tennis, M.J. and Jeffries, S., 2020. California sea lion (*Zalophus californianus)* monitoring in the Lower Columbia River, 1997–2018. *Northwestern Naturalist*, *101*(2), pp.92-103.

BUREAU, O.M.F., 1947. California sea lion census for 1946. *California Fish and Game*, *33*, pp.19-22.

Drago, M., Cardona, L., Crespo, E.A., Grandi, M.F. and Aguilar, A., 2010. Reduction of skull size in South American sea lions reveals density-dependent growth during population recovery. Marine Ecology Progress Series, 420, pp.253-261.

Franco-Moreno, R.A., Cruz-Escalona, V.H., Aurioles-Gamboa, D., Vera-Alfaro, P., Salas, J. and Ravela, S., 2015. Variability and sexual dimorphism in skull morphometry of California Sea Lions (*Zalophus californianus*) in Mexico. Mammalian Biology, 80(4), pp.316-327.

Gearin, P.J., Melin, S.R., DeLong, R.L., Gosho, M.E. and Jeffries, S., 2017. Migration patterns of adult male California sea lions (*Zalophus californianus*). NOAA technical memorandum NMFS-AFSC 346.

Kvarnemo, C. and Ahnesjo, I., 1996. The dynamics of operational sex ratios and competition for mates. *Trends in Ecology & Evolution*, *11*(10), pp.404-408.

Keith, E.O., Condit, R.S. and Le Boeuf, B.J., 1984. California sea lions breeding at Año Nuevo Island, California. *Journal of mammalogy*, *65*(4), pp.695-695.

Laake, J.L., Lowry, M.S., DeLong, R.L., Melin, S.R. and Carretta, J.V., 2018. Population growth and status of California sea lions. The Journal of Wildlife Management, 82(3), pp.583-595.

Lowry, M.S. and Maravilla-Chavez, O., 2005. Recent abundance of California sea lions in western Baja California, Mexico and the United States. In *Proceedings of the sixth California Islands symposium* (pp. 485-497). Institute for Wildlife Studies.

Lowry, M.S., Melin, S.R. and Laake, J.L., 2017. Breeding season distribution and population growth of California sea lions, *Zalophus californianus*, in the United States during 1964-2014. NOAA Technical Memorandum 574.

Lowry, M.S., Jaime, E.M. and Moore, J.E., 2021. Abundance and distribution of pinnipeds at the Channel Islands in southern California, central and northern California, and southern Oregon during summer 2016–2019.

McClatchie, S., Field, J., Thompson, A.R., Gerrodette, T., Lowry, M., Fiedler, P.C., Watson, W., Nieto, K.M., and Vetter, R.D., 2016. Food limitation of sea lion pups and the decline of forage off central and southern California. *Royal Society Open Science*, *3*(3), p.150628.

McHuron, E.A., Robinson, P.W., Simmons, S.E., Kuhn, C.E., Fowler, M. and Costa, D.P., 2016. Foraging strategies of a generalist marine predator inhabiting a dynamic environment. *Oecologia*, *182*(4), pp.995-1005.

Melin, S.R., Delong, R.L., Thomason, J.R. and Vanblaricom, G.R., 2000. Attendance patterns of California sea lion (Zalophus californianus) females and pups during the non-breeding season at San Miguel Island. *Marine Mammal Science*, *16*(1), pp.169-185.

Melin, S.R., Orr, A.J., Harris, J.D., Laake, J.L. and DeLong, R.L., 2012. California sea lions: an indicator for integrated ecosystem assessment of the California Current System. *California Cooperative Oceanic Fisheries Investigations Reports*, *53*, pp.140-152.

Schakner, Z.A. and Blumstein, D.T., 2021. The California sea lion: Thriving in a human-dominated world. In *Ethology and Behavioral Ecology of Otariids and the Odobenid* (pp. 347-365). Springer, Cham.

Schakner, Z.A., Petelle, M.B., Tennis, M.J., Van der Leeuw, B.K., Stansell, R.T. and Blumstein, D.T., 2017. Social associations between California sea lions influence the use of a novel foraging ground. *Royal Society open science*, *4*(5), p.160820.

Timm-Davis, L.L., DeWitt, T.J. and Marshall, C.D., 2015. Divergent skull morphology supports two trophic specializations in otters (Lutrinae). PloS one, 10(12), p.e0143236.

Trites, A.W. and Donnelly, C.P., 2003. The decline of Steller sea lions Eumetopias jubatus in Alaska: a review of the nutritional stress hypothesis. *Mammal review*, *33*(1), pp.3-28.

Trites, A.W. and Calkins, D.G., 2008. Diets of mature male and female Steller sea lions (*Eumetopias jubatus*) differ and cannot be used as proxies for each other. *Aquatic Mammals*, *34*(1), p.25.

Weir, L.K., Grant, J.W. and Hutchings, J.A., 2011. The influence of operational sex ratio on the intensity of competition for mates. *The American Naturalist*, *177*(2), pp.167-176.

CHAPTER 4

WHAT DO WE KNOW ABOUT THE FOSSIL RECORD OF PINNIPEDS?

A HISTORIOGRAPHIC INVESTIGATION

Reproduced with permission from: Valenzuela-Toro, A. and Pyenson, N.D., 2019. What do we know about the fossil record of pinnipeds? A historiographical investigation. *Royal Society Open Science*, *6*(11), p.191394.

ROYAL SOCIETY
OPEN SCIENCE

royalsocietypublishing.org/journal/rsos

Research

Cite this article: Valenzuela-Toro A, Pyenson ND. 2019 What do we know about the fossil record of pinnipeds? A historiographical investigation. *R. Soc. open sci.* **6**: 191394.
http://dx.doi.org/10.1098/rsos.191394

Received: 9 August 2019
Accepted: 22 October 2019

Subject Category:
Biology (whole organism)

Subject Areas:
palaeontology

Keywords:
fossil record, pinnipeds, marine mammals, historiographical revision, paleobiology database, biases in the fossil record

Author for correspondence:
Ana Valenzuela-Toro
e-mail: avalenzuela.toro@gmail.com

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.4739150.

THE ROYAL SOCIETY
PUBLISHING

What do we know about the fossil record of pinnipeds? A historiographical investigation

Ana Valenzuela-Toro[1] and Nicholas D. Pyenson[2,3]

[1]Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Coastal Biology Building, 130 McAllister Way, Santa Cruz, CA 95060, USA
[2]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, PO Box 37012, Washington, DC 20013, USA
[3]Department of Paleontology and Geology, Burke Museum of Natural History and Culture, Seattle, WA 98105, USA

AV-T, 0000-0003-1497-364X; NDP, 0000-0003-4678-5782

The fossil record of pinnipeds (seals, fur seals and walruses) is globally distributed, spanning from the late Oligocene to the Holocene. This record shows a complex evolutionary history that could not otherwise be inferred from their extant relatives, including multiple radiations and iterative ecomorphological specializations among different lineages, many of which are extinct. The fossil record of pinnipeds is not uniformly represented in space and time, however, leaving some gaps in our knowledge. We performed a historiographical investigation of the published fossil record of pinnipeds based on the information available in the Paleobiology Database, with the aim to broadly characterize and evaluate it from a taxonomic, geographical and temporal perspective. We identified major trends, strengths and weaknesses of the pinniped fossil record, including potential biases that may affect our interpretations. We found that 39% of the record corresponds to extant taxa, which are essentially from the Pleistocene and Holocene. There is a larger record from the Northern Hemisphere, suggesting biases in sampling and collection effort. The record is not strongly biased by sedimentary outcrop bias. Specifically, for extinct species, nearly half of them are represented by a single occurrence and a large proportion have type specimens consisting of single isolated postcranial elements. While the pinniped fossil record may have adequate temporal and taxonomic coverage, it has a strong geographical bias and its comparability is hindered by the incompleteness of type specimens. These results should be taken into account when addressing patterns of their past diversity, evolutionary history and paleoecology.

1. Introduction

Among living marine mammals, pinnipeds constitute the second most species-rich clade, comprising 33 widely distributed extant species in three subclades: Phocidae (true seals, with 19 species), Otariidae (fur seals and sea lions, with 14 species) and Odobenidae with only one extant species, walruses (*Odobenus rosmarus*; [1,2]). The fossil record of pinnipeds is based on localities from the late Oligocene to the early Miocene of the North Pacific Ocean and from the early Miocene of the Mediterranean and Paratethys regions, through the Holocene from both the Northern and Southern hemispheres. From the fossil evidence, it is clear that pinnipeds were different in the geologic past, showing greater species richness in some groups, different ecomorphologies, body sizes and geographical distributions [2]. For instance, the fossil record shows that, during the Neogene, Odobenidae comprised at least 20 species (versus the monotypic extant walrus) with a range of body sizes and skull morphologies that imply much greater morphological disparity ([2–4]; and references therein). Faunal comparisons suggest that the rise and fall of different pinniped subclades are likely dependent on changing oceanographic and habitat availability (e.g. haul outs for rookeries) over geologic time [5–7].

As with other marine mammal groups, the fossil record of pinnipeds appears to possess certain qualities, modes and patterns. For example, despite their relative abundance in fossiliferous sites throughout the world, fossil pinnipeds are not uniformly described across the world (see [2]). Furthermore, the fossil record of some groups is represented by isolated and fragmentary remains (e.g. [8,9]). These attributes may bias the fossil record of pinnipeds in a similar way to the fossil record of cetaceans and sirenians, which show biases in geography, preservation and historiography [10,11]. Hence, it remains unclear how potential sources of bias, such as geographical and temporal occurrences, or sampling effort, affect our knowledge and interpretations of the fossil record of pinnipeds.

Here, we perform a historiographical analysis of the published fossil record of pinnipeds using the Paleobiology Database with the aim to qualitatively and quantitatively characterize the record from taxonomic, geographical and temporal perspectives, identifying the principal trends, strengths and weaknesses, as well as to explore the potential biases that may affect our interpretations about the past diversity, evolutionary history and paleoecology of this group of marine mammals.

2. Methods

2.1. Data collection

Raw data were downloaded from the Paleobiology Database (PaleoDB; available at http://www.paleobiodb.org) on 29 April 2019, using the name 'pinnipedimorpha'. We restricted the search to output the files 'fossil occurrences' and 'valid taxa' for our analysis and also to provide a more detailed analysis of the type material of valid extinct species of pinnipeds. In this study, we regard the term 'occurrences' to signify the records of a taxon that are grouped into geographical collections, logged into the PaleoDB. Furthermore, for our study, we only examined published (i.e. documented) occurrences, where fossil remains have been taxonomically identified and also belong to a discrete geographical collection with precise coordinates stipulated in the scientific literature. Thus, we excluded, to the best of our ability, fossil occurrences of pinnipeds that have not been formally published in the peer-reviewed literature; in cases where the PaleoDB's occurrence data (i.e. geographical, stratigraphic or specimen-related) can be more precisely ascertained, we have noted the supplemental information. Because our analysis emphasizes published occurrences reflected in museum collections, we also note that there are additional unpublished fossil occurrences worth further discussion (see more detail below).

For further information about definitions used by the PaleoDB, see Peters & McClennen [12]. Their revision includes fossil (older than 11 000 years old) and subfossil (younger than 11 000 years old) occurrences; however, we refer to them indistinctly as fossils. The raw data were complemented by information from different sources, including the PaleoDB website and peer-reviewed literature.

2.2. Categorical analysis

To characterize the taxonomic identity, the temporal and geographical distributions, and the historiography of fossil pinniped publications, we included the following categories: taxon name, taxonomic rank, geographical provenance (hemisphere, oceanic basin and country), geological formation/locality, geological age, primary language of the publication, year of the publication and full reference (see electronic supplementary material, table S1). When it was not possible to obtain information, we recorded 'No information' in the respective category.

For the taxonomic classification, we used the following groups, as listed in the PaleoDB: enaliarctids, which include basal pinnipedimorphs such as *Enaliarctos* and its relatives (including *Pinnarctidion* and *Pteronarctos*); desmatophocids, which include species belonging to the extinct genera *Allodesmus* and *Desmatophoca*; Pan-Otariidae, which include species belonging to the extinct genus *Eotaria*; and the extant families Phocidae, Otariidae and Odobenidae. For the 'oceanic basins' category, we followed a modified version of Berta *et al*. [13] and Deméré *et al*. [14] as follows: eastern and western North and South Pacific Ocean, eastern and western North and South Atlantic Ocean, Paratethys region, Indian Ocean, Lake Baikal, North Sea, Baltic Sea, Mediterranean Sea, Southern Ocean and Arctic Ocean. In particular, the Paratethys region referred to the occurrences placed in continental Europe and other regions considered remnants of the ancient Neo-Paratethys Sea (e.g. Black and Caspian seas, Austria, Czech Republic, Hungary, Romania, Serbia, Bulgaria, Moldavia, Ukraine, Russia, Georgia, Azerbaijan, Iran and Kazakhstan; see [15]). The Mediterranean Sea comprises occurrences from the adjacent areas to this sea and also northern Africa.

2.3. Analysis of rock outcrop area and fossil occurrences

We explored the association between sedimentary rock outcrop area from the Neogene (measured in km^2) of the USA and the number of reported occurrences of fossil pinnipeds from this area, using unpublished marine rock area data collected by Uhen & Pyenson [10] in 2007.

2.4. Museum collections

We examined the relationship between the number of fossil specimens from two most fossil-rich geologic units in terms of the abundance of extinct pinniped remains in the USA: Calvert and Yorktown formations and the number of published fossil occurrences from those units. For that, we focused on the pinniped collection from those units housed in the Department of Paleobiology at the Smithsonian Institution's National Museum of Natural History in Washington, DC, USA (data downloaded at https://collections.nmnh.si.edu on 2 October 2018).

2.5. Collection curves

Collection curves from the documented occurrences of extinct species data were generated using the software Past (v. 3.23; [16]). In Past, we selected the function individual rarefaction by estimating the number of taxa (extinct species) expected to be collected in a sample with a small initial total number of individuals. The input data file for Past contained occurrences of fossil species for a given geological formation that were grouped by year. For this analysis, we considered the Calvert, Astoria, Yorktown and Purisima Formation, given the number of taxa reported in each one.

2.6. Analysis of extinct species

To identify the principal trends for type specimens of extinct species, the following categories were included: the catalogue number (= collection number within a research institution) of the type specimen, type locality, skeletal element(s) of the type material (skull, cranium, skeleton or postcranium) and their articulation and completeness conditions. For the analysis of the skeletal elements, we followed White & Folkens [17] in defining skull as the entire bony structure of the head (dermatocranium, splanchnocranium and neurocranium) including the lower jaw (or mandible), differing from the terminology cranium, which only corresponds to the skull without the lower jaw. We used a modified version of Pyenson *et al*. [18] and Boessenecker *et al*. [19] for the articulation and element association of type material, defined here as: category 1, complete or almost complete articulated skeleton; category 2, disarticulated skeletons and associated skeletal elements, including cranial and other skeletal elements; and category 3, isolated elements.

Caribbean monk seals (*Neomonachus tropicalis*) and Japanese sea lions (*Zalophus japonicus* according to [20]; or *Z. californianus japonicus* according to [21]) became extinct over the last century; for the purpose of the paper, these species were categorized as extant [22].

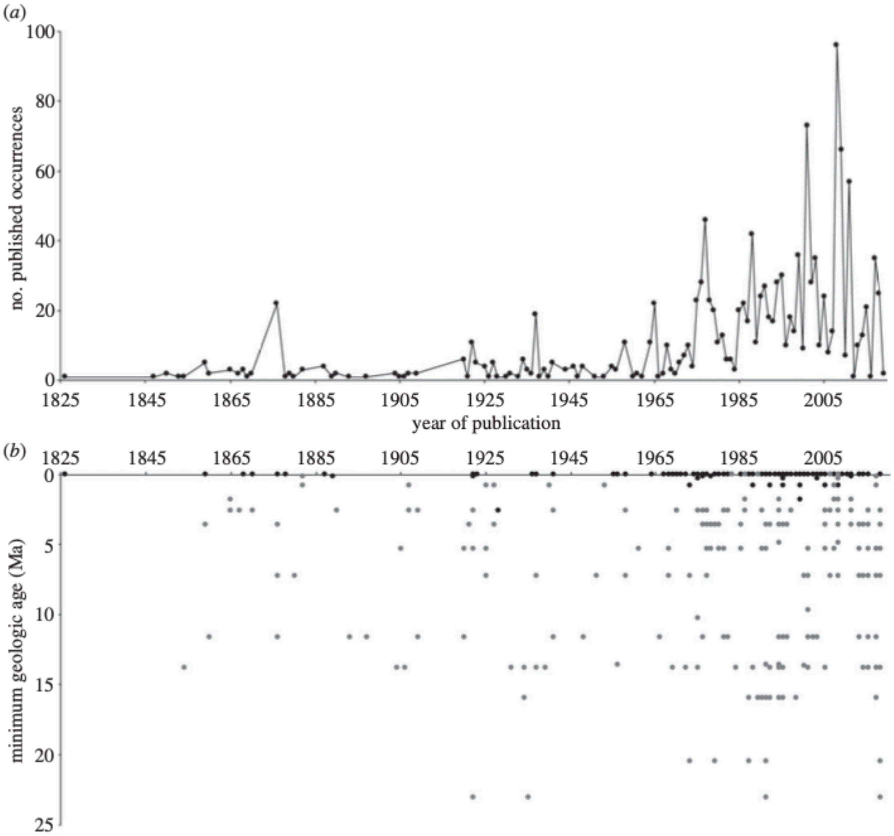

Figure 1. Published fossil occurrences over time. (*a*) Number of publications of fossil pinnipeds through calendar years ($n = 1296$). (*b*) Minimum geological age of fossil occurrences (in millions of years; Ma) identified at level of species through calendar years. Black dots represent occurrences of extant species and grey dots represent occurrences of extinct species.

2.7. Zooarchaeological record

Finally, a note of caution: the zooarchaeological record of pinnipeds is extensive (see [23–33]; and references therein); however, these data are not consistently entered into the PaleoDB. In addition, some of the Holocene occurrences listed in the PaleoDB are modern findings (e.g. living taxa) rather than zooarchaeological or subfossil remains (M. Uhen, personal communication). Thus, we performed a more in-depth verification of these reports, excluding improper zooarchaeological occurrences. Nevertheless, the addition of more comprehensive zooarchaeological data may potentially alter the results presented herein.

3. Results

3.1. Documented fossil record

The compilation resulted in 1296 occurrences of fossil pinnipeds identified at a variety of taxonomical ranks (i.e. superfamily, family, subfamily, genus, subgenus, species, subspecies, tribe and subtribe) and published in the peer-reviewed literature. The number of publications reporting fossil pinnipeds, including extinct and extant taxa, fluctuates through calendar time. There is, however, a general increase in the number of publications reporting new occurrences over the last 3 decades (figure 1*a*). The oldest publication in our survey dates to 1826, with the report of fossil remains of extant harbour

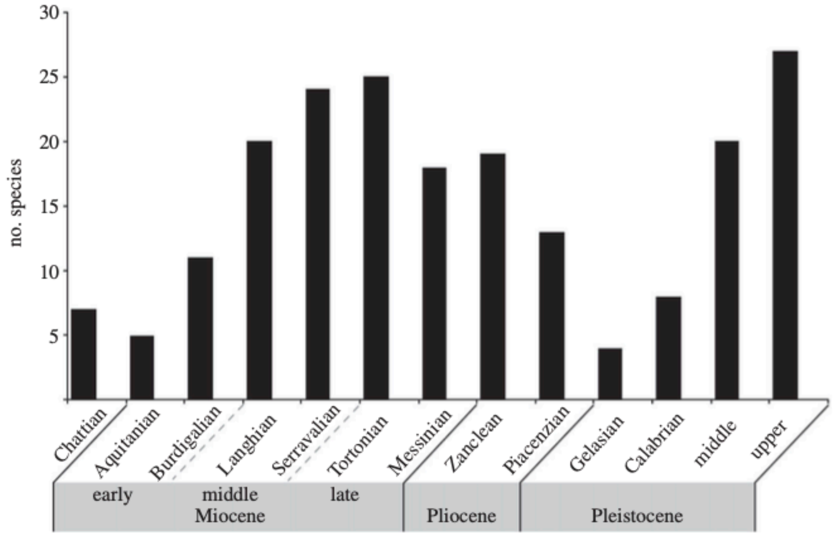

Figure 2. Number of species (both extant and extinct) over geological time. Note that the Chattian Stage belongs to the late Oligocene.

seals (*Phoca vitulina*) from the Pleistocene of the North Sea [34]. This record is followed by the occurrence of an indeterminate phocid from Calvert Formation (middle Miocene) of the eastern coast of North America. More than half of the pinniped fossil record (58%; $n = 752$) has been reported since 1990.

Remarkably, 90% ($n = 1160$) of the published occurrences (including all taxonomic ranks and ages) are derived from the Northern Hemisphere. The most productive geographical sub-regions in terms of occurrences are the eastern North Pacific (29%; $n = 374$), western North Atlantic (17%; $n = 215$) and North Sea (13%; $n = 162$). Occurrences from the Arctic, western North Pacific and the Paratethys Region represent 9% ($n = 120$), 8% ($n = 103$) and 7% ($n = 92$), respectively. Fossil occurrences from other regions (including from the Southern Hemisphere) are minor; the eastern coast of the South Atlantic Ocean, eastern coast of the South Pacific Ocean, the western coast of the South Pacific Ocean and the western coast of the South Atlantic Ocean represent only 5% ($n = 59$), 4% ($n = 47$), 2% ($n = 21$) and 1% ($n = 8$), respectively, of published fossil pinniped occurrences.

The distribution of the published occurrences over geologic time spans from the late Oligocene (approx. 26 Ma) to the Holocene (figure 1*b*; electronic supplementary material, figure S1). Additionally, there are a few putative older occurrences of fossil pinnipeds ($n = 2$) from the early Oligocene [35,36]. However, the validity of these occurrences and their stratigraphic provenance remain controversial (see [14,37]). The Quaternary (Pleistocene and Holocene) yielded the largest amount of fossil occurrences, encompassing 51% ($n = 665$) of the record (see below). Occurrences from the Pliocene represent 14% ($n = 187$). Reports from the Miocene–Pliocene and Miocene represent 33% ($n = 430$). Occurrences from the late Oligocene represent 1% ($n = 14$). It is worth noting that those differences are possibly correlated with the extension of the time span comprising the temporal bins used, and not necessarily implying particular properties during those temporal windows.

The number of species of both extinct and extant pinnipeds over geological time (at level of stage) is variable with peaks during the Serravallian and Tortonian and the Pleistocene (figure 2). Furthermore, to assess the effect of the availability of pre-Quaternary sedimentary rocks over the number of fossil pinnipeds, we plotted pinniped richness data of extinct and extant taxa against rock outcrop area for marine rock units of the western and eastern coasts of the USA (figure 3). These rocks comprise one of the more consistently sampled areas for fossil pinnipeds and other fossil marine mammals in the world. We used unpublished marine rock area data collected for similar analyses with fossil cetaceans reported in Uhen & Pyenson [10]. These geological data range at the subepoch level from the early Eocene through Pliocene of North America, following Uhen & Pyenson [10]'s data. Middle Eocene rocks, especially from the southeastern US coastal plain, account for the bulk area of Cenozoic rock outcrop in North America, but even excluding rocks of this age from our analysis (because of the lack of Eocene age pinnipeds in this continent), we did not find a correlation between the map area of

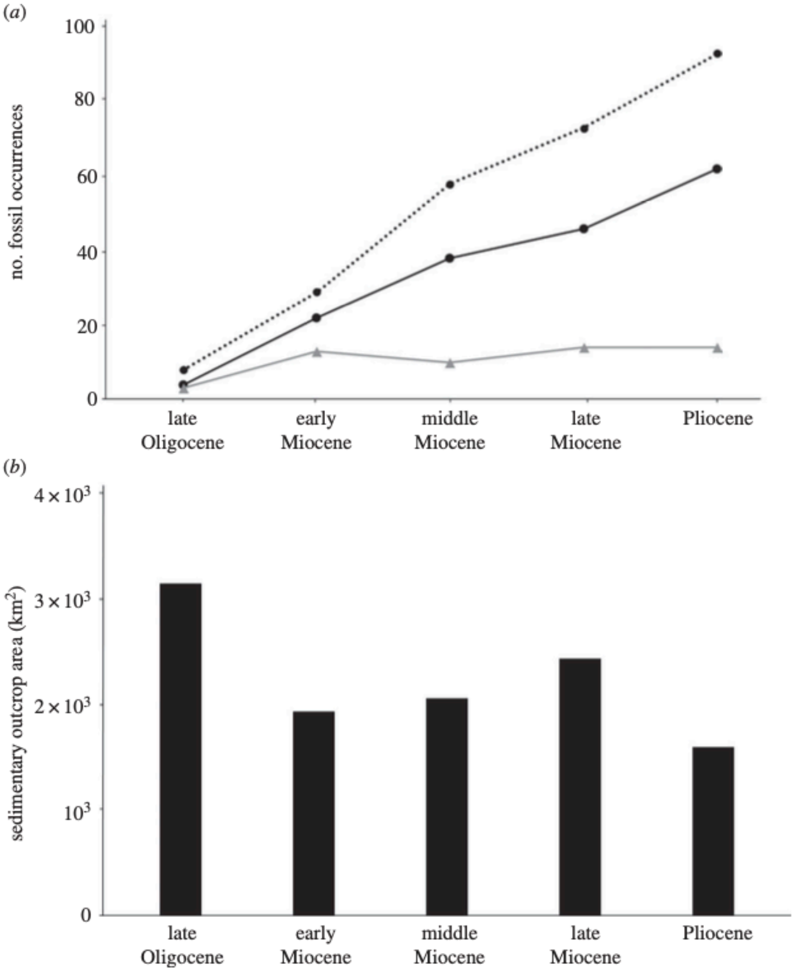

Figure 3. (*a*) Number of pinniped occurrences from the eastern and western coasts of the USA through geological time. Dashed line represents the number of fossil occurrences including an assortment of taxonomic ranks. Black line represents the number of fossil occurrences identified at the level of species. Grey line represents the species richness of pinnipeds. (*b*) Rock outcrop area for North American marine rock units, using unpublished data collected for the analyses published in Uhen & Pyenson [10].

rocks from USA and the number of published occurrences of pinnipeds through geological time (figure 3). Furthermore, we did not find a correspondence between the species richness over geological time and the sedimentary map area. For this analysis, we excluded putative occurrences of pinnipeds older than the late Oligocene and two occurrences identified as phocids from the late Oligocene because their validity is controversial (see above). It is worth noting that strong differences between rock area along the eastern and western coasts of the USA do exist: for example, abundant early Miocene rocks are known from California and Oregon, whereas similarly aged rocks are far less abundant (by areal map data) along the east coast of the USA.

3.2. Fossil record of extant pinnipeds

Of the 1296 documented fossil occurrences of pinnipeds, 37% ($n = 480$) correspond to fossil and zooarchaeological occurrences of extant species. Species belonging to Phocidae are the most abundant representing 48% ($n = 231$) of record of extant species, which is followed by members of Otariidae (29%; $n = 141$) and Odobenidae (23%; $n = 108$). The extant species with larger representation in the fossil record are *O. rosmarus* (walruses), *Arctocephalus townsendi* (Guadalupe fur seals), *Pusa hispida* (ringed seals), *Erignathus barbatus* (bearded seals), *Phoca vitulina* (harbour seals) and *Mirounga angustirostris* (Northern elephant seals).

Almost all (99%; *n* = 478) of the fossil and zooarchaeological occurrences of extant species are referred to occurrences from the Pleistocene and the Holocene epoch (electronic supplementary material, figure S1). The only exceptions are constituted by a single occurrence of *O. rosmarus* from the Miocene of Belgium [38]; and remains assigned to *Eumetopias jubata* (Steller sea lions) from the Pliocene of Japan [39]. A third record, corresponding to remains of *Phocarctos hookeri* (New Zealand sea lions) from the Pliocene of New Zealand [40] is included in PBDB; however, it has been argued that this record corresponds to a Holocene specimen, younger than 1000 years old, rather than a Pliocene occurrence [41].

3.3. Fossil record of extinct pinnipeds

A total of 388 occurrences of extinct species belonged to one of the 102 valid extinct species (electronic supplementary material, tables S1 and S2). We observed a positive trend of growing publications on extinct species over calendar years (figure 4*a*). In particular, 1977, 2001 and 2008 represent outstanding years, correlating with the publication of more than 30 occurrences of extinct species in each calendar year in three seminal and monographic publications ([8,42,43]; figure 3*a*). Furthermore, 61% (*n* = 235) of the occurrences of extinct species have been reported since 1990. Of the 102 species, only five extinct species belong to an extant genus (*Callorhinus gilmorei*, *Histriophoca alekseevi*, *Neophoca palatina*, *Otaria fisheri* and *Phoca moori*), representing approximately 5% of the extinct species.

The fossil record of extinct species spans from the late Oligocene to the late Pleistocene (figure 1). When analysed by geologic stages, we found there is normal-like distribution of occurrences over the Neogene and Quaternary (electronic supplementary material, figure S1) with a peak of known occurrences from the Serravallian, Tortonian, Zanclean and Piacenzian, comprising together 63% (*n* = 246) of the record. More recent occurrences of extinct species from the Pleistocene (including the Gelasian, Calabrian and Middle and Upper Pleistocene) represent 8% (*n* = 30) of the record.

In terms of their geographical origin, 93% (*n* = 362) of the record of extinct species is from the Northern Hemisphere, which is practically identical to the results found for the all published occurrences (including extant and extinct taxa, see above). North America concentrates more than half of the record, followed by Europe, Asia, Africa and South America (electronic supplementary material, figure S2). Six North American sedimentary formations lead the list of the most prolific pinniped-producing units, in terms of the number of published occurrences of extinct pinnipeds (identified at level of species), in decreasing rank: Calvert (eastern USA), Yorktown (eastern USA), Purisima (western USA), Santa Margarita (western USA), Astoria (western USA) and Bone Valley (eastern USA) formations. In fact, the Calvert and Yorktown formations (Middle Miocene and late Miocene-early Pliocene in age, respectively) comprise 6% (*n* = 25), each of the published occurrences of extinct pinniped species. Surprisingly, the Pisco Formation of Peru represents the seventh most prolific unit comprising 2% (*n* = 9) of the fossil occurrences of extinct taxa. Unfortunately, it was not possible to determine a clear and unambiguous geological formation for 11% (*n* = 42) of the occurrences of extinct taxa. The taxonomic accumulation curves (rarefaction curves; electronic supplementary material, figure S3) show that neither Calvert, Astoria, Yorktown and Purisima formations have reached a saturation in sampling over time. In turn, this analysis suggests that more fossil pinniped species should be found from these rock units.

Using data from museum collections of the two most fossil-rich units (Calvert and Yorktown formations; electronic supplementary material, tables S4 and S5), we investigated whether there is a correspondence between the number of pinniped specimens in these collections and the published record from those units. We discovered that the museum collections for the Calvert Formation comprise a disproportionately smaller number of specimens (*n* = 125) compared with the number of specimens from Yorktown Formation (*n* = 4153), which contrasts with the published fossil record from both units (*n* = 25 from Calvert Formation and *n* = 21 from Yorktown Formation). When examining the taxonomic richness of Calvert and Yorktown formations, we obtained dissimilar results. Despite having the highest number of published fossil occurrences with 25 reports of extinct taxa, only 2 species of phocids have been identified from the Calvert Formation: *Leptophoca proxima* and *Monotherium? wymani*. On the other hand, six species of pinnipeds have been reported from the Yorktown Formation, including odobenids and phocids (*Ontocetus emmonsi*, *Phocanella pumila*, *Homiphoca* sp., *Platyphoca vulgaris*, *Callophoca obscura*, *Auroraphoca atlantica* and *Gryphoca similis*). Remarkably, in Pisco Formation, the seventh most prolific unit with nine fossil occurrences of extinct taxa, four species of phocids (*Acrophoca longirostris*, *Piscophoca pacifica*, *Hadrokirus martini* and *Australophoca changorum*) and one species of otariid (*Hydrarctos lomasiensis*) have been described.

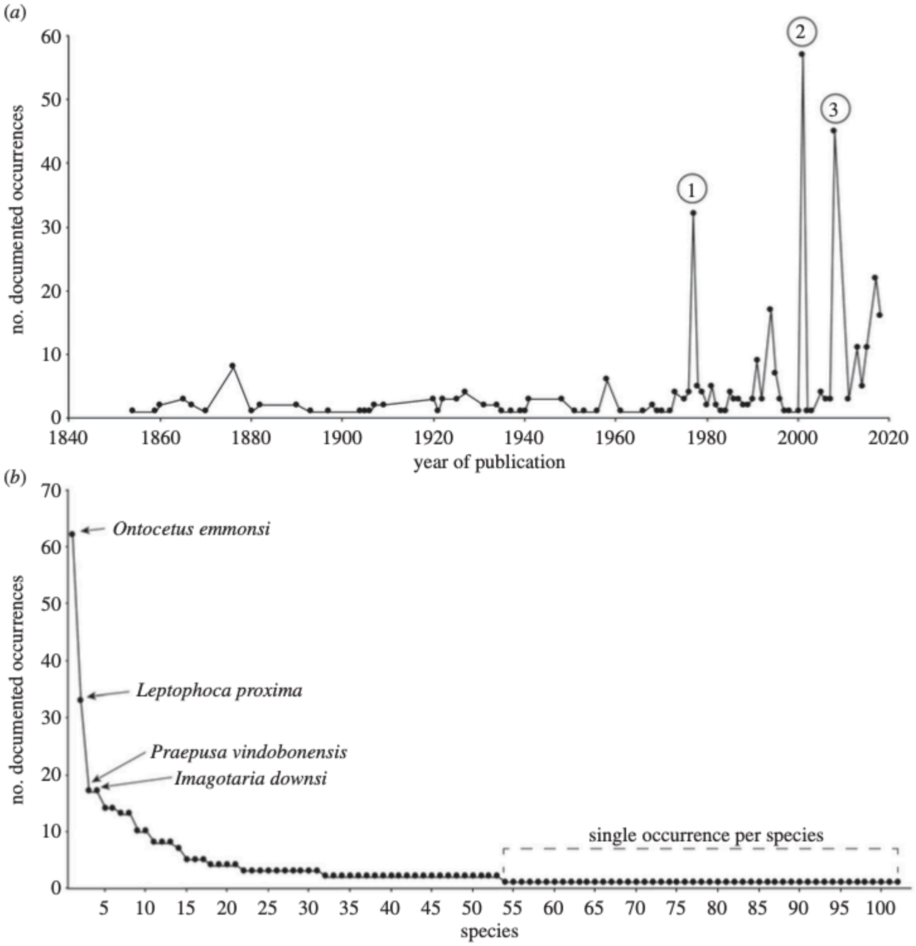

Figure 4. (*Caption overleaf.*)

Of the 388 occurrences of extinct pinnipeds identified at level of species, 50% ($n = 194$) of them belong to Phocidae, 30% ($n = 116$) belong to Odobenidae, 10% ($n = 37$) belong to Otariidae and Pan-Otariidae, 5% ($n = 20$) belong to Desmatophocidae and 5% ($n = 20$) belong to the so-called enaliarctids. Similarly, in terms of the taxonomic counts throughout the Cenozoic, of the 102 recognized extinct species, Phocidae constitute the largest taxonomically diverse clade, comprising 45 extinct species. Odobenidae is the second richest clade including 21 extinct species, contrasting with their monotypic extant diversity represented only by *O. rosmarus*. Otariidae and Pan-Otariidae comprise together 13 extinct species. The extinct clade Desmatophocidae comprises 11 species, and the so-called enaliarctids are represented by 10 species. Only *Palaeotaria henriettae* from the late Oligocene of France [44] was not assigned to any known group because the lack of unequivocal information to confirm its identity [45], remaining Pinnipedia *incertae sedis* in this study.

Overall, the odobenid *Ontocetus emmonsi* is the most represented extinct species constituting 16% ($n = 62$; figure 4*b*) of the total of the published fossil record of extinct species. Phocids, such as *L. proxima* and *Praepusa vindobonensis*, the odobenid *Imagotaria downsi* and the phocid *Homiphoca capensis*, are frequent findings in the fossil record, constituting 9% ($n = 33$), 4% ($n = 17$), 4% ($n = 17$) and 4% ($n = 14$), respectively (figure 4*b*). Notably, nearly half ($n = 49$) of the total of extinct species are established by a single fossil occurrence, which means the presence of a single specimen representing a single individual (figure 4*b*).

It should be noted that these results might point to a hidden diversity of other extinct species that are relatively abundant in the fossil record. For example, the phocid *Homiphoca capensis* from the Pliocene of

Figure 4. Fossil record of extinct species ($n = 388$). (*a*) Number of pinniped occurrences of extinct species through calendar years. We identified years with outstanding publications of fossil occurrences, which are indicated by numbers. 1: Repenning and Tedford (1977); 2: Koretsky (2001); 3: Kohno and Ray (2008). (*b*) Number of published occurrences per extinct species. Abbreviations: 1. *Ontocetus emmonsi* ($n = 62$); 2. *Leptophoca proxima* ($n = 33$); 3. *Praepusa vindobonensis* ($n = 17$); 4. *Imagotaria downsi* ($n = 17$); 5. *Cryptophoca maeotica* ($n = 14$); 6. *Homiphoca capensis* ($n = 14$); 7. *Callophoca obscura* ($n = 13$); 8. *Monachopsis pontica* ($n = 13$); 9. *Callorhinus gilmorei* ($n = 10$); 10. *Phocanella pumila* ($n = 10$); 11. *Dusignathus santacruzensis* ($n = 8$); 12. *Pliophoca etrusca* ($n = 8$); 13. *Pithanotaria starri* ($n = 8$); 14. *Pontophoca sarmatica* ($n = 7$); 15. *Gryphoca similis* ($n = 5$); 16. *Prophoca rousseaui* ($n = 5$); 17. *Allodesmus kernensis* ($n = 5$); 18. *Pachyphoca ukrainica* ($n = 4$); 19. *Thalassoleon mexicanus* ($n = 4$); 20. *Dusignathus seftoni* ($n = 4$); 21. *Thalassoleon macnallyae* ($n = 4$); 22. *Pteronarctos goedertae* ($n = 3$); 23. *Australophoca changorum* ($n = 3$); 24. *Praepusa pannonica* ($n = 3$); 25. *Platyphoca vulgaris* ($n = 3$); 26. *Batavipusa neerlandica* ($n = 3$); 27. *Desmatophoca oregonensis* ($n = 3$); 28. *Enaliarctos emlongi* ($n = 3$); 29. *Acrophoca longirostris* ($n = 3$); 30. *Allodesmus sinanoensis* ($n = 3$); 31. *Nanophoca vitulinoides* ($n = 3$); 32. *Enaliarctos mealsi* ($n = 2$); 33. *Piscophoca pacifica* ($n = 2$); 34. *Pteronarctos piersoni* ($n = 2$); 35. *Frissiphoca aberrantum* ($n = 2$); 36. *Pontolis magnum* ($n = 2$); 37. *Gomphotaria pugnax* ($n = 2$); 38. *Prototaria primigenia* ($n = 2$); 39. *Gryphoca nordica*; 40. *Titanotaria orangensis* ($n = 2$); 41. *Allodesmus demerei*; 42. *Pliopedia pacifica* ($n = 2$); 43. *Hydrarctos lomasiensis* ($n = 2$); 44. *Monotherium wymani* ($n = 2$); 45. *Proterozetes ulysses* ($n = 2$); 46. *Pelagiarctos thomasi* ($n = 2$); 47. *Enaliarctos mitchelli* ($n = 2$); 48. *Aivukus cedrosensis* ($n = 2$); 49. *Enaliarctos tedfordi* ($n = 2$); 50. *Pinnarctidion bishopi* ($n = 2$); 51. *Valenictus imperialensis* ($n = 2$); 52. *Pinnarctidion rayi* ($n = 2$); 53. *Phoca moori* ($n = 2$); 54. *Properyptychus argentinus* ($n = 1$); 55. *Brachyallodesmus packardi* ($n = 1$); 56. *Neotherium mirum* ($n = 1$); 57. *Virginiaphoca magurai* ($n = 1$); 58. *Noriphoca gaudini* ($n = 1$); 59. *Praepusa magyaricus* ($n = 1$); 60. *Odobenus mandanoensis* ($n = 1$); 61. *Prototaria planicephala* ($n = 1$); 62. *Allodesmus naorai* ($n = 1$); 63. *Eotaria citrica* ($n = 1$); 64. *Oriensarctos watasei* ($n = 1$); 65. *Pontophoca simionescui* ($n = 1$); 66. *Otaria fischeri* ($n = 1$); 67. *Atopotarus courseni* ($n = 1$); 68. *Pachyphoca chapskii* ($n = 1$); 69. *Miophoca vetusta* ($n = 1$); 70. *Desmatophoca brachycephala* ($n = 1$); 71. *Pseudotaria muramotoi* ($n = 1$); 72. *Pacificotaria hadromma* ($n = 1$); 73. *Thalassoleon inouei* ($n = 1$); 74. *Palaeotaria henriettae* ($n = 1$); 75. *Valenictus chulavistensis* ($n = 1$); 76. *Palmidophoca callirhoe* ($n = 1$); 77. *Archaeodobenus akamatsui* ($n = 1$); 78. *Eotaria crypta* ($n = 1$); 79. *Praepusa boeska* ($n = 1$); 80. *Hadrokirus martini* ($n = 1$); 81. *Enaliarctos barnesi* ($n = 81$); 82. *Histriophoca alekseevi* ($n = 1$); 83. *Proneotherium repenningi* ($n = 1$); 84. *Eumetopias kishidai* ($n = 1$); 85. *Messiphoca mauretanica* ($n = 1$); 86. *Frisiphoca affine* ($n = 1$); 87. *Protodobenus japonicus* ($n = 1$); 88. *Allodesmus kelloggi* ($n = 1$); 89. *Afrophoca libyca* ($n = 1$); 90. *Devinophoca claytoni* ($n = 1$); 91. *Auroraphoca atlantica* ($n = 1$); 92. *Platyphoca danica* ($n = 1$); 93. *Sarmatonectes sintsovi* ($n = 1$); 94. *Devinophoca emryi* ($n = 1$); 95. *Allodesmus megallos* ($n = 1$); 96. *Kamtschatarctos sinelnikovae* ($n = 1$); 97. *Necromites nestoris* ($n = 1$); 98. *Allodesmus uraiporensis* ($n = 1$); 99. *Neophoca palatina* ($n = 1$); 100. *Kawas benegasorum* ($n = 1$); 101. *Pontophoca jutlandica* ($n = 1$); 102. *Nanodobenus arandai* ($n = 1$).

South Africa is only represented by 14 fossil occurrences in electronic supplementary material, table S1. However, Govender *et al*. [46] identified 40 specimens belonging to this species and suggested that 'two or possible three seal taxa' existed among this material. Furthermore, Govender *et al*. [46] mentioned that more than 3000 specimens have been identified belonging to *H. capensis*, currently housed at the Iziko South African Museum, in Cape Town, South Africa, although a large portion remain undescribed [46]. A similar case is represented by the phocid *Callophoca obscura*, which is represented by an extensive fossil record from the western coast of North America (see electronic supplementary material, table S5); however, only 13 records of this species are included in electronic supplementary material, table S1. Considering this taxonomical uncertainty, we remain conservative and we only included the specimens recognized by the PaleoDB.

Finally, the most prolific author describing fossils of extinct taxa (including a variety of taxonomical ranks) is I. Koretsky, who is responsible for 20% of the taxonomic reporting. She is followed by N. Kohno (12%), C. A. Repenning (8%), L. Barnes (6%), A. Berta and R. Boessenecker (the latter two with 4%, each). To further explore in their efforts by geographical research area, we analysed the study sites for each of these authors and found that without exception the authors have described specimens from the Northern Hemisphere. In more detail, when analysed the geographical region of the specimens described for each of them, we noted a proclivity for those authors for working on fossil specimens from their own region versus other areas or continents (see electronic supplementary material, figure S4).

3.4. Type specimens of extinct species

It was not possible to state the catalogue number (i.e. the collection number of the research institution such as museums and universities in which the materials are deposited) for the type specimen (or holotype) of 13 extinct species: *Allodesmus sinanoensis, Eumetopias kishidai, Hydrarctos lomasiensis, Miophoca vetusta, Necromites nestoris, Oriensarctos watasei, Otaria fischeri, Pala. henriettae, Phoca (Phoca)*

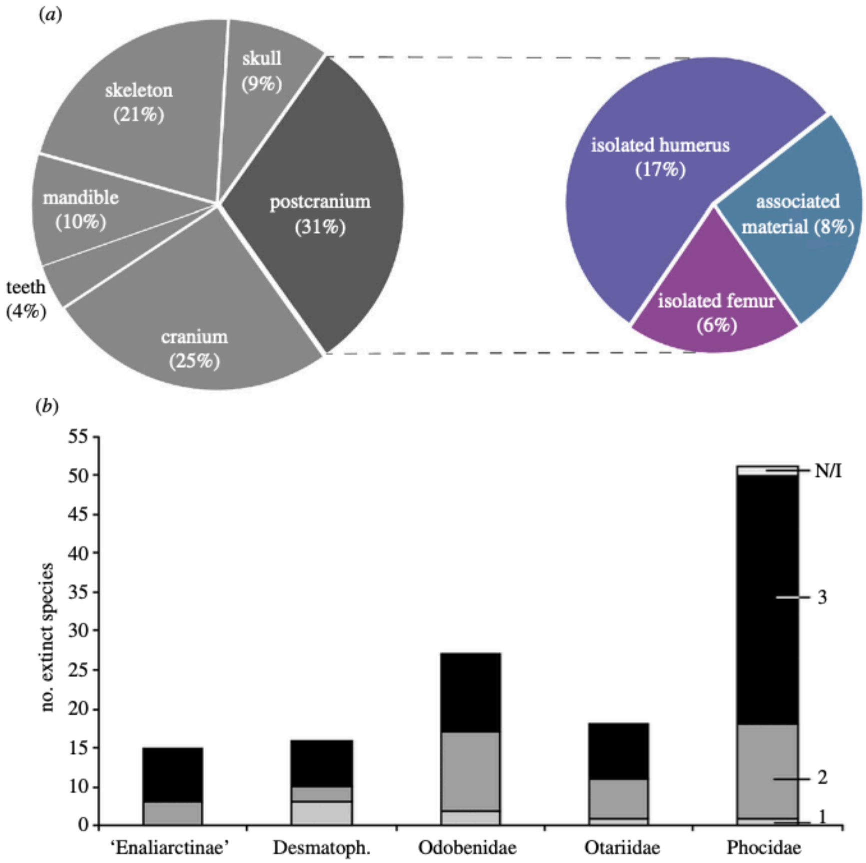

Figure 5. Features of the type material of extinct species ($n = 103$) recognized by the PaleoDB. (*a*) Identity of the type specimens of the extinct species. The bar representing postcranial remains shows the proportion of species which type materials is only represented by an isolated humerus (light grey), isolated femur (medium grey) and associated elements (dark grey). (*b*) Completeness of type specimens of extinct species by family. Light grey represents category 1 (complete or mostly complete skeletons), medium grey represents category 2 (associated elements) and dark grey represents category 3 (isolated elements). One species of phocid could not be assigned to any of the categories and it is stated as N/I.

moori, *Pontophoca sarmatica*, *Pontophoca simionescui*, *Praepusa vindobonensis* and *Protodobenus japonicus*. Some of them (*A. sinanoensis*, *E. kishidai*, *O. watasei* and *P. japonicus*) are housed at small institutions in Japan; therefore, our inability to state a catalogue number could be due to language constraints and limited accessibility to the specimens by researchers. In other cases, these taxonomic entities were erected in the nineteenth or early twentieth century without a designated type specimen, or remain problematic in other ways. Establishing their validity ought to be the focus of future systematic work.

Regarding the anatomical basis of these latter type specimens (figure 5*a*), 31% ($n = 32$) of extinct species have a holotype represented only by postcranial elements; 25% ($n = 26$) by cranium only, 21% ($n = 22$) by associated or articulated skeleton; 9% ($n = 9$) by skull (cranium and mandible); 10% ($n = 10$) by isolated mandibular remains; and 4% ($n = 4$) by dentition alone (figure 5*a*). We identified that the most common postcranial elements used as type specimen are isolated humeri and femora, representing a non-trivial quantity of 17% ($n = 18$) and 6% ($n = 6$), respectively (figure 5*a*). Similarly, 8% ($n = 8$) extinct species are based on type material constituted by associated postcranial elements. Thus, we identified that 23% of the extinct species of pinnipeds are founded only on isolated (and sometimes incomplete) appendicular elements as humeri and femora.

Regarding the completeness of type specimens of extinct species, we identified 61% ($n = 63$) belonging to category 3 (isolated elements), 31% ($n = 32$) to category 2 (associated or more complete remains), 7% ($n = 7$) to category 1 (complete or almost complete skeletons). For 1% ($n = 1$), it was not possible to assign a category because of the missing information (i.e. *Mi. vetusta*). Therefore, the majority of fossil pinniped taxa are based on the type material that belong to a single isolated element (figure 5*b*).

4. Discussion

Uhen & Pyenson [10] were the first to examine the potential biases affecting diversity counts in fossil marine mammals, focusing on fossil cetaceans (with a brief comparison to fossil sirenians). They identified that taxonomic practices, such as the use of non-diagnostic-type specimens and taxonomic over-splitting, may artificially increase diversity indices. Other factors, such as the sedimentary outcrop area, sedimentation, preservation, collection and publication efforts, have the potential to bias diversity estimations [10]. Unfortunately for fossil pinnipeds, a few studies have directly addressed the influence of these factors, with the exception of Marx [11], who discussed, in part, the European fossil record of pinnipeds. While far from an exhaustive review of the potential biases affecting the pinniped fossil record and biodiversity estimations, our results show some relevant points.

4.1. Sampling biases of the pinniped fossil record

The effect of sampling biases (e.g. Pull of the Recent, outcrop area, among others) on diversity estimates from the fossil record has been the topic of extensive discussion in the paleobiological literature for nearly half a century (e.g. [47–52]; and references therein). In particular, it has been shown that the fossil record of cetaceans and sirenians lacks significant sampling bias, nor is there a display of strong the 'Pull of the Recent' (*sensu* [48]).

Our broad evaluation of the fossil occurrences of pinnipeds, along with their species richness through time, showed no correspondence with sedimentary outcrop area (figures 2 and 3; electronic supplementary material, table S3), suggesting that changes in the pinniped diversity may reflect genuine biological patterns rather than manifest geological factors [48,50,51]. Aside from this apparent lack of rock record bias, the pinniped record does appear to exhibit a Pull of the Recent trend with a relative increase in the number of species in younger time bins, towards the Recent (figure 2). This pattern is not surprising given broad-scale patterns in the marine tetrapod fossil record [18,53] that largely echo this trend in clades with larger numbers of extant and extinct species. Several authors have argued that environmental shifts increasing the patchiness and abundance of the primary productivity were likely strong factors in driving this trend in taxonomic and ecological diversity in both coastal and pelagic seas (see [54–56]). This argument seems to be supported by the timing of the diversification among otariids in the North Pacific during the late Miocene [57] and also the Mio-Pliocene record of odobenids [3].

Furthermore, we found that the most prolific geological units for fossil pinnipeds in the USA, Calvert and Yorktown formations did not show a correspondence with the number of species described in those units, nor with the number of fossils recovered from those collections (electronic supplementary material, tables S4 and S5). These results highlight that the amount of fossil remains recognized in geologic units and the number of species identified are not correlated, probably because the influence of taphonomic processes (among others) that limit the preservation of features with a diagnostic value (see below).

Taphonomy represents an important factor in the preservation of pinnipeds. Their amphibious lifestyle—equally dependent on land for breeding and on water for foraging—causes pinnipeds to be exposed to very different taphonomic processes depending on where they die (rookeries versus coastal or even pelagic environments). In this regard, we conceive three possible scenarios in which pinniped remains might enter into the fossil record: (i) death at sea and deposition offshore; (ii) death at sea followed by beaching of the carcass on the coast; and (iii) death and burial on land, either at haul out or rookery sites, or after stranding due to illness or injury. The potential effect of the taphonomic processes associated with these scenarios on the pinniped fossil record is largely unexplored, although they likely share some similarities with processes for other marine mammals, such as cetaceans (see [58]). The pre- and post-mortem processes that might accompany each of these modes of death are very different and are likely to affect the completeness of skeletons found, bone weathering state, bone modifications, the species composition at the site and the demography of sites with multiple individuals of the same species. While many studies have addressed taphonomic processes involving pinniped remains in part [6,19,59–63], future work needs to address and evaluate the full range of biotic and abiotic factors, as well intrinsic factors (e.g. body size, morphology, physiology, ontogeny and natural history) that potentially bias preservation across the entire clade of pinnipeds.

4.2. Geographical biases of the fossil record

Our analysis revealed that 89% of the published fossil record of pinnipeds (from the Cenozoic and Quaternary) is represented by occurrences from the Northern Hemisphere, denoting an enormous disparity in the location of the fossil findings between both hemispheres. There are several potential explanations for this dissimilarity, including differences in the past geographical distribution and abundance of the group (including the fact that pinnipeds originated along the North Pacific), as well other extrinsic explanations related with their fossilization and preservation; and other human-related factors including the sampling and collection effort and the likelihood of publication (e.g. [64–71]). Because of the unpredictability of the processes involved in the preservation and discovery of fossil remains, we cannot reject any of these potential explanations. Nevertheless, the stark differences in the published record from the eastern coasts of the North and South Pacific Ocean do deserve further consideration. Both regions exhibit analogous physical and ecological conditions, including high primary productivity [72,73] and the occurrence of a rich and diverse marine vertebrate fauna [74]. Notably, both regions exhibit broad fossiliferous sedimentary outcrops with a mostly remarkable contemporaneous fossil record of pinnipeds (and other marine mammals) from the middle Miocene and Pliocene (see [2] and references therein). Fossiliferous outcrops from the middle Miocene and Pliocene along the coast of California and along the western coast of South America both extend across a vast latitudinal gradient relatively constant range encompassing almost the entire southern coast of Peru and the northern and central coast of Chile, comprising two of the most important geologic units of the Southern Hemisphere: the Pisco and Bahía Inglesa formations in southern Peru and northern Chile, respectively [75,76]. In fact, both formations have yielded several species of marine vertebrates including, at least, four species of pinnipeds and still several species and morphotypes remain to be described (A.V.-T., personal observations), and rank among the world's richest fossil marine mammal faunas.

We propose that the disparity in the number of published fossil record of pinnipeds during the middle Miocene and Pliocene between the two regions is likely associated with differential sampling and publication efforts, along with the number of vertebrate paleontologists working in the field. For example, we detected that, the six most productive systematists were Northern Hemisphere-based researchers (electronic supplementary material, figure S2). Furthermore, these researchers show a strong tendency of publishing specimens from regions where they live and work. Thus, field explorations and publication efforts in the Southern Hemisphere may be a key factor explaining these differences. Overall, this suggests a very promising future for the study of fossil pinnipeds (and other marine mammals) in the Southern Hemisphere.

4.3. Fossil record of extant species

Surprisingly, the fossil record of extant species of pinnipeds represents 39% of the overall fossil record of this group (including Pleistocene and Holocene occurrences), contrasting with the proportions of the fossil record of other marine mammals, such as cetaceans and sirenians, in which the record of modern species represents a small fraction of the fossil record (e.g. only 2% of the fossil record of sirenians correspond to extant species; PaleoDB). Also, with a few exceptions, including remains of *O. rosmarus* from the Miocene of Belgium and *E. jubata* from the Pliocene of Japan [38,39], the fossil record of extant species is mostly referred to recent occurrences from the Holocene and Pleistocene (figure 1), exhibiting, in general, a very similar geographical distribution to contemporary patterns (a notable exception is constituted by a Ross seal (*Ommatophoca* rossii) from the early Pleistocene of New Zealand; [21]). In fact, in some regions, such as the eastern and western North American coast and Europe, the Pleistocene pinniped assemblage is identical in composition to the modern local fauna. By contrast, we found that fewer than 15 occurrences of extinct taxa occur in this interval. The relative paucity of Quaternary extinct species may explain the lack of knowledge about the evolutionary history of extant species.

Equally, we suggest that careful and exhaustive studies of pinniped faunas from the Pleistocene and Holocene might represent an exceptional opportunity to better understand the most historically recent community-wide changes in this clade, as exemplars for the response of marine mammals to changing environmental conditions over time (including shifting baselines from human hunting; see [6]). Furthermore, the use of biogeochemistry and molecular techniques, such as stable isotopes and ancient DNA, respectively, would provide new clues regarding how humans interacted and potentially affected different populations of marine mammals during the past (e.g. [31,77]), and has the potential to shed light on questions as to what degree the modern distribution of pinnipeds is a reflection of their human-caused decimation in the past few hundred years [78,79].

4.4. Fossil record of extinct species

Our analysis highlights some features of the fossil record of extinct species that deserve further attention. First, nearly half of the extinct species are based on a single (published) occurrence confined to single time interval. While our study does not account for subsequent follow-up work that refers to more skeletal material or increases the geographical and stratigraphic range data of a novel taxon, this strong modal pattern to the description of fossil pinniped has a major impact on the historiography of paleobiological research with this group. In this regard, an important caveat is that these results do not necessarily represent the true plenitude of the fossil record of extinct species. In fact, we argue that there are discrepancies between the published fossil record and museum collections, which remain mostly unpublished (see the Results section for more details, and electronic supplementary material, table S5), much as 'dark data' obscure many patterns in the Cenozoic marine invertebrate record that co-occurs with fossil pinniped-bearing units of the west coast of North America [80].

Separately, 23% of the extinct species rely on type specimens consisting of a single isolated postcranial element (e.g. humeri or femora). We think this practice among systematists has largely not been grounded in a quantitative comparative context that accounts for the osteological variation and sexual dimorphism in some extant pinniped species [81–83]. To our knowledge, most of the studies addressing the osteological variation from sexual dimorphism in modern and fossil pinnipeds have been based on skulls (see [84–86]), with only a few studies testing such patterns using postcranial elements [8,83,87,88]. For instance, Koretsky [8] examined the humeri and femora of extinct and modern phocine seals, finding that most of the dimorphic variation between males and females is related to differences in the size (e.g. absolute length and length of the deltoid crest of the humerus), overall shape and proportions of the structures (e.g. dorsoventral thickness of the diaphysis and length and thickness of the neck of the femur) and the depth of muscle insertions (e.g. depth and shape of the coronoid fossa). Koretsky [8] did not find a correlation in the variation of those features among fossil and modern species of seals, showing a high specificity of the variation among seals. Based on the qualitative observations of the humeri of leopard seals (*Hydrurga leptonyx*) and a Weddell seal (*Leptonychotes weddellii*), Dewaele *et al.* [88] proposed that complete or nearly complete humeri can be considered as diagnostic bones to differentiate among monachinae phocids, although this was not tested statistically. More recently, Churchill & Uhen [83] performed an exhaustive morphometric analysis of the interspecific variation in the humeri and femora of phocids. They found the existence of large intraspecific variation, suggesting that the diagnostic efficacy of isolated femora and humeri is unjustified, questioning their validity as diagnostic elements for new species.

A more critical issue is the lack of a standardized approach for systematists to deal with non-associated elements referred to a new extinct taxon. Koretsky [8] asserted that a presumed 'principle of correlation of parts' and an 'ecomorphotype hypothesis' were sufficient to establish association, in the absence of taphonomic, stratigraphic or locality data. The 'ecomorphotype hypothesis' is based on the notion that the ecological niche of modern phocine seals is reflected in bones of the postcranial skeleton (humeri and femora) and mandible. It also assumes that extinct phocine seals have analogous morphological units to modern phocine species, making possible the recognition of fossil species from isolated postcranial elements and mandibles [8]. This author then defined five morphological groups of phocine seals, each comprising both modern and fossil species based on specific features of the mandible, humeri and femora. Unfortunately, no exhaustive ecomorphological study has been performed in modern pinnipeds, and the validity of this hypothesis remains to be tested, despite its weak paleoecological foundation. An example of the taxonomic consequences of this unsupported practice is represented by the recently described phocids *Terranectes magnus* and *T. parvus*, from the late Miocene age Eastover and St Marys formations of the eastern USA [89]. Despite the fragmentary nature of their holotypes (proximal half of the left humerus and a partial femur, respectively), Rahmat *et al.* [89] erected taxonomic names for these species based on non-overlapping and non-associated cranial, axial and appendicular elements (including some from different stratigraphic levels). Later, Dewaele *et al.* [88] considered both *T. magnus* and *T. parvus* to be a *nomen dubium*.

This practice (the use of non-associated elements) might lead not merely to artificial increases in taxonomic diversity, but also to inaccurate inferences about phylogenetic relationships among fossil pinnipeds. For instance, the extinct phocids *Prophoca proxima* and *Leptophoca lenis* are both species originally based on fragmentary isolated postcranial remains from the Miocene of Belgium. An exhaustive re-description and phylogenetic analysis of *Pr. proxima* and *L. lenis* resulted in the synonymization of both species, with the proposition of a new combination *L. proxima* [37]. A similar case is represented by desmatophocids belonging to the genus *Allodesmus*, from the Round Mountain Silt of California. Three species of *Allodesmus* have been described (*Allodesmus gracilis*, *A. kelloggi* and *A. kernensis*; [90]), distinguished by the morphological variation on the mandibles (e.g. symphysial angle, interalveolar septa, depth of the masseteric fossa, shape of the coronoid process; [91,92]). However, it has been argued that these differences fall within levels of intraspecific variation in extant pinnipeds [93]. Thus, *A. kelloggi* and *A. gracilis* should be identified as junior synonyms of *A. kernensis* (following [90]). Further studies focusing on intraspecific morphological variation within extant and extinct species are needed to clarify these issues. These taxonomic re-evaluations (e.g. declaration of *nomina dubia* and junior synonyms) should add an additional complexity to the fossil record of this group since taxa, based on isolated and non-overlapping materials, are more prone to changes in their systematic and taxonomic identity. Similarly, taxa described longer ago are more prone to re-evaluations over time.

Finally, we could not pinpoint a specimen voucher for the holotype of 13 extinct species; in some cases, no type specimen had been formally designated, which is an occasional aspect of ninteenth-century taxonomic practices (see [10]). This situation is particularly relevant to the issues identified in our study because it creates a number of negative consequences, including lack of traceability with the identification, validation and comparability with other putative fossil occurrences (see [94]). It is incumbent on the community of practising systematic researchers to develop best practices in specimen-based research that prevent these problems (e.g. deposit fossil specimens in accessible natural history collections such as museums or research institutions; avoid studying specimens derived from illegal or informal trade, as well as those collected outside of established natural history museums). Surprisingly, many of these problems still occur among marine mammal researchers in the twenty-first century (see [95,96,97]).

5. Conclusion

We performed a historiographical revision of the published fossil record of pinnipeds based in the Paleobiology Database. Our historiographical analysis revealed several clear trends in the pinniped fossil record:

1. Most of the record is from deposits in the Northern Hemisphere, despite favourable paleoecological and depositional conditions in the Southern Hemisphere. There appears to be a strong collection and publication bias given strong imprint from the legacy of study in major centres of learning in the Northern Hemisphere, especially in North America and Europe, which have larger population centres, more researchers and longer traditions of study.
2. Nearly half of all fossil species are represented by a single occurrence—and a single specimen of a single individual. Additionally, a substantial number of extinct species have type material represented only by isolated postcranial elements, which might lead to artificial increases in taxonomic diversity. Considering these results, studies focusing on intra- and interspecific variation in the morphology of cranial and postcranial elements in modern and fossil taxa are needed.
3. Overall, despite the large geographical bias exhibited by the fossil record of pinnipeds, it is relatively adequately represented for evolutionary and paleoecological studies depending on the geographical region (and time interval) investigated.

Although this investigation is far from being exhaustive, it still provides a starting point for future research addressing changes in diversity, paleobiogeography and paleoecology in pinnipeds.

Data accessibility. Additional data are in the electronic supplementary material.

Authors' contributions. A.V.-T. and N.D.P. conceived and designed the research, analysed the data and wrote the paper.

Competing interests. We declare we have no competing interests.

Funding. This study was supported by CONICYT PCHA/Becas Chile, Doctoral Fellowship (grant no. 2016-72170286) to A.V.-T. and a Smithsonian Institution Graduate Fellowship. Additional funding for this work comes from a National Museum of Natural History (NMNH) Small Grant Award, and the Smithsonian Institution's Remington Kellogg Fund.

Acknowledgements. We would like to thank P. Koch and D. Costa (UCSC), J. Parham (CSUF), J. Velez-Juarbe (LACM), D. Bohaska (NMNH), M. Gilmour (UCSC), D. Glynn (UCSC), C. Ravelo (UCSC), F. Parada (U. Chile) and C. Gutstein (U. Chile) for providing comments and suggestions during the performance of this study, C. Carter (NMNH) for her help in the literature search. Additionally, we would like to thank four anonymous reviewers for their helpful comments that significantly improved the manuscript. The paper is Paleobiology Database contribution number 350.

References

1. Berta A, Churchill M. 2011 Pinniped taxonomy: review of currently recognized species and subspecies, and evidence used for their description. *Mamm. Rev.* **15**, 1–19. (doi:10.1111/j.1365-2907.2011.00193.x)
2. Berta A, Churchill M, Boessenecker RW. 2018 The origin and evolutionary biology of Pinnipeds: seals, sea lions, and walruses. *Annu. Rev. Earth Planet. Sci.* **46**, 203–228. (doi:10.1146/annurev-earth-082517-010009)
3. Magallanes I, Parham JF, Santos G, Velez-Juarbe J. 2018 A new tuskless walrus from the Miocene of Orange County, California, with comments on the diversity and taxonomy of odobenids. *PeerJ* **6**, e5708. (doi:10.7717/peerj.5708)
4. Velez-Juarbe J, Salinas-Marquéz FM. 2018 A dwarf walrus from the Miocene of Baja California Sur, Mexico. *R. Soc. open sci.* **5**, 180423. (doi:10.1098/rsos.180423)
5. Valenzuela-Toro AM, Gutstein CS, Varas-Malca RM, Suarez ME, Pyenson ND. 2013 Pinniped turnover in the South Pacific Ocean: new evidence from the Plio-Pleistocene of the Atacama Desert, Chile. *J. Vertebr. Paleontol.* **33**, 216–223. (doi:10.1080/02724634.2012.710282)
6. Boessenecker RW. 2013 A new marine vertebrate assemblage from the Late Neogene Purisima Formation in Central California. Part II. Pinnipeds and cetaceans. *Geodiversitas* **35**, 815–940. (doi:10.5252/g2013n4a5)
7. Velez-Juarbe J. 2017 *Eotaria citrica*, sp. nov., a new stem otariid from the 'Topanga' formation of Southern California. *PeerJ* **5**, e3022. (doi:10.7717/peerj.3022)
8. Koretsky IA. 2001 Morphology and systematics of the Miocene Phocinae (Mammalia: Carnivora) from Paratethys and the North Atlantic Region. *Geol. Hungarica Ser. Palaeontol.* **54**, 1–109.
9. Valenzuela-Toro AM, Pyenson ND, Gutstein CS, Suárez ME. 2015 A new dwarf seal from the late Neogene of South America and the evolution of pinnipeds in the southern hemisphere. *Pap. Palaeontol.* **2**, 101–115. (doi:10.1002/spp2.1033)
10. Uhen MD, Pyenson ND. 2007 Diversity estimates, biases, and historiographic effects: resolving cetacean diversity in the Tertiary. *Palaeontol. Electron.* **10**, 1–22.
11. Marx FG. 2008 Marine mammals through time: when less is more in studying palaeodiversity. *Proc. R. Soc. B* **276**, 887–892. (doi:10.1098/rspb.2008.1473)
12. Peters S, McClennen M. 2016 The Paleobiology Database application programming interface. *Paleobiology* **42**, 1–7. (doi:10.1017/pab.2015.39)
13. Berta A, Sumich JL, Kovaks KM. 2006 *Marine mammals—evolutionary biology*, pp. 1–547, 2nd edn. Amsterdam, The Netherlands: Elsevier-Academic Press.
14. Deméré TA, Berta A, Adam PJ. 2003 Pinnipedimorph evolutionary biogeography. *Bull. Am. Mus. Nat. Hist.* **13**, 32–76. (doi:10.1206/0003-0090(2003)279<0032:C>2.0.CO;2)
15. Piller WE, Harzhauser M, Mandic O. 2007 Miocene Central Paratethys stratigraphy—current status and future directions. *Stratigraphy* **4**, 151–168.
16. Hammer Ø, Harper DAT, Ryan PD. 2001 PAST: Paleontological Statistics Software package for education and data analysis. *Palaeontol. Electron.* **4**, 9 p.
17. White T, Folkens PA. 2005 *The human bone manual*. Boston, MA: Elsevier and Academic Press.
18. Pyenson ND *et al.* 2014 Repeated mass strandings of Miocene marine mammals from Atacama Region of Chile point to sudden death at sea. *Proc. R. Soc. B* **281**, 20133316. (doi:10.1098/rspb.2013.3316)
19. Boessenecker RW, Perry FA, Schmitt JG. 2014 Comparative taphonomy, taphofacies, and bonebeds of the Mio-Pliocene Purisima formation, Central California: strong physical control on marine vertebrate preservation in shallow marine settings. *PLoS ONE* **9**, e91419. (doi:10.1371/journal.pone.0091419)
20. Itoo T. 1985 New cranial materials of the Japanese sea lion, *Zalophus californianus japonicus* (Peters, 1866). *J. Mammal. Soc. Jpn* **10**, 135–148.
21. King JE. 1983 The Ohope skull—a new species of Pleistocene sealion from New Zealand. *New Zeal. J. Mar. Freshwater Res.* **17**, 105–120. (doi:10.1080/00288330.1983.9515990)
22. Melin SR, Trillmich F, Aurioles-Gamboa D. 2018 California, Galapagos, and Japanese Sea lions. In *Encyclopedia of marine mammals* (eds B Wursig, JGM Thewissen, KM Kovacs), 3rd edn. New York, NY: Academic Press.
23. Lyman R. 1988 Zoogeography of Oregon coast marine mammals: the last 3,000 years. *Mar. Mamm. Sci.* **4**, 247–264. (doi:10.1111/j.1748-7692.1988.tb00205.x)
24. Lyman R, Harpole J, Darwent C, Church R. 2002 Prehistoric occurrence of Pinnipeds in the Lower Columbia River. *Northwest. Nat.* **83**, 1–6. (doi:10.2307/3536507)
25. Rick TC, DeLong RL, Erlandson JM, Braje TJ, Jones TL, Kennett DJ, Wake TA, Walker PL. 2009 A trans-Holocene archaeological record of Guadalupe fur seals (*Arctocephalus townsendi*) on the California coast. *Mar. Mamm. Sci.* **25**, 487–502. (doi:10.1111/j.1748-7692.2008.00273.x)
26. Rick TC, Erlandson JM, Braje TJ, DeLong RL. 2009 Seals, sea lions, and the erosion of archaeological sites on California's Channel Islands. *J. Island Coast. Archaeol.* **4**, 125–131. (doi:10.1080/15564890902791391)
27. Rick TC, Braje TJ, DeLong RL. 2011 People, pinnipeds, and sea otters of the northeast Pacific. In *Human Impacts on Seals, Sea Lions, and Sea Otters* (eds TC Rick, TJ Braje), pp. 1–17. Berkeley, CA: University of California Press.
28. Jew NP, Braje TJ, Erlandson JM. 2016 Pinnipeds and Paleocoastal middens: a case study from Point Bennett, San Miguel Island, California. *J. Island Coast. Archaeol.* **11**, 294–303. (doi:10.1080/15564894.2015.1096870)
29. Braje TJ, Costello JG, Erlandson JM, DeLong R. 2014 Of seals, sea lions, and abalone: the archaeology of an historical multiethnic base camp on San Miguel Island, California. *Hist. Archaeol.* **48**, 122. (doi:10.1007/BF03376930)
30. Olguín L, Castro V, Castro P, Peña-Villalobos I, Ruz J, Santander B. 2015 Exploitation of faunal resources by marine hunter–gatherer groups during the Middle Holocene at the Copaca 1 site, Atacama Desert coast. *Quat. Int.* **373**, 4–16. (doi:10.1016/j.quaint.2015.02.004)
31. Moss ML, Yang DY, Newsome SD, Speller CF, McKechnie I, McMillan AD, Losey RJ, Koch PL. 2006 Historical ecology and biogeography of North Pacific Pinnipeds: isotopes and ancient DNA from three archaeological assemblages. *J. Island Coast. Archaeol.* **1**, 165–190. (doi:10.1080/15564890600934129)
32. Castilho P, Lopes PC. 2008 Sea mammals in archaeological sites on the southern coast of Brazil. *Revista Do Museu De Arqueologia E Etnologia* **18**, 101–113. (doi:10.11606/issn.2448-1750.revmae.2008.89831)
33. Childerhouse S, Gales N. 1998 Historical and modern distribution and abundance of the New Zealand sea lion *Phocarctos hookeri*. *New Zeal. J. Zool.* **25**, 1–16. (doi:10.1080/03014223.1998.9518131)
34. Knox R. 1826 Report of a seal from a bed of clay near Camelon. *Mem. Wernerian Nat. Hist. Soc., Edinb.* **5**, 260–572.
35. Koretsky IA, Sanders AE. 2002 Paleontology of the late Oligocene Ashley and Chandler Bridge formations of South Carolina, 1: Paleogene pinniped remains; the oldest known seal (Carnivora: Phocidae). *Smiths. Contrib. Paleobiol.* **93**, 179–183.
36. Richard M. 1946 Contribution a l'étude du basin d'Aquitaine, Les Gisements de Mammiferes Tertiares. *Memoires de la Societe Geologique de France, Nouvelle Serie* **24**, 1–380.
37. Dewaele L, Lambert O, Louwye S. 2017 On *Prophoca* and *Leptophoca* (Pinnipedia, Phocidae) from the Miocene of the North Atlantic realm: redescription, phylogenetic affinities and paleobiogeographic implications. *PeerJ* **5**, e3024. (doi:10.7717/peerj.3024)
38. Van Beneden PJ. 1876 Les phoques fossiles du basin d'Anvers. *Bulletin de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* **41**, 783–802.
39. Miyazaki S, Horikawa H, Kohno N, Hirota K, Kimura M, Hasegawa Y, Tomida Y, Barnes LG, Ray CE. 1995 Summary of the fossil record of pinnipeds of Japan, and comparisons with that from the eastern North Pacific. *Island Arc* **3**, 361–372. (doi:10.1111/j.1440-1738.1994.tb00120.x)
40. Berry JA, King JE. 1970 The identity of the Pliocene Seal from Cape Kidnappers, New Zealand, previously known as *Arctocephalus caninus*. *Tuatara* **18**, 15–18.
41. Weston RJ, Repenning CA, Fleming CA. 1973 Modern age of supposed Pliocene seal, *Arctocephalus caninus* Berry (= *Phocarctos hookeri* Gray), from New Zealand. *New Zeal. J. Sci.* **16**, 591–598.
42. Repenning CA, Tedford RH. 1977 Otarioid seals of the Neogene. Professional Papers 992, US Geological Survey, Washington, DC. pp. 1–93. (doi:10.3133/pp992)

43. Kohno N, Ray CE. 2008 Pliocene walruses from the Yorktown Formation of Virginia and North Carolina, and a systematic revision of the North Atlantic Pliocene walruses. *Virginia Mus. Nat. Hist. Spec. Publ.* **14**, 39–80.
44. Leriche M. 1910 Les Poissons oligocènes de la Belgique. *Mémoires du Musée Royal d'Histoire naturelle de Belgique, T.V. Mémoire* **20**, 329–364.
45. Kellogg R. 1922 Pinnipeds from Miocene and Pleistocene Deposits of California. *Bull. Dep. Geol. Sci., Univ. Calif. Publ.* **13**, 23–132.
46. Govender R, Chinsamy A, Ackermann RR. 2012 Anatomical and landmark morphometric analysis of fossil phocid seal remains from Langebaanweg, West Coast of South Africa. *Trans. R. Soc. South Africa* **67**, 135–149. (doi:10.1080/0035919X.2012.724471)
47. Raup DM. 1976 Species diversity in the Phanerozoic: an interpretation. *Paleobiology* **2**, 289–297. (doi:10.1017/S0094837300004929)
48. Jablonski D, Roy K, Valantine JW, Price R, Anderson PS. 2003 The impact of the pull of the recent on the history of marine diversity. *Science* **300**, 1133–1136. (doi:10.1126/science.1083246)
49. Benton MJ, Wills MA, Hitchin DR. 2000 Quality of the fossil record through time. *Nature* **403**, 534–537. (doi:10.1038/35000558)
50. Peters SE, Foote M. 2001 Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology* **27**, 583–601. (doi:10.1666/0094-8373(2001)027<0583:BITPAR>2.0.CO;2)
51. Foote M. 2000 Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology* **26**, 578–605. (doi:10.1666/0094-8373(2000)026<0578:OAECOT>2.0.CO;2)
52. Tarver JE, Braddy SJ, Benton MJ. 2007 The effects of sampling bias on Palaeozoic faunas and implications for macroevolutionary studies. *Palaeontology* **50**, 177–184. (doi:10.1111/j.1475-4983.2006.00618.x)
53. Kelley NP, Pyenson ND. 2015 Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science* **348**, 301.aaa3716. (doi:10.1126/science.aaa3716)
54. Vermeij GJ. 2012 The evolution of gigantism on temperate seashores. *Biol. J. Linnean Soc.* **106**, 776–793. (doi:10.1111/j.1095-8312.2012.01897.x)
55. Pyenson ND, Vermeij GJ. 2016 The rise of ocean giants: maximum body size in Cenozoic marine mammals as an indicator for productivity in the Pacific and Atlantic Oceans. *Biol. Lett.* **12**, 20160186. (doi:10.1098/rsbl.2016.0186)
56. Slater GJ, Goldbogen JA, Pyenson ND. 2017 Independent evolution of baleen whale gigantism linked to Plio- Pleistocene ocean dynamics. *Proc. R. Soc. B* **284**, 20170546. (doi:10.1098/rspb.2017.0546)
57. Churchill M, Boessenecker RW, Clementz MT. 2014 Colonization of the Southern Hemisphere by fur seals and sea lions (Carnivora: Otariidae) revealed by combined evidence phylogenetic and Bayesian biogeographical analysis. *Zool. J. Linn. Soc.* **172**, 200–225. (doi:10.1111/zoj.12163)
58. Pyenson ND. 2010 Carcasses on the coastline: measuring the ecological fidelity of the cetacean stranding record in the eastern North Pacific Ocean. *Paleobiology* **36**, 453–480. (doi:10.1666/09018.1)
59. Bigelow PK 1994 Occurrence of a squaloid shark (Chondrichthyes: Squaliformes) with the pinniped *Allodesmus* from the Upper Miocene of Washington. *J. Paleontol.* **68**, 680–684. (doi:10.1017/S0022336000026032)
60. Serrán M, Centeno N, Weiler N, Otero JG. 2008 Massive death of pinnipeds 1200 years ago: taphonomic history of the 'Lobos site' (Golfo Nuevo, Patagonia, Argentina). *Quat. Int.* **183**, 135–142. (doi:10.1016/j.quaint.2006.12.001)
61. Boessenecker RW, Perry FA. 2011 Mammalian bite marks on juvenile fur seal bones from the late Neogene Purisima Formation of Central California. *Palaios* **2**, 115–120. (doi:10.2110/palo.2010.p10-088r)
62. Pyenson ND, Irmis RB, Lipps JH, Barnes LG, Mitchell Jr ED, McLeod SA. 2009 Origin of a widespread marine bonebed deposited during the middle Miocene Climatic Optimum. *Geology* **37**, 519–522. (doi:10.1130/G25509A.1)
63. Schäfer W. 1972 *Ecology and palaeoecology of marine environments (translated by Irmgard Oertel, edited by G.Y. Craig)*, xiii+568 pp. Chicago, IL: University of Chicago Press.
64. Puchalski SS, Eernisse DJ, Johnson CC. 2008 The effect of sampling bias on the fossil record of chitons (Mollusca, Polyplacophora). *American Malacological Bulletin* **25**, 87–96. (doi.org/10.4003/0740-2783-25.1.87)
65. Koch CF. 1978 Bias in the published fossil record. *Paleobiology* **4**, 367–372. (doi:10.1017/S0094837300006060)
66. Behrensmeyer AK, Kidwell SM, Gastaldo RA. 2000 Taphonomy and paleobiology. *Paleobiology* **26**, 103–147. (doi:10.1017/S0094837300026907)
67. Lloyd GT, Pearson PN, Young JR, Smith AB. 2002 Sampling bias and the fossil record of planktonic foraminifera on land and in the deep sea. *Paleobiology* **38**, 569–584. (doi:10.1666/11041.1)
68. Vilhena DA, Smith AB. 2013 Spatial bias in the marine fossil record. *PLoS ONE* **8**, e74470. (doi:10.1371/journal.pone.0074470)
69. Holland SM. 2016 The non-uniformity of fossil preservation. *Phil. Trans. R. Soc. B* **371**, 20150130. (doi:10.1098/rstb.2015.0130)
70. Dean CD, Mannion PD, Butler RJ. 2016 Preservational bias controls the fossil record of pterosaurs. *Palaeontology* **59**, 225–247. (doi:10.1111/pala.12225)
71. Kloess PA, Parham JF. 2016 A specimen-based approach to reconstructing the late Neogene seabird communities of California. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **468**, 473–484. (doi:10.1016/j.palaeo.2016.12.042)
72. Barber RT, Smith RL. 1981 Coastal upwelling ecosystems. In *Analysis of marine ecosystems* (ed. AR Longhurst), pp. 31–68. New York, NY: Academic Press.
73. Blanchette CA, Wieters EA, Broitman BR, Kinlan BP, Schiel DR. 2009 Trophic structure and diversity in rocky intertidal upwelling ecosystems: a comparison of community patterns across California, Chile, South Africa and New Zealand. *Prog. Oceanogr.* **83**, 107–116. (doi:10.1016/j.pocean.2009.07.038)
74. Forcada J. 2018 Distribution. In *Encyclopedia of marine mammals* (eds B Wursig, JGM Thewissen, KM Kovacs), pp. 259–262, 3rd edn. New York, NY: Academic Press.
75. Brand L, Urbina M, Chadwick A, DeVries TJ, Esperante R. 2011 A high resolution stratigraphic framework for the remarkable fossil cetacean assemblage of the Miocene/Pliocene Pisco Formation, Peru. *J. South Am. Earth Sci.* **31**, 414–425. (doi:10.1016/j.jsames.2011.02.015)
76. Le Roux JP, Achurra L, Henríquez A, Carreño C, Rivera H, Suárez ME, Ishman SE, Pyenson ND, Gutstein CS. 2016 Orodinal bending of the Juan Fernández Ridge suggested by geohistory analysis of the Bahía Inglesa Formation, north-central Chile. *Sediment. Geol.* **333**, 32–49. (doi:10.1016/j.sedgeo.2015.12.003)
77. Alter SE, Rynes E, Palumbi SR. 2007 DNA evidence for historic population size and past ecosystem impacts of gray whales. *Proc. Natl Acad. Sci. USA* **104**, 5162–5167. (doi:10.1073/pnas.0706056104)
78. Costa D, Weise M, Arnould J. 2006 Potential influences of whaling on the status and trends of pinniped populations. In *Whales, whaling and ocean ecosystems* pp. 344–359.
79. Stoffel MA, Humble E, Paijmans AJ, Acevedo-Whitehouse K, Chilvers BL, Dickerson B *et al.* 2018 Demographic histories and genetic diversity across pinnipeds are shaped by human exploitation, ecology and life-history. *Nat. Commun.* **9**, 4836. (doi:10.1038/s41467-018-06695-z)
80. Marshall CR *et al*. 2018 Quantifying the dark data in museum fossil collections as palaeontology undergoes a second digital revolution. *Biol. Lett.* **14**: 20180431. (doi:10.1098/rsbl.2018.0431)
81. Brunner S, Bryden MM, Shaughnessy PD. 2004 Cranial ontogeny of otariid seals. *Syst. Biodivers.* **2**, 83–110. (doi:10.1017/S1477200004001367)
82. Jones KE, Goswami A. 2010 Quantitative analysis of the influences of phylogeny and ecology on phocid and otariid pinniped (Mammalia; Carnivora) cranial morphology. *J. Zool.* **280**, 297–308. (doi:10.1111/j.1469-7998.2009.00662.x)
83. Churchill M, Uhen MD. 2019 Taxonomic implications of morphometric analysis of earless seal limb bones. *Acta Palaeontol. Pol.* **64**, 213–230. (doi:10.4202/app.00607.2019)
84. Zammit M, Norris RM. 2013 Sex determination in adults of two otariid species (*Neophoca cinerea* and *Arctophoca australis forsteri*) based on osteology of the pelvis. *Mar. Mamm. Sci.* **29**, E515–E519. (doi:10.1111/mms.12011)
85. Tarnawski BA, Cassini GH, Flores DA. 2014 Allometry of the postnatal cranial ontogeny and sexual dimorphism in *Otaria byronia* (Otariidae). *Acta Theriol.* **59**, 81–97. (doi:10.1007/s13364-012-0124-7)
86. Loza CM, Scarano AC, Soibelzon LH, Negrete J, Carlini AA. 2015 Morphology of the tympanic-basicranial region in *Mirounga leonina* (Phocidae, Carnivora), postnatal ontogeny and sexual dimorphism. *J. Anat.* **226**, 354–372. (doi:10.1111/joa.12286)

87. Van Bree PJH, Bosscha Erdbrink DP. 1987 Fossil Phocidae in some Dutch collections (Mammalia, Carnivora). *Beaufortia* **37**, 43–66.
88. Dewaele L, Peredo CM, Meyvisch P, Louwye S. 2018 Diversity of late Neogene Monachinae (Carnivora, Phocidae) from the North Atlantic, with the description of two new species. *R. Soc. open sci.* **5**, 172437. (doi:10.1098/rsos.172437)
89. Rahmat SJ, Koretsky IA, Osborne JE, Alford AA. 2017 New Miocene Monachinae from the western shore of the Chesapeake Bay (Maryland, USA). *Vestnik zoologii* **51**, 221–242. (doi:10.1515/vzoo-2017-0029)
90. Boessenecker RW, Churchill M. 2018 The last of the desmatophocid seals: a new species of *Allodesmus* from the upper Miocene of Washington, USA, and a revision of the taxonomy of Desmatophocidae. *Zoological Journal of the Linnean Society* **184**, 211–235. (doi.org/10.1093/zoolinnean/zlx098)
91. Mitchell E. 1966 Miocene pinniped *Allodesmus*. *University of California Publications in Geological Sciences* **61**, 1–46.
92. Barnes LG, Hirota K. 1994 Miocene pinnipeds of the otariid subfamily Allodesminae in the North Pacific Ocean: systematics and relationships. *Island Arc.* **3**, 329–360. (doi.org/10.1111/j.1440-1738.1994.tb00119.x)
93. Barnes LG. 1970 A re-evaluation of mandibles of *Allodesmus* (Otariidae, Carnivora) from the Round Mountain Silt, Kern County, California. *PaleoBios* **10**, 1–24.
94. Kaiser H, Crother BI, Kelly CM, Luiselli L, O'Shea M, Ota H, Passos P, Schleip WD, Wüster W. 2013 Best practices: in the 21st century, taxonomic decisions in herpetology are acceptable only when supported by a body of evidence and published via peer-review. *Herpetol. Rev.* **44**, 8–23.
95. Crerar LD, Crerar AP, Domning DP, Parsons ECM. 2014 Rewriting the history of an extinction—was a population of Steller's sea cows (*Hydrodamalis gigas*) at St Lawrence Island also driven to extinction? *Biol. Lett.* **10**, 20140878. (doi:10.1098/rsbl.2014.0878)
96. Pyenson ND, Parham JF, Velez-Juarbe J. 2016 The dilemma of trade samples and the importance of museum vouchers: caveats from a study on the extinction of Steller's sea cow. *Biol. Lett.* **12**, 20150149. (doi:10.1098/rsbl.2015.0149)
97. Crerar LD, Parsons ECM, Domning DP. 2016 Serendipity in research—investigation into illegal wildlife trade discovers a new population of Steller's sea cows: a reply to Pyenson *et al.* (2016). *Biol. Lett.* **12**, 20150670. (doi:10.1098/rsbl.2015.0670)

CHAPTER 4

4.1 SUPPLEMENTARY INFORMATION

Supplementary information available online at https://royalsocietypublishing.org/doi/suppl/10.1098/rsos.191394

CHAPTER 5

STABLE ISOTOPE EVIDENCE FOR THE PALEOECOLOGY AND NICHE PARTITIONING IN FOSSIL PINNIPEDS

5.1 ABSTRACT

Living pinnipeds which include otariids (fur seals and sea lions), phocids (true seals), and odobenids (walruses), play essential roles in the structure and function of marine ecosystems and display divergent foraging and habitat preferences. How these strategies emerged along the evolutionary history of pinnipeds and how they partitioned their niche remain unclear. We analyzed the stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope compositions of tooth enamel from fossil pinnipeds and coeval marine and terrestrial mammals from the middle Miocene Round Mountain Silt and Temblor formations and the lower levels of the Monterey Formation from the eastern North Pacific, and the early Pliocene Yorktown Formation in the western North Atlantic. As expected for fully aquatic mammals, pinnipeds and control marine mammals had low $\delta^{18}O$ variability relative to coeval terrestrial mammals, and corresponded with the published values for some taxa, indicating the absence of diagenetic alteration. We reveal that fossil marine mammal assemblages exhibited foraging and habitat partitioning, as indicated by differences in $\delta^{13}C$ and $\delta^{18}O$ compositions. We recognized the occurrence of nearshore and offshore foraging across pinniped assemblages. The exploitation of estuarine ecosystems and long-distance foraging were also identified and likely contributed to resource partitioning. Among middle Miocene pinnipeds from the eastern North Pacific, *Allodesmus* had consistently lower $\delta^{13}C$ values than coeval taxa, indicating offshore foraging, supporting predictions based on morphology. The basal otariid *Pithanotaria* had significantly higher enamel $\delta^{13}C$ values than co-occurring pinnipeds, indicating preferentially nearshore foraging. The basal odobenid *Neotherium* had intermediate foraging preferences between nearshore and offshore predators,

whereas the odobenid cf. *Imagotaria* displayed relatively low enamel $\delta^{18}O$ but comparable enamel $\delta^{13}C$ values to contemporary pinnipeds, suggesting the exploitation of estuarine resources. Morphological and taxonomic uncertainties prevented us from genus-level identifications based on isolated phocid teeth from the Yorktown Formation. Nevertheless, a hierarchical cluster analysis revealed that at least two ecologically distinct pinniped groups occurred at this formation. The odobenid *Ontocetus* and a subgroup of monachinae phocids were predominantly nearshore foragers, as concluded from higher enamel $\delta^{13}C$ and $\delta^{18}O$ values than coeval marine mammals. A second phocid group was characterized by significantly lower $\delta^{13}C$ and $\delta^{18}O$ values than coexisting phocids (and other marine mammal taxa), which is compatible with northward long-distance foraging movements along the western North Atlantic coastlines. Resembling patterns of foraging and resource partitioning, with the co-occurrence of nearshore, offshore, and alternative foraging modes, have been identified in living pinniped communities. These results suggest that these foraging modes were early acquired in pinniped communities across their evolutionary history, hinting that niche partitioning have contributed to the structure of pinniped communities over time.

5.2 INTRODUCTION

Among marine mammals, pinnipeds (seals, fur seals, sea lions, and walruses) have evolved and maintained a semiaquatic lifestyle – breeding on land but foraging in the water – over the past ~30 million years (Berta et al., 2018). Pinnipeds have a globally distributed and well represented fossil record (Valenzuela-Toro and Pyenson, 2019); however, their macroevolutionary history and their ecological transitions have been comparatively understudied. In fact, one central aspect of pinniped macroevolution – their foraging ecology over their evolutionary history, remains obscure (Berta et al., 2018; Berta and Lanzetti, 2020).

The foraging ecology of extant pinnipeds has been intensively investigated through scat, fatty-acid, and stable isotope analyses, as well as animal-borne telemetry (e.g., Zeppelin and Orr, 2010; Goetsch et al., 2018; Brault et al., 2019; Chilvers, 2019; Steingass et al., 2019). These studies have shown that co-occurring pinniped species display divergent foraging and habitat preferences. For instance, northern elephant seals (*Mirounga angustirostris*) are highly pelagic foragers, contrasting with co-occurring harbor seals (*Phoca vitulina*), which are nearshore residents and relatively benthic feeders (Eguchi and Harvey, 2005; Robinson et al., 2012; Gibble and Harvey, 2015; Schramm and Heckel, 2021). How these strategies emerged along the evolutionary history of pinnipeds and how patterns of niche segregation prevalent in living pinnipeds communities compared to those by extinct ones have not been thoroughly addressed.

Knowledge about the foraging paleoecology of pinnipeds is primary sourced from comparative morphology of fossils. These studies show that basal pinnipeds, such as *Enaliarctos* might have a coastal rather than a pelagic lifestyle and used a pierce feeding strategy analogous to modern sea otters (*Enhyndra lutris*) (Berta and Wyss, 1994; Adam and Berta, 2002). Based on morphology, desmatophocids, an extinct group of sexually dimorphic stem seals including *Allodesmus*, have been proposed as pelagic feeders (Mitchell, 1966; Barnes and Hirota, 1994) with specializations for deep diving like elephant seals (Debey and Pyenson, 2013). Extinct odobenids (walruses) might have displayed a broad diversity of foraging ecologies, with basal and small-bodied taxa (e.g., *Neotherium*) feeding in coastal areas, while later diverging taxa (e.g., *Ontocetus*) have been inferred to be coastal and benthic feeders, analogous to *Odobenus rosmarus*, the only living walrus species (Magallanes et al., 2018; Deméré, 1994; Boessenecker, 2017). Some have proposed a range of ecomorphologies for extinct phocids (true seals) (Koretsky, 2001), but no specific tests of their past foraging ecology, including habitat preferences, have been performed. The same is true for extinct otariids (fur seals and sea lions).

Studies on living pinnipeds have demonstrated that neither skull nor dental morphology alone can fully capture the diversity of feeding and foraging behaviors (Adam and Berta, 2002; Kienle, 2018; Churchill and Clementz, 2016). Additional quantitative and comparative trait studies are needed to support and reject any palaeoecological hypothesis and examine the occurrence of niche partitioning. Stable isotope analysis is a widely used tool in ecology and paleobiology for studying habitat use, diet, movement, physiology, and life history in terrestrial and aquatic organisms (Koch, 2007; Newsome et al., 2010). Analysis of stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope variations in tooth enamel bioapatite has emerged as a robust approach to investigate the foraging ecology and habitat preferences of marine mammals in both recent and deep time (e.g., Clementz and Koch, 2001, 2003, 2006; MacFadden et al., 2004). Together, $\delta^{13}C$ and $\delta^{18}O$ variations provide insights into habitat use and foraging ecology in aquatic mammals (e.g., discriminating coastal vs. pelagic feeding and marine vs. freshwater vs. estuarine environments).

Here we examine the enamel $\delta^{13}C$ and $\delta^{18}O$ composition of fossil pinnipeds and coeval marine mammals from the middle Miocene of the eastern North Pacific and the Pliocene of the western North Atlantic to assess their foraging paleoecology and examine how extinct pinnipeds partitioned their ancient communities.

.

5.3 BACKGROUND INFORMATION

5.3.1 Enamel as a deep time ecological recorder

Tooth enamel forms by accretionary growth; however, this takes place early in ontogeny, with no remodeling or replacement later in life. In pinnipeds, tooth enamel forms during the development in the uterus; hence its isotopic composition will reflect the foraging and metabolism of pregnant females (Stewart and Stewart, 1987; Stewart et al., 1998; Clementz and Koch, 2001). Mineralized animal tissues (e.g., tooth enamel) are combinations of minerals, proteins, and lipids. Specifically, the minerals in teeth are a modified form of hydroxylapatite (i.e., bioapatite). The proportion of mineral vs. organic matter and the size of the bioapatite crystals among mineralized tissues affect their structure, leading to differences in their resistance to diagenetic alteration and preservation of the isotopic signature over time. Tooth enamel has large bioapatite crystals with a low percentage of organic matter (~5%). These conditions make enamel highly resistant to diagenetic alterations preserving the original isotopic signal over millions of years and yielding an exceptional substrate for isotopic studies of extinct taxa.

5.3.2 Stable carbon isotopes as proxies of preferred foraging zone

In marine ecosystems, the $\delta^{13}C$ values of primary producers track productivity with values decreasing from highly productive nearshore regions (e.g., upwelling zones) to offshore and stratified areas (Fry and Wainright, 1991; Rau et al., 1992). The preferential uptake of ^{12}C by photosynthetic plants can explain this pattern, which leads to an increment of the $\delta^{13}C$ values of residual dissolved inorganic carbon. As growth rates in productive nearshore upwelling zones increase, more ^{13}C enriched carbon is incorporated during photosynthesis, enriching the $\delta^{13}C$ composition of primary producers. Moreover, warm temperatures in the tropics are typically linked with lower CO_2 solubility in seawater, leading to high $\delta^{13}C$ values in phytoplankton. These conditions are reversed at higher latitudes (>40º) as cooler temperatures result in enhanced CO_2 solubility, leading to lower in $\delta^{13}C$ values. The magnitude of the $\delta^{13}C$ decrease is variable in across hemispheres, and it has been estimated to be as much as ~2‰ in the Northern Hemisphere. Estuarine and freshwater ecosystems have lower mean $\delta^{13}C$ values than marine primary producers. However, mixing atmospheric and respired CO_2 variations drive more variable $\delta^{13}C$ values among primary producers (Osmond et al. 1981; Fry and Sherr 1984; MacLeod and Barton 1998). Together, these processes create spatial $\delta^{13}C$ gradients among primary producers, driving differences in the $\delta^{13}C$ among consumers (Burton and Koch, 1999; Clementz and Koch, 2001).

Carbon in animal tissues is obtained from the diet. The $\delta^{13}C$ composition of animals largely reflect the isotopic signature of their diet, including dietary proteins, lipids, and carbohydrates. In carnivores, the $\delta^{13}C$ composition of dental enamel is driven by the bulk diet (proteins and lipids) (Clementz and Koch, 2001). The tissue-to-diet fractionation for bioapatite in carnivorous marine mammals has not been experimentally determined; however, it has been assumed to mirror that of terrestrial carnivorous (+9‰; Tieszen and Fagre 1993). Comparisons of the $\delta^{13}C$ composition among mammals can be influenced by trophic level (there is ~1‰ enrichment in $\delta^{13}C$ with each trophic step) and disparities in the timing of formation and eruption of teeth (Clementz and Koch, 2001), which in the case of pinnipeds has been documented to occur almost synchronically in utero. Therefore, the $\delta^{13}C$ composition will reflect the $\delta^{13}C$ values of the mother's diet.

5.3.3 Stable oxygen isotopes as a habitat tracer

The $\delta^{18}O$ values in marine ecosystems are primarily driven by fractionation processes associated with the hydrologic cycle, with a significant contribution of evaporation and precipitation. During the evaporation process, molecules of water possessing lighter isotopes of oxygen (^{16}O) will preferentially evaporate, forming clouds, leaving the remaining sea surface water enriched in the heavier isotope (^{18}O). Thus, sea water in regions with net evaporation (e.g., tropics) will have higher $\delta^{18}O$ values than water in regions with lower net evaporation. Water vapor molecules containing the heavy isotope will condense first from clouds through precipitation resulting in ^{18}O-enriched rainfall, which will become progressively ^{18}O-depleted as the vapor mass continues to circulate poleward into colder regions, resulting in lower $\delta^{18}O$ values at high latitudes (Bowen 2010). The magnitude of this decrease has been estimated to be as much 2.0‰ in the Northern Hemisphere (Clementz et al., 2014). The $\delta^{18}O$ values in seawater ($\delta^{18}O_{seawater}$) can also be influenced by freshwater runoff into the ocean. Rivers and glacial meltwater are ^{18}O-depleted (increasingly so at high latitudes), producing a reduction in the $\delta^{18}O$ values of coastal waters as salinity decreases. This phenomenon is particularly evident at high latitudes (Bowen, 2010). Together, these spatial $\delta^{18}O_{seawater}$ gradients label the $\delta^{18}O$ values of organisms living in these regions. Consequently, the $\delta^{18}O$ composition of marine organisms can be used as habitat tracer for those with ranges that span over regions with distinct $\delta^{18}O_{seawater}$, such as marine mammals (e.g., Yoshida and Miyazaki, 1991; Borrell et al., 2013; Vighi et al., 2014, 2016; Matthews et al., 2016; Drago et al., 2020).

The $\delta^{18}O$ composition of bioapatite depends on the magnitude and isotopic composition of the oxygen fluxes into and out of the animal and potentially isotopic fractionations associated with metabolism, which influence, the $\delta^{18}O$ composition of the body fluid from which bioapatite precipitates, as well as the temperature at which it forms (Clementz et al., 2001, 2003; Kohn and Cerling, 2002). Body temperature is constant in mammals, inducing a fixed offset relative to body water. While water diffusion through the skin accounts for body water in cetaceans, water in consumed prey is one of the main influxes of water in pinnipeds (Nagy and Costa 1980). Metabolic water (water produced by oxidation of food, which contains ^{18}O-enriched atmospheric O_2, contributes to body water, but the magnitude of this flux relative to that associated with water in prey remains largely unexplored. Overall, $\delta^{18}O$ values in bioapatite of pinnipeds will primarily reflect the seawater isotope values when the mother was gestating, reflecting their foraging zone.

5.4 MATERIALS AND METHODS

5.4.1 Fossiliferous localities and specimen information

We analyzed the $\delta^{13}C$ and $\delta^{18}O$ values of fossil teeth (n = 66) of marine and terrestrial mammals recovered from Neogene localities on the eastern and western coast of North America. We included fossil specimens from the Middle Miocene Round Mountain Silt and Temblor formations and the lower levels of the Monterey Formation in Southern California, as well as the early Pliocene Yorktown Formation from North Carolina (Table 5.1).

5.4.1.1 Temblor Formation

The formation represents diverse depositional environments from shallow marine to bathyal marine to terrestrial deposits along the San Joaquin Valley in Southern California (Bate, 1985; Graham, 1985; Bartow, 1991). The "Reef beds" in the Ridge Reef sequence have yielded several marine invertebrate and vertebrate remains (Cooley, 1982; Graham, 1985) and are considered the original unit of the fossils studied here. This sequence contains shoreline shallow-marine shelf deposits in a close embayment environment (Cooley, 1982). The age of the Temblor Formation has been estimated to the middle Miocene, ranging from 14.8 to 15.8 Ma and corresponding to the early Barstovian North American Land Mammal Age (NALMA) (Kelley and Steward, 2008).

5.4.1.2 Round Mountain Silt Formation

As described for the Temblor Formation, sedimentological evidence indicates that Round Mountain Silt corresponds to relatively shallow but dynamic marine basin that inundated the interior of the San Joaquin Valley during the middle Miocene. The foraminiferal assemblage in the lower part of the Round Mountain Silt indicates the prevalence of inner to outer shelf depths followed by upper bathyal depths higher in the stratigraphic section. Terrestrial mammals described from this sequence indicate that the adjacent continental mass encompassed riparian, woodland, and open grassland habitats (Prothero et al., 2008). Fossil marine mammal specimens were principally collected from one locality, Sharktooth Hill, a marine bonebed containing a diverse marine fauna, including marine mammals, sea birds, and sharks (Pyenson et al., 2009; Velez-Juarbe, 2018). While the age of the bonebed at Sharktooth Hill has been estimated from 15.2 to 15.9 Ma, the contiguous Round Mountain Silt deposits would have occurred in an extended time span between 14.5 and 16 Ma corresponding to the early Barstovian NALMA (middle Miocene; Pyenson et al., 2009; Welton, 2014).

Remains of several pinnipeds, including desmatophocids (i.e., *Allodesmus*) and stem odobenids (i.e., *Neotherium* and *Pelagiarctos*), have been reported from the Temblor and Round Mountain Silt formations (Velez-Juarbe 2017, 2018). The fossil record from these localities includes other marine tetrapods (e.g., turtles, birds), sharks, fishes, and terrestrial mammals (Velez-Juarbe, 2018). Here we evaluated the stable isotope composition of specimens of *Allodesmus* sp. (n = 7) and *Neotherium* sp. (n = 1). We also included original (n = 6) and published data of *Desmostylus* sp., an enigmatic hippo-like herbivorous marine mammal, *Allodesmus*, and some unidentified odontocetes from these localities for comparison purposes (Table 5.1, 2).

5.4.1.3 Monterey Formation

The formation represents an open-marine deposit of middle to upper bathyal conditions (Graham and Williams, 1985; Finger, 1988; Bartow, 1991; Blake, 1991). Deposits from the Monterey Formation range from the mid Langhian to earliest Messinian (14.9–7.1 Ma; Velez-Juarbe and Valenzuela-Toro, 2019). Specifically, the pinniped specimens analyzed here were collected from the lower section of the Monterey Formation at a Laguna Hills site in Orange County (LACM locality 1945; Howard and Barnes, 1987). This locality is characterized by having a diverse assemblage of benthic foraminifera assigned to the Luisian Benthic Foraminifera Stage (Finger, 1988, 1992; Stanton and Alderson, 2013) corresponding to the Serravallian (Smith, 1960; Poore et al., 1981; Stadum and Finger, 2016). More recently, Parham et al. (2022) concluded that the lower section of the Monterey Formation, including this locality, ranges between 15.9 and 12.9 Ma, indicating a late middle Miocene age (falling within the Barstovian NALMA) for the remains included here.

Abundant pinniped remains have been described from the Monterey Formation, including phocids, desmatophocids (*Allodesmus*), odobenids (*Imagotaria*), and stem otariids (*Pithanotaria*) (Barnes et al., 1985; Velez-Juarbe and Valenzuela-Toro, 2019 and refences therein). Specifically, the pinniped assemblage from the lower levels of the Monterey Formation shows a mosaic composition (Parham et al. in 2022). From this level, fauna known from other Middle Miocene localities such as *Allodesmus* and *Neotherium* co-occur with fauna known for the Late Miocene, including *Pithanotaria* and some early odobenids (Velez-Juarbe and Valenzuela-Toro, 2019; Parham et al., 2022). Remains of morphologically basal odobenids have been recovered from the lower part of the Monterey Formation (Parham et al., 2022). However, basal odobenids show substantial intraspecific dental variation (Biewer et al., 2020), impeding their taxonomic identification at the genus or species levels. The odobenid specimens included in this study resemble the aspect of those exhibited by *Imagotaria downsi*. However, their isolated condition prevents us from making a precise designation, and we identify them as cf. *Imagotaria* sp. In this study, we report original stable isotope data for *Allodesmus* sp. (n = 3), cf. *Imagotaria* sp. (n = 3) and *Pithanotaria* sp. (n = 2) from the lower levels of the Monterey Formation (Table 5.1).

5.4.1.4 *Yorktown Formation*

The formation represents a widespread transgression in the central Atlantic Coastal Plain in eastern North America. This formation consists of four members; the basal Sunken Meadow Member, which is overlain by the Rushmere, Morgarts Beach, and the Moore House members (Dowsett and Wiggs, 1992). The open-pit phosphate mine at Lee Creek, near Aurora in North Carolina, exposes a nearly complete section of the Yorktown Formation and has yielded abundant remains of fossil marine and terrestrial vertebrates (e.g., Eshelman et al., 2008; Dewaele et al., 2018) and it is the original site of the fossils studied here.

The age of the Yorktown Formation has ranges from the early Pliocene to the late Pliocene based on planktonic foraminifera, mollusk, and ostracod fauna (Hazel, 1971; Gibson, 1983; Snyder et al., 1983; Dowsett and Wiggs, 1992; Dowsett et al., 2019, 2021). Deposits of the Yorktown Formation at Lee Creek Mine are considered to range from 3.7 to 4.8 Ma (Hazel, 1983), corresponding to the Blancan NALMA. The mining operation at Lee Creek penetrates and scatters sediments and fossils from the underlying Pungo River Formation (middle Miocene) and it is possible that older fossils might be mixed with the Pliocene Yorktown fauna (Zug, 2001). However, the vertebrate fossils from the mine are considered to largely derive from the basal part of the Yorktown Formation (i.e., the Sunken Meadow Member; Olson and Rasmussen, 2001; Eshelman et al., 2008; Gibson and Geisler, 2009). Also, no fossil pinniped remains have been reported from the Pungo River Formation, further supporting the attribution of the specimens reported in this study to the lower section of the Yorktown Formation.

Planktonic foraminifera from the Sunken Meadow Member are dominated by cold affine taxa, contrasting with the dominance of warm-tolerant species in overlaying members (Snyder et al., 1983; Gibson, 1983). Faunal evidence has revealed that during the deposition of the Yorktown Formation, the marine climate shifted from predominantly temperate and less seasonally variable conditions to subtropical settings (Hazel, 1983; Krantz, 1990; Dowsett et al., 2019). These shifting conditions might have resulted from the impact of the closure of the Central American Seaway on oceanic currents, including the weakening of the cool southward Labrador Current in the northwestern Atlantic during the early deposition of this unit (Williams et al., 2008; Johnson et al., 2017). The depositional environment of the lower sections of the Yorktown Formation has been interpreted as a relatively deep and open marine environment (Fitch and Lavenberg, 1983; Olson and Rasmussen, 2001). Moreover, the presence of terrestrial mammals like camelids, canids, horses, and mastodonts (Ward, 2008) hints that the adjacent continental land was dominated by dry wooded environments.

Abundant phocid remains have been documented from the Sunken Meadow Member in the Yorktown Formation. They largely correspond to isolated or fragmentary remains with uncertain diagnostic value (Valenzuela-Toro and Pyenson, 2019). Nevertheless, they have been frequently identified to the genus or species level based on ambiguous and untested ecomorphological attributes, even when they do not morphologically overlap with type specimens (e.g., Koretsky, 2001; Koretsky and Ray, 2008). Although the taxonomic identity of fossil phocids from this locality remains highly controversial, more recent morphological reassessments declared *nomen dubium* some previously identified taxa and recognized, instead, the occurrence of at least five phocid taxa (i.e., *Auroraphoca*, *Homiphoca*, *Gryphoca*, *Sardonectes*, and *Virginiaphoca*; Dewaele et al., 2018; Rule et al., 2020). In addition, one odobenid species (*Ontocetus emmonsi*) have been reported from this locality (Kohno and Ray, 2008; Dewaele et al., 2018), making the pinniped assemblage from the Yorktown Formation one of the most diverse ever reported and only comparable to living pinniped assemblages in the eastern North Pacific.

We reported the original stable isotope data of *O. emmonsi* (n = 2) and phocid seals (n = 16) from the Yorktown Formation. The phocid specimens comprise isolated teeth, resembling the general morphology of Monachinae seals in having double-rooted, multicuspate cuspid post canines, which are mesiodistally longer than tall and relatively wide. These specimens were characterized by having relatively high main cusps with a notch between the main cusps and the immediate accessory cusp, similar to *Sardonectes* (Rule et al., 2020). Nevertheless, the other monachinae seals from this locality, *Auroraphoca* and *Virginiaphoca,* are known only from isolated postcranial remains (Dewaele et al., 2020). No cranial remains have been referred to these species, and their dental morphology is indeterminate. Therefore, it is impossible to establish the taxonomic identity of phocid specimens using only isolated teeth. Considering these limitations, we recognize the phocid specimens included in this study as Monachinae indet. We also reported the stable isotope composition of odontocete cetaceans such as *Globicephala* sp. (n = 7), *Ninoziphius* sp. (n = 3), *Pseudorca* sp. (n = 1), and "*Scaldicetus*" (n = 6), and the terrestrial mammal *Rhynchotherium cf. euhypodon* (n = 9) for comparison (Table 5.1, 2).

5.4.2 Stable isotope analyses

The tooth surface was abraded to remove potential contaminants. Bioapatite pretreatment followed the protocols described by Koch et al. (1997) and Clementz and Koch (2001). Approximately 5 mg of powder were drilled from each tooth. Powders were soaked for 24 h in ~2% H_2O_2 to oxidize organic matter, rinsed five times with distilled water, soaked for 24 h in 1 M calcium acetate/acetic acid buffer to remove carbonate contaminants, rinsed five times with distilled water, and then freeze-dried (Koch et al. 1997; Clementz and Koch, 2001). Approximately 1 mg of powder were analyzed in the Stable Isotope Laboratory at the University of California Santa Cruz by acid digestion using an individual vial acid drop Themo Scientific Kiel IV carbonate device interfaced to Thermo Scientific MAT 253 dual-inlet isotope ratio mass spectrometer (iRMS). Samples were loaded into individual vials and dried overnight in a 70°C vacuum oven. During analysis, samples reacted at 75°C in orthophosphoric acid (specific gravity = 1.92 g/cm^3) to generate carbon dioxide and water. Water was cryogenically separated and non-condensible gases were pumped away before introducing the CO_2 analyte into the iRMS. All samples were measured with several replicates of the externally calibrated Carrera Marble in-house standard reference material CM12 and the NBS-18 limestone international standard reference material. Samples with natural abundance carbonate isotope ratios are corrected to VPDB

(Vienna Pee Dee Belemnite) for offset and linearity in a two-point correction with CM12 and NBS-18. Samples with carbonate isotope ratios outside the range of natural abundance were corrected to VPDB only for offset in a single-point correction with either CM12 or NBS-18. Two natural samples of "Atlantis II" powdered coral were run daily as independent quality control to monitor performance. Typical reproducibility of replicate measurements is significantly better than 0.05‰ for $\delta^{13}C_{CO3}$ and significantly better than 0.10‰ for $\delta^{18}O_{CO3}$.

All samples were run in duplicates. Isotope data are expressed in delta (δ) notation and calculated as follows: $[(R_{sample} / R_{standard}) - 1] \times 1000$, where R_{sample} or $R_{standard}$ are the $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios in the sample or standard for carbon and oxygen, respectively. Carbon and oxygen values are reported relative to the VPDB standard. The oxygen isotope ratios were later calculated relative to SMOW (standard mean ocean water) to compare them with published data, using the formula:

$$\delta^{18}O_{VSMOW} = 30.91 + (1.03091 \text{ x } \delta^{18}O_{VPDB})$$

We assumed that the stable carbon and oxygen isotope values of marine mammal populations from the Temblor and Round Mountain Silt Formations were ecologically comparable based on the following evidence: (1) the Temblor and the Round Mountain Silt Formations represent equivalent depositional environments consisting of shallow marine basins with a tropical and outer tropical climate (Figure S5.1), and (2) the oceanic $\delta^{18}O$, and benthic $\delta^{13}C$ values prevalent during the deposition of these two fossiliferous localities (i.e., ~14.5 and 16 Ma) are similar and remained relatively stable (Figure S5.2; Zachos et al., 2001; Hall, 2002; Holbourn et al., 2014), hinting at no significant baseline differences. The lower sequences of the Monterey Formation (15.9-12.9 Ma; Parham et al., 2022) have been interpreted as open marine habitats with a dominant climate corresponding to outer tropical conditions, comparable to those in Temblor and Round Mountain Silt Formations (Figure S5.1). Yet, benthic foraminifera records from the eastern North Pacific show a conspicuous decrease in their $\delta^{13}C$ values between 13.8 and 12.9 Ma (Holbourn et al., 2014), coinciding with the upper limit of the lower levels of the Monterey Formation (Figure S5.2). Consequently, comparisons between the marine mammal assemblages from the Monterey Formation with those from the Temblor and Round Mountain Silt Formations must account for baseline shifts. To do that, we corrected the $\delta^{13}C$ values of specimens from the Monterey Formation by the difference between the mean $\delta^{13}C$ values of benthic foraminifera ranging from (1) 14.5 to ~16 Ma (the estimated deposition time of the Temblor and the Round Mountain Silt Formations) and those between (2) ~12.9 to 16 Ma (corresponding to the deposition of the lower levels of the Monterey Formation). We used published $\delta^{13}C$ values of benthic foraminifera from Holbourn et al. (2014) to calculate differences in the $\delta^{13}C$ values during these time bins, which corresponded to 0.165‰. These values were added to the $\delta^{13}C$ values for specimens from the Monterey Formation, allowing direct comparisons with fossil marine mammals from the nearly contemporaneous Temblor and the Round Mountain Silt Formations.

5.4.3 Data analyses

Statistical analyses were performed in R statistical software version 4.0.3. The significance of differences in mean isotopic values among multiple groups was calculated using the parametric one-factor analysis of variance (ANOVA) followed by a posthoc Tukey test for pairwise comparisons. When the assumptions of equal variance and normality among populations were not meet, we used a nonparametric Kruskal-Wallis one factor analysis, followed by the non-parametric Wilcoxon–Mann–Whitney test. Comparisons of the variance between populations were conducted using simple F-tests or the Barlett and the Levene tests (when comparing two or more groups with normal and non-normal distributions, respectively). Statistical significance of the correlation between δ^{13}C and the δ^{18}O values was evaluated using the Pearson and Spearman rank correlation test, for normally and non-normally distributed data, respectively. All these analyses were conducted using their respective functions in base R.

Considering the taxonomic uncertainty associated with phocids from the Yorktown Formation, we examined whether structured isotopic variability existed in this assemblage. We conducted a hierarchical cluster analysis (HCA) using Euclidean distances and Ward linkage method on the δ^{13}C and δ^{18}O values and body length estimates for the studied taxa. Body size for phocids was calculated as the average of the estimated body length of Monachinae taxa described in Yorktown Formation (i.e., *Auroraphoca*, *Homiphoca*, *Sardonectes*, and *Virginiaphoca*) from Rule et al. (2020). The body length for other taxa was directly obtained from the literature. We used the Bootstrap re-sampling (with 10,000 iterations) and the Jaccard coefficient for evaluation of the cluster's stability using the package fpc (Hennig, 2020).

5.5 RESULTS

The marine mammal samples from Temblor, Round Mountain Silt, Monterey, and Yorktown Formations are scattered in their respective isospaces (Figure 5.2). Their δ^{13}C and $\delta^{18}O$ values resemble the range displayed by extant marine mammal communities and show low general variability in their $\delta^{18}O$ values (Table 5.2), as expected for aquatic mammals (Clementz and Koch, 2001).

5.5.1 Miocene marine mammal assemblages from Southern California

Specimens covered a large range in $\delta^{13}C$ values (9.5‰), extending from -12.7‰ for one specimen of *Allodesmus* to -3.2‰ for *Desmostylus*, resembling the scattering of modern marine mammal communities in central and Southern California (Figure 5.1A, B). The range of $\delta^{18}O$ values was smaller (3.3‰) and extended from 25.3‰ for cf. *Imagotaria* to 28.6‰ for *Neotherium* (Figure 5.1A, Table 5.2). We did not find a significant relationship between the $\delta^{13}C$ and $\delta^{18}O$ values (Spearman, $p = 0.34$; $n = 22$).

Desmostylus and pinnipeds varied in their mean $\delta^{13}C$ values (one-way ANOVA: $F(1,20) = 32.28$, $p < 0.001$); *Desmostylus* had higher $\delta^{13}C$ values than pinnipeds as a whole (Tukey test: $p < 0.001$). Differences in the median $\delta^{18}O$ value between these groups were insignificant (Kruskal-Wallis test: $p = 0.12$). We found no significant differences in $\delta^{13}C$ (Barlett test: $p = 0.42$) and $\delta^{18}O$ (Levene test: $p = 0.075$) variance between desmotylians and pinnipeds. The average $\delta^{13}C$ value varied among genera (Kruskal-Wallis test: $\chi^2(3) = 18.22$, $p = 0.00040$). Wilcoxon tests revealed that *Desmostylus* had significantly higher mean $\delta^{13}C$ value than *Allodesmus* ($p = 0.0081$) and odobenids (*Neotherium* and cf. *Imagotaria*) ($p = 0.028$), and that *Allodesmus* had lower mean $\delta^{13}C$ values than odobenids ($p = 0.017$) and the stem otariid *Pithanotaria* ($p = 0.061$), although this latter comparison was non-significant because of the low *Pithanotaria* sample size. The mean $\delta^{18}O$ value was less variable and we found no significant differences between populations (Kruskal-Wallis test: $p = 0.27$).

5.5.2 *Pliocene marine mammal assemblages from Yorktown Formation*

Specimens covered a large range in $\delta^{13}C$ values (5.0‰), extending from -11.0‰ to -6.0‰ for specimens of monachinae indet. (Figure 5.1C). The range of $\delta^{18}O$ values was smaller (3.0‰) and extended from 25.5‰ for a specimen of monachinae indet. to 28.5‰ for "*Scaldicetus*" (Figure 5.1C). No significant relationship between the $\delta^{13}C$ and $\delta^{18}O$ values existed (Pearson, $p = 0.11$).

Fossil marine and terrestrial mammals significantly differed in their mean $\delta^{18}O$ values ($F(5,38) = 8.9$, $p < 0.001$) but not in their mean $\delta^{13}C$ values (one-way ANOVA, $p = 0.26$). Tukey test revealed that the gomphotheriid *Rhynchotherium* had significantly lower mean $\delta^{18}O$ than "*Scaldicetus*" ($p = 0.0040$). While no significant differences were found in $\delta^{13}C$ variance (Barlett test: $p = 0.22$), the $\delta^{18}O$ variance differed significantly (Barlett test: $p = 0.028$) between marine and terrestrial mammals with the latter having higher $\delta^{18}O$ variance than cetaceans, but comparable to those of pinnipeds. No differences in mean $\delta^{13}C$ values were detected between *Globicephala*, *Ontocetus*, monachinae seals, "*Scaldicetus*", and *Ninoziphius* (one-way ANOVA: $p = 0.22$). Mean $\delta^{18}O$ values were statistically distinct between populations (one-way ANOVA: $F(4,30) = 13.48$, $p < 0.001$). Tukey test revealed that phocids had consistently lower mean $\delta^{18}O$ than co-occurring *Globicephala* ($p = 0.00011$), "*Scaldicetus*" ($p < 0.001$), and *Ninoziphius* ($p = 0.017$).

The HCA using the $\delta^{13}C$ and $\delta^{18}O$ values and estimated body length, revealed that populations from the Yorktown Formation grouped into three clusters (Figure 5.2A,B). Cluster 1 ($n = 9$) included a subset of monachinae seals, and the extinct walrus *Ontocetus*. Cluster 2 ($n = 9$) included the remaining phocids, and Cluster 3 ($n = 17$)

comprised large body-sized cetaceans. The mean $\delta^{13}C$ value was significantly different between clusters (one-way ANOVA: $F(2,32) = 10.23$, $p < 0.001$), with phocids from Cluster 2 having a significantly lower mean $\delta^{13}C$ value (-9.3 ± 1.1‰) than pinnipeds grouped in Cluster 1 (-7.1 ± 0.9‰) (Tukey test: $p < 0.001$), and cetaceans from Cluster 3 (-7.9 ± 1.1‰) (Tukey test: $p = 0.0064$). Likewise, the mean $\delta^{18}O$ between clusters was significantly different (one-way ANOVA: $F(2,32) = 45.73$, $p < 0.001$). Cluster 3 (cetaceans) had significantly higher mean $\delta^{18}O$ value (28.0 ± 0.3‰) than pinnipeds in Cluster 1 (27.3 ± 0.3‰) (Turkey test: $p < 0.001$) and phocids in Cluster 2 (26.5 ± 0.6‰) (Tukey test: $p < 0.001$), whereas Cluster 1 had significantly higher mean $\delta^{18}O$ value than Cluster 2 (Tukey test: $p < 0.001$).

5.6 DISCUSSION

5.6.1 Evaluation of diagenetic alteration

Enamel bioapatite is more highly resistant to diagenetic alteration of stable isotope composition than other mineralized tissues, capable of retaining the original isotopic signatures for millions of years (Koch, 2007). Yet, alterations can still occur (Lee-Thorp and Van Der Merwe, 1991; Schoeninger et al., 2003), implying that the diagenetic alteration of the bioapatite must be assessed when using stable isotopes from tooth enamel for paleoecological inferences.

Patterns of variation in stable isotope composition can serve as one monitor the occurrence of diagenetic alteration in marine mammals. Oceanic environments are relatively homogenous, resulting in relatively low $\delta^{18}O$ variability compared to terrestrial environments. For homeothermic marine organisms like marine mammals (in which water evaporation and other processes leading to substantial isotopic fractionation are negligible), the $\delta^{18}O$ values should mirror the water in which the organism lives, resulting in little variability within species that inhabit the same water mass (Clementz and Koch, 2001). If the fossil marine mammal's tooth enamel has retained their original isotopic composition, very low $\delta^{18}O$ variance (≤0.5‰) compared to coeval terrestrial mammals (>1‰) is expected (Clementz and Koch, 2001). As anticipated, our results show that the $\delta^{18}O$ variance among fossil marine mammal populations was low (≤0.5‰; Table 5.2), except for slightly high values (0.6‰) for *Allodesmus* and Monachinae indet. from the Round Mountain Silt and the Yorktown Formations, respectively. Based on comparisons to co-occurring terrestrial mammals (Table 5.2), we suggest that all the specimens preserve the original stable isotope composition, and that the higher variance shown by these two pinniped taxa are likely explained by ecological attributes rather than diagenetic alteration.

A higher variance was recorded only in *Allodesmus* and Monachinae indet. from the Round Mountain Silt and Yorktown formations, respectively. Yet, these variations are likely explained by ecological attributes of these species (see below) rather than diagenetic alteration.

Terrestrial control taxa were only gauged for the Yorktown Formation corresponding to the gomphotheriid *Rhynchotherium* (n = 7) (Family Gomphotheriidae; Table 5.2; Figure S5.3). The calculated $\delta^{18}O$ variance for this group was 0.6‰, higher than any coeval marine mammal population. However, this value is lower than the published variance (>1‰) of living terrestrial carnivores and herbivores elsewhere (e.g., Clementz and Koch, 2001). Yet, *Gomphotherium*, a closely related gomphotheriid from the Temblor Formation also had lower $\delta^{18}O$ variance (0.8‰; Clementz et al., 2003) than coeval terrestrial mammals as well. The consistent low $\delta^{18}O$ variance observed in *Rhynchotherium* and *Gomphotherium* (Table 5.2) may be explained by a larger water consumption from sources with relatively homogenous $\delta^{18}O$ composition as it has been described for modern elephants (Clementz et al., 2003). Consequently, the relatively low $\delta^{18}O$ variance observed in *Rhynchotherium* from Yorktown Formation likely reflects ecological processes, further supporting the lack of diagenetic alteration.

Despite the lack of terrestrial control taxa for marine units in the eastern North Pacific, we argue that the consistency between our novel stable isotope data with previously reported data (Table 5.2) would support the preservation of the original isotope composition. The isotopic ranges encompassed by our original $\delta^{13}C$ and $\delta^{18}O$ dataset for *Allodemus* and desmostylians (*Desmostylus*) from the contemporaneous middle Miocene Temblor and Round Mountain Silt Formations are consistent with those described by other studies which had their corresponding terrestrial control taxa (Table 5.2; Clementz et al., 2003). Moreover, these taxa had significantly different mean $\delta^{13}C$ (but not $\delta^{18}O$), denoting different foraging habitat as it has been portrayed by paleoecological studies (e.g., Clementz et al., 2003).

Expected differences in stable isotope composition between marine mammal taxa may also contribute to evaluating diagenetic alteration in fossil specimens. Previous studies on modern marine mammals have shown that cetaceans are consistently ~1 to 2‰ ^{18}O-enriched compared to pinnipeds (Clementz and Koch, 2001). While the mechanisms underlying this difference remain unknown, the occurrence of consistent ^{18}O-enrichment among cetaceans compared to pinnipeds might serve as alternative evidence for the preservation of the original stable isotope composition. Our study found that fossil cetaceans from the Yorktown Formation had significantly higher median $\delta^{18}O$ values than co-occurring pinnipeds (~1‰ difference), supporting the preservation of the original isotopic composition in this unit. Conversely, the non-significant differences in the $\delta^{18}O$ composition of the cetaceans and other marine mammals from fossil localities from the eastern North Pacific might be justified by the low sample size of the fossil cetaceans reported.

Based on the low $\delta^{18}O$ variance of fossil marine mammals, the comparable $\delta^{18}O$ variance obtained for *Rhynchotherium* relative to other gomphoteriids, the consistency between the newly reported stable isotope data with those previously reported for the same units (with terrestrial control taxa), and the occurrence of differences in the $\delta^{18}O$ values between concurrent cetaceans and pinnipeds, we conclude that diagenesis has not affected marine mammals' $\delta^{13}C$ and $\delta^{18}O$ composition at the study sites, supporting the validity of the ecological interpretations derived from their analyses.

5.6.2 Paleoecology of Miocene marine mammals from Southern California

Coeval Miocene marine mammals from the eastern North Pacific showed little variance in their $\delta^{18}O$ composition but broadly varied in their $\delta^{13}C$ values, resembling the configuration of living marine mammal communities in the region. Yet, the elevated $\delta^{13}C$ values (~2‰) among Miocene marine mammals relative to modern communities (Figure 5.1A, B) likely reflect both natural and post-industrial anthropogenic changes in the carbon isotopic composition of atmospheric CO_2 since the Miocene (Suess, 1955; Tipple et al., 2010). Indeed, present-day atmospheric CO_2 has a $\delta^{13}C$ value of -8.0‰, approximately, which is lower than the estimated values for the Cenozoic, including the Miocene (-6.1 ± 0.6‰; Clementz et al., 2014). The mean $\delta^{18}O$ values for living and fossil marine mammals had a similar range, suggesting that the $\delta^{18}O_{seawater}$ at this time (ca. 16 Ma) was close to present-day conditions.

While fossil marine mammal assemblages from Southern California contain groups with modern analogs like pinnipeds and cetaceans, it also includes others with no modern representatives, like *Desmostylus*. *Desmostylus* is a genus of herbivores known from the Oligocene through the Miocene of the eastern North Pacific (Matsui and Tsuihji, 2019). Previous biogeochemical analyses revealed that they were aquatic mammals inhabiting estuarine or freshwater environments, consuming different pools of aquatic vegetation (Clementz et al., 2003). Our study shows that *Desmostylus* from the Temblor Formation had little $\delta^{18}O$ variation, but it had significantly higher and more variable $\delta^{13}C$ values than coeval pinnipeds. These results mirror previous assessments, denoting that *Desmostylus* had aquatic lifestyles but exploited distinct foraging habitats than coeval marine mammals, likely consuming seagrasses, and other vegetation in estuarine or freshwater habitats (Clementz et al., 2003).

Allodesmus is an extinct genus of pinnipeds that has been frequently recovered from Miocene marine localities across the eastern and western North Pacific. Based on their body size, simplified dentition, and enlarged orbits, *Allodesmus* have been interpreted as a pelagic and deep-diving predator, comparable to extant elephant seals (Mitchell, 1966; Debey and Pyenson, 2013). Previous stable isotope analyses showed that *Allodesmus* from Middle Miocene localities from Southern California had low $\delta^{18}O$ variance and consistently lower $\delta^{13}C$ values than co-occurring *Desmostylus*, supporting their offshore marine foraging preference (Clementz et al., 2003). Our work aligns with these previous findings and shows that *Allodesmus* had consistently low $\delta^{13}C$ values relative to coeval species with little $\delta^{18}O$ variance. Stable isotope analyses on living marine mammals from California reveal that species with pelagic and offshore foraging preferences, like female elephant seals and northern fur seals, are 2 to 4‰ ^{13}C-depleted relative to nearshore and resident predators (e.g., harbor seals) (Figure 5.1B). Our results resemble that pattern and show that *Allodesmus* had significantly lower $\delta^{13}C$ values than co-occurring marine mammals. Isotopic values from *Allodesmus* were ~3.5‰ and ~2‰ ^{13}C-depleted relative to pinnipeds like *Pithanotaria* and odobenids, hinting at a pelagic and offshore foraging preferences, supporting predictions derived from morphology.

Various factors could explain the significantly low $\delta^{13}C$ value by a single *Allodesmus* specimen (~-14‰) from the Round Mountain Silt. Still, we argue that it likely reflects the occurrence of intraspecific dietary differences. The enamel $\delta^{13}C$ values correlate with the $\delta^{13}C$ of bulk diet, including proteins and lipids (Clementz and Koch, 2001). Lipids have lower $\delta^{13}C$ values than other body tissues (DeNiro and Epstein 1978), and the preferential consumption of a lipid-rich diet is expected to lower a predator's $\delta^{13}C$ value. Among living pinnipeds from California, similar extremely low but $\delta^{13}C$ values have been observed in some female northern elephant seals, which have even lower values than concurrent pelagic and offshore female northern fur seals (Figure 5.2B). While they opportunistically consume diverse pelagic prey species, the diet of female elephant seals is preferentially composed of mesopelagic myctophids (Goetsch et al., 2018; Yoshino et al., 2020), which have significantly higher lipid content than other pelagic prey (Van Pelt et al., 1997). Therefore, female elephant seals' low but variable enamel $\delta^{13}C$ values (Figure 5.1B) likely result from the additive influence of their lipid-rich diet, the opportunistic consumption of other pelagic species, and offshore foraging (Clementz and Koch, 2001). Moreover, food webs at depths >100 m can be partially fueled by primary organic matter that is significantly lower in $\delta^{13}C$ values compared to phytoplankton at the oceanic surface (Benner et al. 1997).

Therefore, elephant seals feeding at greater depths (Robinson et al., 2012) might have lower values than expected from surface primary producer values. It is conceivable that the variability displayed by some *Allodesmus* individuals results from a similar mechanism, hinting at the prevalence of intraspecific dietary differences including the consumption of prey with distinct lipid-content and/or the performance of deep diving. Further morphological and biogeochemical examinations of additional *Allodesmus* from these and other Neogene units will be required to unravel the occurrence of ecological diversity in this taxon.

Pithanotaria and other stem otariids have been consistently interpreted as piercing feeders based on their simplified postcanine dentition (Adam and Berta, 2002; Boessenecker, 2011; Velez-Juarbe, 2017). Moreover, it has been argued that they might be offshore foragers, which would explain their paucity in fossiliferous nearshore localities predating the late Miocene (Boessenecker and Churchill, 2015). Contrary to this prediction, *Pithanotaria* enamel $\delta^{13}C$ values are ~4‰ and ~1‰ ^{13}C-enriched relative to coeval *Allodesmus* and stem odobenids, respectively, pointing to the use of nearshore foraging zones. If this interpretation is correct, different factors may explain their rarity in nearshore fossiliferous localities. Among coeval pinnipeds, *Pithanotaria* had the smallest estimated body length, approaching ~1.3 m, within the range of living sea otters and harbor seals. Coincidentally, these nearshore species also exhibit a meager fossil record, consisting of a few isolated occurrences from Pleistocene nearshore localities (Boessenecker, 2015; Valenzuela-Toro and Pyenson, 2019). Together, these observations suggest that shared taphonomic factors such as body size or natural history might bias their preservation, explaining the poor fossil record (Cuitiño et al., 2019).

Pinniped assemblages from the Temblor and Round Mountain Silt Formations contained the extinct odobenids *Neotherium* and *Pelagiarctos* (Velez-Juarbe, 2017). Among them, morphological evaluations have shown that *Neotherium* lacked cranial specializations for benthic feeding, suggesting the consumption of pelagic resources and a piscivorous diet (Kohno et al., 1994; Deméré and Berta, 2001), resembling the inferred diet of Pelagiarctos (Boessenecker and Churchill, 2013; Loch et al., 2016). While our study only included a single *Neotherium* specimen, it had higher $\delta^{13}C$ composition than co-occurring *Allodesmus*, it was 1‰ lower than those of the nearly contemporaneous *Pithanotaria* and cf. *Imagotaria* from the lower levels of the Monterey Formation, and partially overlapped with *Desmostylus* and unidentified odontocetes from Temblor and Round Mountain Silt formations (Figure 5.1). Combined with their nearly equivalent $\delta^{18}O$ value, these results hint that *Neotherium* might have inhabited similar water masses than coeval pinnipeds but exploited intermediate habitats between those used by *Allodesmus* and *Pithanotaria* as indicated by their intermediate $\delta^{13}C$ value.

The odobenids cf. *Imagotaria* from the lower levels of the Monterey Formation had intermediate $\delta^{13}C$ values between coeval *Allodesmus* and *Pithanotaria*, corresponding with those of *Neotherium*. Yet, cf. *Imagotaria* were ~1.5‰ ^{18}O-depleted relative to coeval marine mammal populations. Their low enamel $\delta^{18}O$ values could be explained by their foraging at higher latitudes (with lower $\delta^{18}O_{seawater}$). However, cf. *Imagotaria* enamel $\delta^{13}C$ values are not significantly lower than coeval pinnipeds, suggesting that foraging at higher latitudes is unlikely. Alternatively, foraging in estuarine environments might explain their distinctive isotopic composition. Studies of living aquatic mammals have shown that populations that favor estuarine habitats have enamel $\delta^{13}C$ values equivalent to nearshore marine consumers but significantly lower

$\delta^{18}O$ values because of the reduced salinities in estuaries (Clementz and Koch, 2001). Together, these results are the first evidence of the use of estuarine environments by extinct pinnipeds. Additional biogeochemical analyses in odobenid specimens from the lower levels of the Monterey Formation are needed to test this interpretation. Specifically, the examination of strontium isotopes ($\delta^{87}Sr$) in addition to $\delta^{13}C$ and $\delta^{18}O$ values will be critical for evaluating whether cf. *Imagotaria* inhabited marine vs. estuarine ecosystems (Clementz et al., 2003).

5.6.3 Paleoecology of Pliocene marine mammals from the Western North Atlantic

At least five phocid taxa (i.e., *Auroraphoca*, *Homiphoca*, *Gryphoca*, *Sardonectes*, *Virginiaphoca*), one odobenid (*Ontocetus*), and several odontocetes have been recognized from the Sunken Meadow Member at the Yorktown Formation (Valenzuela-Toro and Pyenson, 2019; Rule et al., 2020), making it one of the most diverse marine mammal assemblages ever reported. Although morphological uncertainties prevented us from conducting genus-level identifications based on isolated phocid teeth, our study revealed that at least three ecologically distinct groups of marine mammals occurred in this site.

Little is known about the paleoecology of coeval phocids from the Yorktown Formation. Based on its relatively large body size and robust feeding morphology, it has been proposed that *Sardonectes* was a large pierce feeder, consuming larger prey (Rule et al., 2020). Morphological comparisons also have suggested that the medium-sized *Homiphoca* were piercing feeders with some capacity for filter feeding, analogous to modern leopard seals (Govender, 2018; Kienle and Berta, 2018). No paleoecological inferences have been conducted for other phocid species from this formation mainly because of their incomplete fossil record (see Dewaele et al., 2018). Using isolated teeth that cannot be identified to genus, we show that at least two ecologically distinct pinniped groups co-occurred during the early Pliocene in the western North Atlantic as inferred from their $\delta^{13}C$ and $\delta^{18}O$ variability (Figure 5.2). The odobenid *Ontocetus* and a subgroup of Monachinae phocids (Cluster 1) were predominantly nearshore foragers, as is concluded from their higher $\delta^{13}C$ and $\delta^{18}O$ values than coeval marine mammals. The remaining phocids were recovered as a separate group (Cluster 2) and characterized by having significantly lower $\delta^{13}C$ and $\delta^{18}O$ values than coeval phocids (Cluster 1) and odontocetes (Cluster 3). Neither the exploitation of estuarine nor freshwater ecosystems is consistent with the stable isotope composition shown by the latter phocid subpopulation, since both foraging modes generate opposite patterns of variation of the enamel $\delta^{13}C$ and $\delta^{18}O$ in aquatic mammals (Clementz and Koch, 2001). Other mechanisms must account for their variability.

The $\delta^{13}C$ and $\delta^{18}O$ composition of marine phytoplankton and seawater is strongly influenced by latitudinal gradients of temperature, sea surface salinity, and primary productivity, creating a widespread and negative correlation with latitude that has been maintained since the Paleogene (Clementz et al., 2014). The early Pliocene in the western North Atlantic was characterized by warmer than present-day conditions, decreased seasonality, and increased sea surface salinity, which likely increased with latitude (Dowsett et al., 2009; Lawrence et al., 2009). We are unaware of early Pliocene $\delta^{18}O_{seawater}$ records from the western North Atlantic. However, the ~1‰ difference between the enamel $\delta^{18}O$ values by some Monachinae phocids (Cluster 2) relative to coeval pinnipeds from the Yorktown Formation (Figure 5.2) is equivalent to the difference observed in the $\delta^{18}O_{seawater}$ between low (~35ºN) and high (~45º) latitudes inferred from enamel $\delta^{18}O$ values in fossil sirenians inhabiting this region (Clementz and Sewall, 2011). The isotopic composition of cetaceans stranded along the western North Atlantic coastlines further supports this hypothesis (Figure 5.1D). The $\delta^{13}C$ and $\delta^{18}O$ values of modern pilot whales (*Globicephala* spp.) stranded along the North Carolina coastlines (~35ºN) are ~2‰ higher than those at higher latitudes (40º - 42ºN), presumably reflecting latitudinal differences in their foraging grounds (Clementz et al., 2014). Consequently, we interpret that the lower $\delta^{13}C$ and $\delta^{18}O$ values of a subgroup of Monachinae seals (Cluster 2) from the Yorktown Formation is consistent with long-distance foraging movements to presumably highly productive northern foraging grounds, enhanced by the influence of the Labrador Current during the early Pliocene (Williams et al., 2009; Johnson et al., 2017).

Ontocetus is one of the closest extinct relatives of modern walruses (Berta et al., 2018). Based on its skull morphology, enlarged tusks, and large body size (~15% larger than living walruses; Boessenecker et al., 2018), it has been inferred to have a foraging ecology analogous to living walruses but deployed in a warmer environment. *Odobenus rosmarus*, the only living walruses, are relatively shallow and benthic foragers that prey on bottom-dwelling invertebrates, especially bivalve mollusks (Gjertz et al., 2001; Garde et al., 2018; Gebruk et al., 2021). If predictions based on morphology are correct, and *Ontocetus* were nearshore foragers with a mollusk-specialized diet, we expect them to have relatively higher $\delta^{13}C$ values than coeval marine mammals. Following predictions, we found that *Ontocetus* had a mean $\delta^{13}C$ value ~1‰ higher than the average of coeval nearshore phocids (within Cluster 1), and 1.5‰ than phocids showing long-distance-movement (Cluster 2) (Figure 5.2). It is possible that *Ontocetus* feed on the abundant invertebrate fauna reported in the lower levels of the Yorktown Formation (e.g., Krantz, 1990).

Our study also provides insights into the paleoecology of large-bodied odontocetes (Cluster 3) from the Yorktown Formation (Figure 5.2). Although "*Scaldicetus*" likely represents a polyphyletic group, their dental morphology hints that they were macroraptorial predators analogous to modern killer whales (Bianucci and Landini, 2006; Hampe, 2006; Toscano et al., 2013; Lambert and Bianucci, 2019). While "*Scaldicetus*" enamel $\delta^{18}O$ values showed low variability (~0.2‰), their $\delta^{13}C$ variability was higher (~1.4‰), likely indicating the prevalence of diverse foraging strategies. Similar variations in $\delta^{13}C$ values (with small $\delta^{18}O$ variance) in living killer whale populations have been described (e.g., Foote et al., 2013; Matthews et al., 2021). The specific factors driving this variability remain unclear; however, it likely results from the combined effect of their vast geographical ranges and intraspecific foraging specializations (Foote et al., 2013; Matthews and Ferguson, 2014). It is conceivable that the enamel $\delta^{13}C$ variability observed in "*Scaldicetus*" might result from similar mechanisms, supporting the occurrence of distinct foraging strategies analogous to killer whales.

Living *Globicephala* spp. are predominantly offshore foragers feeding on pelagic squids (Santos et al., 2014). However, they periodically reach nearshore zones where they consume neritic prey (Gannon et al., 1997; Becker et al., 2021). *Globicephala* from the Yorktown Formation had variable $\delta^{13}C$ values with little $\delta^{18}O$ variance, overlapping with the isospace occupied by "*Scaldicetus*". Likewise, high variability in the $\delta^{13}C$ values has been recorded in living pilot whales (Mèndez-Fernandez et al., 2012). Moreover, their $\delta^{18}O$ composition is indistinct from living short-finned pilot whales (*G.*

macrorhynchus) stranded along the eastern coast of North America (see Figure 5.1C, D), further suggesting the occurrence of similar foraging preferences over time.

Ninoziphius is a stem ziphiid known from the late Miocene and Pliocene of Peru (Muizon, 1984) and the Pliocene of western North Atlantic. Compared to the extant and deep diving ziphiids, *Ninoziphius* lacked traits associated with deep diving and exhibited a more elongated rostrum, longer and more flexible neck, and shorter and less powerful tail. They also showed dental wear patterns that are consistent with probing and scouring the seafloor during prey search as described in some long-snouted river dolphins (Lambert et al., 2013). Based on this morphological evidence, it has been proposed that *Ninoziphius* were raptorial predators, feeding on movable prey along the seafloor in shallow environments (Lambert et al., 2013, 2015). We show that *Ninoziphius* displayed relatively higher $\delta^{13}C$ values than their coeval cetaceans, suggesting the prevalence of nearshore foraging preferences and confirming morphological predictions.

5.6.4 Niche partitioning of coeval pinnipeds

The pinniped taxa from the assemblages examined here are largely phylogenetically unrelated. For instance, *Allodesmus* belongs to the extinct family Desmatophocidae (Boessenecker and Churchill, 2018), whereas the concurrent *Neotherium* and cf. *Imagotaria* are, respectively, one of the most basal and relatively derived members of the family Odobenidae (Magallanes et al., 2018; Biewer et al., 2020). *Pithanotaria* also is not closely related to any of their coeval taxa, constituting one of the most basal members of the family Otariidae (Boessenecker and Churchill, 2015; Velez-Juarbe, 2017). While the taxonomic identification at the species level of phocids from the Yorktown Formation is uncertain, they are non-closely related to *Ontocetus*, which is one of the most derived odobenids. Phylogenetic analyses have shown that two of the phocid Monachinae taxa described from this formation (i.e., *Sardonectes* and *Homiphoca*) are not sister taxa. *Sardonectes* pertains to the clade Monachini, whereas *Homiphoca* forms a separate clade with *Acrophoca*, *Hadrokirus*, and *Piscophoca*, which are extinct phocids from the eastern South Pacific (Rule et al., 2020). Further analyses are needed to resolve the phylogenetic relationships of *Auroraphoca* and *Virginiaphoca* within monachinae and, from there, to refine the relatedness of the specimens included in this study.

Modern pinniped communities are less taxonomically diverse than those chronicled by the fossil record (Valenzuela-Toro et al., 2015; Velez-Juarbe, 2017). However, paleontological, zooarchaeological, and historical records indicate that pinnipeds' current abundance and distribution do not reflect their pre-historical past, implying that the structure and dynamics observed in modern communities have emerged from the relatively recent synergic effects of human exploitation and climate change (e.g., Braje and Rick, 2011; Valenzuela-Toro et al., 2013, 2015). For instance, paleontological and historical evidence indicates that until two centuries ago, southern elephant seals inhabited a broader area in the Southern Hemisphere than today (Philippi, 1889; Sielfeld, 1983; Valenzuela-Toro et al., 2015), implying that pinnipeds' community structure was different than those observed in the same coastlines and elsewhere today (i.e., exclusively dominated by otariids).

Our stable isotope analyses revealed that fossil pinniped assemblages exhibited consistent foraging partitioning among co-occurring taxa. We recognized the occurrence of nearshore and offshore foraging modes within fossil pinniped assemblages across the

Northern Hemisphere. The exploitation of estuarine ecosystems and long-distance foraging were also identified in these assemblages, which likely contributed to niche partitioning. Similar patterns of foraging and resource partitioning have been identified in living pinniped communities with the co-occurrence of nearshore, offshore, and some alternative foraging modes (Figure 5.1B). These results suggest that foraging patterns were early acquired in pinniped communities across their evolutionary history, hinting that niche partitioning has been an important driver for the structure of pinniped communities over time.

Because of sampling constraints, our study only included a subset of the co-occurring taxa across some pinniped assemblages. Therefore, resource partitioning patterns (e.g., nearshore vs. offshore) might result from incomplete taxonomic sampling. Nevertheless, we argue that described body size and morphological differences between co-occurring fossil taxa further support our interpretations. Body size and cranial morphology affect foraging dynamics. Larger taxa can, in theory, reach greater depths and exploit a greater diversity of prey resources than smaller ones (e.g., Thompson et al., 1998; Weise et al., 2010). Feeding morphology can also limit prey size and processing efficiency, influencing foraging dynamics and resource partitioning (e.g., Jones et al., 2013; Segura et al., 2015). While the direction of the correlation between body size, feeding morphology, and foraging remains understudied, our study showed that co-occurring species with disparate body sizes (e.g., *Allodesmus*, *Neotherium*, and *Pithanotaria*) exhibited distinct foraging methods, exposing some level of resource partitioning. Consequently, we expect that the addition of missing taxa from middle Miocene fossil assemblages from Southern California and the improvement of the taxonomic sorting of phocids from the Pliocene Yorktown Formation (which largely varied in body size) will result in intricate patterns of resource partitioning. We anticipate these patterns would be analogous to those displayed by the most taxonomically diverse pinnipeds community today, inhabiting the eastern North Pacific (Figure 5.1B). Future morphological and stable isotope analyses on additional co-occurring pinniped species are required to further examine the foraging and niche segregation strategies, and test hypotheses about the role of body size and feeding morphology in these ecological dynamics.

5.7 CONCLUSIONS AND PROSPECTS

We showed that among fossil pinnipeds from the eastern North Pacific, *Allodesmus* had consistently lower $\delta^{13}C$ values than coeval taxa, indicating offshore foraging, supporting interpretations based on morphological evidence. The basal otariid *Pithanotaria* had significantly higher enamel $\delta^{13}C$ values than co-occurring pinnipeds, indicating preferentially nearshore foraging, opposing predictions based on taphonomy. The basal odobenid *Neotherium* had intermediate foraging preferences between nearshore and offshore predators, whereas the odobenid cf. *Imagotaria* displayed low enamel $\delta^{18}O$ but comparable enamel $\delta^{13}C$ values to contemporary pinnipeds, suggesting the exploitation of estuarine resources.

Among fossil pinnipeds from the western North Atlantic, at least two ecologically distinct pinniped groups co-occurred. The odobenid *Ontocetus* and a subgroup of monachinae phocids were predominantly nearshore foragers characterized by higher enamel $\delta^{13}C$ and $\delta^{18}O$ values than coeval marine mammals. The second phocid group had lower $\delta^{13}C$ and $\delta^{18}O$ values than co-eval phocids (and other marine mammal taxa) and is consistent with individuals performing northward long-distance foraging movements along the western North Atlantic coastlines. The foraging and resource partitioning observed in fossil pinniped communities (i.e., the co-occurrence of nearshore, offshore, and alternative foraging modes) resemble the ecological configuration of living pinniped communities (Chapters 1, 2). These results suggest that these distinct foraging modes were early acquired in pinniped communities across their evolutionary history, hinting that niche partitioning have contributed to the structure of pinniped communities over time.

In addition to including larger sample sizes and additional taxa, future biogeochemical analyses implementing other stable isotope systems will likely offer further insights into pinniped paleoecology. For instance, strontium stable isotope analysis (δ^{87}Sr) on tooth enamel might provide ways to disentangle the use of marine and estuarine ecosystems by some groups (e.g., cf. *Imagotaria*; Clementz et al., 2003). Likewise, the recent implementation of non-traditional stable isotopes like magnesium (δ^{25}Mg) as a trophic tracer has yielded promising results in extant, and extinct terrestrial mammals (e.g., Martin et al., 2015); ongoing studies by our group are testing their feasibility in marine ecosystems. Moreover, the performance of additional quantitative paleoecological assessments such as enamel and bone microstructure of extant and extinct taxa will be instrumental in advancing the knowledge of the evolution of ecological transitions and the evolution of foraging strategies over geologic time (e.g., Amson et al., 2014; Loch et al., 2013; Amson and Bibi, 2021; Dewaele et al. 2021). Taphonomic experiments examining the effect of life-history features (e.g., habitat preferences, reproductive strategies) on taphonomic processes and fossil preservation in marine predators are also critical for improving our understanding of pinniped paleoecology.

5.8 REFERENCES

Adam, P.J. and Berta, A., 2002. Evolution of prey capture strategies and diet in the Pinnipedimorpha (Mammalia, Carnivora). *Oryctos*, *4*, pp.83-107.

Amson, E., de Muizon, C., Laurin, M., Argot, C. and de Buffrénil, V., 2014. Gradual adaptation of bone structure to aquatic lifestyle in extinct sloths from Peru. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1782), p.20140192.

Amson, E. and Bibi, F., 2021. Differing effects of size and lifestyle on bone structure in mammals. *BMC biology*, *19*(1), pp.1-18.

Bartow, J.A., 1991. *The Cenozoic evolution of the San Joaquin Valley, California* (No. 1501).

Bate, M.A., 1985. Depositional sequence of Temblor and Big Blue Formations, Coalinga anticline, California.

Barnes, L.G. and Hirota, K., 1994. Miocene pinnipeds of the otariid subfamily Allodesminae in the North Pacific Ocean: systematics and relationships. *Island Arc*, *3*(4), pp.329-360.

Becker, Y.A., Fioramonti, N.E., Dellabianca, N.A. and Riccialdelli, L., 2021. Feeding ecology of the long-finned pilot whale, *Globicephala melas edwardii*, in the southwestern Atlantic Ocean, determined by stable isotopes analysis. *Polar Biology*, *44*(8), pp.1655-1667.

Benner, R., Biddanda, B., Black, B. and McCarthy, M., 1997. Abundance, size distribution, and stable carbon and nitrogen isotopic compositions of marine organic matter isolated by tangential-flow ultrafiltration. *Marine chemistry*, *57*(3-4), pp.243-263.

Berta, A. and Wyss, A., 1994. Pinniped phylogeny. *Contributions in marine mammal paleontology honouring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History*, *29*, pp. 33-56.

Berta, A., Churchill, M. and Boessenecker, R.W., 2018. The origin and evolutionary biology of pinnipeds: seals, sea lions, and walruses. *Annual Review of Earth and Planetary Sciences*, *46*, pp.203-228.

Berta, A. and Lanzetti, A., 2020. Feeding in marine mammals: an integration of evolution and ecology through time. *Palaeontologia Electronica*, *23*, p.a40.

Bianucci, G. and Landini, W., 2006. Killer sperm whale: a new basal physeteroid (Mammalia, Cetacea) from the Late Miocene of Italy. *Zoological Journal of the Linnean Society*, *148*(1), pp.103-131.

Biewer, J.N., Velez-Juarbe, J. and Parham, J.F., 2020. Insights on the dental evolution of walruses based on new fossil specimens from California. *Journal of Vertebrate Paleontology*, *40*(5), p.e1833896.

Blake, G.H., 1991. Review of the Neogene Biostratigraphy and Stratigraphy of the Los Angeles Basin and Implications for Basin Evolution: Chapter 4.

Boersma, A.T. and Pyenson, N.D., 2015. *Albicetus oxymycterus*, a new generic name and redescription of a basal physeteroid (Mammalia, Cetacea) from the Miocene of California, and the evolution of body size in sperm whales. *PloS one*, *10*(12), p.e0135551.

Boessenecker, R.W., 2011. New records of the fur seal *Callorhinus* (Carnivora: Otariidae) from the Plio-Pleistocene Rio Dell Formation of Northern California and comments on otariid dental evolution. *Journal of Vertebrate Paleontology*, *31*(2), pp.454-467.

Boessenecker, R.W., 2017. A new early Pliocene record of the toothless walrus *Valenictus* (Carnivora, Odobenidae) from the Purisima Formation of Northern California. *PaleoBios*, *34*.

Boessenecker, R.W., 2018. A middle Pleistocene sea otter from northern California and the antiquity of *Enhydra* in the Pacific Basin. *Journal of Mammalian Evolution*, *25*(1), pp.27-35.

Boessenecker, R.W. and Churchill, M., 2013. A reevaluation of the morphology, paleoecology, and phylogenetic relationships of the enigmatic walrus *Pelagiarctos*. *PLoS One*, *8*(1), p.e54311.

Boessenecker, R.W. and Churchill, M., 2015. The oldest known fur seal. *Biology Letters*, *11*(2), p.20140835.

Boessenecker, R.W. and Churchill, M., 2018. The last of the desmatophocid seals: a new species of Allodesmus from the upper Miocene of Washington, USA, and a revision of the taxonomy of Desmatophocidae. *Zoological Journal of the Linnean Society*, *184*(1), pp.211-235.

Boessenecker, S.J., Boessenecker, R.W. and Geisler, J.H., 2018. Youngest record of the extinct walrus *Ontocetus emmonsi* from the Early Pleistocene of South Carolina and a review of North Atlantic walrus biochronology. *Acta Palaeontologica Polonica*, *63*(2).

Borrell, A., Velásquez Vacca, A., Pinela, A.M., Kinze, C., Lockyer, C.H., Vighi, M. and Aguilar, A., 2013. Stable isotopes provide insight into population structure and segregation in eastern North Atlantic sperm whales. *PLoS One*, *8*(12), p.e82398.

Bowen, G.J., 2010. Isoscapes: spatial pattern in isotopic biogeochemistry. *Annual review of earth and planetary sciences*, *38*, pp.161-187.

Braje, T.J. and Rick, T.C. eds., 2011. *Human Impacts on Seals, Sea Lions, and Sea Otters*. University of California Press.

Brault, E.K., Koch, P.L., Costa, D.P., McCarthy, M.D., Hückstädt, L.A., Goetz, K.T., McMahon, K.W., Goebel, M.E., Karlsson, O., Teilmann, J. and Harkonen, T., 2019. Trophic position and foraging ecology of Ross, Weddell, and crabeater seals revealed by compound-specific isotope analysis. *Marine Ecology Progress Series*, *611*, pp.1-18.

Burton, R.K. and Koch, P.L., 1999. Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds. *Oecologia*, *119*(4), pp.578-585.

Chilvers, B.L., 2019. Whisker stable isotope values indicate long-term foraging strategies for female New Zealand sea lions. *Endangered Species Research*, *38*, pp.55-66.

Churchill, M. and Clementz, M.T., 2016. The evolution of aquatic feeding in seals: insights from *Enaliarctos* (Carnivora: Pinnipedimorpha), the oldest known seal. *Journal of evolutionary biology*, *29*(2), pp.319-334.

Clementz, M.T. and Koch, P.L., 2001. Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. *Oecologia*, *129*(3), pp.461-472.

Clementz, M.T. and Sewall, J.O., 2011. Latitudinal gradients in greenhouse seawater $\delta^{18}O$: evidence from Eocene sirenian tooth enamel. *Science*, *332*(6028), pp.455-458.

Clementz, M.T., Hoppe, K.A. and Koch, P.L., 2003. A paleoecological paradox: the habitat and dietary preferences of the extinct tethythere *Desmostylus*, inferred from stable isotope analysis. *Paleobiology*, *29*(4), pp.506-519.

Clementz, M.T., Goswami, A., Gingerich, P.D. and Koch, P.L., 2006. Isotopic records from early whales and sea cows: contrasting patterns of ecological transition. *Journal of Vertebrate Paleontology*, *26*(2), pp.355-370.

Clementz, M.T., Fordyce, R.E., Peek, S.L. and Fox, D.L., 2014. Ancient marine isoscapes and isotopic evidence of bulk-feeding by Oligocene cetaceans. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *400*, pp.28-40.

Cuitiño, J.I., Buono, M.R., Viglino, M., Farroni, N.D. and Bessone, S., 2019. Factors affecting the preservation and distribution of cetaceans in the lower Miocene Gaiman Formation of Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *526*, pp.110-125.

DeNiro, M.J. and Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et cosmochimica acta*, *42*(5), pp.495-506.

Debey, L.B. and Pyenson, N.D., 2013. Osteological correlates and phylogenetic analysis of deep diving in living and extinct pinnipeds: what good are big eyes?. *Marine Mammal Science*, *29*(1), pp.48-83.

Deméré, T.A., 1994. Two new species of fossil walruses (Pinnipedia: Odobenidae) from the upper Pliocene San Diego Formation, California. In *Proceedings of the San Diego Society of Natural History* (Vol. 29, pp. 77-98).

Deméré, T.A. and Berta, A., 2001. A reevaluation of Proneotherium repenningi from the Miocene Astoria Formation of Oregon and its position as a basal odobenid (Pinnipedia: Mammalia). *Journal of Vertebrate Paleontology*, *21*(2), pp.279-310.

Dewaele, L., Peredo, C.M., Meyvisch, P. and Louwye, S., 2018. Diversity of late Neogene Monachinae (Carnivora, Phocidae) from the North Atlantic, with the description of two new species. *Royal Society Open Science*, *5*(3), p.172437.

Dewaele, L., Gol'din, P., Marx, F.G., Lambert, O., Laurin, M., Obadă, T. and de Buffrénil, V., 2022. Hypersalinity drives convergent bone mass increases in Miocene marine mammals from the Paratethys. *Current Biology*, *32*(1), pp.248-255.

Dowsett, H.J. and Wiggs, L.B., 1992. Planktonic foraminiferal assemblage of the Yorktown Formation, Virginia, USA. *Micropaleontology*, pp.75-86.

Dowsett, H.J., Chandler, M.A. and Robinson, M.M., 2009. Surface temperatures of the Mid-Pliocene North Atlantic Ocean: implications for future climate. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *367*(1886), pp.69-84.

Dowsett, H.J., Robinson, M.M., Foley, K.M., Herbert, T.D., Otto-Bliesner, B.L. and Spivey, W., 2019. Mid-piacenzian of the north Atlantic Ocean. *Stratigraphy*, *16*(3), pp.119-144.

Dowsett, H.J., Robinson, M.M., Foley, K.M. and Herbert, T.D., 2021. The Yorktown Formation: Improved Stratigraphy, Chronology, and Paleoclimate Interpretations from the US Mid-Atlantic Coastal Plain. *Geosciences*, *11*(12), p.486.

Drago, M., Valdivia, M., Bragg, D., González, E.M., Aguilar, A. and Cardona, L., 2020. Stable oxygen isotopes reveal habitat use by marine mammals in the Río de la Plata estuary and adjoining Atlantic Ocean. *Estuarine, Coastal and Shelf Science*, *238*, p.106708.

Eguchi, T. and Harvey, J.T., 2005. Diving behavior of the Pacific harbor seal (*Phoca vitulina richardii*) in Monterey Bay, California. *Marine Mammal Science*, *21*(2), pp.283-295.

Eshelman, R.E., Whitmore Jr, F.C., Ray, C.E., Bohaska, D.J., Koretsky, I.A., Ward, L.W. and Barnes, L.G., 2008. Early Pliocene (late Hemphillian) land mammals from the Lee

Creek Mine, Aurora, North Carolina. *Geology and paleontology of the Lee Creek Mine, North Carolina, IV*, *14*, pp.17-38.

Finger, K.L., 1988. Depositional paleoecology of Miocene ostracodes in the Monterey Formation, Laguna Hills, Southern California, USA. In *Developments in Palaeontology and Stratigraphy* (Vol. 11, pp. 1101-1111). Elsevier.

Finger, K.L., 1992. *Biostratigraphic atlas of Miocene foraminifera from the Monterey and Modelo Formations, central and southern California*. Cushman Foundation for foraminiferal research.

Fitch, J.E. and Lavenberg, R.J., 1983. Teleost fish otoliths from Lee Creek Mine, Aurora, North Carolina (Yorktown Formation: Pliocene). *Smithsonian Contributions to Paleobiology*, *53*(1), pp.509-529.

Foote, A.D., Newton, J., Ávila-Arcos, M.C., Kampmann, M.L., Samaniego, J.A., Post, K., Rosing-Asvid, A., Sinding, M.H.S. and Gilbert, M.T.P., 2013. Tracking niche variation over millennial timescales in sympatric killer whale lineages. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1768), p.20131481.

Fry, B. and Sherr, E.B., 1989. δ 13 C measurements as indicators of carbon flow in marine and freshwater ecosystems. In *Stable isotopes in ecological research* (pp. 196-229). Springer, New York, NY.

Fry, B. and Wainright, S.C., 1991. Diatom sources of 13 C-rich carbon in marine food webs. *Marine Ecology Progress Series*, pp.149-157.

Gannon, D.P., Read, A.J., Craddock, J.E., Fristrup, K.M. and Nicolas, J.R., 1997. Feeding ecology of long-finned pilot whales Globicephala melas in the western North Atlantic. *Marine Ecology Progress Series*, *148*, pp.1-10.

Garde, E., Jung-Madsen, S., Ditlevsen, S., Hansen, R.G., Zinglersen, K.B. and Heide-Jørgensen, M.P., 2018. Diving behavior of the Atlantic walrus in high Arctic Greenland and Canada. *Journal of Experimental Marine Biology and Ecology*, *500*, pp.89-99.

Gebruk, A., Mikhaylyukova, P., Mardashova, M., Semenova, V., Henry, L.A., Shabalin, N., Narayanaswamy, B.E. and Mokievsky, V., 2021. Integrated study of benthic foraging resources for Atlantic walrus (*Odobenus rosmarus rosmarus*) in the Pechora Sea, south-eastern Barents Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(1), pp.112-125.

Gibble, C.M. and Harvey, J.T., 2015. Food habits of harbor seals (*Phoca vitulina richardii*) as an indicator of invasive species in San Francisco Bay, California. *Marine Mammal Science*, *31*(3), pp.1014-1034.

Gibson, T.G., 1983. Stratigraphy of Miocene through Lower Pleistocene strata of the United States central Atlantic coastal plain. *Smithsonian Contributions to Paleobiology*, *53*, pp.35-80.

Gibson, M.L. and Geisler, J.H., 2009. A new Pliocene dolphin (Cetacea: Pontoporiidae), from the Lee Creek Mine, North Carolina. *Journal of Vertebrate Paleontology*, *29*(3), pp.966-971.

Gjertz, I., Griffiths, D., Krafft, B.A., Lydersen, C. and Wiig, Ø., 2001. Diving and haul-out patterns of walruses *Odobenus rosmarus* on Svalbard. *Polar Biology*, *24*(5), pp.314-319.

Goetsch, C., Conners, M.G., Budge, S.M., Mitani, Y., Walker, W.A., Bromaghin, J.F., Simmons, S.E., Reichmuth, C.J. and Costa, D.P., 2018. Energy-Rich Mesopelagic Fishes Revealed as a Critical Prey Resource for a Deep-Diving Predator Using Quantitative Fatty Acid Signature Analysis. *Frontiers in Marine Science*, *5*, p.430.

Govender, R., 2018. Extension of the geographic range of Homiphoca into Northern Cape Province, South Africa, with comments on the possible feeding strategies used by Homiphoca. *Journal of Vertebrate Paleontology*, *38*(3), p.e1463536.

Graham, S.A. and Williams, L.A., 1985. Tectonic, depositional, and diagenetic history of Monterey Formation (Miocene), central San Joaquin basin, California. *AAPG bulletin*, *69*(3), pp.385-411.

Hall, C.A. ed., 2002. Nearshore marine paleoclimatic regions, increasing zoogeographic provinciality, molluscan extinctions, and paleoshorelines, California: Late Oligocene (27 Ma) to Late Pliocene (2.5 Ma) (Vol. 357). *Geological Society of America.*

Hampe, O., 2006. Middle/late Miocene hoplocetine sperm whale remains (Odontoceti: Physeteridae) of North Germany with an emended classification of the Hoplocetinae. *Fossil Record*, *9*(1), pp.61-86.

Hazel, J.E., 1971. Ostracode biostratigraphy of the Yorktown Formation (upper Miocene and lower Pliocene) of Virginia and North Carolina (No. 704). *US Govt. Print. Off.*

Hazel, J.E., 1983. Age and correlation of the Yorktown (Pliocene) and Croatan (Pliocene and Pleistocene) formations at the Lee Creek Mine. *Smithsonian Contributions to Paleobiology*, *53*, pp.81-199.

Hennig, C., 2020. fpc: Flexible Procedures for Clustering. R package version 2.2-9. https://CRAN.R-project.org/package=fpc

Holbourn, A., Kuhnt, W., Lyle, M., Schneider, L., Romero, O. and Andersen, N., 2014. Middle Miocene climate cooling linked to intensification of eastern equatorial Pacific upwelling. *Geology*, *42*(1), pp.19-22.

Howard, H. and Barnes, L.G., 1987. *Middle Miocene marine birds from the foothills of the Santa Ana Mountains, Orange County, California*. Natural History Museum of Los Angeles County.

Inuzuka, N., 兼子尚知 and 高畠孝宗, 2016. 北海道歌登産 *Desmostylus* の骨格 Ⅲ. 歌登第8標本の再記載と第1標本頭蓋形態の再考. *地質調査研究報告*, *67*(5), pp.167-181. [in japanese].

Jones, K.E., Ruff, C.B. and Goswami, A., 2013. Morphology and biomechanics of the pinniped jaw: mandibular evolution without mastication. *The Anatomical Record*, *296*(7), pp.1049-1063.

Johnson, A.L., Valentine, A., Leng, M.J., Sloane, H.J., Schoene, B.R. and Balson, P.S., 2017. Isotopic temperatures from the early and mid-pliocene of the us middle atlantic coastal plain, and their implications for the cause of regional marine climate changepliocene marine temperaturesa. *Palaios*, *32*(4), pp.250-269.

Kelly, T.S. and Stewart, J.D., 2008. New records of middle and late Miocene Perissodactyla and Artiodactyla from the western border of the San Joaquin Valley, Diablo Range, Fresno County, California. *Natural History Museum of Los Angeles County*.

Kienle, S.S. and Berta, A., 2018. The evolution of feeding strategies in phocid seals (Pinnipedia, Phocidae). *Journal of Vertebrate Paleontology*, *38*(6), p.e1559172.

Koch PL. 2007 Isotopic study of the biology of modern and fossil vertebrates. *Stable Isotopes in Ecology and Environmental Science*. 2nd edition, 99-154. Malden, Massachusetts: Blackwell Publishing.

Koch, P.L., Tuross, N. and Fogel, M.L., 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. *Journal of Archaeological Science*, *24*(5), pp.417-429.

Kohn, M.J. and Cerling, T.E., 2002. 12 Stable Isotope Compositions of Biological Apatite. *Phosphates-Geochemical, Geobiological, and Materials Importance. Reviews in Mineralogy and Geochemistry*, pp.455-488.

Kohno, N., Barnes, L.G. and Hirota, K., 1994. Miocene fossil pinnipeds of the genera *Prototaria* and *Neotherium* (Carnivora; Otariidae; Imagotariinae) in the North Pacific Ocean: evolution, relationships and distribution. *Island Arc*, *3*(4), pp.285-308.

Kohno, N. and Ray, C.E., 2008. Pliocene walruses from the Yorktown Formation of Virginia and North Carolina, and a systematic revision of the North Atlantic Pliocene walruses. *Virginia Museum of Natural History Special Publication*, *14*, pp.39-80.

Koretsky, I. A., 2001. Morphology and systematics of Miocene Phocinae (Mammalia: Carnivora) from Paratethys and the North Atlantic region. *Geologica Hungarica*, Budapest, 54, p.1-109.

Koretsky, I.A. and Ray, C.E., 2008. Phocidae of the Pliocene of eastern USA. *Virginia Museum of Natural History Special Publication*, *14*, pp.81-140.

Krantz, D.E., 1990. Mollusk-isotope records of Plio-Pleistocene marine paleoclimate, US middle Atlantic coastal plain. *Palaios*, pp.317-335.

Lambert, O., De Muizon, C. and Bianucci, G., 2013. The most basal beaked whale *Ninoziphius platyrostris* Muizon, 1983: clues on the evolutionary history of the family Ziphiidae (Cetacea: Odontoceti). *Zoological Journal of the Linnean Society*, *167*(4), pp.569-598.

Lambert, O., Collareta, A., Landini, W., Post, K., Ramassamy, B., Di Celma, C., Urbina, M. and Bianucci, G., 2015. No deep diving: evidence of predation on epipelagic fish for a stem beaked whale from the Late Miocene of Peru. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1815), p.20151530.

Lambert, O. and Bianucci, G., 2019. How to break a sperm whale’s teeth: dental damage in a large Miocene physeteroid from the North Sea Basin. *Journal of Vertebrate Paleontology*, *39*(4), p.e1660987.

Larramendi, A., 2015. Shoulder height, body mass, and shape of proboscideans. *Acta Palaeontologica Polonica*, *61*(3), pp.537-574.

Lawrence, K.T., Herbert, T.D., Brown, C.M., Raymo, M.E. and Haywood, A.M., 2009. High-amplitude variations in North Atlantic Sea surface temperature during the early Pliocene warm period. *Paleoceanography*, *24*(2).

Lee-Thorp, J.A. and Van Der Merwe, N.J., 1991. Aspects of the chemistry of modern and fossil biological apatites. *Journal of Archaeological Science*, *18*(3), pp.343-354.

Loch, C., Boessenecker, R.W., Churchill, M. and Kieser, J., 2016. Enamel ultrastructure of fossil and modern pinnipeds: evaluating hypotheses of feeding adaptations in the extinct walrus *Pelagiarctos*. *The Science of Nature*, *103*(5), pp.1-8.

MacLeod, N.A. and Barton, D.R., 1998. Effects of light intensity, water velocity, and species composition on carbon and nitrogen stable isotope ratios in periphyton. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(8), pp.1919-1925.

MacFadden, B.J., 1986. Fossil horses from “*Eohippus*” (*Hyracotherium*) to *Equus*: scaling, Cope's Law, and the evolution of body size. *Paleobiology*, *12*(4), pp.355-369.

MacFadden, B.J., Higgins, P., Clementz, M.T. and Jones, D.S., 2004. Diets, habitat preferences, and niche differentiation of Cenozoic sirenians from Florida: evidence from stable isotopes. *Paleobiology*, *30*(2), pp.297-324.

Magallanes, I., Parham, J.F., Santos, G.P. and Velez-Juarbe, J., 2018. A new tuskless walrus from the Miocene of Orange County, California, with comments on the diversity and taxonomy of odobenids. *PeerJ*, *6*, p.e5708.

Martin, A.R., Reynolds, P., and Richardson, M.G., 1987. Aspects of the biology of pilot whales (*Globicephala melaena*) in recent mass strandings on the British coast. *Journal of Zoology*, *211*(1), pp.11-23.

Martin, J.E., Vance, D. and Balter, V., 2015. Magnesium stable isotope ecology using mammal tooth enamel. *Proceedings of the National Academy of Sciences*, *112*(2), pp.430-435.

Matsui, K. and Tsuihiji, T., 2019. The phylogeny of desmostylians revisited: proposal of new clades based on robust phylogenetic hypotheses. *PeerJ*, *7*, p.e7430.

Matthews, C.J. and Ferguson, S.H., 2014. Spatial segregation and similar trophic-level diet among eastern Canadian Arctic/north-west Atlantic killer whales inferred from bulk and compound specific isotopic analysis. *Journal of the Marine Biological Association of the United Kingdom*, *94*(6), pp.1343-1355.

Matthews, C.J., Longstaffe, F.J. and Ferguson, S.H., 2016. Dentine oxygen isotopes ($\delta^{18}O$) as a proxy for odontocete distributions and movements. *Ecology and Evolution*, *6*(14), pp.4643-4653.

Matthews, C.J., Longstaffe, F.J., Lawson, J.W. and Ferguson, S.H., 2021. Distributions of Arctic and Northwest Atlantic killer whales inferred from oxygen isotopes. *Scientific Reports*, *11*(1), pp.1-14.

Mèndez-Fernandez, P., Bustamante, P., Bode, A., Chouvelon, T., Ferreira, M., Lopez, A., Pierce, G.J., Santos, M.B., Spitz, J., Vingada, J.V. and Caurant, F., 2012. Foraging ecology of five toothed whale species in the Northwest Iberian Peninsula, inferred using carbon and nitrogen isotope ratios. *Journal of Experimental Marine Biology and Ecology*, *413*, pp.150-158.

Mitchell, E.D., 1966. The Miocene pinniped *Allodesmus*. *University of California Publications in Geological Sciences*, *61*, pp.1-105.

Muizon, C.D., DE. 1984. Les vertébrés fossiles de la Formation Pisco (Pérou) II. Les odontocetes (Cetacea, Mammalia) du Pliocene inférieur de Sud-Sacaco. *Travaux de l'Institut Français d'Études Andines*, *27*, pp.1-188.

Nagy, K.A. and Costa, D.P., 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *238*(5), pp.R454-R465.

Newsome, S.D., Clementz, M.T. and Koch, P.L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science*, *26*(3), pp.509-572.

Olson, S.L. and Rasmussen, P.C., 2001. Miocene and Pliocene birds from the Lee Creek Mine, North Carolina. *Smithsonian Contributions to Paleobiology*, *90*, pp.233-365.

Osmond, C.B., Valaane, N., Haslam, S.M., Uotila, P. and Roksandic, Z., 1981. Comparisons of $\delta^{13}C$ values in leaves of aquatic macrophytes from different habitats in Britain and Finland; some implications for photosynthetic processes in aquatic plants. *Oecologia*, *50*(1), pp.117-124.

Parham, J.F., Barron, J.A.and Velez-Juarbe, J., 2022. Middle and late Miocene marine mammal assemblages from the Monterey Formation of Orange County, California, in Aiello, I., Barron, J., and Ravelo, C., eds., Understanding the Monterey Formation and Similar Biosiliceous Units across Space and Time: *Geological Society of America Special Paper* 556.

Philippii, R. A. 1889. Rectificación de algunos errores con respecto á las focas ó lobos de mar de Chile. *Anales de la Universidad*, pp. 61–64.

Poore, R.Z., McDougall, K., Barron, J.A., Brabb, E.E. and Kling, S.A., 1981. Microfossil biostratigraphy and biochronology of the type Relizian and Luisian Stages of California.

Prothero, D.R., Liter, M.R., Barnes, L.G., Wang, X., Mitchell, E., McLeod, S., Whistler, D.P., Tedford, R.H. and Ray, C., 2008. Land mammals from the Middle Miocene Sharktooth Hill Bonebed, Kern County, California. *New Mexico Museum of Natural History and Science Bulletin*, *44*, pp.299-314.

Pyenson, N.D., Irmis, R.B., Lipps, J.H., Barnes, L.G., Mitchell Jr, E.D. and McLeod, S.A., 2009. Origin of a widespread marine bonebed deposited during the middle Miocene Climatic Optimum. *Geology*, *37*(6), pp.519-522.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rau, G.H., Takahashi, T., Des Marais, D.J., Repeta, D.J. and Martin, J.H., 1992. The relationship between $\delta^{13}C$ of organic matter and [CO_2 (aq)] in ocean surface water: data from a JGOFS site in the northeast Atlantic Ocean and a model. *Geochimica et Cosmochimica Acta*, *56*(3), pp.1413-1419.

Robinson, P.W., Costa, D.P., Crocker, D.E., Gallo-Reynoso, J.P., Champagne, C.D., Fowler, M.A., Goetsch, C., Goetz, K.T., Hassrick, J.L., Hückstädt, L.A. and Kuhn, C.E., 2012. Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PloS one*, *7*(5), p.e36728.

Rule, J.P., Adams, J.W., Rovinsky, D.S., Hocking, D.P., Evans, A.R. and Fitzgerald, E.M., 2020. A new large-bodied Pliocene seal with unusual cutting teeth. *Royal Society open science*, *7*(11), p.201591.

Santos, M.B., Monteiro, S.S., Vingada, J.V., Ferreira, M., López, A., Martínez Cedeira, J.A., Reid, R.J., Brownlow, A. and Pierce, G.J., 2014. Patterns and trends in the diet of long-finned pilot whales (*Globicephala melas*) in the northeast Atlantic. *Marine Mammal Science*, *30*(1), pp.1-19.

Segura, A.M., Franco-Trecu, V., Franco-Fraguas, P. and Arim, M., 2015. Gape and energy limitation determine a humped relationship between trophic position and body size. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(2), pp.198-205.

Schramm, Y. and Heckel, G., 2021. Pacific Harbor Seal (Phoca vitulina richardii, Gray 1864). In *Ecology and Conservation of Pinnipeds in Latin America* (pp. 209-231). Springer, Cham.

Schoeninger, M.J., Hallin, K., Reeser, H., Valley, J.W. and Fournelle, J., 2003. Isotopic alteration of mammalian tooth enamel. *International Journal of Osteoarchaeology*, *13*(1-2), pp.11-19.

Sielfeld, W. K. 1983. Mamíferos marinos de Chile. Ediciones de la Universidad de Chile. Santiago. 199 pp.

Smith, P.B., 1960. *Foraminifera of the Monterey Shale and Puente Formation, Santa Ana Mountains and San Juan Capistrano Area, California* (No. 294-M).

Snyder, S.W., Mauger, L.L., Akers, W.H. and Ray, C.E., 1983. Planktonic foraminifera and biostratigraphy of the Yorktown Formation, Lee Creek Mine. *Smithsonian Contributions to Paleobiology*, *53*, pp.455-482.

Stadum, C.J. and Finger, K.L., 2016. Paleontology and stratigraphy of the Miocene Saddleback Valley Limestone, Orange County, southern California. *Natural History Museum of Los Angeles County Contributions in Science*, *524*, pp.31-49.

Stanton, R.J. and Alderson, J.M., 2013. Limestone interbedded with submarine volcanics: The early–middle Miocene Conejo volcanics, California. *Facies*, *59*(3), pp.467-480.

Steingass, S., Horning, M. and Bishop, A.M., 2019. Space use of Pacific harbor seals (*Phoca vitulina richardii*) from two haulout locations along the Oregon coast. *PloS one*, *14*(7), p.e0219484.

Stewart, R.E.A. and Stewart, B.E., 1987. Dental ontogeny of harp seals, *Phoca groenlandica*. *Canadian journal of zoology*, *65*(6), pp.1425-1434.

Stewart, B.E., Innes, S. and Stewart, R.E., 1998. Mandibular dental ontogeny of ringed seals (*Phoca hispida*). *Marine Mammal Science*, *14*(2), pp.221-231.

Suess, H.E., 1955. Radiocarbon concentration in modern wood. *Science*, *122*(3166), pp.415-417.

Thompson, P.M., Mackay, A., Tollit, D.J., Enderby, S. and Hammond, P.S., 1998. The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology*, *76*(6), pp.1044-1053.

Tieszen, L.L. and Fagre, T., 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO 2, bone collagen, bioapatite, and soft tissues. In *Prehistoric human bone* (pp. 121-155). Springer, Berlin, Heidelberg.

Tipple, B.J., Meyers, S.R. and Pagani, M., 2010. Carbon isotope ratio of Cenozoic CO2: A comparative evaluation of available geochemical proxies. *Paleoceanography*, *25*(3).

Toscano, A., Abad, M., Ruiz, F., Muñiz, F., Álvarez, G., García, E.X.M. and Caro, J.A., 2013. Nuevos restos de *Scaldicetus* (Cetacea, Odontoceti, Physeteridae) del Mioceno superior, sector occidental de la Cuenca del Guadalquivir (sur de España). *Revista mexicana de ciencias geológicas*, *30*(2), pp.436-445.

Valenzuela-Toro, A.M., Gutstein, C.S., Varas-Malca, R.M., Suarez, M.E. and Pyenson, N.D., 2013. Pinniped turnover in the South Pacific Ocean: new evidence from the Plio-Pleistocene of the Atacama Desert, Chile. *Journal of Vertebrate Paleontology*, *33*(1), pp.216-223.

Valenzuela-Toro, A.M., Gutstein, C.S., Suárez, M.E., Otero, R. and Pyenson, N.D., 2015. Elephant seal (*Mirounga* sp.) from the Pleistocene of the Antofagasta Region, northern Chile. *Journal of Vertebrate Paleontology*, *35*(3), p.e918883.

Valenzuela-Toro, A. and Pyenson, N.D., 2019. What do we know about the fossil record of pinnipeds? A historiographical investigation. *Royal Society Open Science*, *6*(11), p.191394.

Van Pelt, T.I., Piatt, J.F., Lance, B.K. and Roby, D.D., 1997. Proximate composition and energy density of some North Pacific forage fishes. *Comparative Biochemistry and Physiology Part A: Physiology*, *118*(4), pp.1393-1398.

Velez-Juarbe, J., 2017. *Eotaria citrica*, sp. nov., a new stem otariid from the "Topanga" formation of Southern California. *PeerJ*, *5*, p.e3022.

Velez-Juarbe, J., 2018. New data on the early odobenid *Neotherium mirum* Kellogg, 1931, and other pinniped remains from the Sharktooth Hill Bonebed, California. *Journal of Vertebrate Paleontology*, *38*(4), pp.1-14.

Velez-Juarbe, J. and Valenzuela-Toro, A.M., 2019. Oldest record of monk seals from the North Pacific and biogeographic implications. *Biology letters*, *15*(5), p.20190108.

Vighi, M., Borrell, A., Crespo, E.A., Oliveira, L.R., Simões-Lopes, P.C., Flores, P.A., García, N.A. and Aguilar, A., 2014. Stable isotopes indicate population structuring in the Southwest Atlantic population of right whales (*Eubalaena australis*). *PLoS One*, *9*(3), p.e90489.

Vighi, M., Borrell, A. and Aguilar, A., 2016. Stable isotope analysis and fin whale subpopulation structure in the eastern North Atlantic. *Marine Mammal Science*, *32*(2), pp.535-551.

Ward, L. W. 2008. Synthesis of paleontological and stratigraphic investigations at the Lee Creek Mine, Aurora, NC (1958–2007). *Geology and Paleontology of the Lee Creek Mine, North Carolina, IV. Virginia Museum of Natural History Special Publication* 14: 325-436.

Weise, M.J., Harvey, J.T. and Costa, D.P., 2010. The role of body size in individual-based foraging strategies of a top marine predator. *Ecology*, *91*(4), pp.1004-1015.

Welton, B.J., 2014. A new fossil basking shark (Lamniformes: Cetorhinidae) from the middle Miocene Sharktooth Hill Bonebed, Kern County, California. *Contributions in Science*, *522*, pp.29-44.

Williams, M., Haywood, A.M., Harper, E.M., Johnson, A.L., Knowles, T., Leng, M.J., Lunt, D.J., Okamura, B., Taylor, P.D. and Zalasiewicz, J., 2009. Pliocene climate and seasonality in North Atlantic shelf seas. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *367*(1886), pp.85-108.

Yoshida, N. and Miyazaki, N., 1991. Oxygen isotope correlation of cetacean bone phosphate with environmental water. *Journal of Geophysical Research: Oceans*, *96*(C1), pp.815-820.

Yoshino, K., Takahashi, A., Adachi, T., Costa, D.P., Robinson, P.W., Peterson, S.H., Hückstädt, L.A., Holser, R.R. and Naito, Y., 2020. Acceleration-triggered animal-borne videos show a dominance of fish in the diet of female northern elephant seals. *Journal of Experimental Biology*, *223*(5), p.jeb212936.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. and Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *science*, *292*(5517), pp.686-693.

Zeppelin, T.K. and Orr, A.J., 2010. Stable isotope and scat analyses indicate diet and habitat partitioning in northern fur seals *Callorhinus ursinus* across the eastern Pacific. *Marine Ecology Progress Series*, *409*, pp.241-253.

Zug, G.R., 2001. Turtles of the Lee Creek Mine (Pliocene: North Carolina). *Smithsonian Contributions to Paleobiology*, *90*, pp.203-218.

TABLES

Table 5.1. Taxonomic, geologic, and ecological information of marine and terrestrial mammals included in this study. Body size corresponds to body length (in cm), except for Gomphotheriidae which is the shoulder height (in cm), and for Merychippus for which the body mass (in Kg) is presented .Letter superscript indicates the information source: [a]Boersma and Pyenson (2015), [b]Lambert et al. (2013), [c]Marine mammals Research and Conservation of India, [d]Martin et al. (1987), [e]Rule et al. (2020), [f]Knutsen and Born (1994), [g]Churchill et al. (2014), [h]Inuzuka et al. 2017, [i]Larramendi (2016), [j]MacFadden (1986). Body length of indeterminate Monachinae from Yorktown Formation was estimated as the average body length of identified monachinae seals from this unit for which this information is available (i.e., *Sardonectes* and *Homiphoca*). Body length of Gomphotheriidae corresponds to the shoulder height.

Order	**Family**	**Genus**	**Geologic formation**	**Age**	**Body size**	**Ecological interpretation from morphological evidence**
Cetacea	Physeteriidae	*Scaldicetus*	Yorktown	Pliocene	600[a]	Macroraptorial predator
Cetacea	Ziphiidae	*Ninoziphius*	Yorktown	Pliocene	450[b]	Shallow benthic predator
Cetacea	Delphinidae	*Pseudorca*	Yorktown	Pliocene	550[c]	
Cetacea	Delphinidae	*Globicephala*	Yorktown	Pliocene	590[d]	Offshore predator
Pinnipedia	Phocidae	Monachinae indet.	Yorktown	Pliocene	242[e]	Pierce feeder (*Sardonectes* and *Homiphoca*)
Pinnipedia	Odobenidae	*Ontocetus*	Yorktown	Pliocene	291[f]	Benthic feeder
Pinnipedia	Desmatophocidae	*Allodesmus*	Monterey/Round Mountain Silt/Temblor	middle Miocene	>250[g]	Pelagic and deep-diving predator
Pinnipedia	Odobenidae	cf. *Imagotaria*	Monterey	middle Miocene	257[g]	Pelagic and piscivorous predator
Pinnipedia	Otariidae	*Pithanotaria*	Monterey	middle Miocene	126[g]	Offshore predator
Pinnipedia	Odobenidae	*Neotherium*	Round Mountain Silt	middle Miocene	202[g]	Pelagic and piscivorous predator

Desmostylia	Desmostylidae	*Desmostylus*	Round Mountain Silt/Temblor	middle Miocene	>380[h]	Estuarine or freshwater herbivore
Proboscidea	Gomphotheriidae	*Rhynchotherium*	Yorktown	Pliocene	> 250[i]	Terrestrial herbivore
Proboscidea	Gomphotheriidae	*Gomphotherium*	Temblor	middle Miocene	> 250[i]	Terrestrial herbivore
Perissodactyla	Equidae	*Merychip pus*	Temblor	middle Miocene	71[j]	Terrestrial herbivore

Table 5.2. Mean $\delta^{13}C$ and $\delta^{18}O$ values and respective standard deviation (σ^2) for fossil mammals included in the study. [1]indicates data from Clementz et al. (2003).

Taxa	**n**	**Loc.**	**Geologic formation**	**$\delta^{13}C$**	**σ^2**	**$\delta^{18}O$**	**σ^2**
Allodesmus	3	1945	Monterey	-9.9	0.7	27.1	0.5
cf. *Imagotaria*	3	1945	Monterey	-7.7	0.4	25.4	0.5
Pithanotaria	2	1945	Monterey	-6.0		27.6	
Allodesmus	4		Round Mountain Silt	-10.4	1.7	27.2	0.6
Neotherium	1	3162	Round Mountain Silt	-7.5		28.6	
Desmostylus[1]	6	1292	Round Mountain Silt	-5.6	1.6	27.8	0.5
Allodesmus[1]	7	1292	Round Mountain Silt	-9.5	0.8	27.1	0.5
Odontocete large[1]	4	1292	Round Mountain Silt	-7.4	1.9	28.2	0.3
Odontocete small[1]	6	1292	Round Mountain Silt	-7.7	0.3	27.5	0.4
Allodesmus	3		Temblor	-10.0	0.1	27.7	0.3
Desmostylus	6		Temblor	-4.5	1.3	27.7	0.3
Desmostylus[1]	5	2124	Temblor	-7	2.5	27.2	0.2
Desmostylus[1]	8	V3301	Temblor	-3.5	1	27.6	0.2
Monachinae indet.	16	42246	Yorktown	-8.4	1.5	26.8	0.6
Globicephala	7	42246	Yorktown	-7.9	1.0	28.0	0.3
Ninoziphius	3	42246	Yorktown	-6.8	0.4	27.8	0.2
Ontocetus emmonsi	2	42246	Yorktown	-6.8		27.6	
Pseudorca	1	42246	Yorktown	-8.5		27.4	
Scaldicetus	6	42246	Yorktown	-8.3	1.4	28.3	0.2
Rhynchotherium cf. euhypodon	9	42246	Yorktown	-7.2	2.0	27.1	0.7

FIGURES

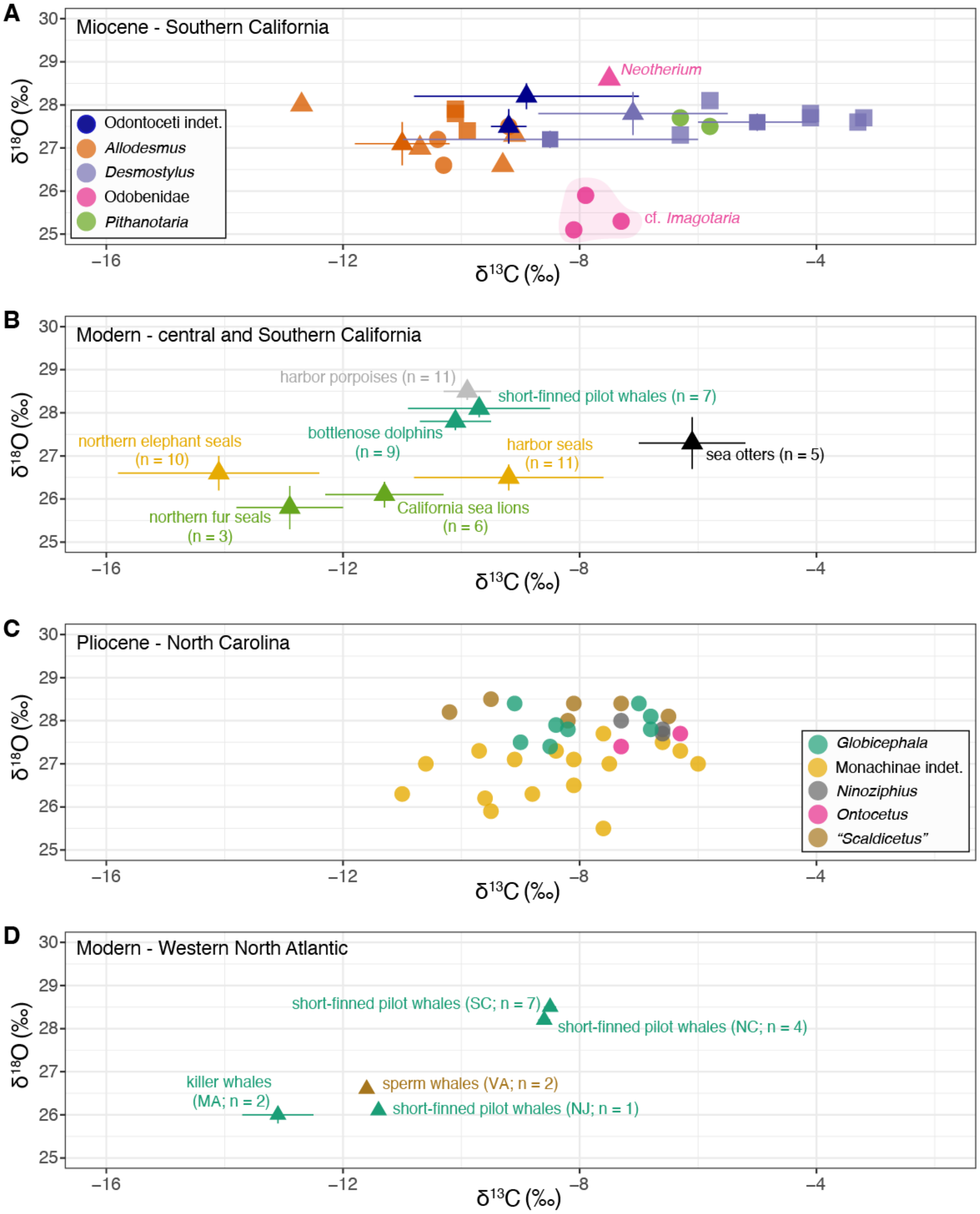

Figure 5.1. Biplot of $\delta^{13}C$ and $\delta^{18}O$ values for fossil (A, C) and living (B, D) marine mammals from California (eastern North Pacific Ocean) and North Carolina (western North Atlantic Ocean). The mean and variance of fossil and modern marine mammals is indicated for data gathered from the literature. Shapes in (A) represent specimens from the Round Mountain Silt (triangles), Monterey (circles), and Temblor (squares) Formations. Measurements were made from tooth enamel carbonate, except for killer

whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) of panel (D), which were from bone and dentine carbonate, respectively. n represents the sample size. Data from the literature was taken from Clementz and Koch (2001), Clementz and Sewall (2011), and Clementz et al. (2014).

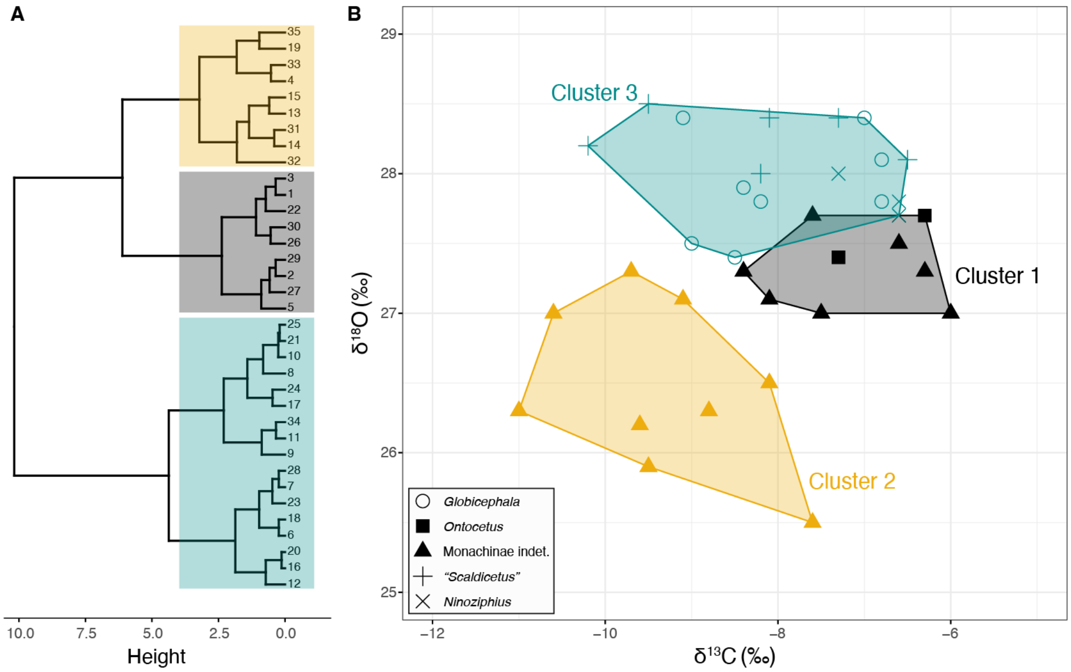

Figure 5.2. (A) Hierarchical Cluster Analysis using the $\delta^{13}C$ and $\delta^{18}O$ composition, and the estimated body length for each marine mammal populations from the Yorktown Formation. (B) Biplot of $\delta^{13}C$ and $\delta^{18}O$ depicting the distribution of Clusters in the isospace.

SUPPLEMENTARY FIGURES

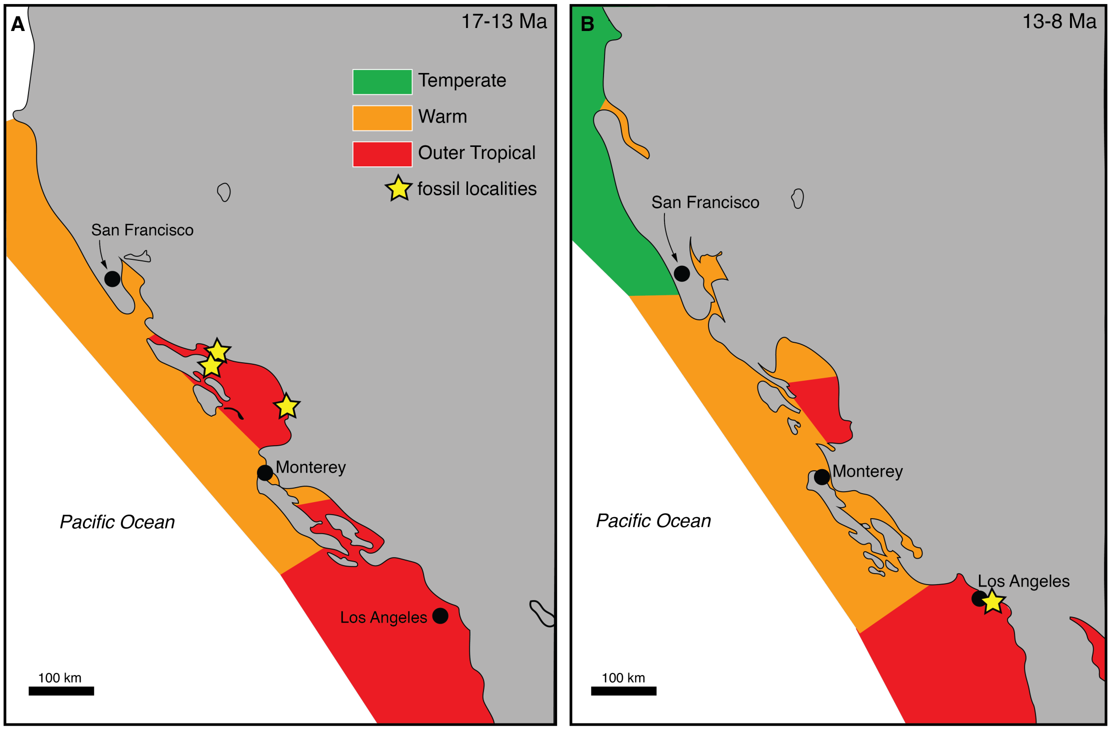

Figure S5.1. Maps showing the paleoshoreline and the marine paleoclimatic regions of western California between 17 and 8 Ma, encompassing the depositional period of Round Mountain Silt, Temblor, and Monterey formations. Yellow stars indicate localities from the Round Mountain Silt formations (A), and the Monterey Formation (lower and upper levels) (B). Figure modified from Hall (2002).

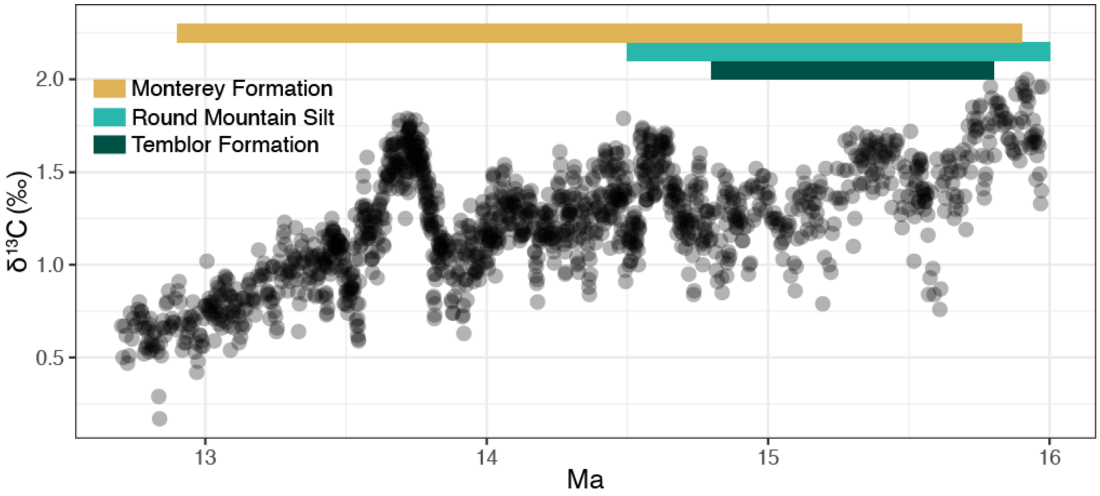

FIGURE S5.2. Records of the δ13C of benthic foraminifers from the middle Miocene. Data corresponds to the Integrated Ocean Drilling Program Site U1338 located in the tropical eastern North Pacific. Color bars represent the span encompassed by the fossiliferous localities that yielded the fossil specimens included in this study. Data from Holbourn et al. (2014).

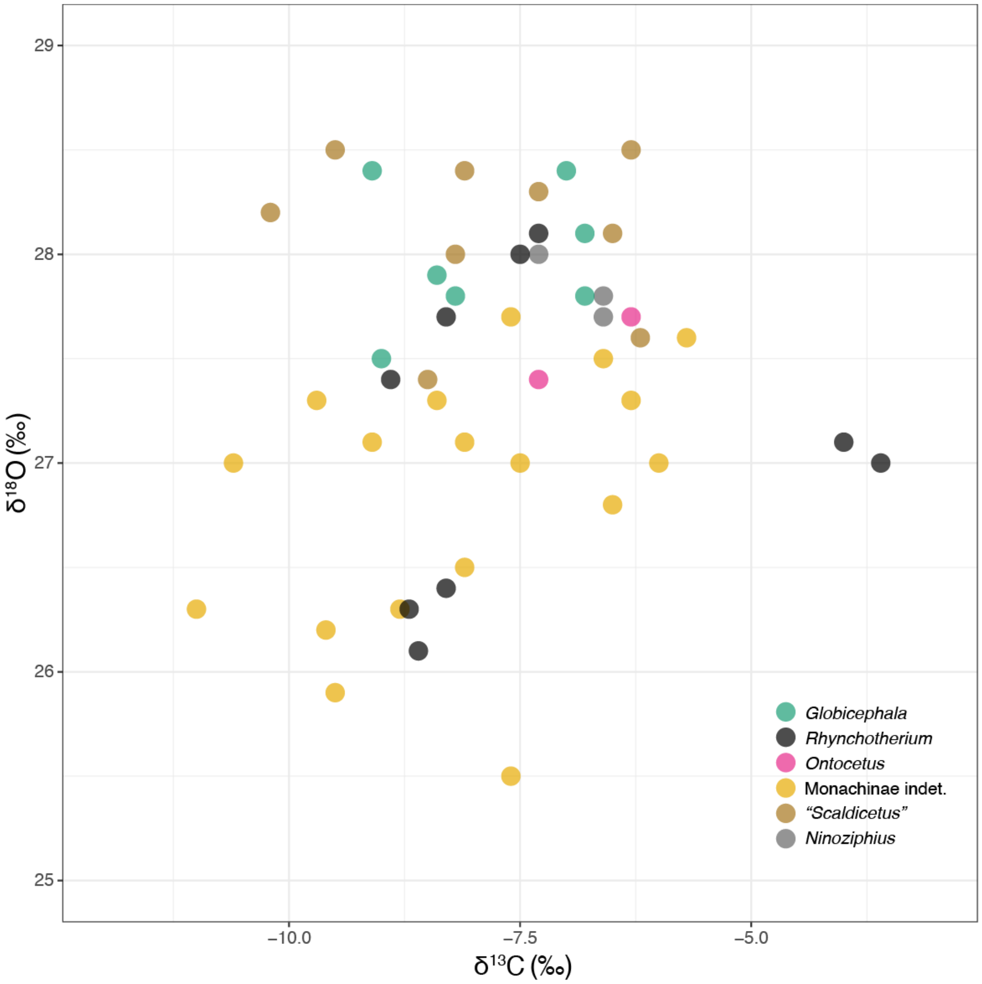

FIGURE S5.3. Carbon and oxygen isotope ratios of marine and terrestrial mammals from the Yorktown Formation.

CONCLUSION

How organisms coexist and structure their ecological communities and how these dynamics have changed through time are long-standing questions in ecology and evolutionary biology (e.g., Diamond, 1975; Connor and Simberloff, 1979; Weiher et al., 1998; Drake, 1990; Gotelli and McCabe, 2002). Functional traits can affect the organisms' performance, including their foraging ecology, shaping the structure and function of ecological communities (e.g., Bowers and Brown, 1982; Stevens and Willig, 2000; Dayan and Simberloff, 2005; McGill et al., 2006; Cadotte et al., 2015). Among them, body size and feeding morphology can affect foraging and resource partitioning in terrestrial mammals, playing a driving role in the structure of their communities through competitive interactions (e.g., Van Valkenburgh, 1985, 1988). Whether and how these traits might affect the foraging ecology and, ultimately, the community structure in taxa with different life and evolutionary histories and ecological constraints, such as marine mammals, remains unknown. Indeed, the coexistence mechanisms underlying pinniped communities and how these have changed through time have not been thoroughly addressed. My dissertation contributed to filling this knowledge gap by offering a multiscale examination of the pinniped foraging dynamics and ecomorphology, illuminating the patterns of their communities, the mechanisms underlying these patterns, and how they might have changed over time.

Chapter 1 showed that sympatric eared seals display consistent foraging and resource partitioning patterns across their distributional range. Fur seals feed offshore and on pelagic prey, whereas co-occurring sea lions rely on nearshore and benthic resources. Although some species (or populations of species) depart from this pattern, divergent foraging modes still prevail in their respective communities. These foraging distinctions are consistent with energetic trade-offs emerging from their body size disparities (fur seals are significantly smaller than sea lions) and the distinct ecological dynamics in benthic and pelagic food webs. Although Chapter 1 revealed that body size disparities contribute to resource and niche partitioning in sympatric otariids, the precise role of body size and feeding morphology in niche segregation and community structure remained undetermined. In this regard, Chapter 2 showed a significant relationship between body size, feeding morphology, and foraging and habitat preferences in sympatric otariids from the eastern North Pacific, by which larger individuals have stronger bite forces and are preferentially coastal and benthic, and they consume slightly higher trophic level prey than smaller ones, making this one of the first definitive ecomorphological quantifications in a living pinniped community.

This work focused on a single community, but the community-wide ecomorphological relationships examined here may exist in other geographic areas. As shown in Chapter 1, living otariid communities throughout the Southern Hemisphere display comparable body size, morphological, and foraging disparities. Likewise, the fossil record reveals that pinniped assemblages had body size and morphological differences analogous to modern otariid and other pinniped communities (e.g., Valenzuela-Toro et al., 2016). These observations suggest that variation in body size and feeding morphology among co-occurring otariids (and other pinnipeds) have repeatedly evolved, likely contributing to niche segregation over geologic time, as shown for some marine herbivore and terrestrial carnivore communities (Van Valkenburgh, 1988, 1994; Velez-Juarbe et al., 2012). Future community-wide ecomorphological examinations using different methodologies (e.g., tracking data, bone microstructure, stable isotopes) might further clarify the mechanisms involved in their coexistence, niche segregation, and community structure.

Factors different from foraging ecology can affect the body size and feeding morphology of mammals (e.g., Tseng and Flynn, 2018; Pérez-Ramos et al., 2020; Law, 2021). Chapter 3 showed that density-dependent sexual selection can drive changes in the body size and biomechanical properties of pinniped feeding morphology, affecting, in turn, their feeding performance. Over 46 years of population recovery, adult male California sea lions increased rather than decreased their average body size and the size of their oral cavity and developed more powerful bite strength. These morphological shifts are consistent with strengthening density-dependent sexual selection of more competitive individuals with larger sizes and more potent biting forces. Whereas increased body size results in higher absolute energy requirements, adult males have concurrently expanded their isotopic niche, suggesting diversification of their dietary preferences over time. While female sea lions' body size remained stable, they were rare in central and northern California (the region represented by our collection) until the mid-2010s. Therefore, during the study period (1983-2007), female sea lions inhabiting central and northern California were sparse, experiencing low density-dependent intraspecific competition for resources, contributing to their body size stability.

Chapter 3 revealed that direct selective pressures for foraging performance are not the only factors controlling body size and feeding morphology. Population density and life history can also shift size and feeding biomechanics in polygynous sea lions through density-dependent sexual selection. These results demonstrate that mechanisms controlling the feeding ecomorphology of extant and extinct pinnipeds (and likely other marine predators) may be more complex than traditionally accepted narratives involving functional tradeoffs between cranial morphology and feeding performance (Tzeng and Flynn, 2018). Consequently, over evolutionary time, the morphological and functional disparity observed in co-occurring species (Chapter 1) might have indirectly resulted from selection pressures not necessarily linked with feeding performance. Future studies exploring additional mechanisms with the prospect of affecting feeding ecomorphology, such as environment (e.g., Torres-Romero et al., 2016; Mori et al., 2019; Adamczak et al., 2020), hormone secretion (Kamaluddin et al., 2019; Leitch et al., 2020; DeRango et al., 2021), or cranial sutures (White et al., 2021) might offer opportunities to investigate other nonfeeding factors affecting feeding morphology.

From a conservation standpoint, Chapter 3 also showed that body size decrease is not a general response to increased resource competition in marine predators during recovery. It revealed that marine mammals can evolve energetic compensations to overcome increased competition due to their population recovery. However, independent dietary records showed that these compensations were achieved during periods in which California sea lions' diet was consistently dominated by the commercially relevant and energy-rich pelagic prey such as Pacific sardines and northern anchovies. As depletions of these pelagic prey associated with climate change intensify, California sea lions will not be able to achieve and benefit from these ecological and energetic compensations, leading to a reduction in their capability to overcome increased resource competition, likely forcing abrupt population declines. Additional analyses of the size and morphological dynamics experienced by female California sea lions breeding in Southern California, which have likely reached their carrying capacity, will further disentangle the effect of density-dependent dynamics on body size and feeding ecomorphology. Moreover, studies examining decadal shifts in reproductive hormones or secondary sexual traits (e.g., baculum) in archival museum specimens might provide ways to test and quantify density-dependent sexual selection in adult male sea lions during population recovery.

Paleoecological research is essential for addressing long-standing questions about how ecological dynamics and processes operate over large geographical, taxonomic, and temporal scales (e.g., Jablonski and Sepkoski, 1996; Louys et al., 2012; Barnosky et al., 2017). Paleoecology relies upon the ecological information chronicled by the fossil record, offering a coarse but extensive geographic and temporal perspective on how these interactions and dynamics have originated, operated, and shifted over time and space (e.g., Smith et al., 2015; Blanco et al., 2021; Wooller et al., 2021). However, as with other marine mammal groups, the pinniped fossil record possesses certain qualities, modes, and patterns. For example, despite their relative abundance in fossiliferous sites throughout the world, fossil pinnipeds are not uniformly described across regions (Berta et al., 2018). Moreover, the pinniped fossil record is constituted by isolated and fragmentary remains (e.g., Dewaele et al., 2017; Velez-Juarbe and Valenzuela-Toro, 2019). These attributes may bias their fossil record, like occur for cetaceans and sirenians (Uhen and Pyenson 2007). It remained unclear how sources of bias, such as geographic and temporal occurrences, or sampling efforts, might affect our knowledge and interpretations derived from their fossil record.

Chapter 4 revealed that most of the published pinniped fossil record is constituted by occurrences from deposits in the Northern Hemisphere, despite favorable paleoecological and depositional conditions in the Southern Hemisphere. There appears to be a substantial collection and publication bias associated with the legacy of study in learning centers in the Northern Hemisphere, especially in North America and Europe.

Extant species from Quaternary deposits represent more than half of the pinniped fossil record. Likewise, more than half of all fossil species are described from a single occurrence of a single specimen of a single individual, hampering the examination of intraspecific morphological variation. Many extinct species have type material constituted only by isolated postcranial elements, which might lead to artificial increases in taxonomic diversity. Still, despite the geographic and sampling biases, the pinniped fossil record is sufficiently represented, allowing evolutionary and paleoecological studies depending on the geographic region and time interval investigated. Novel examinations of the intra- and interspecific osteological variation in modern and fossil taxa (e.g., Churchill and Uhen, 2019), the performance of taphonomic studies in modern fauna (see Behrensmeyer, 1978; Behrensmeyer et al., 2003; Kidwell and Flessa, 1995), and the investigation of fossil remains from the Southern Hemisphere (e.g., Valenzuela-Toro et al., 2013, 2015; Rule et al., 2020, 2021) will likely contribute to overcoming these challenges, potentially expanding the frontiers of studies based on the fossil record.

Pinniped foraging paleoecology has been primarily sourced from the comparative morphology of fossils (Berta et al., 2018). Yet, studies have revealed that neither skull or dental morphology fully capture the diversity of feeding and foraging behaviors on living pinnipeds (e.g., Adam and Berta, 2002; Churchill and Clementz, 2016). Additional quantitative studies were needed to test any paleoecological hypotheses based on comparative morphology. In Chapter 5, I conducted a quantitative examination of the foraging paleoecology of some extinct pinnipeds from the middle Miocene and Pliocene of the eastern North Pacific and western North Atlantic coasts, respectively. In addition to confirming and rejecting some of the prevalent paleoecological hypotheses, Chapter 5 demonstrated that pinniped foraging patterns (i.e., nearshore vs. offshore) developed early in their evolutionary history, hinting that niche partitioning has been a significant factor in the structure of communities over ecologic and geologic time. Future ecomorphological and biogeochemical analyses using these and other nontraditional stable isotope systems such as δ^{25}Mg will likely offer novel insights into pinniped paleoecology.

REFERENCES

Adam, P.J. and Berta, A., 2002. Evolution of prey capture strategies and diet in the Pinnipedimorpha (Mammalia, Carnivora). *Oryctos*, *4*, pp.83-107.

Adamczak, S.K., Pabst, D.A., McLellan, W.A. and Thorne, L.H., 2020. Do bigger bodies require bigger radiators? Insights into thermal ecology from closely related marine mammal species and implications for ecogeographic rules. *Journal of Biogeography*, *47*(5), pp.1193-1206.

Badgley, C., Barry, J.C., Morgan, M.E., Nelson, S.V., Behrensmeyer, A.K., Cerling, T.E. and Pilbeam, D., 2008. Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proceedings of the National Academy of Sciences*, *105*(34), pp.12145-12149.

Barnosky, A.D., Hadly, E.A., Gonzalez, P., Head, J., Polly, P.D., Lawing, A.M., Eronen, J.T., Ackerly, D.D., Alex, K., Biber, E., Blois, J., 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science*, *355*(6325), p.eaah4787.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology*, *4*(2), pp.150-162.

Behrensmeyer, A.K., Stayton, C.T. and Chapman, R.E., 2003. Taphonomy and ecology of modern avifaunal remains from Amboseli Park, Kenya. *Paleobiology*, *29*(1), pp.52-70.

Berta, A., Churchill, M. and Boessenecker, R.W., 2018. The origin and evolutionary biology of pinnipeds: seals, sea lions, and walruses. *Annual Review of Earth and Planetary Sciences*, *46*, pp.203-228.

Blanco, F., Calatayud, J., Martín-Perea, D.M., Domingo, M.S., Menéndez, I., Müller, J., Fernández, M.H. and Cantalapiedra, J.L., 2021. Punctuated ecological equilibrium in mammal communities over evolutionary time scales. *Science*, *372*(6539), pp.300-303.

Bowers, M.A. and Brown, J.H., 1982. Body Size and Coexistence in Desert Rodents: Chance or Community Structure? Ecological Archives E063-002. *Ecology*, *63*(2), pp.391-400.

Cadotte, M.W., Arnillas, C.A., Livingstone, S.W. and Yasui, S.L.E., 2015. Predicting communities from functional traits. *Trends in Ecology & Evolution*, *30*(9), pp.510-511.

Churchill, M. and Uhen, M.D., 2019. Taxonomic implications of morphometric analysis of earless seal limb bones. *Acta Palaeontologica Polonica*, *64*(2).

Churchill, M. and Clementz, M.T., 2016. The evolution of aquatic feeding in seals: insights from *Enaliarctos* (Carnivora: Pinnipedimorpha), the oldest known seal. *Journal of evolutionary biology*, *29*(2), pp.319-334.

Connor, E.F. and Simberloff, D., 1979. The assembly of species communities: chance or competition?. *Ecology*, *60*(6), pp.1132-1140.

Dayan, T. and Simberloff, D., 2005. Ecological and community-wide character displacement: the next generation. *Ecology letters*, *8*(8), pp.875-894.

DeRango, E.J., Schwarz, J.F., Piedrahita, P., Páez-Rosas, D., Crocker, D.E. and Krüger, O., 2021. Hormone-mediated foraging strategies in an uncertain environment: Insights into the at-sea behavior of a marine predator. *Ecology and Evolution*, *11*(12), p.7579.

Dewaele, L., Lambert, O. and Louwye, S., 2017. On Prophoca and Leptophoca (Pinnipedia, Phocidae) from the Miocene of the North Atlantic realm: redescription, phylogenetic affinities and paleobiogeographic implications. *PeerJ*, *5*, p.e3024.

Diamond, J.M., 1975. Assembly of species communities. *Ecology and evolution of communities*, pp.342-444.

Drake, J.A., 1990. Communities as assembled structures: do rules govern pattern?. *Trends in Ecology & Evolution*, *5*(5), pp.159-164.

Gotelli, N.J. and McCabe, D.J., 2002. Species co-occurrence: a meta-analysis of JM Diamond's assembly rules model. *Ecology*, *83*(8), pp.2091-2096.

Jablonski, D. and Sepkoski Jr, J.J., 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology*, *77*(5), pp.1367-1378.

Kidwell, S.M. and Flessa, K.W., 1995. The quality of the fossil record: populations, species, and communities. *Annual Review of Ecology and Systematics*, *26*(1), pp.269-299.

Kamaluddin, S.N., Tanaka, M., Wakamori, H., Nishimura, T. and Ito, T., 2019. Phenotypic plasticity in the mandibular morphology of Japanese macaques: captive–wild comparison. *Royal Society open science*, *6*(7), p.181382.

Law, C.J., 2021. Ecological drivers of carnivoran body shape evolution. *The American Naturalist*, *198*(3), pp.406-420.

Leitch, V.D., Bassett, J.H. and Williams, G.R., 2020. Role of thyroid hormones in craniofacial development. *Nature Reviews Endocrinology*, *16*(3), pp.147-164.

Louys, J., Wilkinson, D.M. and Bishop, L.C., 2012. Ecology needs a paleontological perspective. In *Paleontology in ecology and conservation* (pp. 23-38). Springer, Berlin, Heidelberg.

McClenachan, L., Cooper, A.B., McKenzie, M.G. and Drew, J.A., 2015. The importance of surprising results and best practices in historical ecology. *BioScience*, *65*(9), pp.932-939.

McGill, B.J., Enquist, B.J., Weiher, E. and Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends in ecology & evolution*, *21*(4), pp.178-185.

Mori, E., Ancillotto, L., Lovari, S., Russo, D., Nerva, L., Mohamed, W.F., Motro, Y., Di Bari, P. and Plebani, M., 2019. Skull shape and Bergmann's rule in mammals: hints from Old World porcupines. *Journal of Zoology*, *308*(1), pp.47-55.

Pérez-Ramos, A., Tseng, Z.J., Grandal-D'Anglade, A., Rabeder, G., Pastor, F.J. and Figueirido, B., 2020. Biomechanical simulations reveal a trade-off between adaptation to glacial climate and dietary niche versatility in European cave bears. *Science advances*, *6*(14), p.eaay9462.

Rule, J.P., Adams, J.W., Marx, F.G., Evans, A.R., Tennyson, A.J., Scofield, R.P. and Fitzgerald, E.M., 2020. First monk seal from the Southern Hemisphere rewrites the evolutionary history of true seals. *Proceedings of the Royal Society B*, *287*(1938), p.20202318.

Rule, J.P., Adams, J.W. and Fitzgerald, E.M., 2021. Colonization of the ancient southern oceans by small-sized Phocidae: new evidence from Australia. *Zoological Journal of the Linnean Society*, *191*(4), pp.1160-1180.

Smith, C.R., Glover, A.G., Treude, T., Higgs, N.D. and Amon, D.J., 2015. Whale-fall ecosystems: recent insights into ecology, paleoecology, and evolution. *Annual Review of Marine Science*, *7*, pp.571-596.

Stevens, R.D. and Willig, M.R., 2000. Community structure, abundance, and morphology. *Oikos*, *88*(1), pp.48-56.

Tseng, Z.J. and Flynn, J.J., 2018. Structure-function covariation with nonfeeding ecological variables influences evolution of feeding specialization in Carnivora. *Science advances*, *4*(2), p.eaao5441.

Uhen, M.D. and Pyenson, N.D., 2007. Diversity estimates, biases, and historiographic effects: resolving cetacean diversity in the Tertiary. *Palaeontologia Electronica*, *10*(2), pp.1-22.

Valenzuela-Toro, A.M., Gutstein, C.S., Varas-Malca, R.M., Suarez, M.E. and Pyenson, N.D., 2013. Pinniped turnover in the South Pacific Ocean: new evidence from the Plio-Pleistocene of the Atacama Desert, Chile. *Journal of Vertebrate Paleontology*, *33*(1), pp.216-223.

Valenzuela-Toro, A.M., Gutstein, C.S., Suárez, M.E., Otero, R. and Pyenson, N.D., 2015. Elephant seal (*Mirounga* sp.) from the Pleistocene of the Antofagasta Region, northern Chile. *Journal of Vertebrate Paleontology*, *35*(3), p.e918883.

Valenzuela-Toro, A.M., Pyenson, N.D., Gutstein, C.S. and Suárez, M.E., 2016. A new dwarf seal from the late Neogene of South America and the evolution of pinnipeds in the southern hemisphere. *Papers in Palaeontology*, *2*(1), pp.101-115.

Van Valkenburgh, B., 1985. Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology*, *11*(4), pp.406-428.

Van Valkenburgh, B., 1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology*, *14*(2), pp.155-173.

Van Valkenburgh, BV., 1994. Ecomorphological analysis of fossil vertebrates and their paleocommunities. In: Wainwright PC, Riley SM, editors. Ecological morphology: integrative organismal biology. Chicago (IL): University of Chicago Press. pp. 140 – 66.

Velez-Juarbe, J., Domning, D.P. and Pyenson, N.D., 2012. Iterative evolution of sympatric seacow (Dugongidae, Sirenia) assemblages during the past~ 26 million years. *PLoS One*, *7*(2), p.e31294.

Velez-Juarbe, J. and Valenzuela-Toro, A.M., 2019. Oldest record of monk seals from the North Pacific and biogeographic implications. *Biology letters*, *15*(5), p.20190108.

Weiher, E., Clarke, G.P. and Keddy, P.A., 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, pp.309-322.

White, H.E., Goswami, A. and Tucker, A.S., 2021. The intertwined evolution and development of sutures and cranial morphology. *Frontiers in Cell and Developmental Biology*, *9*, p.690.

Wooller, M.J., Bataille, C., Druckenmiller, P., Erickson, G.M., Groves, P., Haubenstock, N., Howe, T., Irrgeher, J., Mann, D., Moon, K. and Potter, B.A., 2021. Lifetime mobility of an Arctic woolly mammoth. *Science*, *373*(6556), pp.806-808.

APPENDIX 1

Original raw $\delta^{13}C$ and $\delta^{15}N$ values of eared seals obtained for Chapters 1, 2, and 3

APPENDIX 2

Original raw $\delta^{13}C$ and $\delta^{18}O$ values of eared seals obtained for Chapter 5