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“MECANISMOS DE COEXISTENCIA DE DOS ESPECIES SIMPÁTRICAS DE LOBOS MARINOS, *Arctocephalus australis* y *Otaria byronia*, EN PUNTA SAN JUAN, PERÚ”

TESIS PARA OPTAR EL GRADO DE
DOCTORA EN CIENCIAS DE LA VIDA

SUSANA CARDENAS ALAYZA

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“MECHANISMS OF COEXISTENCE OF TWO SYMPATRIC SPECIES OF PINNIPEDS, *Arctocephalus australis* AND *Otaria byronia*, IN PUNTA SAN JUAN, PERU”

THESIS FOR COMPLETING DOCTORAL
DEGREE IN LIFE SCIENCES

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Un lugar importante dónde empezar es agradecer a todo el personal del Programa de Punta San Juan. En los últimos años, desde que me convertí en la Directora del Programa, agradezco a mi equipo por estar abierto a mis ideas y planes para recolectar información, muestras y marcar animales en el campo. Y, también por continuar el trabajo mientras he estado ocupado con este doctorado. El Programa de Punta San Juan sólo es posible gracias a personas motivadas que están dispuestas a aprender e innovar para la investigación y la conservación. Por ello agradezco al personal de campo pasado y presente Marco Cardeña, Paulo Colchao, Daniel Torres, Juan Carlos Jerí; a las asistentes de investigación María José Ganoza, Karla Calderón, Lyanne Ampuero y al personal administrativo/operativo Ken Rojas y Fernando Nishio que también han sido piezas importantes para "lograr las cosas". Y por supuesto, una larga lista de increíbles pasantes y voluntarios que a través de los años han hecho posible la toma de muestras y los análisis como parte de su formación en el Programa Punta San Juan.

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Empecé a trabajar en el seguimiento de pinnípedos (capítulo 3) cuando regresé a Perú después de obtener mi maestría en dinámica de la población de lobos marinos finos, que me dejó con más preguntas que respuestas (¡lo cual considero positivo!). Quería saber dónde obtenían su alimento los lobos marinos finos y si competían con los lobos marinos chuscos. Cuando empecé esta aventura, ¿quién iba a pensar que esas viejos viejos transmisores satelitales, amablemente donadas por Andrew Trites en 2013, serían los loggers de los primeros lobos marinos chuscos rastreados en Perú? Gracias Andrew, por la confianza. El capítulo 3 ha involucrado a mucha gente en el campo. Me gustaría dar las gracias a mi *partner* en marcaje de lobos, el veterinario de fauna silvestre Mike Adkesson. Con Mike hemos organizado muchas temporadas de campo con pinnípedos en PSJ con múltiples objetivos. Juntos hemos conseguido financiamiento para hacer posible temporadas de campo en Perú, hemos importado una innumerable cantidad de equipos (¡y personas!) a Perú; así como contactado con expertos para preparar nuestras temporadas de campo para hacer las cosas bien. Mientras aprendíamos cómo hacerlo, hemos formado a muchos biólogos, veterinarios y técnicos veterinarios y, junto a ellos, seguimos aprendiendo. Mi más profundo agradecimiento a todos los equipos que han trabajado con nosotros en el campo durante las temporadas de pinnípedos 2013-2019 de PSJ incluidas en esta tesis. Me gustaría recordar especialmente a Gwen Jankowski, una veterinaria y persona increíble que rápidamente conectó con la magia de Punta San Juan y con la que trabajé estrechamente marcando lobos marinos finos en PSJ. Gwen, tu ausencia es irremplazable y sé que te interesaría mucho conocer todos estos resultados. ¡Por tí, amiga!

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PUBLICATIONS

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Edwards MR, **Cárdenas-Alayza S**, Adkesson MJ, Daniels-Abdulahad M, Hirons AC (2021) Peruvian Fur Seals as Archivists of El Niño Southern Oscillation Effects. *Front. Mar. Sci.* 8:651212 https://doi.org/10.3389/fmars.2021.651212 (**Capítulo 4**)

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Cárdenas-Alayza S, Torres, D.A., Gutiérrez D, Tremblay Y. Resource partitioning as a mechanism for trophic segregation in sympatric otariids from the productive upwelling Peruvian Humboldt Current System. Manuscrito enviado a la revista Austral Ecology. (**Capítulo 2**)

Cárdenas-Alayza S, Adkesson, M.J., Gutiérrez D, Demarcq, H, Tremblay Y. Multiple strategies for segregation during foraging in sympatric otariids of the Peruvian upwelling Humboldt Current System. Manuscrito enviado a la revista Marine Ecology Progress Series (**Capítulo 3**)

Cárdenas-Alayza S, Adkesson, M.J., Edwards, M.R., Hirons, A.C., Gutiérrez D, Tremblay Y, Franco-Trecu, V. Sympatric otariids increase trophic segregation in response to warming ocean conditions in Peruvian Humboldt Current System. Manuscrito enviado a la revista PLOS ONE (**Capítulo 4**)

TABLE OF CONTENTS

TABLE OF FIGURES

TABLE OF TABLES

RESUMEN DE TESIS

El principio de exclusión competitiva predice que las especies mostrarán mecanismos de segregación para coexistir. En el Sistema de la Corriente de Humboldt (HCS) en Perú, los lobos marinos chuscos (SASL, *Otaria byronia*) coexisten con lobos marinos finos (SAFS, *Arctocephalus australis*). Sin embargo, la segregación trófica, temporal y espacial durante la búsqueda de alimento no está claramente definida. El presente estudio describe y compara los nichos ecológicos de las dos especies para determinar si existe diferenciación / sobreposición interespecífica e intraespecífica de nichos. Este estudio se desarrolla en Punta San Juan (PSJ) en Perú, donde se reproducen ambas especies. Las trayectorias poblacionales demuestran que ambas poblaciones se encuentran en un estado de declive. Una reducción en juveniles sugiere que una limitación de recursos explica el declive actual (Capítulo 1). Se detectó la segregación alimentaria interespecífica según tipo de presa. Sin embargo, también se encontró un solapamiento trófico durante un El Niño, lo cual sugiere que los eventos climáticos pueden exacerbar la competencia (Capítulo 2). Un análisis de locaciones en el mar determinó que los machos se segregan en el espacio y tiempo; mientras que las hembras se traslapan en el espacio pero tienen mecanismos de segregación temporal. Las variables ambientales asociadas a hembras sugieren afinidad al hábitat pelágico en SAFS y costero en SASL. Mientras que, los machos presentan mayor variabilidad interindividual, que aún falta explorar (Capítulo 3). Finalmente, se investigó la segregación de nicho a largo plazo en las firmas isotópicas en las vibrisas de SAFS y SASL. En general, los otáridos ampliaron sus nichos tróficos como respuesta al aumento del nivel del mar y a temperaturas oceanográficas más cálidas. La disminución general en la señal de $\delta^{15}N$ sugiere un empobrecimiento en la base de la red trófica, con efectos *bottom-up* (Capítulo 4). Juntos, estos resultados ayudan a explicar el declive poblacional actual, y sirven para extender recomendaciones de conservación para las poblaciones de otáridos en HCS.

PALABRAS CLAVES

COEXISTENCIA; SEGREGACIÓN; PINNÍPEDOS; ECOLOGÍA TRÓFICA; NICHOS; SISTEMA DE LA CORRIENTE DE HUMBOLDT

THESIS ABSTRACT

The principle of competitive exclusion predicts that species will exhibit segregation mechanisms to coexist. In the Humboldt Current System (HCS) in Peru, sea lions (SASL, *Otaria byronia*) coexist with fur seals (SAFS, *Arctocephalus australis*). However, trophic, temporal and spatial segregation during foraging is not clearly understood. The present study describes and compares the ecological niches of the two species to determine if there is interspecific and intraspecific niche differentiation/overlap. This study is conducted at Punta San Juan (PSJ) in Peru, where both species breed. Population trajectories show that both populations are in a state of decline. A reduction in juveniles suggests that resource limitation explains the current decline (Chapter 1). Interspecific feeding segregation according to prey type was detected. However, trophic overlap was also found during an El Niño, suggesting that climatic events may exacerbate competition (Chapter 2). An analysis of at-sea locations determined that males segregate in space and time; whereas females overlap in space but have temporal segregation mechanisms. Environmental variables associated with females suggest an affinity for pelagic habitat in SAFS and coastal habitat in SASL. Males, on the other hand, show greater inter-individual variability, which remains to be explored (Chapter 3). Finally, long-term niche segregation in isotopic signatures was investigated in SAFS and SASL vibrissae. In general, otariids expanded their trophic niches in response to sea level rise and warmer oceanographic temperatures. The overall decrease in the $\delta^{15}N$ signal suggests an impoverishment at the base of the food web, with bottom-up effects (Chapter

4). Together, these results help to explain the current population decline, and serve to extend conservation recommendations for otariid populations in HCS.

KEYWORDS

COEXISTENCE; SEGREGATION; PINNIPEDS; TROPHIC ECOLOGY; NICHES; HUMBOLDT CURRENT SYSTEM

RÉSUMÉ DE THÉSE

Le principe d'exclusion compétitive prédit que les espèces feront preuve de mécanismes de ségrégation pour coexister. Dans le système du courant de Humboldt (HCS) au Pérou, les lions de mer sud-américains (SASL, *Otaria byronia*) coexistent avec les otaries à fourrure sud-américaines (SAFS, *Arctocephalus australis*). Cependant, la ségrégation trophique, temporelle et spatiale pendant la recherche de nourriture reste largement inconnu. La présente étude décrit et compare les niches écologiques des deux espèces afin de déterminer s'il existe une différenciation/un chevauchement des niches interspécifiques et intraspécifiques. Cette étude se déroule à Punta San Juan (PSJ) au Pérou, où les deux espèces se reproduisent. Les trajectoires des populations montrent que les deux populations sont en état de déclin. Une réduction des juvéniles suggère que la limitation des ressources explique le déclin actuel (Chapitre 1). Une ségrégation alimentaire interspécifique en fonction du type de proie a été détectée. Cependant, un chevauchement trophique a également été constaté lors d'un El Niño, ce qui suggère que les événements climatiques peuvent exacerber la compétition (Chapitre 2). Une analyse des localisations en mer a permis de déterminer que les mâles se séparent dans l'espace et dans le temps, tandis que les femelles se chevauchent dans l'espace mais disposent de mécanismes de ségrégation temporelle. Les variables environnementales associées aux femelles suggèrent une affinité pour l'habitat pélagique chez les SAFS et l'habitat côtier chez les SASL. Les mâles, en revanche, présentent une plus grande variabilité interindividuelle, qui reste à explorer (Chapitre 3). Enfin, la ségrégation de niche à long terme dans les signatures isotopiques a été étudiée dans les vibrisses SAFS et SASL. En général, les otariidés ont étendu leurs niches trophiques en réponse à l'élévation du niveau de la mer et au réchauffement des températures océanographiques. La diminution globale du signal δ15N suggère un appauvrissement à la base du réseau alimentaire, avec des effets *bottom-up* (Chapitre 4). Ces résultats aident à expliquer le déclin actuel de la population, et servent à étendre les recommandations de conservation pour les populations d'otariidés dans le HCS.

MOTS CLÉS

COEXISTENCE ; SEGREGATION ; PINNIPEDES ; ECOLOGIE TROPHIQUE ; NICHES ; SYSTEME DU COURANT DE HUMBOLDT

INTRODUCTION

> "WHAT WORLD LIES BEYOND THAT STORMY SEA
> I DO NOT KNOW,
> BUT EVERY OCEAN HAS A DISTANT SHORE,
> AND I SHALL REACH IT."
> *- Cesare Pavese*

1. Introduction

Understanding how sympatric species with similar requirements coexist, is an important theme in ecology. Competition is an ecological processes permeated by natural selection, that shapes species in present time, in reference to the conditions of their ecological setting. Competition can compromise the fitness of the species involved and may ultimately lead to the competitive exclusion of one species (Pacala & Roughgarden, 1985). The ways in which species within ecological communities partition available resources among themselves is a major determinant of the species diversity. A community with more resource sharing or greater niche overlap, will support more species than one with less niche overlap. Thus, coexisting species must differ in their ecological requirements by at least some minimal amount to avoid competitive exclusion (Pianka, 1974).

This study focuses on two sympatric top predator populations of otariid species South American fur seals (SAFS, *Arctocephalus australis*) and South American sea lions (SASL, *Otaria byronia*), that appear to have similar trophic requirements. After population declines caused by extreme food shortage due to 1997-98 El Niño Southern Oscillation (ENSO), SASL in Peru have been growing steadily, with an estimated population of over ca. 130,000 individuals (IMARPE, 2014b). In comparison SAFS in Peru have not been able to recover in the same extent, barely reaching a population of ca. 11,000 individuals (IMARPE, 2014b). This study focuses on information collected via instrumentation of animals, counts and samples collected at Punta San Juan (PSJ, Latitude: 15°22’) in south

Peru, where these two species share a common coastal haul-out site for reproduction. In PSJ, breeding populations concentrate up to 5,000 SAFS and 12,000 SASL within the 2013-2019 study period of this thesis. In Peru, these species have temporal segregation in their breeding seasons, which are 1-3 months a part. Allochrony, which is recognized as a major driver behind speciation, can be considered to facilitate resource partition during energetically critical times (Taylor & Friesen, 2017). In Peru, SAFS breed during October-December and SASL breed during January-March. However, lactation of offspring can be extended compared to other otariid species, and time of weaning is flexible with reports of 6 - 36 months, with high interannual variability (Majluf, 1987; Soto, 2004). This generates a temporal overlap in the time of high energetic demand during which females have to ensure the survival of their young.

To understand the level of competition between these two species, it is necessary to understand the overlap and/or segregation between trophic niches (e.g., niche differentiation)). This will only be possible by determining the species mechanisms of exploitation and resource partitioning in their environment. When species are living in the same habitat, the ways in which they can partition their resources are: spatial separation (e.g. feeding in different depths or geographic locations); temporal separation of resources (e.g. utilizing resources that are available at different times of day or different seasons) or dietary segregation (e.g. consumption of different prey types) (Begon et al., 2006). However, it is crucial to take into account the environmental context of coexisting species; in which varying conditions can produce new responses before patterns are completely

established (Figure I.1).

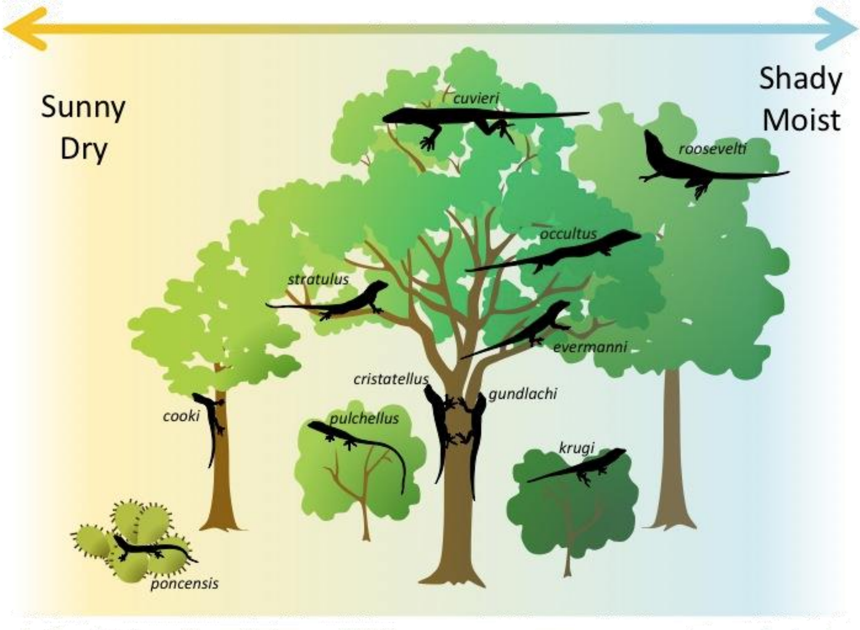


Figure I. 1 Diagram showing resource partitioning among 11 species of anole lizards found on the island of Puerto Rico. Each species occupies a different type or elevation of vegetation. The habitat is further partitioned by the amount of sunlight and moisture available. Image by Eva Horne modified from (Williams, 1983). Source: https://www.khanacademy.org/science/ap-biology/ecology-ap/community-ecology/a/niches-competition

Another important influential feature on the foraging mode in otariids may be local marine productivity and its effect on prey availability. It may be that, except in very productive regions, smaller body size favors foraging on a highly patchy but dense prey resource near the surface (zooplankton, small fish or squid) compared to larger body sized air breathing mammals are better adapted for searching for more evenly distributed but less dense prey resource

on the benthos (larger fishes or octopus). This coincides with the trend of greater mass of prey items being consumed by benthic foraging sea lions and the greater proportions of time spent at sea diving compared to smaller epipelagic fur seals (Arnould & Costa, 2006). More recent studies have elucidated that this pattern is not always the norm, and there are some sea lion populations that inhabit upwelling areas that display pelagic foraging (Hückstädt et al., 2014), fur seals that are benthic divers (Arnould & Hindell, 2001) and some otariids that display a combination of shallow and deep dives according to metabolic needs and local prey availability (Harcourt et al., 2002; Villegas-Amtmann et al., 2008). This demonstrates the plasticity in the adaptations of populations and individuals to local spatial and temporal conditions, and which may also vary according to sex and age (Weise & Costa, 2007).

Thus, the main goal of this study is to describe the ecological niches of sympatric otariid species to determine intraspecific and interspecific niche differentiation / overlap in the marine environment of the HCS. It is particularly important to understand the partitioning mechanisms that drive coexistence of predator populations. Predators usually affect ecosystems through top-down control and behaviorally mediate impacts on prey species. Thus, the maintenance of predator population is key to preserve healthy ecosystems. Accurate assessments of foraging ecology are essential to help understand the function of predators and structure of ecosystems. As ecosystems and trophic webs are highly dynamic, the coupling of traditional

diet information (e.g. hard parts identified in scats) with foraging location data can add a spatial and temporal dimension to dietary estimates (Jeanniard du Dot et al., 2017). Furthermore, long time series of population counts and isotopic signatures from whiskers will provide a different temporal windows to explore trophic habits in SAFS and SASL during 15 to 20 year timeframes. To achieve this, the current study proposes to combine a suite of datasets and analytical tools that will offer insight into the trophic dimension of both species at different temporal and spatial scales to explain current divergent trends in population abundance of sympatric otariid predators. Theoretical Framework

1.1 *Ecological niche*

A niche is an n-dimensional hypervolume which defines the limits within which a given species can survive and reproduce for a number of environmental factors, including both conditions and resources (Hutchinson & MacArthur, 1959). The resource dimensions of a species niche can sometimes be represented in similar manner to that adopted for conditions, with lower and upper limits within which a species can thrive. Thus, a predator may only be able to detect and handle prey between lower and upper limits of size. Together, resources and conditions, define a species niche.

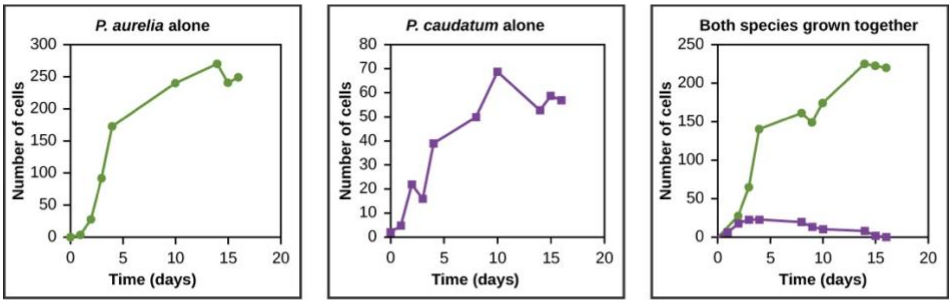
The ecological niche of a species needs to be multidimensional. In an *n*-dimensional hypervolume, n is the number of dimensions that make up the niche. Usually a species has a larger ecological niche in the absence of competitors and

predators. Thus, there are a certain number of combinations of conditions and resources that can allow a species to maintain a viable population, but only if it is not being adversely affected by competitors (Hutchinson & MacArthur, 1959).

All environments are heterogeneous. The extent to which an environment is heterogeneous depends on the scale of the organism that senses it. There may also be gradients in space (e.g. depth) or gradients in time (e.g. seasonal cycles). Gradients can be directional (e.g. accumulation of pollutants) or erratic (e.g. tsunami) as well. When a species is exposed to variations in the physical factors of the environment, the two species that interact can change and produce alterations in the life of the other, and each may generate selective forces that direct the evolution of the other (Begon et al., 2006). Behavior and metabolism constrain the animal within a narrow niche and deny it access to what otherwise may appear as a suitable alternative food source (Begon et al., 2006). Temperature, for example, limits the growth and reproduction of all organisms, but different organisms tolerate different ranges of temperature. Thus, in this example, the temperature range is one dimension of the organisms' ecological niche.

1.2 ***Competition and coexistence***

From a historical evolutionary point of view, natural selection have shaped species. The ecological effects are broad and species may be eliminated from a habitat by competition from individuals of other species or reductions in fecundity and survival appear (Begon et al., 2006). Under current ecological conditions, competition and resources availability shape species *in vivo*. In this context, competition can compromise the fitness of the species involved and may ultimately lead to the competitive exclusion of one species (Figure I.2), following the Competitive Exclusion Principle (Hardin, 1960; Pacala & Roughgarden, 1985).



(a) (b) (c)

Figure I. 2 Competitive exclusion example showing Paramecium caudatum grow well individually, but when they compete for the same resources, P. aurelia outcompetes P. caudatum. Image from: Fowler et al., 2013. Source: https://openstax.org/books/concepts-biology/pages/19-4-community-ecology

When two species compete, individuals of one or both species may suffer reductions in fecundity or survivorship. The fittest individuals of each species may be those that escape competition because they utilize the habitat in ways that differ from most of those adopted by individuals of the other species. Natural selection can favor such individuals and eventually the population can consist entirely of them. The two species become more different from one another, compete less and can evolve to coexist (Begon et al., 2006). The Lotka-Volterra model predicts the stable coexistence of competitors in situations where interspecific competition is, for both species, less significant than intraspecific competition (Begon et al., 2006). Thus, niche differentiation will tend to concentrate competitive effects more within species than between them. The Lotka-Volterra model and the Competitive Exclusion Principle imply that complete competitors cannot coexist and species must have ecological differentiation as a necessary condition for coexistence (Figure I.3, Hardin, 1960).

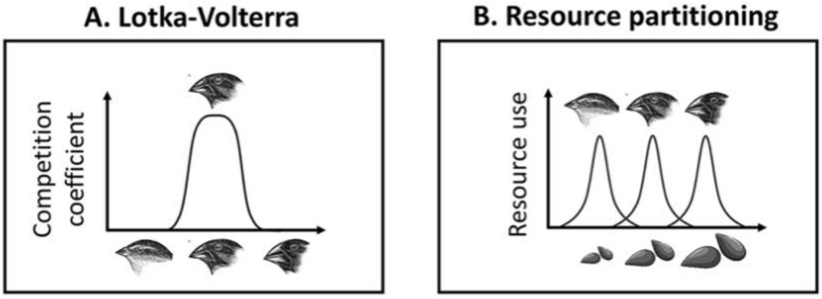

A. Lotka-Volterra
B. Resource partitioning

Figure I. 3 Schematic representation of Lotka-Volterra competition. Image from D’Andrea et al., 2019

1.3 *Sympatry in otariids*

Sympatric species are those species whose breeding ranges and distribution overlap and in which individuals can coexist without hybridizing. Thus, it is defined as the occurrence of two or more species breeding in the same location (Cain, 1953). If two non-interbreeding populations occupy the same geographical territory and the same ecological niche, they are sympatric. Many species of fur seals and sea lions occur in sympatry throughout the world (Bailleul et al., 2005; Dellinger & Trillmich, 1999; Franco-Trecu et al., 2012; Jeglinski et al., 2013; Page et al., 2005; Villegas-Amtmann et al., 2013; Waite, Trumble, et al., 2012). Areas of sympatry, however, represent only a small proportion of the allopatric or non-breeding ranges. The duration of coexistence in sympatric otariid seals is not known, and it is possible that sympatry has resulted from recent population recoveries and recolonization following the cessation of commercial sealing (Costa et al., 2007). If sympatry is a result of recent events, it is possible that divergence is not yet evident or that competitive exclusion is currently occurring. Some authors suggest that the differences in the population dynamics of sea lions and fur seals are associated with the observed divergent trends of epipelagic and benthic foraging (Arnould & Costa, 2006). All species of otariid seals throughout the world were subject to extensive and, in most cases, excessive hunting pressure during the eighteenth and nineteenth centuries. By the late 1800s, however, most species had acquired total legislative protection or were subject to only regulated harvests. Despite this protection, populations of various sea lion species have

experienced very little recovery and in some cases are declining; whereas fur seal species have generally experienced rapid population recovery rates (Costa et al., 2007; Wickens & York, 1997).

1.4 *Interspecific segregation*

Interspecific competition, defined as reciprocal negative effects of one species on another, is an important process determining the structure of natural communities (Chase et al., 2002). This can occur either directly or indirectly mediated by changes in resource availability. Lotka–Volterra competition theory states that coexistence of two species is possible when the per capita effects of intraspecific competition on per capita rates of population growth are greater than those of interspecific competition (Chase et al., 2002; Chesson & Warner, 1981; Schoener, 1983).

In conditions of limited resources, competition between species implies a reduction in some population attributes, such as growth, survival or fecundity (Begon et al., 2006). Closely related species with similar life-history strategies often share similar niches. Non-migratory, central-place foraging species with overlapping ranges may compete for similar resources, such as prey or breeding sites. Among the sympatric marine mammal species with similar life-history traits and foraging habits are the otariids: fur seals and sea lions. In general, where fur seals and sea lions live in sympatry, the fur seal population is typically larger and they appear to outcompete sea lions. Many studies have examined potential

competition between sympatric fur seal and sea lions, and their results are mixed. Some have found ecological segregation with no trophic overlap (Antonelis et al., 1990; Aurioles-Gamboa & Camacho-Ríos, 2007; Dellinger & Trillmich, 1999; Franco-Trecu et al., 2012), while others have found some dietary overlap (Páez-Rosas & Aurioles-Gamboa, 2010; Page et al., 2005; Waite, Burkanov, et al., 2012).

Recent studies that include stable isotope analysis have elucidated findings that provide new insights into understanding how sympatric species exposed to strong interspecific competition can develop foraging strategies that may decrease competition and facilitate survival in stochastic environments with variable resource availability. Individual long-term dietary specialization from two sympatric otariid species using isotopic ratios in whiskers was analyzed in SAFS and SASL of the Uruguayan coast showed that fur seals had a larger trophic niche resulting from generalist individuals, whereas sea lions have a smaller trophic niche, from individuals with higher degree of trophic specialization (Franco-Trecu et al., 2014). Also, a study comparing stable isotopes in Galapagos sea lions (*Zalophus wollebaeki*) and Galapagos fur seals (*Arctocephalus galapagoensis*), found that differences in habitat use. *Z. wollebaeki* was persistent in repeating the use of the same benthic / inshore feeding grounds, whereas *A. galapagoensis* feeds on pelagic / offshore prey items; while both species isotopic signatures vary according to oceanographic conditions (El Niño, La Niña, normal years) (Páez-Rosas et al., 2012).

1.5 *Intraspecific segregation*

Sexual differentiation in the ecological niches in pinniped species is expected due to high dimorphism between sex. Males are originally thought to have higher diving capacity to exploit larger three dimensional foraging areas, and considering that they are not involved in postnatal care, they could feed farther away from the rookery than females and exploit wider ranges and more exclusive foraging habitats (González-Suárez & Cassini, 2014). Stable isotope studies are challenging this assumption and demonstrating that this is not always the case. Several recent studies demonstrate the role of the local environment as a major driver of resource partitioning in otariid populations (Drago et al., 2015).

Individual long-term dietary specialization of male and females sympatric otariid species using isotopic ratios in whiskers was analyzed in sympatric South American fur seals *A. australis* and South American sea lions *O. byronia* on the Uruguayan coast. Sexual dimorphism in body size, present in both species, suggests that males will exploit larger preys often at higher trophic levels. However, in the study, δ^{15}N values showed that both sexes of sea lions and fur seals consumed preys at similar trophic levels. Females in both species, showed wider ranges of δ^{15}N that are associated with a higher consumption of prey at lower trophic levels than males. This differentiation was interpreted by the additional constraint on female foraging trips, since this group is obligated to return to shore to nurse their pup (Franco-Trecu et al., 2014).

In terms of differences in δ13C, different signals between sexes may reflect

physiological (body mass) or behavioral (parental care) differences. An expected result of the same beforementioned study was that males, who are not involved in postnatal care, could use their higher diving capacity to exploit larger, deeper and more distant foraging areas than females. This would lead to wider ranges of a $\delta^{13}C$ in more exclusive foraging habitats. Study results showed that sea lion males had a lower $\delta^{13}C$ values than females; and the opposite was true for fur seals. Although the range of $\delta^{13}C$ was wider for males of both species, there was a large overlap in the overall areas of isotopic niches between the sexes of both sea lions and fur seals. Thus, males despite not being linked to the colonies, have a similar foraging behavior to females off the coast of Uruguay (Franco-Trecu et al., 2014).

1.6 ***Otariids' foraging***

Animals should forage in a way that optimizes their energy intake and, ultimately, fitness. Multiple factors influence foraging behavior, including predation risk and prey availability. Air-breathing mammals and birds foraging underwater are additionally constrained by the duration of their dives as they need to supply oxygen stores frequently (Sigler et al., 2009). The foraging behaviors of top marine predators are related to the energetic requirements of individuals and environmental features (Costa & Gales, 2003). Indeed, according to optimal foraging theory, organisms are supposed to adopt foraging behaviors that optimize fitness for given environmental conditions. In the marine environment, food resources are distributed heterogeneously in space and time and their distribution

is related to oceanographic features. Distribution and behavior of top marine predators are related to physical and biological features (bathymetry, sea-surface temperature, primary productivity), as found in seabirds (Bost et al., 1997; Guinet et al., 1997) and pinnipeds (Georges, Bonadonna, et al., 2000; Jessopp et al., 2004).

Many pinniped studies in the 1980s and 1990s were conducted on lactating females, since this is the age-class with highest energetic constraint, and to increase in the recovery of biologging devices compared to males. Results from these studies have grouped sea lions and fur seals to have two broadly divergent foraging patterns. Lactating sea lions generally undertake short trips (1-2 days) foraging mostly on the benthos of continental shelf areas where they have a continuous dive pattern with no diel variation, foraging mostly on benthic or demersal prey in continental shelf areas (Riet-Sapriza et al., 2013; Thompson et al., 1998; Werner & Campagna, 1995). In contrast, lactating fur seals generally undertake longer trips (4-23 days) foraging mostly on vertically migrating prey in oceanic frontal structures or continental shelf-edges with upwelling regions (Arnould & Costa, 2006), during which diving is mostly nocturnal. This mode of foraging is hereafter referred to as “epipelagic” foraging and mainly occurs in oceanic frontal structures or continental shelf-edges with upwelling regions (Gentry & Kooyman, 1987). The dives occur in the deep scattering layer, with a pronounced diel variation in depth that reflects the vertical migration of their prey (Boyd & Croxall, 1992; Francis et al., 1998; Georges, Tremblay, et al., 2000).

1.7 *Body size and oxygen storage*

A main feature that differentiates fur seals and sea lions is their fur layer. The insulating feature of fur seal integument traps a layer of air within the fur and is inefficient at great depths preventing them from foraging as deep as sea lions (Arnould & Costa, 2006; Gentry & Kooyman, 1987). Also, it has been suggested that the larger body size of sea lions compared to fur seals results in greater oxygen storage capabilities, enabling them to aerobically dive for longer periods and reach higher depths (Costa et al., 1998) and can have implications on the metabolic and reproductive output. The Aerobic Dive Limit (ADL) is a model to understand if pinnipeds and seabirds are performing dives that approach their maximum aerobic capacity. ADL is defined as the maximum dive duration before blood lactic acid levels rises as a result of an increase in anaerobic metabolism, and is therefore a function of both oxygen stores and oxygen consumption (metabolic rate).

Calculated ADL (cADL) is a commonly used proxy for ADL, and is calculated from estimates of volumes of usable oxygen stores divided by oxygen consumption in a particular species (Butler, 2006). Exceeding cADL has been reported for some benthic and deep diving otariids. There is evidence indicating that the diving capacity of fur seals measured in their aerobic dive limit is relatively smaller (1.6 to 1.7 min) compared to sea lions (2.3 to 3.8 min), which imposes a constraint for the depth fur seals are capable of reaching during foraging dives (Costa et al., 2001). It has been proposed that deep diving strategies can put

the population at risk if individuals are unable to cope with environmental variability and fluctuations. Thus, otariids that display benthic foraging usually exhibit smaller population sizes and lower population growth rates compared with those that feed pelagically. A revision on reproductive outputs showed that benthic feeding otariids have been documented to have significant lower birth rates compared to epipelagic feeders (Arnould & Costa, 2006). As mentioned, recent studies have elucidated that the ‘benthic sea lions and pelagic fur seals’ pattern is not always the norm, demonstrating the plasticity in the adaptations of populations and individuals to local spatial and temporal conditions (Villegas-Amtmann et al. 2008, Schwarz et al. 2021). Other studies (Hückstädt et al., 2014) have found a weak relationship between pinniped size and total oxygen stores amongst individuals with different foraging strategies (pelagic and benthic). Thus, local environment is an important driver in diving performance among pinnipeds shaping foraging strategies that needs to be explored in each ecosystem.

1.8 *Peruvian Humboldt Current System*

The Humboldt Current System (HCS) in Peru is recognized as the most productive of the Eastern Boundary Upwelling Systems in the world (Bakun & Weeks, 2008). As other upwelling ecosystems, cold nutrient rich water rises to the euphotic layer by a combination of the South east trade winds and the Coriolis force that fuel Ekman transport, giving rise to primary productivity in the upper pelagic and nearshore areas. Peru’s coast is characterized by a narrow continental shelf,

reaching over 1000 m in less than 50 km offshore (Figure I.4). The shallow productive upwelling waters and shallow thermocline are related to an upper minimum oxygen layer at similar depths of approximately 50-80m on average, constraining expansion of vertical habitat (Figure I.5, Bertrand et al., 2010; Demarcq, 2009; Echevin et al., 2008). These features limit the potential habitat for otariid prey to be linked to the benthos. Thus, in this productive shallow environment foraging on highly patchy, but dense prey resources near the surface, may preclude the advantages of searching for more evenly distributed, but less dense, prey resources on the benthos, constrained by bottom water hypoxia.

Fig. 2. Modelo de elevación digital de la morfología del fondo marino frente a la costa peruana, mostrando en detalle vistas perpendiculares a la costa de cañones que surcan el talud continental: A) cañón de Talara); B) cañón de Chiclayo); y C) cañón de Arequipa. *Erick Chacón y Federico Velazco.*

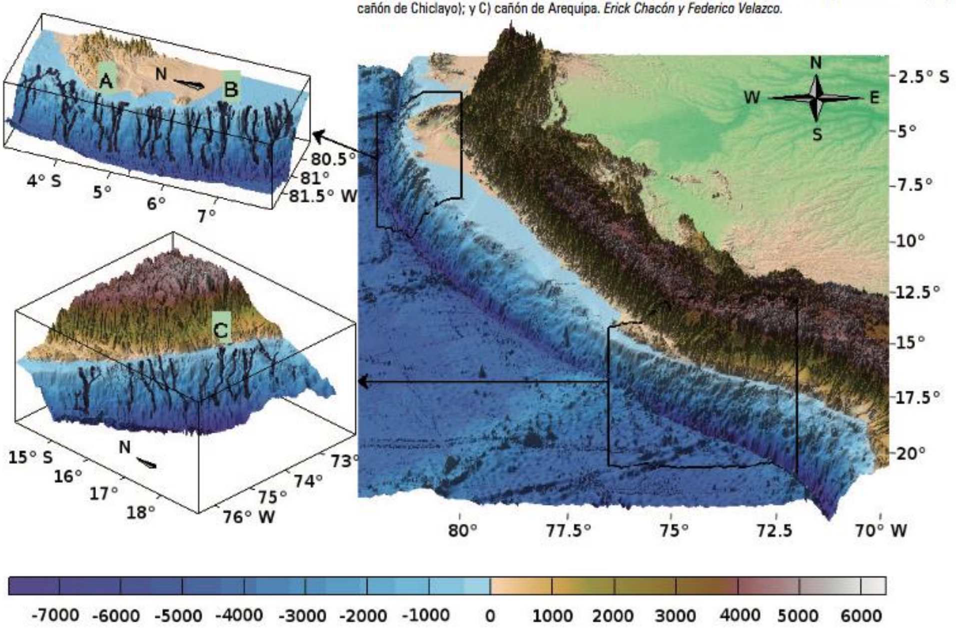


Figure I. 4 Morphology of seafloor along the coast of Peru. Punta San Juan study area located in box C, region with a very narrow continental shelf. Image from IMARPE, 2014a.

Furthermore, HCS is characterized by recurring El Niño Southern Oscillation (ENSO) events, which can vary in intensity and duration. ENSO is known as a cycle of alternating warm El Niño and cold La Niña events and is the most prominent climate signal on Earth (McPhaden et al., 2006). When HCS is affected by warming events, such as the El Niño Southern Oscillation (ENSO) or Kelvin waves, food web composition is altered (Tam et al., 2008). These changes impact the success of predator foraging events and, depending on their intensity and duration, can decrease reproductive output and survival rates in top predators (Majluf, 1991; Trillmich & Dellinger, 1991). Extraordinary ENSO events have triggered significant changes in the food web composition causing nutritional stress and mortality in many species (Bond & Lavers, 2014; Forcada et al., 2006; Oliveira, 2011; Sprogis et al., 2018).

The ENSO events that occurred in 1982-83 and 1997-98, were categorized as ‘Extraordinary’ and are well documented for dramatically altering species composition and reducing marine biomass (Barber & Chavez, 1983; Tam et al., 2008). These climatic events were strong and felt worldwide, changing the availability of prey items and causing declines in reproduction and survival of top marine predator populations around the globe (Milena Arias-Schreiber & Rivas, 1998; Bond & Lavers, 2014; Cárdenas-Alayza, 2012; Forcada et al., 2006; Sprogis et al., 2018; Trathan et al., 2007). For example, the 1997-98 ENSO event caused a reduction of wildlife along Peru’s coast with 75% and 80% reductions in the populations of SAFS and SASL, respectively (Oliveira et al., 2006, 2012). Since

1998 populations have recovered to an extent, but are currently in a state of decline (Cárdenas-Alayza et al., 2021).

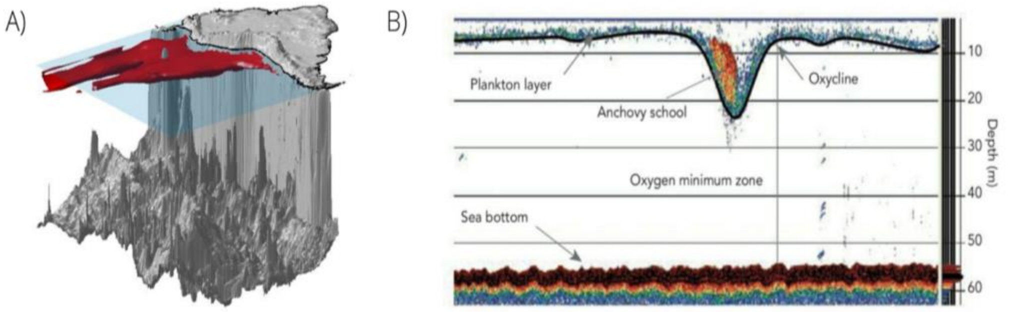


Figure I. 5 A) Example of the distribution of the shallow oxygen minimum zone in the Southeast Pacific Ocean. Source: http://omz.udec.cl ; B) Example of the oxycline delimiting the vertical distribution of plankton and anchovy schools in relation to sea bottom in Peru. Image from IRD /Marbec. Source: https://books.openedition.org/irdeditions/docannexe/image/34324/img-5.jpg

1.9 *A warming climate*

A warming climate is currently altering global ecosystem structure and driving species distributions to higher latitudes, thereby leading to altered interspecific interactions with unspecified consequences (du Pontavice et al., 2020; Walther et al., 2002). Climate driven shifts are more pronounced at the poles where deviations from long-term climatic variables are more striking (Kortsch et al., 2015; Parmesan & Yohe, 2003). However, in the past decade, a series of warming events have taken place in the Pacific Ocean that may affect the organization of predator communities in the Peruvian HCS.

Long-term warming climatic/oceanic events, or heatwaves known as “The

Blob”, have impacted the Pacific Ocean in recent years (Bond et al., 2015). The Blob was first detected in the Gulf of Alaska in 2013-2014 and is a result of a persistent pattern of higher than normal rates of sea level pressure and weak coastal winds. In the past decade in Peru, El Niño conditions occurred between 2014 and 2015 (Graco et al., 2016), and was followed by the strong El Niño event of 2015-2016 that affected the entire Pacific Ocean (Robinson, 2016). This event was then followed by the effects of ‘El Niño costero’ that was a more localized event detected in the El Niño 1+2 region between January and February of 2017 (Paulino et al., 2019). During these years, studies suggest that physical anomalies of these warming ocean events generated a biological response similar to those of El Niño (Espinoza-Morriberón et al., 2017). All the beforementioned events involve the rise of sea level forced by the passage of remotely generated and coastal trapped waves in response to heat expansion (Ryan & Noble, 2002). The thermocline, nearshore depth of chlorophyll-a, and the nutricline deepened, decreasing nutrient enrichment in the euphotic zone. Weak winds caused the reduction in vertical nutrient fluxes to the depleted euphotic zone. A deeper concentration of chlorophyll-a decreased phytoplankton biomass, causing a shift in community structure toward smaller phytoplankton which can have bottom-up effects on food and energy availability at higher trophic levels (Zaba & Rudnick, 2016).

Pinniped researchers have found that body-size declines in aquatic ecosystems is a universal response to climate change. Body size directly

affects energy and water requirements for thermoregulation, energy, mass acquisition and utilization rates and life-history characteristics (Daufresne et al., 2009). For example, Galapagos fur seals from Fernandina Island, in Galapagos Archipelago, that are significantly smaller than sympatric Galapagos sea lions exhibited lower foraging effort when compared. Although sympatric, fur seals are less successful; it is possible that their low plasticity in foraging behavior, expressed by their lower individual variability, has contributed to their overall smaller population size. Compared to the high plasticity in sea lions, fur seals are more impacted by variations in prey abundance, such as during ENSO events (Villegas-Amtmann et al., 2013). Oceanographic processes are changing as a result of climate change and direct anthropogenic influence, altering features of the current pelagic habitat. This, in synergy with competition for prey with fisheries can severely hamper future recoveries of otariids after future ENSO events.

1.10 *Punta San Juan study site*

Within the HCS there are few sites where otariids are found in important sympatric colonies. Punta San Juan (PSJ, 15°22’S, 75°12’W), a peninsula on the southern coast of Peru, is one such site. PSJ is a peninsula protected from land by a 1.2 km concrete wall that is part of a marine coastal national reserve system called ‘Reserva Nacional Sistema de Islas, Islotes y Puntas Guaneras’ (RNSIIPG, Spanish acronym). The PSJ peninsula consists of 20 sites, which

are beaches and coves all used for breeding and/or as haul-out sites by SASL and SAFS (Figure I.6). PSJ supports important breeding rookeries of both species with an annual range of 6-12,000 SASL and 2-5,000 SAFS over the past 5 years (Cárdenas-Alayza et al., 2021). In PSJ, SAFS and SASL colonies are found year round, making it an ideal setting for interspecific comparison studies. In PSJ operates the Punta San Juan Program, a unique long-term research program that monitors otariid populations *in-situ* for over 20 years. This has permitted the routine collection of scats and counts as well as research projects that include instrumentation, morphometrics and whisker collection of pinnipeds, analyzed for this doctoral thesis project.

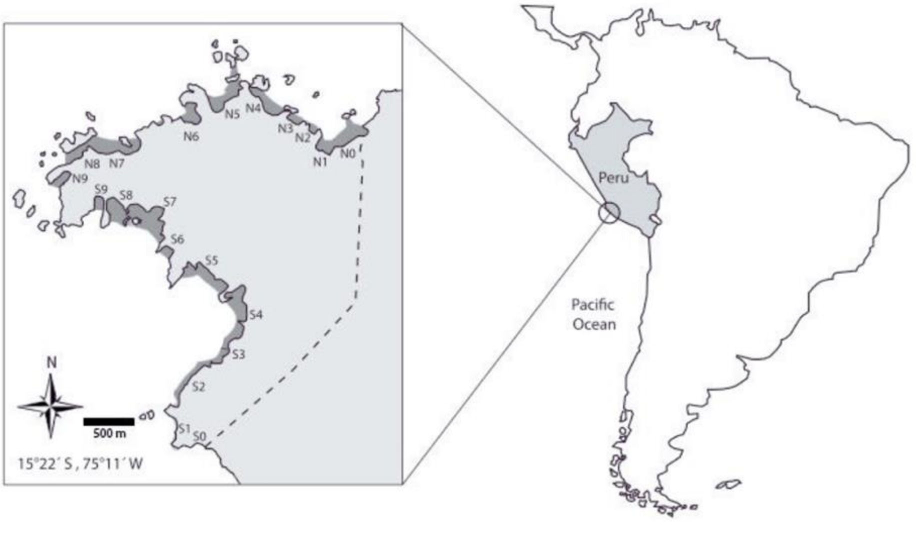


Figure I. 6 Location of Punta San Juan peninsula (left) on the south coast of Peru, South America (right). Image modified from S. Cárdenas-Alayza, 2012.

2. Thesis Objectives

The main goal of this thesis is to describe and compare the ecological niches of sympatric otariid species *Arctocephalus australis* and *Otaria byronia* that coexist in Punta San Juan; and determine intraspecific and interspecific niche differentiation/overlap. This will be addressed through three specific goals. The first, is to describe and compare the trophic ecology of sympatric pinnipeds according to species and sex. The second is to describe and compare the environmental variables that characterize ecological niches between the sympatric pinnipeds according to species and sex. Finally, the third objective is to describe and compare the foraging strategies (spatial and temporal dimensions) within the ecological niches of the sympatric pinnipeds according to species and sex.

3. Structure of the Thesis

To contextualize the current state of the study species, population trends in abundance and biomass of sympatric study species are analyzed to understand the potential interspecific competition at PSJ. To address trophic ecology, the coupling of traditional diet information (e.g., hard parts recovered in scats), foraging location data and stable isotopes information are explored with the aim to better understand the use of the marine environment by male and female SAFS and SASL, at different resolutions. As part of each analysis, descriptions of the environment are included that help characterize the conditions for each trophic dataset. In sum, the current study proposes to combine a suite of datasets, divided into four data chapters, in order to shed light into the foraging ecology of both species and sexes (Figure I.7) at different temporal and spatial scales to explain current population trends.

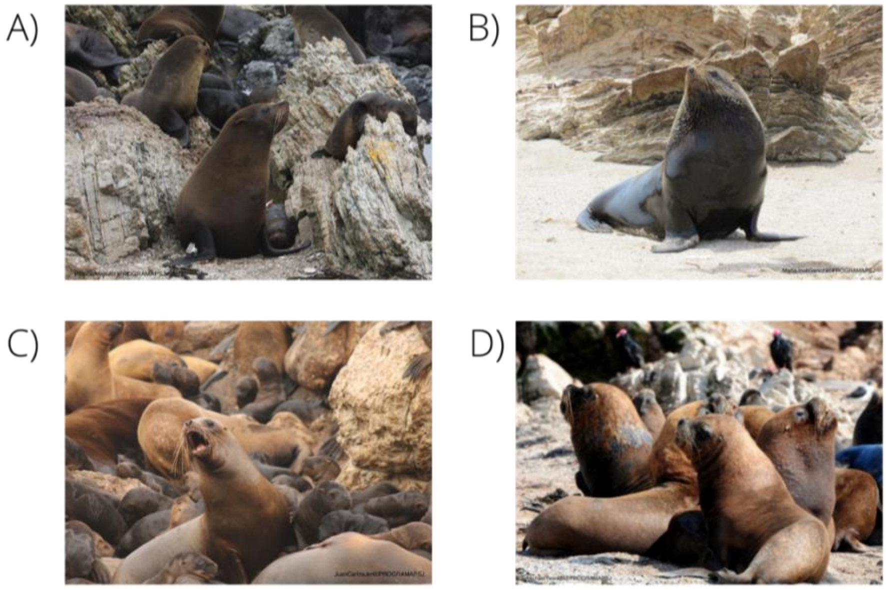


Figure I. 7 Study species and groups included in this study: South American fur seal (Arctocepalus australis) A) adult female with pup; B) territorial male and South American sea lion (Otaria byronia) C) adult female with pup; D) sub-adult males. Images provided by Punta San Juan Program, CSA-UPCH.

Chapter 1 – Trends in sympatric pinniped populations suggest resource limitations in the Peruvian Humboldt Current System

I evaluate population trajectories of Peruvian sympatric otariids and discuss mechanisms for competition and/or resource limitation. In this chapter, I analyze population trajectories of SASL and SAFS in a sympatric breeding site in Punta San Juan, Peru between 2001-2019. By using a combination of abundance time series, age-class proportions and biomass time series within and between species. This is

considered as a first step towards exploring if larger body mass (SASL), a proxy for higher consumption of prey resources, can offer a greater competitive advantage in comparison to a smaller species (SAFS) to sustain population abundance in a common environmental setting.

Chapter 2 – Resource partitioning as a mechanism for trophic segregation in sympatric otariids from the productive upwelling Peruvian Humboldt Current System

To understand if resource partitioning contributes towards sympatric breeding of otariids in Peru’s dynamic HCS I compared seasonal diet composition SAFS and SASL, over 15 seasons between 2015 and 2018 which included ENSO and non-ENSO conditions. The objective of this research is to assess if resource partitioning exists in the sympatric otariid populations at PSJ over a four year study period. My hypothesis is that for sympatry to occur both otariids species should exploit food resources differently, being resource partitioning a potential mechanism to avoid competitive exclusion. Furthermore, this chapter updates knowledge on resource consumption by each species and contribute towards the understanding of the current foraging strategies of sympatric otariids in the highly productive and dynamic HCS.

Chapter 3 - Multiple strategies for segregation during foraging in sympatric otariids of the Peruvian upwelling Humboldt Current system

I analyzed locations of 18 SASL and 17 SAFS (12 females, 23 males) equipped

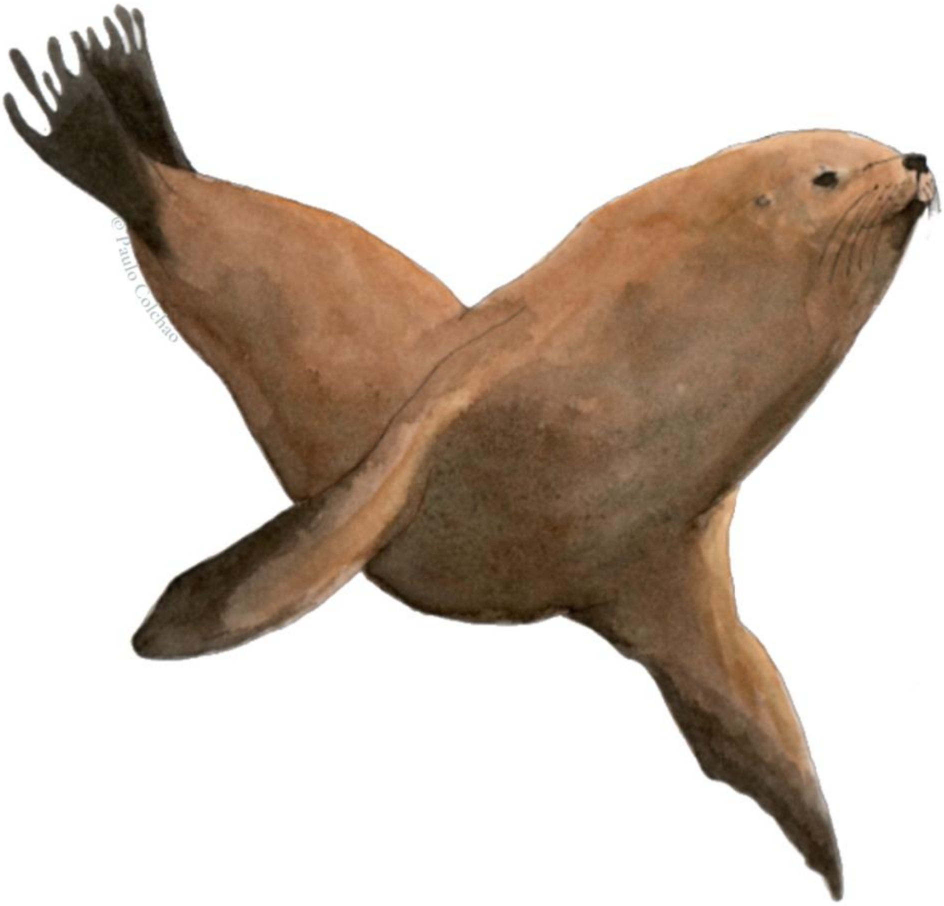
with satellite tags in Punta San Juan, Peru during 2013-2017. I determine if temporal and spatial segregation among species-sex groups is influenced by morphological (body mass), behavioral or environmental conditions during foraging. Due to larger body mass in SASL, sexual dimorphism and different parental care, I expect SASL will travel longer distances, duration and cover larger areas than SAFS; and that males of both species will also travel longer distances, duration and cover larger areas in comparison to females. Tracks were constructed, analyzed and behaviors categorized to understand when individuals were actively exploiting a prey patch with the ultimate goal to understand spatial and temporal overlap and the associated environmental conditions (Sea surface temperature, Chlorophyll-a, Distance from Coast, Proximity to Fronts and Front Gradient) that characterize foraging events identified at sea.

Chapter 4 - Sympatric otariids increase trophic segregation in response to warming ocean conditions in Peruvian Humboldt Current System

Recent ocean warming events (2014 – 2017) that can decrease and impoverish prey biomass have occurred in HCS. In this context, my aim was to assess the effect of warming events on long-term inter- and intra-specific niche segregation. Whisker samples from SAFS (55 females and 21 males) and SASL (14 females and 22 males) collected in Punta San Juan, Peru were used to determine interspecific isotopic niche segregation based on $\delta^{13}C$ and $\delta^{15}N$ values organized at a monthly scale for 2005 – 2019. I determined and compared niche width of species-sex groups and their overlap to assess response to environmental changes.

CHAPTER 1

Trends in sympatric otariid populations suggest resource limitations in the Peruvian Humboldt Current System



Cárdenas-Alayza S, Gutiérrez D, Tremblay Y. (2021) Trends in sympatric otariid populations suggest resource limitations in the Peruvian Humboldt Current System. Mar Environ Res:105349.
https://doi.org/10.1016/j.marenvres.2021.105349

Abstract

Sympatric species evolve mechanisms to avoid competition and coexist. In the Humboldt Current System (HCS), populations of South American sea lions (SASL, *Otaria byronia*) and South American fur seals (SAFS, *Arctocephalus australis*) fluctuate mostly due to ENSO events and prey availability. We evaluate population trajectories of Peruvian sympatric otariids and discuss mechanisms for competition and/or resource limitation. For this purpose, we analyzed population trajectories of SASL and SAFS in a sympatric breeding site in Punta San Juan, Peru between 2001-2019. Wavelet analysis was used to extract trends and derivatives to estimate rates and turning points. Age-class proportions and biomass times series were constructed from weekly counts and evaluated. Both populations show a growth phase and subsequent decline. SAFS started decline ~2.25 years before and at a rate 1.5 times faster than SASL. Decrease in juvenile age-class suggests that resource limitation is the main contributing factor for current population decline.

Keywords: Peru; Punta San Juan; population decline; competition; fur seal; sea lion; *Otaria byronia*; *Arctocephalus australis*; pinniped

1. Introduction

Understanding how species coexist is an important theme in ecology. Coexistence theory is a framework to understand how competitor traits can maintain species diversity and prevent competitive exclusion, even among similar species in ecologically similar habitats (Chesson & Kuang 2008). Competition can compromise the fitness of one of the species involved, and may ultimately lead to its exclusion (Pacala & Roughgarden, 1985). Under the resource-utilization niche concept, two species cannot occupy the same ecological niche without exerting strong competition on each other (Schoener 1974). The Lotka–Volterra competition model states that coexistence of two species is possible when the competitive effect that a species has on another species (interspecific competition) is less than the competitive effect that it has on its own species (intraspecific competition) (Chesson & Warner 1981, Schoener 1983, Chase et al. 2002). Furthermore, competitive interactions are known to be stronger between morphologically and phylogenetically closely related sympatric species (Schoener 1983, Loveridge & Macdonald 2003, Di Bitetti et al. 2009).

Otariids, composed of fur seals and sea lions, occur in sympatry in a number of upwelling regions in the world and have many similar life-history traits and foraging habits (Dellinger & Trillmich 1999, Bailleul et al. 2005, Page et al. 2005, Franco-Trecu et al. 2012, Waite et al. 2012b, Jeglinski et al. 2013, Villegas-Amtmann et al. 2013a). Coexisting species are expected to develop

strategies for niche differentiation when resources become scarce, to mitigate the reduction in population attributes, such as growth, survival or fecundity (Begon et al. 2006). The duration of coexistence in sympatric otariid seals is not known, and it is possible that sympatry has resulted from recent population recoveries posterior to the period of commercial sealing (Arnould & Costa 2006). If sympatry is a result of recent events, it is possible that divergence is not yet evident or that competitive exclusion is now occurring.

In sympatric fur seals and sea lions, past research have found mixed results with regards to competition and segregation. Contrary to the situation in Peru, in many locations fur seal populations are typically larger and they appear to outcompete sea lions (Wickens & York 1997). Researchers studying sympatric otariids have found trophic segregation, differing foraging strategies and contrasting population trends as mechanisms that explain coexistence (Páez-Rosas et al. 2012, Franco-Trecu et al. 2014, Pablo-Rodríguez et al. 2016). More recent studies demonstrate that intraspecific segregation, driven by interindividual specialization, takes place in colonial species (such as otariids) that are constrained to limited foraging ranges that overlap with conspecifics in similar niches (Jeglinski et al. 2013, Villegas-Amtmann et al. 2013b, Schwarz et al. 2021).

Some authors suggest that trophic segregation between sea lions and fur seals is associated with the observed divergent trends in epipelagic and benthic foraging characteristic of each group (Arnould & Costa 2006) and argue that

body size is a central feature that characterizes foraging modes between larger sized benthic foraging sea lions and smaller epipelagic foraging fur seals. In those studies, sea lions showed greater oxygen storage capabilities; enabling them to aerobically dive longer and deeper resulting in higher metabolic and reproductive outputs (Costa et al. 1998). However, other studies have also demonstrated that sea lions of different age-classes (Jeglinski et al. 2013, Villegas-Amtmann et al. 2013b) and within the same age-class (Schwarz et al. 2021) display specialized types of benthic, pelagic and nocturnal epipelagic foraging. Other studies have shown that foraging modes can vary regionally in the same species, therefore demonstrating the importance of prey availability as a driver for foraging mode (Hückstädt et al. 2016).

The Humboldt Current System (HCS) in Peru is recognized as the most productive of the Eastern Boundary Upwelling Systems in the world (Bakun & Weeks 2008). As other upwelling ecosystems, cold nutrient rich water rises to the euphotic layer by a combination of the South east trade winds and the Coriolis force that fuel Ekman transport, giving rise to primary productivity in the upper pelagic and nearshore areas. Peru’s coast is characterized by a narrow continental shelf, shallow productive upwelling waters and a relatively shallow thermocline related to an upper minimum oxygen layer at similar depths of approximately 50-80m, on average (Echevin et al. 2008, Demarcq 2009, Bertrand et al. 2010). These features limit the potential habitat for otariid prey to be linked to the benthos. Thus, in this productive shallow

environment foraging on highly patchy, but dense prey resources near the surface, may preclude the advantages of searching for more evenly distributed, but less dense, prey resources on the benthos (Arnould & Costa 2006), which are also constrained by bottom water hypoxia.

Furthermore, HCS is characterized by recurring El Niño Southern Oscillation (ENSO) events, which can vary in intensity and duration. ENSO is known as a cycle of alternating warm El Niño and cold La Niña events and is the most prominent climate signal on Earth (McPhaden et al. 2006). When HCS is affected by an ENSO, increments of sea surface temperature and reduction of primary productivity occur in the marine environment, altering distribution of habitats and associated prey biomass. The ENSO events that occurred in 1982-83 and 1997-98, were categorized as 'Extraordinary' and are well documented for dramatically altering species composition and reducing marine biomass (Barber & Chavez 1983, Tam et al. 2008). These climatic signals were strong and felt worldwide, changing the availability of prey items and causing declines in reproduction and survival of top marine predator populations around the globe (Arias-Schreiber & Rivas 1998, Forcada et al. 2006, Oliveira et al. 2006, Trathan et al. 2007, Oliveira 2011, Cárdenas-Alayza 2012, Bond & Lavers 2014, Sprogis et al. 2018).

In Peru two species of otariids coexist that have breeding colonies along the coast, the South American sea lion (SASL) and South American fur seal

(SAFS). Analysis of population trends of coexisting species helps understand population status and response to ecosystem conditions. Otariid surveys for the coast of Peru exist from mid 1960s, providing information on the abundance of these populations, but had heterogeneous sampling effort. Since the mid 1990s, systematic annual surveys are conducted at main colonies and during each species breeding season (February/March for SASL and November/December for SAFS) by scientists from Instituto del Mar del Peru (IMARPE) to monitor their status and fluctuations (Arias-Schreiber & Rivas 1998, Oliveira et al. 2006). Regardless, variability in Peru otariid continues to be observed (Figure 1.1). In the 1970s and early 1980s, historical records show a similar abundance for SASL and SAFS of ~ 20-25,000 individuals. However, in the late 1980s and 1990s SASL were more numerous than SAFS. Furthermore, a decline of 75% and 80% is documented for both SAFS and SASL, respectively due to the 1997-98 ENSO (Oliveira et al. 2006, 2012b). Surveys post ENSO reflect population recoveries for both species but with a larger SASL abundance. Similar fluctuations are observed until 2014, after which, there is a decline in SAFS.

Existence of sympatric colonies of SAFS and SASL implies that some mechanism currently operates (or has in the past), to permit interspecific coexistence in the HCS ecosystem. Sympatry of SAFS and SASL occur at only a few locations along the distribution ranges of our study species in the HCS. Punta San Juan (PSJ), a peninsula on the south coast of Peru is a sympatric site and is considered a historically important breeding center for otariids in Peru. The effects of the 1997-98 ENSO also impacted this breeding site, with local reductions of ~87% in both species. In PSJ, abundance declined from 2,751 to 345 in SAFS from November 1996 to November 1999 and from 12,415 to 1,495 in February 1997 to February 1999 in SASL (Arias-Schreiber & Rivas 1998). Since the decline, weekly counts of otariids were conducted to monitor population recovery. Although high resolution time series of marine megafauna populations are scarce; at this location, weekly counts permit to study fluctuations in abundance, which can help understand interspecific and intraspecific interactions in a common ecological context. Thus, we consider that the long time series collected at PSJ (which accounts roughly for 10-50% of the total Peruvian populations in both species in this only site) provide an adequate setting to study the coexistence of SAFS and SASL and is representative of their dynamics in Peru.

The main goal of this study is to describe population trajectories over the last 20 years, in a sympatric otariid colony in Peru and secondly, to discuss mechanisms (e.g. competition and/or resource limitation), possibly explaining these trends. In terms of the population trajectories, we expect a first phase of fast population recovery post 1997-98 ENSO, followed by a subsequent stabilization in populations' size. Given the larger body size and population size of SASL on the coast of Peru we hypothesize that the abundance and biomass of SASL dominates over SAFS, in PSJ during our study period. By using a combination of abundance time series, age-class proportions and biomass time series within and between species, we consider this is a first step towards exploring if larger body mass (SASL), a proxy for higher consumption of prey resources, can offer a greater competitive advantage in comparison to a smaller species (SAFS) to sustain population abundance in a common environmental setting.

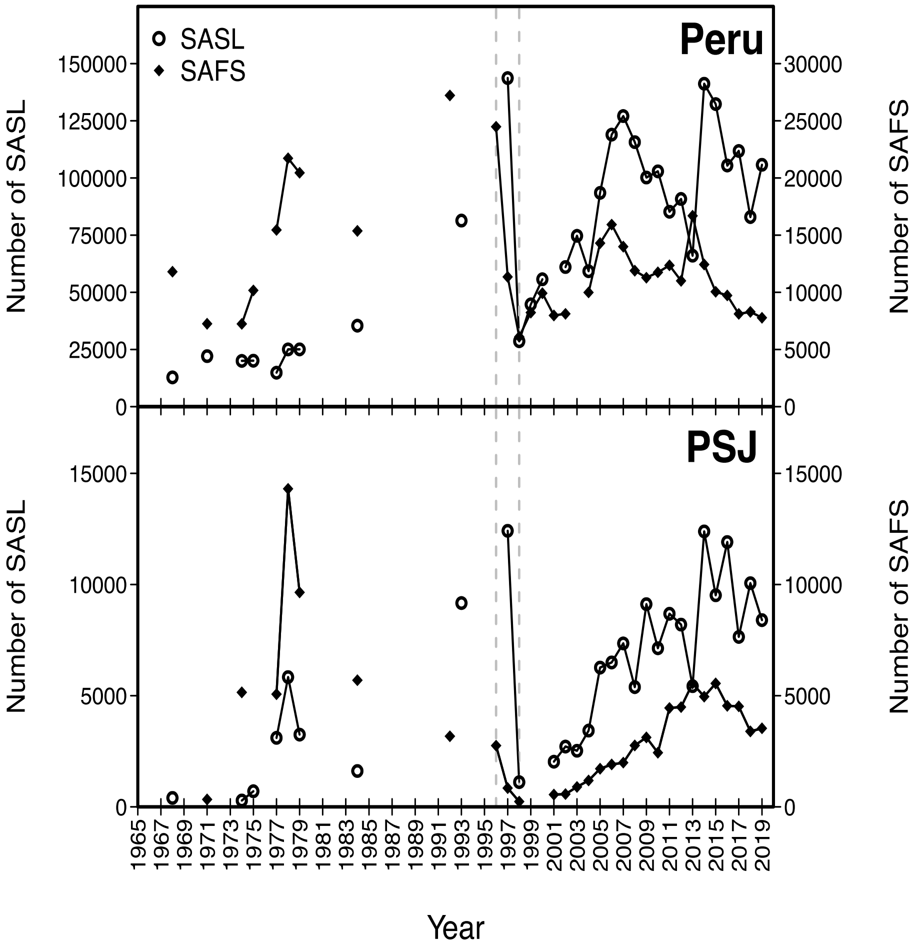


Figure 1. 1 Time series of the total number South American sea lions (SASL, open circles) and South American fur seals (SAFS, filled diamonds) counted on the coast of Peru (top) and Punta San Juan study site (bottom) between 1965-2019. Dashed grey vertical lines delimit the population decline caused by the 1997-98 ENSO. Time series were constructed with official counts from surveys obtained from various sources (Arias-Schreiber & Rivas, 1998; IMARPE, 2012, 2013, 2014b, 2015, 2016, 2017, 2018; Majluf & Trillmich, 1981; Muck & Fuentes, 1987; SERNANP, 2016; Tovar & Fuentes, 1984).

2. Materials and Methods

2.1 *Study Site and Data Collection*

Punta San Juan (15°22’S, 75°12’W) is a peninsula protected from land by a 1.2 km concrete wall that is part of a marine coastal national reserve system called ‘Reserva Nacional Sistema de Islas, Islotes y Puntas Guaneras’ (RNSIIPG, Spanish acronym). The PSJ coastline consists of 20 sites, which are beaches and coves all used for breeding and/or as haul-out sites by SASL and SAFS. In PSJ operates the Punta San Juan Program, a long-term research program that monitors otariid and seabird populations *in-situ*. Access to the PSJ Program database was granted for purpose of this study. At PSJ, land-based counts of accessible otariid sites are conducted at least once per week since 2001 to monitor population dynamics. For this study we accessed the count data during years 2001 to 2019, which have a minimum frequency of once per week. Counts took place between 0600-0900 hours by observers with 10x50 binoculars and tally counters on top of 8 – 30 meter cliffs overlooking otariid sites. Accessible sites are counted for total abundance and age-class categories, for each species. Gaps in count data occurred when roosting seabirds made it impossible to access the cliff-edge to view beaches and coves. More frequent counts available during the breeding seasons (January thru March for SASL and October thru December for SAFS) at selected breeding sites, were also included to enhance time series. Due to the long-term nature of this dataset (19 years), counters changed over time and beaches were counted by

different observers. Standard error of the mean count between three simultaneous observers ranges between 3-4% for SAFS and 3-13% for SASL. Satellite images with 2.8m resolution (image courtesy of CNES/Airbus 31 October 2019 via Google Earth) were used to estimate the area of the main breeding sites for each species. SAFS main breeding site was estimated through *in-situ* measurements collected during low tide in 1999 when animal abundance was zero and used to validate use of satellite images. Finally, a time series of mean monthly density was estimated during the breeding season (January – March for SASL and October – December for SAFS) by dividing mean monthly number of otariids by the area of the site where animals were counted on land and reported as number of individuals per square meter (ind /m^2).

2.2 *Abundance time series*

In otariid breeding sites, the ratios of age-classes change throughout the year. Most evident shifts occur during the breeding season when territorial males, adult females and pups increase and subadult males and juveniles decrease. Breeding season for SAFS and SASL last for approximately 3 months (SAFS: October – December; SASL: January - March). Early in the breeding season males arrive to compete and hold territories; subsequently females arrive to give birth and there is rise in female and pup numbers. Females generally stay with the pup for 5-13 days, depending on the species. After females complete their post-partum fasting period, they will be at sea for varying periods and return to land to nurse the pup. Intra-annual dynamics in each species and age-class was examined (Appendix A1-A2). Due to the intra-annual dynamics due to breeding and non-breeding seasons as well as the long-term population fluctuations, we detrended the abundance time series with the goal to extract an annual trend of abundance for analysis and remove all the high-frequencies' signal in the data.

Total abundance for PSJ was estimated from the sum of all sites individually counted on a given date between 2001 and 2019, for each species. We verified that interannual dynamics of study sites was the same as dynamic of the sum of all sites. Because counts varied on a daily to weekly scale, these were linearly interpolated to generate a time series with an equal sampling interval of every 3 days. To detrend the abundance time series and be able to extract the values we used a wavelet trend decomposition with a "morlet" mother wavelet, since it overcomes the problems of non-stationarity in a time series by performing a local time-scale decomposition of the signal. This method gives the possibility to investigate the temporal evolution of a times series with different rhythmic components.

We identified the wavelength scale corresponding to one year using wavelet analysis in WaveletComp R package v. 1.1 to extract the trend of abundance for both species. To test the study hypothesis, the trend of abundance time series, density and ratios of abundance will be compared between both species. Increasing or decreasing phase of trends, were determined with first order

derivatives. Turning points will permit to detect when the date of change in direction of a species population trajectory occurred. Difference of first order derivatives was used to understand which species was increasing over the other.

2.3 *Age class proportions*

Time series for the proportion of each age-class were constructed using counts available for the main breeding sites of PSJ for SASL and SAFS, respectively. For this, we selected data sets from the main breeding sites in PSJ that are exclusive to one of the two species year-round. Age-class counts from beach site S3 were collected for SAFS between November 2003 to December 2019 (n = 977 observations). For SASL, there was a change in the beach site used to estimate age-classes in years 2012-2013 to improve the number of times the sea lion breeding site could be accessed over the year by observers. Therefore, we constructed a single time series combining counts from beach site S7.S8 for years 2003-2013 and beach N7 for years 2012-2019 (n = 666 observations), including a mean proportion between the two sites for overlapping dates. The pattern in the proportions was inspected carefully to verify that age-classes did not vary abruptly due to site change.

Age-class categories for this study includes: pups, juveniles, adult females, subadult males and territorial males. These are based on the categories used in the field at PSJ for counting animals, based on distinguishable anatomical features and behaviors (Vaz-Ferreira and Ponce de León, 1987). A ‘juvenile’ category was

created in this study to group the ‘yearling’ (1 year old) and ‘immature’ (2-5 years old) categories used in the field. To estimate age-class proportions we only used the dates that considered all the beforementioned categories. Median proportions and interquartile range (IQR) were estimated .

Mean mass ± SD of otariids according to age classes were estimated using PSJ Program database. Mass was collected at PSJ between during otariid tagging and health assessment fieldwork that involved weighing live animals during the study period. Mass of adult age classes were collected during the breeding season while pupping was taking place. Meanwhile, pup mass was collected during pup round-ups, approximately 2 months after the peak of pupping occurs in each species (April for SASL and January for SAFS). Mass for the SAFS subadult male age-class was obtained from the PSJ Program necropsy records of individuals that stranded dead in PSJ due to interactions with longline fisheries, and is reported here. These animals were confirmed to have died from interaction with fishing gear, carcasses were in good body condition and therefore we consider their mass accurately represents their age-class. The only records of mass for dead juveniles available in PSJ were in emaciated body condition, probably due to nutritional stress, thus we do not consider they represent mass of healthy live individuals.

If values for the mean mass of an age-class were not available from PSJ, these were obtained from literature from conspecific or similar sized age-class otariids. We used reported mass of juveniles (Hückstädt et al. 2016); and territorial males (George-Nascimento et al., 1985) SASL collected in Chile. To our knowledge, no

published values exist for mass of juvenile SAFS in the Pacific Ocean and in the Atlantic, studies either report captive animals or small sample sizes (<5) for an class that represents many ages and high variance. We therefore applied the reported mass of conspecific Northern fur seals (*Callorhinus ursinus*) from a study involving live captures and grouped mass of animals of ages 1-2, 2-3, 3-4 and 4-5 years old for the juvenile age class (Baker et al., 1994). To verify our hypothesis about body size, we tested for differences between mean mass of age-classes between species. To evaluate if there is a source of competition between age-classes during breeding and non-breeding season (e.g., overlap in the proportion of territorial males and adult females in non-breeding season) we tested for independence between the weighted age-class proportions (product of proportion and mean mass for each age-class) within each species and season. This was done by applying a t-test or Mann Whitney Wilcoxon Test ($p < 0.05$) after verifying data distribution. Finally, we describe any shifts in the trends of age-class proportion time series to explain the mechanisms behind the population trajectory for each species.

2.4 *Biomass time series*

Biomass time series were constructed for each species in tons (t) by calculating the product of the abundance time series trend, the median age-class proportion and the mean mass per age-class. A time series for total otariid biomass was created from the sum of the SASL and SAFS biomass time series to determine the

proportion of biomass that pertains to each species. To test our hypothesis, the percentages of each of the species biomass over time are used to describe interspecific competition and evaluate if SASL are dominating over SAFS. All analysis were done using R software version 3.6.2.

3. Results

3.1 *Abundance time series*

After removing high frequency signal from count data, annual trends of abundance were extracted for each species. This revealed population trajectories in PSJ that vary between a range of 829 - 4,550 individuals for SASL (Figure 1.2A) and 291 – 3,443 individuals for SAFS (Figure 1.2B) between 2001 to 2019. During this study period mean density of individuals during breeding was 0.40 ± 0.23 ind /m^2 for SASL (January-March) and 0.12 ± 0.08 ind /m^2 for SAFS (October-December).

Throughout the abundance time series, there is always a higher abundance of SASL in comparison to SAFS, with a median ratio of 1.65 SASL : 1 SAFS. The ratio of SASL to SAFS starts at a maximum ratio of 2.84 SASL : 1 SAFS, followed by decreasing phase that hits a minimum of 1.23 SASL : 1 SAFS in October 2012. Then, a final increase phase that rises until a ratio of 2.75 SASL : 1 SAFS in December 2019.

In general, both species started with a positive increasing phase and then both

declined toward a negative phase, with differing dates at each turning point. Turning points were detected as the date when a change from positive to negative phases occurred. First, SAFS changed its phase from positive to negative in November 2014. Then, 2.25 years after (in March 2017), SASL changed its phase and started to decline. Linear regressions ($p<0.05$) were adjusted to standardized data of the (negative) declining phase for each species. Slopes were significantly different from zero in both species ($R^2 = 0.99$, $p<0.05$); being slope incline of SAFS ($B_0 = -179.35$ ± SE 0.21) steeper than SASL slope ($B_0 = -97.33$ ± SE 0.23). The difference between first orders derivatives describes which of the species had a higher growth rate, at a given time, in comparison to the other. We used these values to organize the time series into three different periods. Sea lions had a greater growth rate in comparison to SAFS, during the first period (January 2001 - June 2007) and in the third period (March 2012 - December 2019). SAFS had a stronger growth rate in comparison to SASL during the second period (June 2007 - March 2012).

3.2 *Age-class proportions*

Median age-class proportions (Median, IQR) and mean mass (Mean ± SD) estimated for the entire time series are reported in Table 1. Due to the non-normal distribution of datasets, we applied the Mann Whitney Wilcoxon Test ($p<0.05$) with Bonferroni p-adjustment. Significant differences were found between mean

mass of all age-class proportions within species and between species ($p<0.05$), with SASL being of a significant larger size (x1.5 larger) than SAFS (Table 1). Between the adult sexes, territorial male SAFS are 2.23 larger than adult female SAFS and territorial male SASL are 3.74 times larger than adult female SASL.

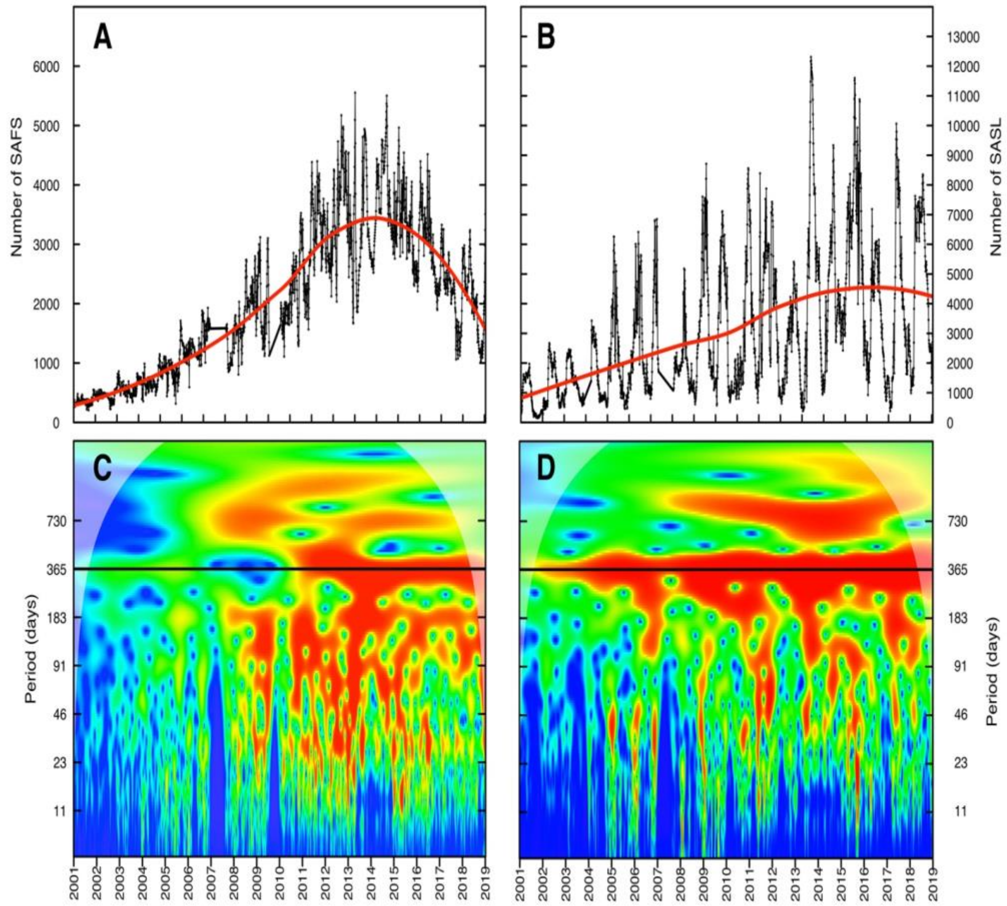


Figure 1. 2 Top panel shows 3-day interpolated counts (black line) with trend of abundance (red line) for A) SAFS and B) SASL collected in Punta San Juan, Peru. Bottom panel shows wavelet spectrum with horizontal line indicating the annual signal at 365 days for C) SAFS and D) SASL abundance time series.

Table 1. 1. Median proportion of age-class per species with inter-quartile range (IQR). Mean mass and standard deviation (± SD) in kilograms. Sample size and source used for each age-class.

	Age-class	Proportion of age-class		Mass of age-class (kg)		
		Median	*IQR*	*Mean ± SD*	*n*	*Source*
SASL	Pups	0.16	0.18	13.98 ± 0.62	77	This study
	Juveniles	0.23	0.17	78.88 ± 17.68	9	Hückstädt et al 2016
	Adult females	0.38	0.19	82.74 ± 11.31	23	This study
	Subadult males	0.12	0.16	173.78 ± 40.96	44	This study
	Territorial males	0.05	0.08	310	-	George-Nascimento et al 1985
SAFS	Pups	0.36	0.13	8.75 ± 0.65	171	This study
	Juveniles	0.26	0.10	24.88 ± 14.4	5606	Baker et al 1994
	Adult females	0.33	0.09	48.56 ± 8.08	91	This study
	Subadult males	0.03	0.02	66.53 ± 8.56	6	This study
	Territorial males	0.04	0.03	108.64 ± 14.20	26	This study

Significant differences were found between weighted age-class proportions (product of mean mass and number of individuals) of each species between breeding and non-breeding seasons (Mann Whitney Wilcoxon Test, $p<0.05$), during the final period of the study (March 2012 - December 2019) (Figure 1.3), suggesting low intraspecific competition between age-classes at this scale.

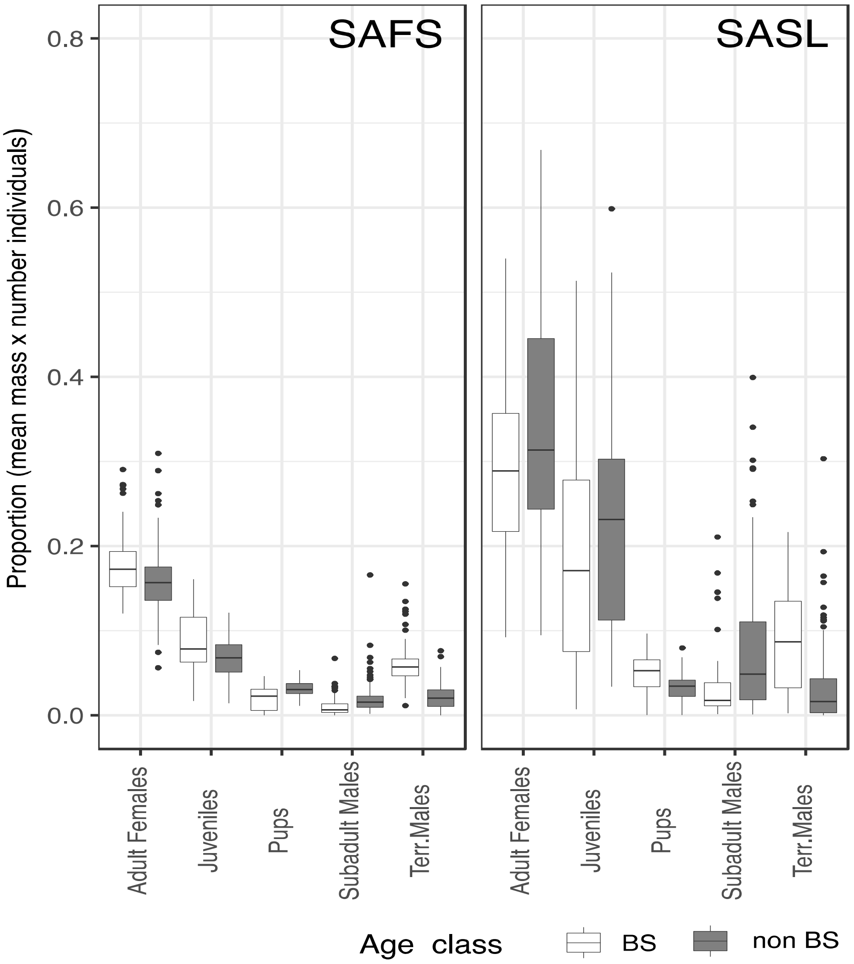


Figure 1. 3. Boxplots of the weighted proportion (product of mean mass and number of individuals) of each age-class for SAFS and SASL during breeding season (BS, white) and non-breeding season (non BS, grey) during March 2012 - December 2019.

Time series of age-class proportions with smooth loess curve and 95% CI were compared during November 2003 – December 2019 (Figure 1.4). Evident shifts in proportion of age-classes include i) increase in adult females (+0.2 SASL and +0.1 SAFS) between 2016 - 2018; ii) decrease in juveniles (-0.40 SASL and -0.30 SAFS) from 2015 – 2019; iii) decrease in sub adult males (-0.10 SASL and -0.05 SAFS) between 2007 - 2015; iv) decrease in territorial males (-0.10 SASL) between 2008 - 2013. All the other ages class proportions are relatively stable. These trends suggest that the population decline in recent years in both species is associated to a decrease in the juvenile and, to a lesser extent, the sub-adult male age-classes at PSJ.

3.3 *Biomass time series*

Total otariid biomass time series was in the range of 83.16 – 506.72 t with a mean of 335.26 ± 139.95 t and reached its maxima in March of 2016. Throughout the time series 82.61 % ± 3.75 of total biomass is composed on average by SASL (range: 77.72 - 88.97 %), and 17.39 % ± 3.75 by SAFS (range: 11.03 – 22.28 %). This trend continues until the end of the study period, with 88.63 % of otariid biomass comprised by SASL and 11.36% by SAFS in the end of 2019. SASL occupy a biomass in the range of 73.99 – 406.25 t with a mean 272.97 ± 108.61 t, reaching its maxima in March 2017. Whereas SAFS occupy a biomass of 9.17 – 108.41 t with a mean of 62.30 ± 33.21 t, reaching its maxima in November 2014 (Figure 1.5).

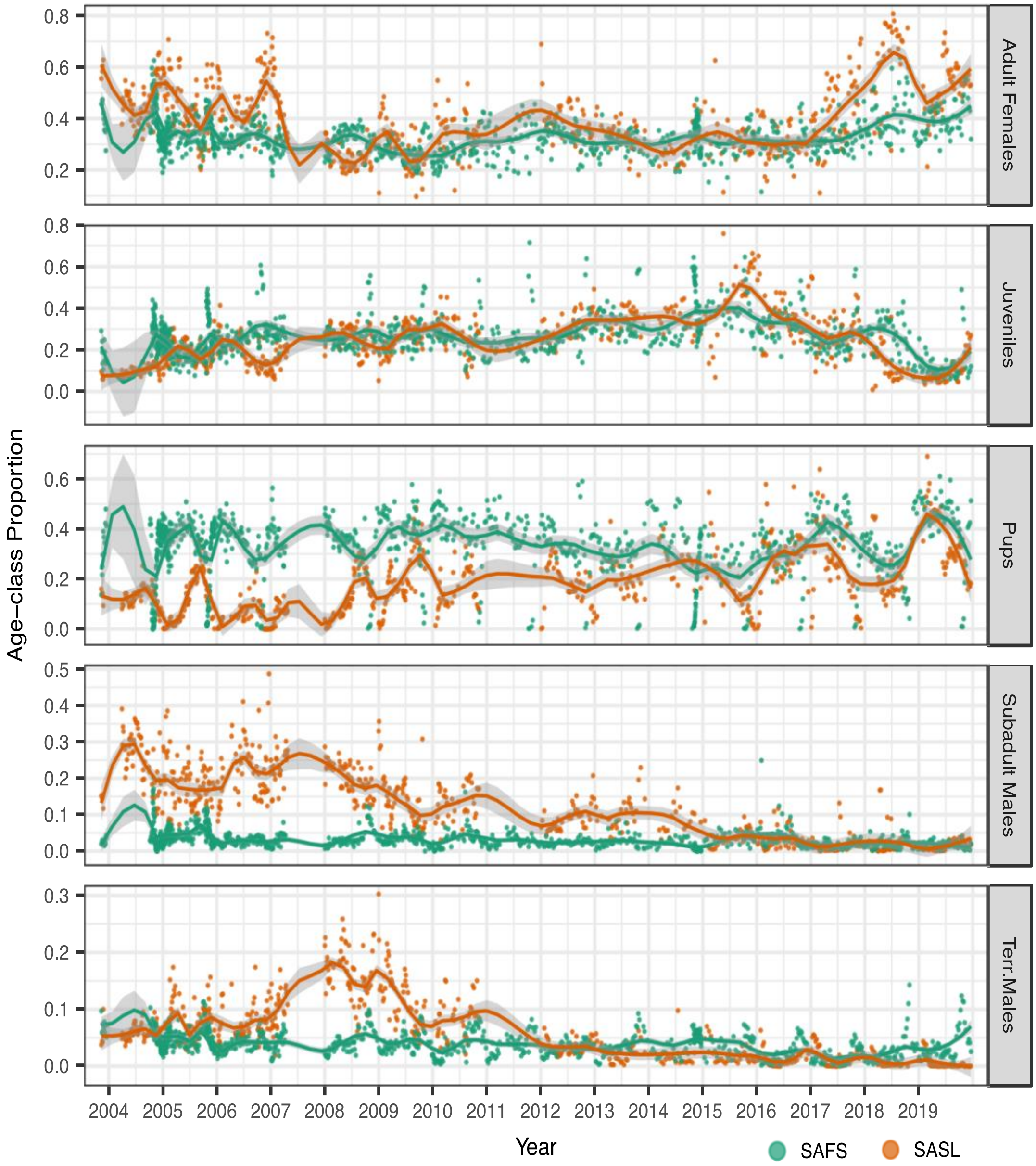


Figure 1. 4 Time series of the proportion of age-classes for SAFS (green) and SASL (orange) constructed from weekly counts (circles) with smooth curve (line) with 95% CI (grey area). Age-class counts collected at Punta San Juan otariid breeding sites between November 2003 - December 2019.

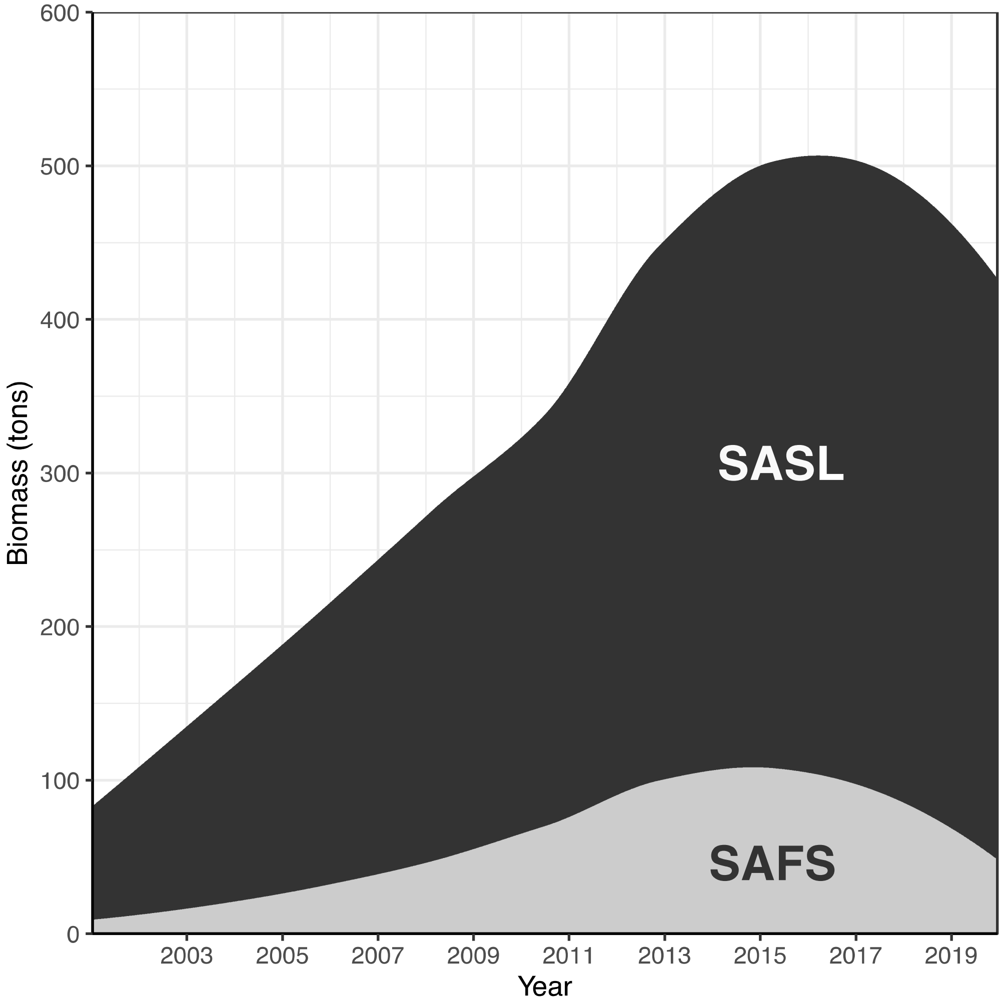


Figure 1. 5 Stacked area chart of constructed biomass time series in tons (t) estimated from otariid abundance in Punta San Juan for SAFS (light gray) and SASL (dark grey) during years 2001-2019.

4. Discussion

4.1 *Changes in abundance, density and population trajectories*

Since the effects of the Extraordinary ENSO in 1997-98 that caused otariid mortality and dispersal, it took SAFS 13 years and SASL 15 years to reach peak abundances similar to levels in 1980s and 1990s. Decomposition of time series of counts and biomass during years 2001-2019 shows that both species had a growth phase, a turning point and are currently in a declining phase. Our analyses reveal that SAFS abundance began to decline ~2.25 years before SASL and at a rate 1.5 times faster than SASL. The current phase of decline in SASL was unexpected and was only detectable with an in-depth analysis of the population trajectories and associated variables. In this study we also found a decrease in the juvenile and (to a lesser extent) in subadult male age-class proportions in both SASL and SAFS that is contributing to the recent decline detected in both species (Figure 1.4). Decrease in juveniles and subadult males can be attributed to an increase in mortality or dispersal of these age-classes, exacerbating failure of recruitment in PSJ. Unfortunately, we do not have information to adequately address mortality or dispersal. Furthermore, in our study we did not find any evidence for intraspecific competition at population level (Table 1.1, Figure 1.3). However it is possible

that intraspecific competition can be operating at another scale, such as in the overlap of resource utilization or in use of foraging grounds, that should be further explored.

The trend in biomass in this study between species shows that, on average, 83% of all otariid biomass is composed by SASL and 17% by SAFS, making SASL the current ‘dominating’ species, as hypothesized. In the final phase of the time series 89% of total otariid biomass belongs to SASL, marking a large difference in the current composition between the two sympatric otariid species that inhabit the PSJ study site. Total SASL abundance is 1.23 - 2.84 times larger in comparison to SAFS, with an median ratio of 1.65 throughout the entire time series. We think this can be related to the different mechanisms of congregation employed by each species, evidenced at PSJ. The aggregation of individuals on land is different when we examine raw counts of otariids at PSJ over time (Figure 1.2A-B). Following recolonization, raw counts show that SAFS increments with what appears to be an exponential rate at PSJ (Cárdenas-Alayza, 2012) that grows accumulating individuals at PSJ. Meanwhile, SASL shows pulse-like increments with seasonal peaks of abundance that can vary widely between years. However, as SAFS abundance increments plateau and then decrease, populations pulses of SASL have been up to four times the abundance of SAFS (Figure 1.2A-B). This variability in the recruitment of individuals in a given breeding season has played an important role in the population growth of SASL at PSJ.

A model for male dispersal proposed by Giardino et al. (2016) developed in the Atlantic population of SASL shows that male sea lions disperse between winter haulouts and breeding sites. Haulouts can be spatially segregated from central breeding areas during the non-breeding season, and are followed by male dispersal towards breeding sites in consecutive years. Males tend to have strong site fidelity to both breeding and haul-out sites maintaining functional connectivity and gene flow throughout their range (Giardino et al., 2016). This same phenomenon contributes towards the recruitment of new individuals at breeding sites and can also be occurring in Peru, with PSJ being a reproductive site where individuals that haul-out at different sites congregate to breed. Furthermore, as evidenced from the raw counts and intra-annual dynamics (Appendix A2), SASLs leave the PSJ breeding rookery decreasing their abundance during non-breeding months. In contrast, SAFS female, juveniles and pups are found year-round at PSJ to complete extended lactation periods (up to 36 months), during which females, juveniles and pups show site fidelity towards lactation sites (Majluf, 1989). Thus, high dispersal rates in SASL seem to be key for augmenting population growth in a given breeding season permitting the recruitment of more individuals for breeding. However, the decline in juvenile and subadult age-classes suggests that PSJ is not a successful site for the recruitment of these age-class in both otariid species in recent years.

Otariid breeding sites tend to show seasonal age-class proportions that reflect

the roles of age-classes and sexual segregation in their polygynous mating system (Bartholomew, 1970). In this study we found that PSJ breeding sites are occupied by different proportions of age-classes during breeding and non-breeding season in both species, with females, pups and juveniles being the most important age-classes throughout the year. Intra-annual dynamics show that from July until December, the abundance of all SASL age-classes decrease to very low and can reach zero abundance in PSJ. In contrast to SAFS, which is present year round, and has a slight decrease in July-August (Appendix A1). The wide variability in SASL in comparison to SAFS over the study period is promoted by the arrival of larger number of animals in a given season and the higher density at the breeding sites. Interestingly SAFS show a higher proportion of pups : female ratio than SASL (Figure 1.4), which suggests that female condition may be better in SAFS. However, this can be explained by the high site fidelity of breeding female SAFS at this site, where experienced breeders return to pup (Majluf, 1989). Whereas in SASL, it is possible that a bulk of the SASL females are young females.

In this study we found that SASL density (0.40 ± 0.23 ind / m^2) at PSJ during breeding was 3-4 times SAFS density (0.12 ± 0.08 ind / m^2). This can be explained by the difference in the social tactics intrinsic to each species. Soto and Trites (2011) reported a lek-like mating system in SASL with the highest female : male ratio recorded for this species in Ballestas Islands in Peru, about 250km from our study site. Large abundances of females congregate to breed

at what some authors identify as population “hotspots”. These high density aggregations have been explained as a means to enhance mate selection (Soto & Trites, 2011). Territorial males line up at the tide line to display themselves to reproductive females. Females benefit from male competition and avoid subadult male harassment while remaining in close proximity to foraging sites (Bradbury & Gibson, 1983; Soto & Trites, 2011). Although there are no studies on the SASL mating system at PSJ, we suppose that the social tactics described above also occurs and PSJ is an important site for SASL breeding (S. Cárdenas-Alayza, personal observation).

We know from historical records that the SAFS population ranged between 9,644 - 14,303 and SASL between 3,249 – 5,836 at the PSJ study site in 1978-79 (Figure 1.1). This shows that PSJ is able to support larger abundances of these species on land and in the surrounding marine environment. Interestingly, during the post 1997-98 ENSO recolonization process, SAFS gathered in lower densities than SASL. Pre ENSO density of SAFS at PSJ was reported between 0.5 - 1 ind /m^2 (Majluf, 1989), considerably higher than average current density of 0.12 ± 0.08 ind / m^2 found in this study. In the 1980s and 1990s, 48% pup mortality was recorded in SAFS in PSJ. This was caused by maladaptive aggression of females towards pups, attributed to the high density aggregations (Harcourt, 1992a, 1992b; Majluf, 1992). Furthermore, SAFS currently occupies many more beaches for breeding in PSJ in lower density, in comparison to the pre 1997-98 ENSO era (Cárdenas-

Alayza, 2007). Other studies have demonstrated that habitat selection for breeding sites by SAFS and SASL varies in Peru, and is driven by access to water or shade for thermoregulation (Stevens & Boness, 2003). Therefore, availability of suitable habitat features will also play a role in the occupation of breeding sites in a given area so that each species can efficiently operate mating tactics characteristic of species social system.

4.2 *Contributing factors of population fluctuations in Peruvian atariids*

All species of otariid seals throughout the world were once subject to extensive and, in most cases, excessive hunting pressure during the eighteenth, nineteenth and twentieth centuries. By the late 1800s, however, most species had acquired total legislative protection or were subject to only regulated managed harvests (Wickens & York, 1997). Despite this protection, populations of various sea lion species have experienced very little recovery, and in some cases, are declining, and fur seal species have generally experienced rapid population recovery rates (Costa et al., 2007; Wickens & York, 1997). In Peru, we have the opposite case, a smaller fur seal population and a more abundant sea lion population. The current lack of recovery of SAFS in Peru may be explained in part by little time for SAFS population to recover from historical commercial exploitation, in synergy with recurring ENSO events and competition with fisheries and other predators (Majluf,

1991; Oliveira, 2011).

In Peru, SAFS were under more exploitation pressure due to the interest driven by the higher value of their pelts in the international fur trade market. By early 1900s, fur seal colonies in Peru were reported as small and isolated, describing this species as “close to the brink of extinction” (Murphy, 1925). The first commercial ban for otariids was legislated in Peru in 1946, prohibiting culling of adult female and pup SAFS (Majluf & Reyes, 1989). In 1950s fur seal abundance continued to be low which resulted in an extension of this ban to include all SAFS age-classes and also female SASL. Exploitation of otariids was reactivated in 1967 until early 1970s. Finally, in 1976 commercial exploitation of both species was banned in Peru (Tovar & Fuentes, 1984).

In mid 1950s began the development of the industrial fishery for Peruvian anchovy (*Engraulis ringens*) in Peru, and has turned into the largest monospecific fishery in the world capturing between 4-12 million tons of fish annually (Chavez et al., 2008). Direct links have been found between anchoveta biomass and population abundance of other top marine predators in HCS, such as seabirds, that rely almost exclusively on this marine resource for growth, reproduction and survival (Barbraud et al., 2018; S. Bertrand et al., 2012; Passuni et al., 2016). In synergy with ENSO conditions, overfishing can have acute effects on the survival of predator populations in HCS (Oliveira, 2011). After the effects of the 1997-98 ENSO, a mere abundance of 6,257 SAFS was recorded on the coast of Peru from a previous count of 24,481 in 1996 (Arias-Schreiber & Rivas, 1998). After some time, nationwide 2006 survey showed that the population had recovered to an abundance of 15,137 SAFS (IMARPE, 2006). However, the SAFS population recovery was also limited geographically. Of the entire current abundance, 80% resides at five sites on the entire coast of Peru (IMARPE, 2013). In comparison, 44,725 SASL were counted in Peru in 1999 after the 1997-98 ENSO, from a previous abundance of 143,713 in early 1997 (Arias-Schreiber & Rivas, 1998; Oliveira, 2011). In 2006, recovery of SASL was documented with a count of 118,220 (IMARPE, 2006). In these years, SASL, breeding colonies and haulouts were already widespread along the coast compared to SAFS. For both species, authors suggest that recovery is due to the re-establishment of prey populations, the lack of strong ENSO events and migration from individuals in the colonies in northern Chile (Cárdenas-Alayza, 2012; Oliveira et al., 2012), but the fact that SASL was not reduced to such a small abundance seems fundamental to their recovery potential.

Our results show that SAFS recently declined at a rate 1.5 faster than SASL. The steeper decline in SAFS, is possibly linked to reduced recruitment in breeding adults at PSJ in recent years in combination with juvenile dispersal and mortality from this site. In our study, the sympatric otariids are exposed to the same environmental conditions, reason why the difference in this response can also be linked to intrinsic species traits that respond differently

to the changes in the environment. A populations risk of extinction will depend both on the deterministic (harvest, commercial exploitation, natural selection, etc.) and stochastic (environmental, genetic, etc.) processes. The latter are more pronounced at small population sizes and can accelerate extinction process started by deterministic factors (Palstra & Ruzzante, 2008). Previous studies have shown that the effective population (Ne) is used as a tool to evaluate viable populations. High Ne values retain high levels of genetic diversity and reduce probability of effects from inbreeding depression (Oliveira et al., 2006, 2012; Wright, 1990). Whereas a population with a low Ne, is susceptible to genetic drift and less apt to respond to selection (Oliveira, 2011).

After the 1997-98 ENSO, SAFS have a critical Ne value of 2,153 (Oliveira et al., 2006) while SASL Ne is 7,715 (Oliveira et al., 2012). According to Oliveira et al (2009) population reductions after the 1997-98 ENSO, may have caused a significant genetic bottleneck in the Pacific population of SAFS and SASL, with loss of genetic diversity and presumably some loss of evolutionary potential for the species (Oliveira et al., 2009, 2012). Furthermore, the rate of loss of genetic diversity via genetic drift is greater in populations where Ne is small and migration is limited, as is the case for SAFS. This can be evidenced in the information gathered through Peru´s nationwide surveys, where >90% of SAFS breeding population is mostly restricted to latitude 15 -17° South, with PSJ supporting at least 40% of entire

Peru SAFS population. Meanwhile, SASL population is distributed continuously along the coast, with important breeding sites in several latitudes (6, 13-14, 15 and 17° South) (IMARPE, 2016, 2017, 2018). Wider distribution of breeding sites with high density aggregations of SASL, suggest that migration and dispersal rates in SASL are higher than SAFS, resulting in higher connectivity. Therefore, even if there was genetic loss due to a bottleneck from a strong ENSO event, SASL has mechanisms to counterbalance loss of genetic diversity with temporal gene flow through migration. The difference in gene flow between these two species in HCS can be a key factor explaining the limited response to achieve population growth under scenarios of environmental change in SAFS in comparison to SASL suggested in this study, and should be further studied.

4.3 *Natural history traits that influence interspecific competition in otariids*

Body size of SASL is overall 1.5 larger in all age-classes compared to SAFS. In this study, although we hypothesize that a larger body size (SASL) could serve as advantageous to consume larger/ more prey, the decline in population abundance of both SAFS and SASL suggests that a resource limitation is affecting trajectories of both species. Between the sexes, territorial male SAFS are 2.23 larger than adult females and SASL males are 3.74 times larger than adult SASL females. Although at population level we did not find

evidence for segregation between age-classes and sex, mechanism to avoid competition may be operating at a different scale. To elucidate differences and how these species are exploiting the environment, further studies need to be conducted to test intra and interspecific trophic niche segregation to understand how these sympatric otariid species exploit the HCS.

In our study we compared otariid biomass as a possible outcome of interspecific competition in PSJ and found that 83 % of total average biomass is composed by SASL throughout our time series. This can be explained by a the difference of 1.6 - 3.3 in mass between SASL and SAFS; in combination with a high density mating system in SASL versus lower density aggregations in SAFS. Researchers have examined potential competition between sympatric fur seal and sea lions at other locations and have found in some cases that trophic segregation is a mechanism to explain differing foraging strategies and contrasting population trends (Franco-Trecu et al., 2014; Pablo-Rodríguez et al., 2016; Páez-Rosas et al., 2012). Some authors suggest that difference in divergent trends is explained thru epipelagic and benthic foraging, being the latter characteristic of sea lions that have larger body size and diving capacity (Arnould & Costa, 2006). Other studies have also demonstrated that different age-classes within the same sea lion population have specialized benthic and epipelagic foraging modes (Jeglinski et al., 2013; Villegas-Amtmann et al., 2013). Therefore, otariid foraging ecology in PSJ needs to be evaluated at interspecific and intraspecific level to understand

how the different groups are exploiting the local environment.

In the coast off PSJ, the continental shelf is extremely narrow limiting the access to benthic habitat. Furthermore, previous studies in Chile have demonstrated that SASL are epipelagic foragers with mean dives of 29.0 ± 34.8m, when they are in an upwelling environment (Hückstädt et al., 2016). Therefore, we expect that competition for similar prey items may be taking place within the upper limit of the oxygen minimum zone off the Peru coast, which is usually located ~50 m in depth (A. Bertrand et al., 2010) making the foraging habitat of pelagic prey readily available for both otariid species diving capacity, independent of differences in body size.

It is well documented that the HCS in Peru holds a world-leading monospecific forage fishery in terms of landings of Peruvian anchovy, sustaining >5 million tons per year on average since 1960s (Bakun & Weeks, 2008; Chavez et al., 2008). In Peruvian otariids, the number of pups born, mean birth dates and anchovy biomass were found to have direct relationships in SASL and SAFS reproductive success, demonstrating that anchovy is a key resource in fulfilling the energetic demands of both species (Cárdenas-Alayza, 2012; Soto et al., 2004). Other studies have evaluated diet composition between these sympatric otariids in the decades of 1980s and late 1990s in south Peru, but conclusions for resource partitioning are not clear. Vásquez (1995) reported that otariid diets were both based on fish and cephalopods; with Peruvian anchovy (*Engraulis ringens*) and Jack Mackerel

(*Trachurus murphyi*) as the main consumed species. Afterwards, Arias-Schreiber (2000) found that Peruvian anchovy, squids and a crustacean, the Red squat lobster (*Pleuroncodes monodon*), were ranked as important prey items shared by the sympatric species. Based on this, we understand that anchovy is an important prey shared by both otariids during these study periods, but mechanisms for trophic segregation are not clearly explained. Furthermore, prey availability may have changed in the last 20 years. Therefore, resource partitioning research needs to be updated and further explored in these sympatric species to disentangle current resource utilization in relation to population trajectories.

4.4 *Current and future trends*

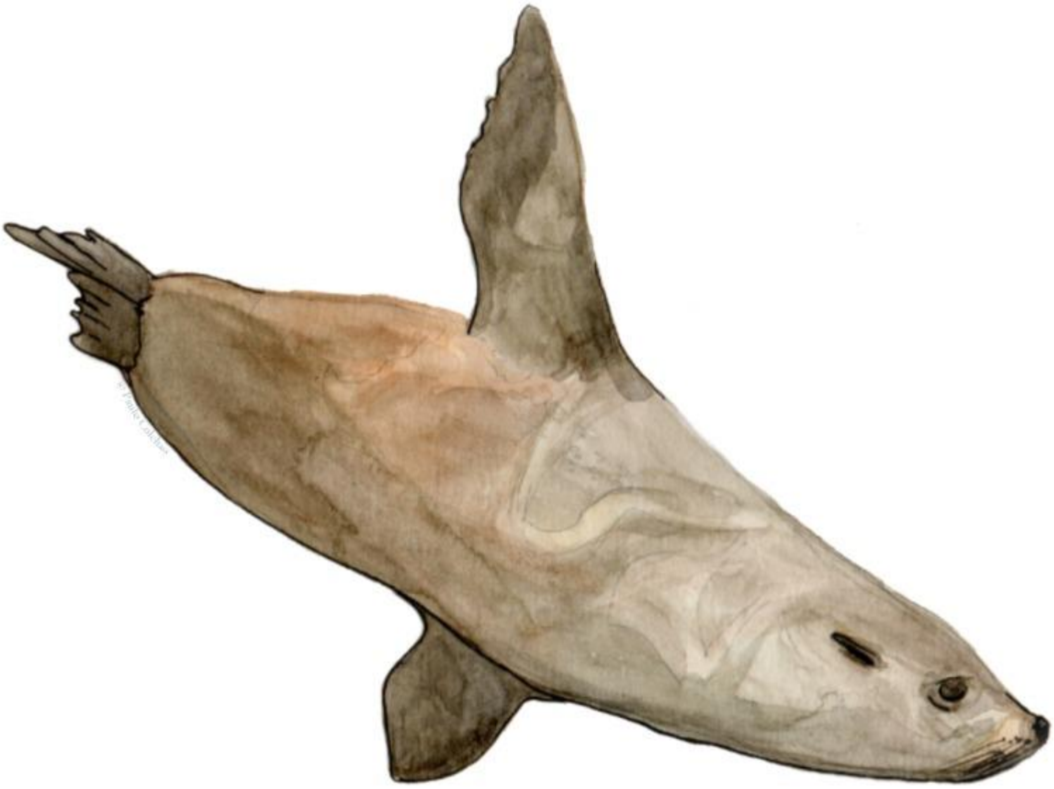
In the final 5 years of our time series, both sympatric otariid populations were found to be in a state of decline. SAFS were the first to decline in 2014, which coincides with a decrease in the anchovy biomass estimated for the coast of Peru during this period. Anchovy biomass dropped from 11,201 tons in 2013 to 3,799 tons in 2014 (Zavala et al., 2019). In 2014 anchovy landings summed 1,302 tons, leaving an available biomass of 2,497 tons for all predators and other fisheries to consume, which may have posed limitations for growth and maintenance of predator populations. Warmer oceanographic conditions in HCS persisted and coincided with a reduced anchovy biomass from 2014 to 2017 (Zavala et al., 2019). Changes in oceanographic conditions can shrink

and expand available habitat for prey items forcing new competition scenarios between coexisting species. Thus, under a scenario of reduced anchovy biomass we consider it is possible that prey availability is limiting population sizes at PSJ and can be responsible for the declines observed in the juvenile and subadult age-class for both SAFS and SASL; as younger individuals do not possess full diving capabilities.

Predictions for the future of HCS include scenarios with shoaling of the oxycline (Brochier et al., 2013), compressing the pelagic habitat that sustains the abundant biomass of small pelagic fish currently in the system (A. Bertrand et al., 2011). If this occurs, it will increase competition between all the predators that depend on pelagic resources, unless they adapt foraging strategies under new conditions. Under this hypothetical predicted scenario and our findings, we suspect SASL will be the more resilient of the two sympatric otariid species that will thrive in HCS, given its population recovery in the past 20 years. Therefore, to propose adequate management for the future of these species, it is important to better understand current underlying foraging strategies used by otariids of HCS and determine if trophic competition rules over space and time between species. These studies are key to tease apart the underlying mechanisms behind the current population trajectories revealed by the present study.

CAPÍTULO 2

Resource partitioning as a mechanism for trophic segregation in sympatric otariids from the productive upwelling Peruvian Humboldt Current System



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Abstract

Resource partitioning can contribute to species coexistence by reducing interspecific competition. To understand if resource partitioning contributes towards sympatric breeding of otariids in Peru’s dynamic Humboldt Current System (HCS), we compared seasonal diet composition of South American fur seals (SAFS, *Arctocephalus australis*) and South American sea lions (SASL, *Otaria byronia*) over 15 seasons between 2015 and 2018 to determine if there is a detectable mechanism for resource partitioning at population level. Diet composition was estimated from identification of hard remains of prey items obtained from 3,325 scats collected from colonies at Punta San Juan, Peru. SAFS diet is primarily composed of Peruvian anchovy (42.8%) and cephalopods (34.7%); with smaller components of myctophids (7.4%), red squat lobsters (5%), and 11 other fish species. SASL diet is mainly composed of red squat lobster (69.9%) and Peruvian anchovy (19.1%); with smaller amounts of cephalopods (4.7%), silversides (4.6%), and five other fish species. In this study, both predators were classified as specialists and interspecific trophic segregation was found in 13 of the 15 seasons sampled. Trophic overlap was detected in the austral summer and fall of 2015 during an extraordinary El Niño event, in which otariids consumed similar proportions of Peruvian anchovy (55% SAFS, 48.6% SASL), cephalopods (21.7% SAFS, 13.6% SASL), and red squat lobsters (9% SAFS, 2% SASL). In conclusion, the analysis demonstrates resource partitioning based on the abundance of primary prey items consumed by two otariid species and helps explain trophic segregation in otariids of HCS. Furthermore, results show that climatic changes can trigger abrupt reduction of prey items and exacerbate interspecific competition.

Keywords: foraging ecology; diet; fur seal; sea lion; Peru

1. Introduction

The ways in which species partition available resources is a major determinant of ecological communities and coexistence. The competitive exclusion principle states that two species in the same habitat cannot have exactly the same niche and coexist in stable form (Begon et al., 2006). Thus, coexisting species must differ in their ecological requirements by at least some minimal amount to avoid competitive exclusion (Pianka, 1974). Otariids (fur seals and sea lions) occur in sympatry in many locations around the globe. Research on sympatric otariids have found differing mechanisms of trophic segregation that explain coexistence (Franco-Trecu et al., 2014; Pablo-Rodríguez et al., 2016; Páez-Rosas et al., 2012). For instance, trophic segregation among otariids has been associated with divergent trends in epipelagic and benthic foraging modes (Arnould & Costa, 2006). Larger body size in sea lions has been linked to the consumption of large demersal fish and cephalopods in the coastal realm, which are accessible by benthic foraging and increased diving time (Costa & Gales, 2003; S. L. Fowler et al., 2006). In contrast, fur seals are often epipelagic feeders that forage on smaller prey resources with highly patchy distributions near the surface (e.g., zooplankton, small fish, or squid) (Arnould & Costa, 2006).

In the Peruvian Humboldt Current System (HCS) two species of otariids coexist, the South American fur seal (SAFS, *Arctocephalus australis*) and the South American sea lions (SASL, *Otaria byronia*). Existence of sympatric colonies of SAFS and SASL implies that a mechanism exists that permits their interspecific coexistence in the HCS ecosystem. Within the HCS there are few sites where

otariids are found in important sympatric colonies. Punta San Juan (PSJ, 15°22’S, 75°12’W), a peninsula on the southern coast of Peru, is one such site. PSJ supports important breeding rookeries of both species with an annual range of 6-12,000 SASL and 2-5,000 SAFS over the past 5 years (Cárdenas-Alayza et al., 2021). In PSJ, SAFS and SASL colonies are found year round. In SAFS, territorial males and adult females increment during breeding months (October to December) and pups are born. In SASL, territorial males, adult females and pups increase during breeding months (January to March). In both species, numbers decrease during the remainder of the year, during which females, pups and juveniles make up the bulk of the age-classes during non-breeding months (Cárdenas-Alayza et al., 2021). During breeding, females arrive pregnant and all viable births to newborn pups occur in a lapse of 2-3 months (Cárdenas-Alayza, 2012; Soto, 2004). After pupping, females remain on land with the pup for 5-13 days and then begin alternating cycles of 2-4 days foraging at sea followed by 2-3 days of nursing on shore (Ganoza, 2016; Majluf, 1987; Soto, 2004). Long lactation that can last up to 36 months as a mechanism to enhance offspring survival during variable oceanographic conditions have been reported in both species in Peruvian HCS (Majluf, 1987; Soto et al., 2004). As in other central place breeding otariids, females are energetically constrained to proximate foraging grounds for nursing and offspring survival in contrast to males that can move freely between different rookeries and foraging grounds (González-Suárez & Cassini, 2014; Hückstädt et al., 2014; Oliveira et al., 2017).

The Peruvian HCS is recognized as the world’s most productive upwelling system in terms of fish biomass (Bakun & Weeks, 2008). The coastline is characterized by a narrow continental shelf and a relatively shallow thermocline related to the upper boundary of the oxygen minimum layer at approximately 50-80m (A. Bertrand et al., 2010; Demarcq, 2009; Echevin et al., 2008). These features limit the habitat for prey biomass of small pelagic fish such as the Peruvian anchovy (*Engraulis ringens*), making them available in high densities for marine predators (A. Bertrand et al., 2011). However, productivity in the HCS decreases when warming events occur, such as the El Niño Southern Oscillation (ENSO) or Kelvin waves, which can alter food web composition (Tam et al., 2008). These changes impact the success of predator foraging events and, depending on their intensity and duration, can decrease reproductive output and survival rates in top predators (Majluf, 1991; Trillmich & Dellinger, 1991). Extraordinary ENSO events have triggered significant changes in the food web composition causing nutritional stress and mortality in many species (A. L. Bond & Lavers, 2014; Forcada et al., 2006; Oliveira, 2011; Sprogis et al., 2018). For example, the 1997-98 ENSO event caused a reduction of wildlife along Peru’s coast with 75% and 80% reductions in the populations of SAFS and SASL, respectively (Oliveira et al., 2006, 2012). Since 1998 populations have recovered to an extent, but are currently in a state of decline (Cárdenas-Alayza et al., 2021).

Identification of hard remains from scat samples is the most widely used technique to identify resource utilization in marine vertebrates. Although the technique has many biases, its wide use permits making interesting comparisons over time. The majority of previous research on the diet composition of otariids within HCS has focused of SAFS and SALS independently (Majluf, 1987; Paredes & Arias-Schreiber, 1999; Sarmiento-Devia et al., 2020; Zavalaga et al., 1998). However,

some few studies have evaluated diet composition between SAFS and SASL concurrently in Peru in the 1980s and late 1990s. The first study conducted by Vásquez (1995), in late 1980s reports otariid diets were based on fish and cephalopods; with the Peruvian anchovy as the main species consumed by both pinnipeds followed by Jack Mackerel (*Trachurus murphyi*). One decade later, Arias-Schreiber (2003) confirms that Peruvian anchovy and squid were main prey items shared by both species, with also red squat lobsters (*Pleuroncodes monodon)* comprising an important part of the diet for SASL. Recent studies in northern Chile also confirms the red squat lobster as a dominating prey item in the diet of SASL, followed by Peruvian anchovy, and squid (Sarmiento-Devia et al., 2020; Sielfeld et al., 2018). However, these recent studies argue that consumption of crustaceans by SASL is influenced by changes in the food web due to ENSO events, and that this resource reflects a coping mechanism when Peruvian anchovy is lacking (Sielfeld et al., 2018). However, there are no studies with consecutive sampling to test if this pattern is true.

Through long term monitoring and onsite research at PSJ, we were able to collect samples from 2015 to 2018, which included ENSO and non-ENSO conditions. The objective of this research was to assess if resource partitioning exists in the resident sympatric otariid populations of SAFS and SASL at PSJ over a four year study period. Our hypothesis is that for sympatry to occur both otariids species exploit food resources differently, being resource partitioning the mechanism to avoid competitive exclusion. Furthermore, we expect to update current patterns of resource consumption by each species and contribute towards the understanding of the current foraging strategies of sympatric otariids in the highly productive and

dynamic HCS.

2. Materials and Methods

2.1 *Study area and sampling*

A total of 3,325 scat samples (1,484 SAFS and 1,841 SASL) were collected at Punta San Juan (PSJ) between January 2015 and December 2018 study period. PSJ (15°22'S, 75°11'W) is a 54 Ha peninsula in Peru with 20 beaches and coves occupied by SASL and SAFS. Samples were collected by personnel of the Punta San Juan Program, CSA, U. Peruana Cayetano Heredia under authorization of the RNSIIPG, (Reserva Nacional Sistema de Islas, Islotes y Puntas Guaneras) administered by SERNANP (Servicio Nacional de Areas Naturales Protegidas). Information and samples for this study were collected in the main breeding rookeries for each species that contain 40-60% of total PSJ population, (beach N7 for SASL and beach S3 for SAFS). During the study period, counts by age-class were carried out in each of the breeding rookeries 2-4 times per month through direct observation from cliff edges using 10x50 binoculars between 0600-0900 hours by specialised personnel. Counts during breeding season (BS, January – March in SASL and October – December in SAFS) and non-breeding season (non BS, April - December in SASL and January - September in SAFS) were examined for the entire study period (see Appendix B1).

This research did not require invasive sample collection from live animals. Samples were collected at beaches exclusively used by each study species, making it impossible to confuse samples between species. All samples were collected from

the ground on a given day of the month, leaving 21-31 days between samplings. Sample collection occurred between 1100 - 1500 hours; a time of day when otariids move towards the shoreline to thermoregulate; thus disturbance towards the colony is minimized. Samples were chosen based on their appearance and tenderness in aims to collect complete, recently defecated faeces. Samples were collected for 40 months for SAFS and for 35 months for SASL. No samples were collected in Spring 2016 for SASL. Samples were stored in plastic bags and labelled. Collected samples were soaked in soap water for 3 - 24 hours to aid dissolving faecal matter. Times varied according to concentration of organic matter in samples. Contents were passed through nested sieves of 1.00 mm and 0.297 mm mesh sizes. Hard remains included otoliths, cephalopod beaks, and crustacean remains, which were all carefully removed. Otoliths and cephalopod beaks that were eroded in >50% were discarded, following Tollit et al. 1997. Sagittal otoliths where identified to species level following García-Godos (2001). Right/left otoliths or upper/lower mandibles were not considered since frequency of occurrence and relative abundance indices (IIMP) were used for diet composition analyses. Cephalopod beaks were identified as one taxonomic group ("Cephalopods"). For crustaceans, only one species (*Pleuroncodes monodon*) was identified and counted using the cephalothorax. Fish otoliths were stored under dry conditions, cephalopod beaks were stored in 70° ethanol, and all crustacean cephalothorax were discarded. Hard parts were not measured.

In order to ensure that sample size is not biased and is sufficient to correctly represent the diversity of prey consumed, we calculated cumulative diversity in a given sampling season and verified the minimum number of samples required to

reach an asymptote. If so, this means that additional samples do not modify the diversity index significantly, indicating a sufficient sample size (Ferry et al., 1997). This was evaluated by calculating the accumulated average and standard deviation of diversity curves generated from matrices of prey abundance data per season. We estimated the Shannon-Wiener Index (H') (Krebs, 1999) with 1,000 random permutations and considered an error of 5% (MATLAB program, v.2019b). Each curve is considered asymptotic if at least two previous values to sample trophic diversity (H') are in the range of H' ± 0.05H'. This permutation routine was adapted from Ferry, Clark and Cailliet (1997) and has been applied to test sample size adequacy in other species (Adams, 2004; Koen Alonso et al., 2002; Páez-Rosas & Aurioles-Gamboa, 2010; Porras-Peters et al., 2008).

2.2 *Diet composition*

The importance of prey was evaluated using the percent number (*PN*), percent frequency of occurrence (*FO*) and the percent Importance Index (*IIMP*). *PN* was used to describe otariid diets according to taxa (fish, cephalopods, and crustaceans), measuring the number of hard remains of taxon *i* in the total number of hard remains from all prey found in scat samples; for the entire study period and by sampling season. *FO* was used to describe the occurrence of a prey item in each of the otariids diet per season, and *IIMP* was used to estimate the importance of each prey item per sampling unit (scat) following García-Rodríguez (1999) and García-Rodríguez & Aurioles-Gamboa (2004). This measure estimates the probability of finding a given prey species in a scat sample, through the following equation:

Equation 1. $$IIMP_i = \frac{1}{U}\sum_{j=1}^{u}\frac{X_{ij}}{X_j}$$

Where X_{ij} is the number of occurrences of species i in scat j, X_j is the total number of identifiable structures in scat j, u is the number of scats in which the taxon i was found and U is the number of scat samples where prey items were found. This index generates results from 0 to 1 that is then converted into percentages ($IIMP_i$ x 100). In this study, we will consider the prey items that contribute an $IIMP \geq 1\%$ (García-Rodríguez & Aurioles-Gamboa, 2004; Koen Alonso et al., 2000). *IIMP* was developed for analysis of hard structures in pinniped scats and is used in this study as the main assessor for prey composition in this study because it is less sensitive to changes in the number of prey in an individual scat (Amador-Capitanachi et al., 2020; García-Rodríguez & Aurioles-Gamboa, 2004; Páez-Rosas & Aurioles-Gamboa, 2010).The *IIMP* allows each scat to contribute an equal amount of information, whereas *PN* can be dominated by a few scats with a large number of a single prey-taxon hard remains and *FO* does not reflect the abundance of prey items in the samples (Garcia-Rodriguez & de la Cruz-Agüero, 2011). With *IIMP* values, ranked abundances were constructed to evaluate the composition of all prey items ranked by their contribution of abundance per each sampling. Also, prey items were classified in ecological groups according to their main habitat / ecology extracted from FishBase (http://www.fishbase.org; Froese and Pauly, 2019). The ecological groups considered were: Pelagic, Demersal-Pelagic, Benthic-Demersal and Demersal, following Koen Alonso *et al.* (2001).

2.3 *Trophic indices*

Species Richness (*S*) was estimated for each sampling season by pooling all years in a season and for each independent season and year. We assume that each faecal sample represents one individual in the rookery, and therefore scat sampling represents a random sample of the population. To determine whether individuals in a given sampling season demonstrate different degrees of feeding expertise, the standardized Levin B_i Index (Krebs, 1999) was estimated to distinguish if each species is a specialist or generalist consumer.

Equation 2.

$$B_i = \frac{1}{n-1}\left\{\left(\frac{1}{\sum {IIMP_{ij}}^2}\right) - 1\right\}$$

Where B_i is the trophic breadth, $IIMP_{ij}$ is the proportion of the prey item *j* in the diet of predator *i*, and *n* is the number of prey species in the diet. The standardized B_i is an index that generates results from 0 to 1. Predators are characterized as a specialist when values are less than 0.6 and as a generalist when values are ≥ 0.6. Confidence intervals (±95) were estimated by applying $\pm 1.96\sqrt{\boldsymbol{\sigma}^2_{\boldsymbol{Bi}}}$ (Krebs, 1999).

Trophic Level (*TL*) was calculated for each species and season (Eq. 3) to identify the trophic level based on its diet composition and the trophic level of their prey (Christensen & Pauly, 1992).

Equation 3.

$$TL = 1 + \left(\sum_{j=1}^{n} DC_{ij}\right)\left(TL_j\right)$$

Where TL_i is the prey's trophic level; DC_{ij} is the proportion of the prey i in the diet of the predator j and n is the total number of prey species in the diet. Trophic level values for prey species were extracted from FishBase (http://www.fishbase.org; Froese and Pauly, 2019). Cephalopod and crustacean values were extracted from literature (Espinoza et al., 2017; Tam et al., 2008). For cephalopods we used the *TL* value for *Loligo gahi*, since it is the only species identified in some of the randomly selected beak squids in our samples and has been previously identified for these study species (Vásquez 1995; Arias-Schreiber 2003; Sielfeld et al. 2018; Sarmiento-Devia et al. 2020).

2.4 *Environmental conditions*

Monthly seasonal sea surface temperature (SST) records collected by the naval base at San Juan de Marcona bay (Dirección de Hidrografía y Navegación, DHN), located less than 5km from the otariid colonies, were used to characterize the environmental conditions during the study period. We constructed a time series of sea surface temperature anomalies (SSTA) by subtracting the monthly record to the long term mean for the complete time series (1976 - 2018) for each month. To compare environmental conditions with scat sampling seasons, we grouped SST and SSTA for austral summer (January - March), fall (April - June), winter (July - September) and spring (October - December), and estimated mean SST and SSTA values.

2.5 *Statistical analyses*

To determine differences in association of the composition of the prey items that were consumed per season and species, matrices with species (columns) and seasons (rows) using *IIMP* values were constructed. It is important to note that *IIMP* is already a form of standardized data because it weighs the contribution of each prey item according to the sample size. Since there are many zeros in the prey items matrix, it was first transformed with $\log(n+1)$ prior to analysis. Bray-Curtis distances between 0-1 were estimated between the sampling seasons (Q-mode). Agglomerative hierarchical clustering was estimated using Ward's method (Ward & Hook, 1963) and p-values for each cluster were calculated with bootstrap resampling (1,000 iterations) using the vegan package in R statistical software (R Core Team, 2018). To interpret the position of sampling seasons and prey items between the two species in a reduced number of dimensions, we used Non-Metric Multidimensional Scaling (NMDS, stress < 0.5) on the standardized matrices. To test assumptions, normality was evaluated using Shapiro-Wilk's Test ($p < 0.05$) and homogeneity of variance was checked with Levene's Test ($p < 0.05$). Differences between groups were evaluated with ANOVA for parametric data and Kruskal-Wallis for non-parametric data ($p < 0.05$). Tukey and Chi-square were used as post-hoc tests for multiple pairwise comparisons ($p < 0.05$) for parametric and non-parametric data, respectively. To determine if there were correlation with environmental conditions, proportion of empty scats, *PN* by taxa (fish, cephalopod and crustaceans), species richness (*S*), trophic breadth (Levin's B_i), and trophic level (*TL*) estimated for SAFS and SASL were correlated with SST and SSTA

metrics using a correlation matrix (Spearman rank, rs, $p < 0.05$) with packages rstatix and corrplot in R statistical software (R Core Team, 2018).

3. Results

3.1 *Study area and sampling*

Of all samples collected, 80.06% (n = 2,662) had identifiable hard remains; the remainder were recorded as empty scats. The proportion of SASL with hard remains (93.10%, n=1,714) was significantly larger (Chi-square test, $X^2 = 17.3$, $p < 0.05$) than the proportion of SAFS with hard remains (63.88%, n=948). This pattern was the same in all years, except 2015 (Chi-square test, $X^2 = 0.337$, $p = 0.561$), when the proportion of empty scats was not significantly different between species (Table 1). Adequate resolution to capture the prey diversity was obtained by grouping samples for three consecutive months during the 2015 - 2018 study period for austral summer (January - March), fall (April - June), winter (July - September) and spring (October – December). A total of 31 matrices were constructed for 16 sampling seasons for SAFS and 15 for SASL. Required samples per season for SAFS were in range of 35 – 120 and 27 – 171 for SASL. Therefore, we grouped monthly sampling into seasons, so sample size was always above the number of required samples to determine diet diversity for both SAFS and SASL.

Table 2. 1 Number of collected and proportion of scat samples with content (in brackets) for South American fur seal (SAFS) and South American sea lion (SASL) per year (2015 - 2018), season (sum = summer, fal = fall, win = winter and spr = spring) and total.

Year	Season	SAFS	SASL
	2015-sum	62 (0.66)	30 (0.43)
	2015-fal	97 (0.63)	97 (0.53)
	2015-win	70 (0.69)	50 (0.96)
	2015-spr	40 (0.70)	151 (0.99)
2015		269	328
	2016-sum	129 (0.74)	183 (0.94)
	2016-fal	111 (0.77)	129 (0.98)
	2016-win	101 (0.78)	183 (0.99)
	2016-spr	40 (0.68)	-
2016		381	495
	2017-sum	120 (0.38)	120 (1.00)
	2017-fal	60 (0.38)	131 (0.98)
	2017-win	110 (0.55)	86 (1.00)
	2017-spr	50 (1.00)	60 (0.92)
2017		340	397
	2018-sum	126 (0.52)	189 (0.97)
	2018-fal	121 (0.83)	185 (0.97)
	2018-win	125 (0.63)	188 (0.93)
	2018-spr	122 (0.67)	59 (1.00)
2018		494	621
Total		**1,484**	**1,841**

3.2 *Diet composition*

SAFS hard remains were composed of 56.47% fish (n = 13,403 otoliths), 30.70% cephalopods (n = 7,286 beaks) and 12.84% crustaceans (n = 3,047 cephalothorax). Meanwhile SASL samples were composed of 6.55% fishes (n = 12,189 otoliths), 1.60% cephalopods (n = 2,981 beaks) and 91.85% crustaceans (n = 171,034 cephalothorax) (Figure 2.1A).

The proportion of fishes (Chi-square test, $X^2 = 7.90$, $p < 0.05$) and cephalopods (Chi-square test, $X^2 = 9.15$, $p < 0.05$) in the hard remains of SAFS samples were ten to thirty times higher than in SASL. Significant differences in fishes were found for all years except for year 2015 (Chi-square test, $X^2 = 0.00$, $p = 1.00$). The proportion of fishes in diet was significantly different between SAFS and SASL in spring (Chi-square test, $X^2 = 4.60$, $p < 0.05$) and winter ($X^2 = 5.33$, $p < 0.05$), but not in fall (Chi-square test, $X^2 = 1.33$, $p= 0.25$) and summer (Chi-square test, $X^2= 1.33$, $p = 0.25$). The proportion of the cephalopods was always higher in SAFS in comparison to SASL samples in summer (Chi-square test, $X^2 = 5.33$, $p < 0.05$), fall (Chi-square test, $X^2 = 4.10$ $p < 0.05$), winter (Chi-square test, $X^2 = 5.33$, $p < 0.05$) and spring (Chi-square test, $X^2 = 4.60$, $p < 0.05$). Finally, the proportion of crustaceans found in SAFS samples was seven times lower than those found in SASL (Chi-square test, $X^2 = 13.70$, $p < 0.05$). This pattern was found in all years except for year 2015, when no significant differences were found for crustaceans ($p = 0.77$). The proportion of crustaceans in diet of SAFS and SASL was significantly different in spring (Chi-square test, $X^2 = 4.50$, $p < 0.05$) and winter

seasons (Chi-square test, $X^2 = 5.33$, $p < 0.05$) but not in summer (Chi-square test, $X^2 = 1.71$, $p = 0.19$) and fall (Chi-square test, $X^2 = 2.08$, $p = 0.15$).

A total of 22 prey items were identified in this study; 19 for SAFS and 15 for SASL. With 22 species accounting for >1% of *IIMP*. When all years and seasons were pooled, the main prey items in the diet of SAFS were 42.8% *Engraulis ringens*, 34.7% cephalopods, 7.4% *Leuroglossus. stilbius*, 5% *Pleuroncodes monodon*, 3.8% *Anchoa nasus*, 2.1% *Sphyraena idiastes*, 1.6% *Odontesthes regia*, and 1.1% *Merluccius gayi*. The main prey items in the diet of SASL were 69.9% *P. monodon*, 19.1% *E. ringens*, 4.7% cephalopods, and 4.6% *O. regia* (Figure 2.1B). The complete list of prey item *IIMP* values for each species, year, and season is available as Appendix B2. Average percent FO for top five prey items during the entire study period for SAFS were 37.0% *Engraulis ringens*, 32.5% cephalopods, 8.0% *Leuroglossus. stilbius*, 5% *Pleuroncodes monodon* and 6.3% *Anchoa nasus*. Meanwhile average percent FO for top five prey items during the entire study period for SASL were 43.8% *P. monodon*, 30.1% *E. ringens*, 12.6% cephalopods, 4.9% *O. regia* and 3.5% *N. crockeri.* Seasonal variations in PN per taxa and *FO* and *IIMP* for prey items are shown in Figure 2.2-2.3. Ecological grouping reveals that SAFS consumed prey items that were 52.6% Pelagic, 47.3% Demersal-Pelagic and 1.5% Demersal-Benthic. Meanwhile SASL consumed prey items that were 23.9% Pelagic, 69.4% Demersal-Pelagic and 1.4% Demersal-Benthic (Figure 2.3D).

3.3 *Trophic indices*

Species richness (*S*) for all SAFS samples (n = 1,484) was estimated at 19 species and for all SASL samples (n = 1,841) at 15 species, with a maximum of 6 species per sample for either SAFS or SASL. No seasonal difference in *S* was found for SAFS (12.06 ± 0.82 for summer, 11.36 ± 0.67 for fall, 12.13 ± 0.84 for winter and 12.97 ± 0.18 for spring) or SASL (10.52 ± 0.65 in summer, 9.29 ± 0.66 in fall, 12.82 ± 0.88 in winter and 11.72 ± 0.51 in spring) (Table 2). Levin's B_i for both species was < 0.6, categorizing both species as "specialists". Regardless, SASL has a more narrow trophic niche breadth ($B_i = 0.11 \pm 0.12$) than SAFS ($B_i = 0.26 \pm 0.13$) (Table 2). Mean *TL* for SAFS was 4.30 ± 0.15 and 4.55 ± 0.10 for SASL, which categorizes them both as tertiary consumers (*TL* > 4), with no significant differences between species (Table 2).

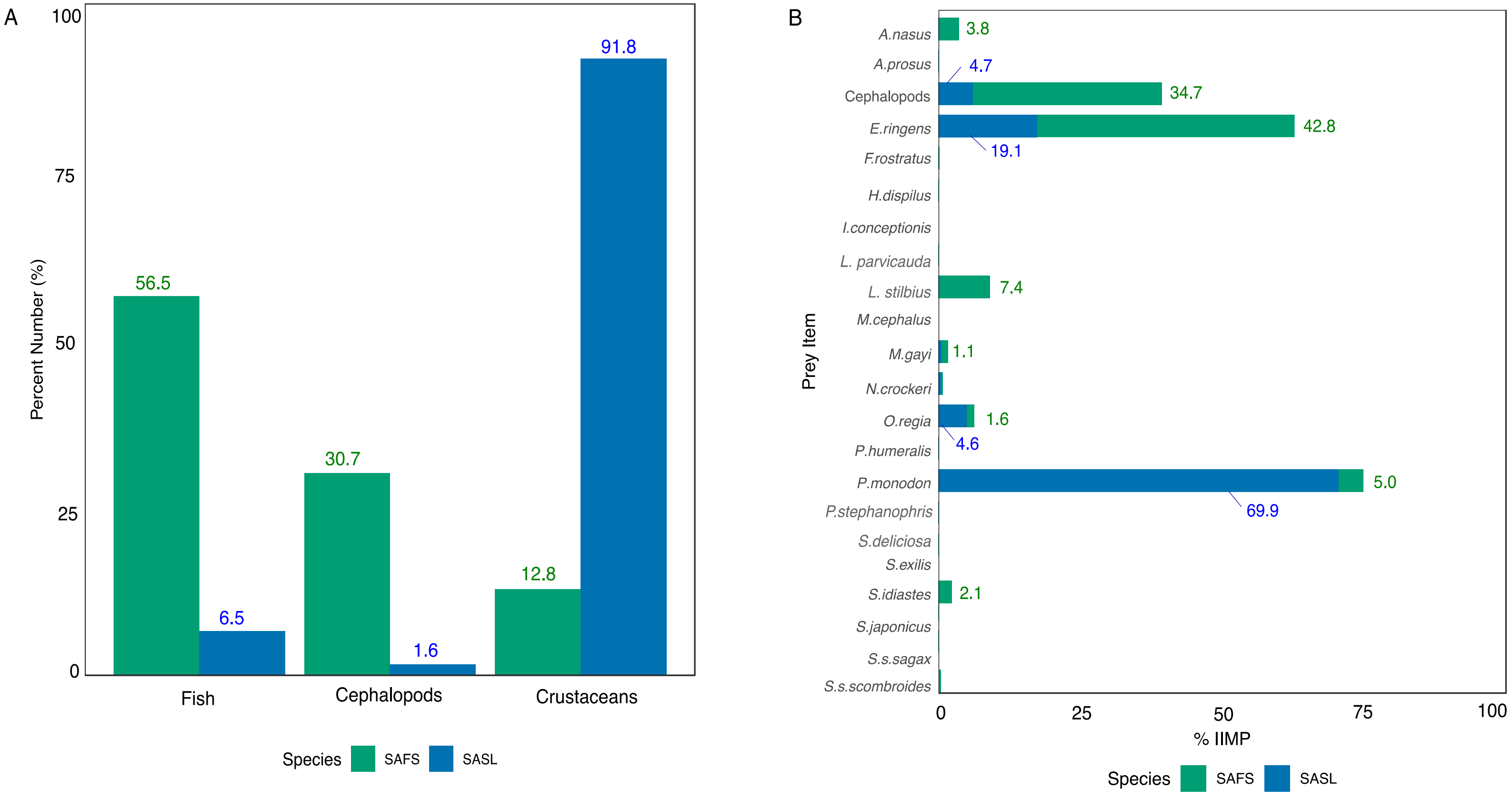

Figure 2. 1 Bar graphs of A) percent number (%) of taxa consumed by each species during the study period and B) stacked % IIMP values for each prey item over the entire study period for South American fur seal (SAFS, green) and South American sea lion (SASL, blue). Prey items (N = 22) detected are listed organized in alphabetical order. Values for IIMP >1% are annotated in each otariid species color

Table 2. 2 Species Richness (S), Levin's Trophic Niche Breadth (Bi ± 95 %CI) and Trophic Level (TL) for South American fur seal (SAFS) andSouth American sea lion (SASL) per year (2015 - 2018), season (sum = summer, fal = fall, win = winter and spr = spring) and Mean ± SD for the study period.

	S		***Bi* ± 95% CI**		***TL***	
Season	**SAFS**	**SASL**	**SAFS**	**SASL**	**SAFS**	**SASL**
2015-sum	8	4	0.18 ± 0.033	0.34 ± 0.125	4.12	4.30
2015-fal	8	7	0.29 ± 0.028	0.41 ± 0.080	4.28	4.51
2015-win	8	8	0.19 ± 0.031	0.15 ± 0.009	4.19	4.39
2015-spr	8	7	0.39 ± 0.050	0.23 ± 0.013	4.49	4.44
2016-sum	11	8	0.35 ± 0.032	0.05 ± 0.002	4.53	4.61
2016-fal	11	9	0.20 ± 0.015	0.07 ± 0.003	4.26	4.61
2016-win	11	12	0.19 ± 0.019	0.01 ± 0.001	4.19	4.67
2016-spr	6	-	0.31 ± 0.063	-	4.46	-
2017-sum	7	8	0.26 ± 0.031	0.03 ± 0.001	4.44	4.64
2017-fal	3	7	0.62 ± 0.179	0.04 ± 0.002	4.28	4.64
2017-win	11	9	0.27 ± 0.029	0.02 ± 0.001	4.40	4.68
2017-spr	8	9	0.15 ± 0.017	0.06 ± 0.002	4.46	4.61
2018-sum	8	9	0.34 ± 0.039	0.07 ± 0.002	4.31	4.53
2018-fal	6	7	0.15 ± 0.014	0.07 ± 0.002	4.11	4.58
2018-win	7	12	0.09 ± 0.013	0.05 ± 0.001	4.05	4.54
2018-spr	8	6	0.22 ± 0.023	0.09 ± 0.004	4.31	4.55
Mean ± SD	**8 ± 2.17**	**8 ± 2.07**	**0.26 ± 0.13**	**0.14 ± 0.16**	**4.31 ± 0.15**	**4.55 ± 0.11**

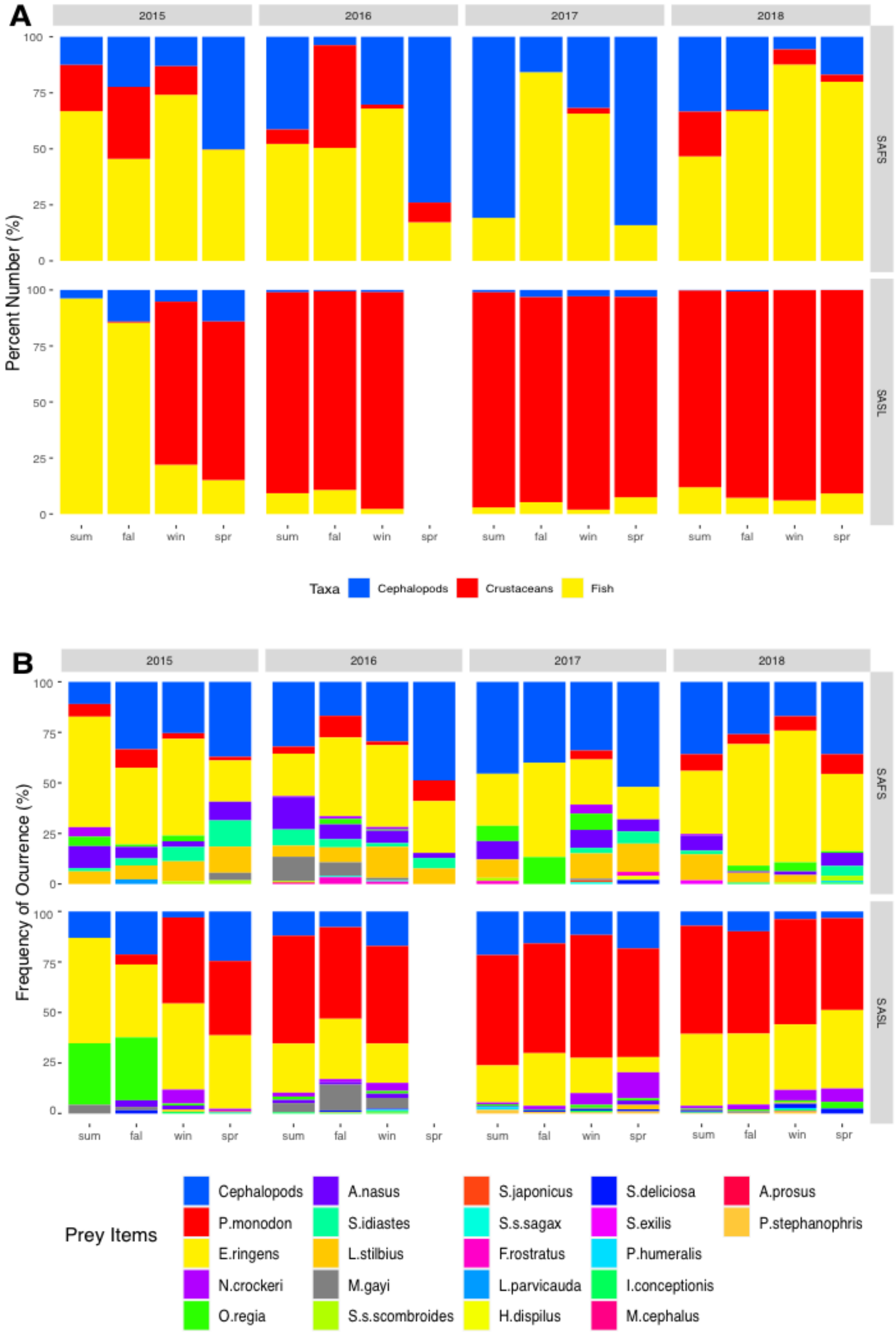

Figure 2. 2 Stacked bar graphs of A) Percent number (%) by taxa; B) Frequency of occurrence (%) by prey item. South American fur seals (SAFS, top panels) and South American sea lions (SASL, bottom panels) for each year (2015-2018) and season (sum = summer, fal = fall, win = winter, spr = spring).

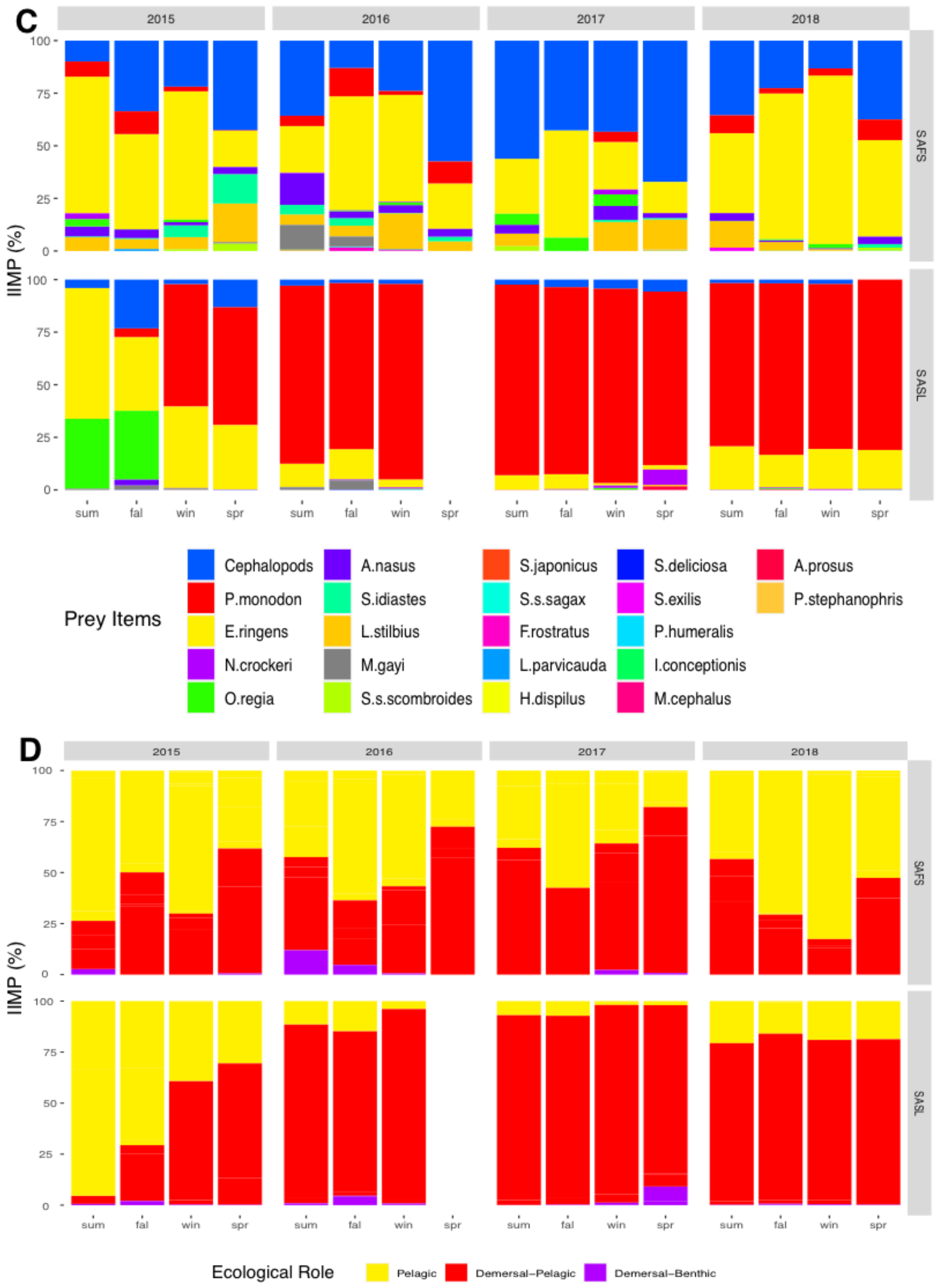

Figure 2. 3 Stacked bar graphs of C) IIMP >1% by prey items and D) IIMP (%) by ecological groups South American fur seals (SAFS, top panels) and South American sea lions (SASL, bottom panels) for each year (2015-2018) and season (sum = summer, fal = fall, win = winter, spr = spring).

3.4 *Clustering*

The hierarchical clustering shows two clear separate clusters for each species. The only exception are summer and fall 2015 with an overlap between SASL and SAFS (Figure 2.4). There are no clear patterns for other seasons and/or years. Non-metric Multidimensional Scaling (NMDS) plot (stress = 0.08) reinforces the separation between SAFS and SASL (Figure 2.4). *E. ringens* is an important prey for both species, due to its central position between the two clusters. Cephalopods are closely associated with the SAFS cluster, whereas *P. monodon* is associated to the SASL cluster. Finally, *O. regia* is positioned close to the sampling season nodes of SASL that correspond to summer 2015 and fall 2015. Fish species *Isacia conceptionis*, *Paralabrax humeralis*, *Sciacena deliciosa*, and *Normanichthys crockeri* are associated with SASL; whereas a larger diversity of other fish species *Merluccius gayi, Lampanyctus parvicauda, Anchoa nasus, Leuroglossus stilbius, Strongylura exilis, Sardinops sagax sagax, Fodiator rostratus, Sphyraena idiastes, Scomber japonicus*, and *Scomberesox saurus scombroides* are more closely associated with SAFS. Abundance rank curves show that during seasons with trophic overlap (summer and fall 2015), SAFS and SASL diets were not significantly different ($p < 0.05$) and were composed of 55% and 48.6% *E. ringens*, plus 21.7% and 13.6% cephalopods, respectively. Furthermore, during these seasons SASL consumed 33% of *O. regia* and SAFS consumed 5.6% *L. stilbius* and 4.6% *A. nasus*. In these seasons, *P. monodon* consumption was 9% and 2%, respectively for SAFS and SASL diets (Figure 2.5).

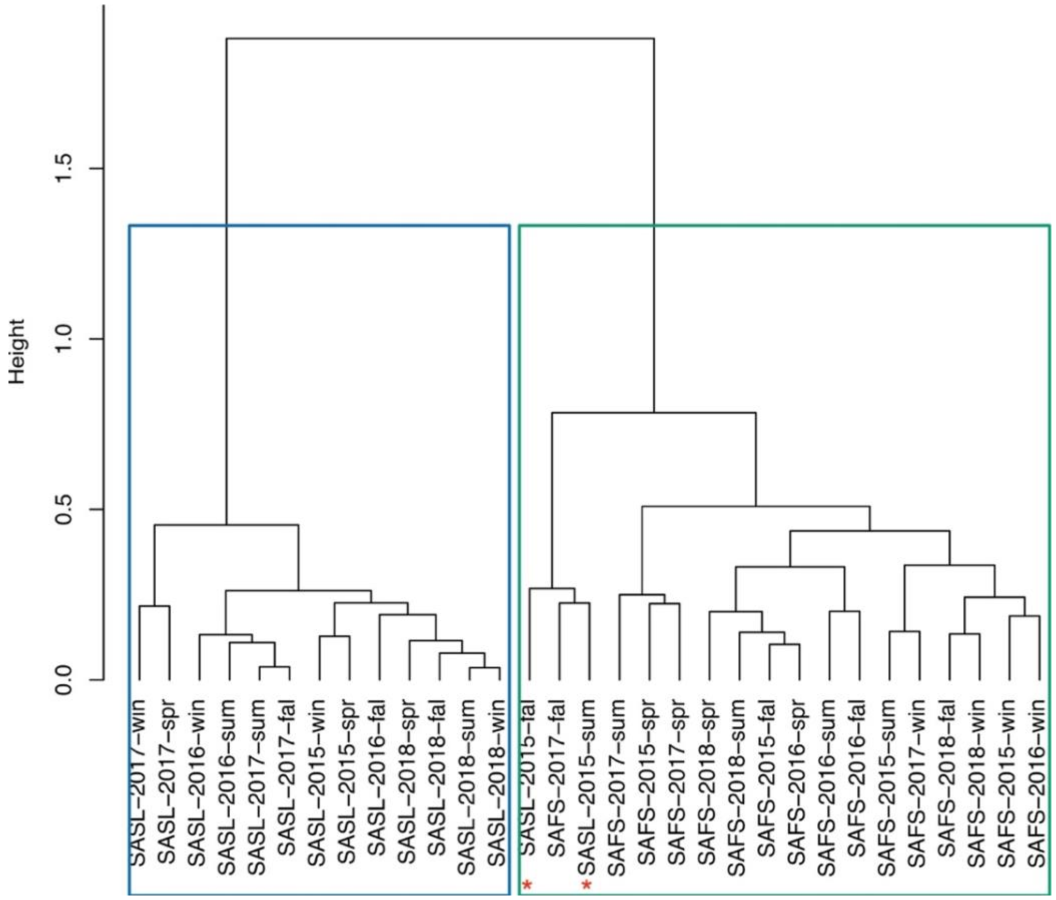

Figure 2. 4 Dendrogram using agglomerative hierarchical clustering with Ward’s method and Bray-Curtis distances, showing two separate clusters for South American sea lion (SASL, blue) and South American fur seal (SAFS, green). Two SASL seasons (SASL-2015-fal and SASL-2015-sum) are inside the SAFS cluster (red asterisks).

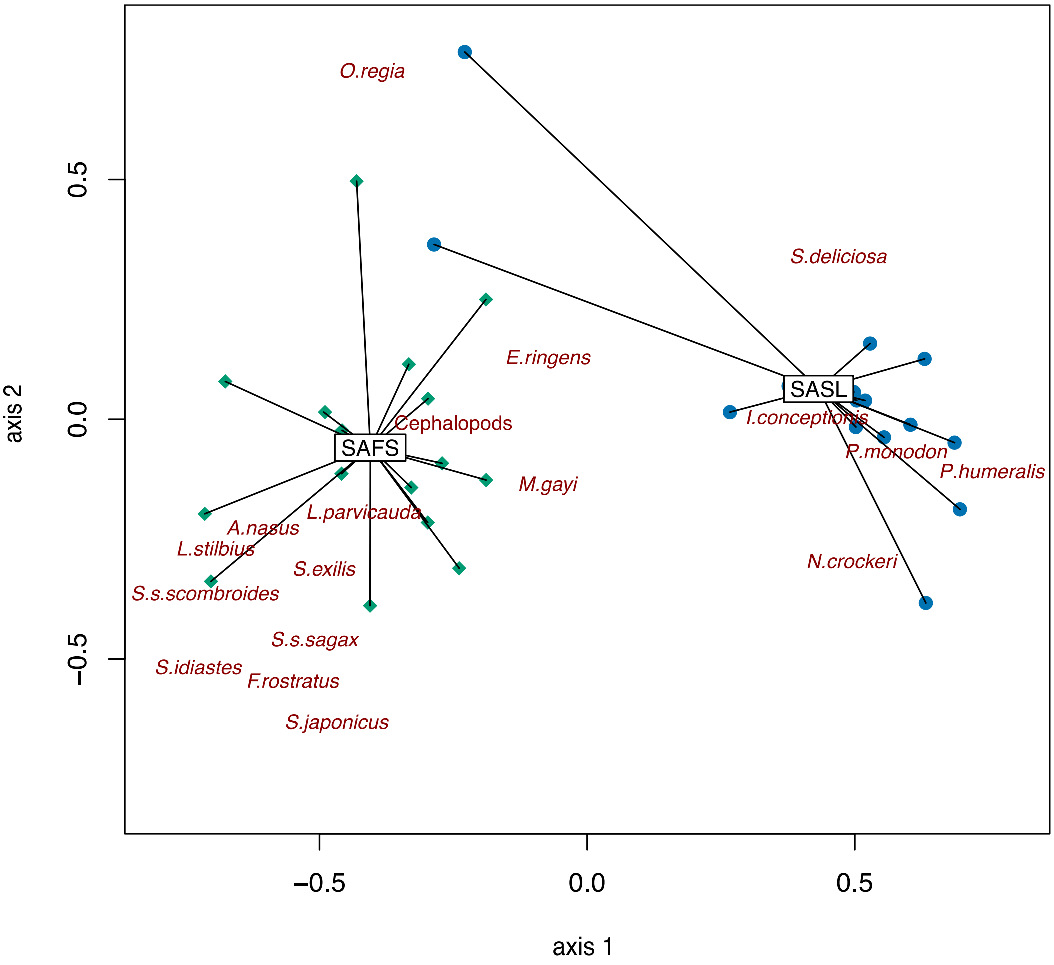

Figure 2. 5 NMDS spider plot (stress = 0.08) showing two separate clusters for each otariid species. Each node represents a sampling season for South American sea lion (SASL, blue) and South American fur seal (SAFS, green). Relevant prey items for principal dimensions (axis 1 and axis 2), overlaid in dark red.

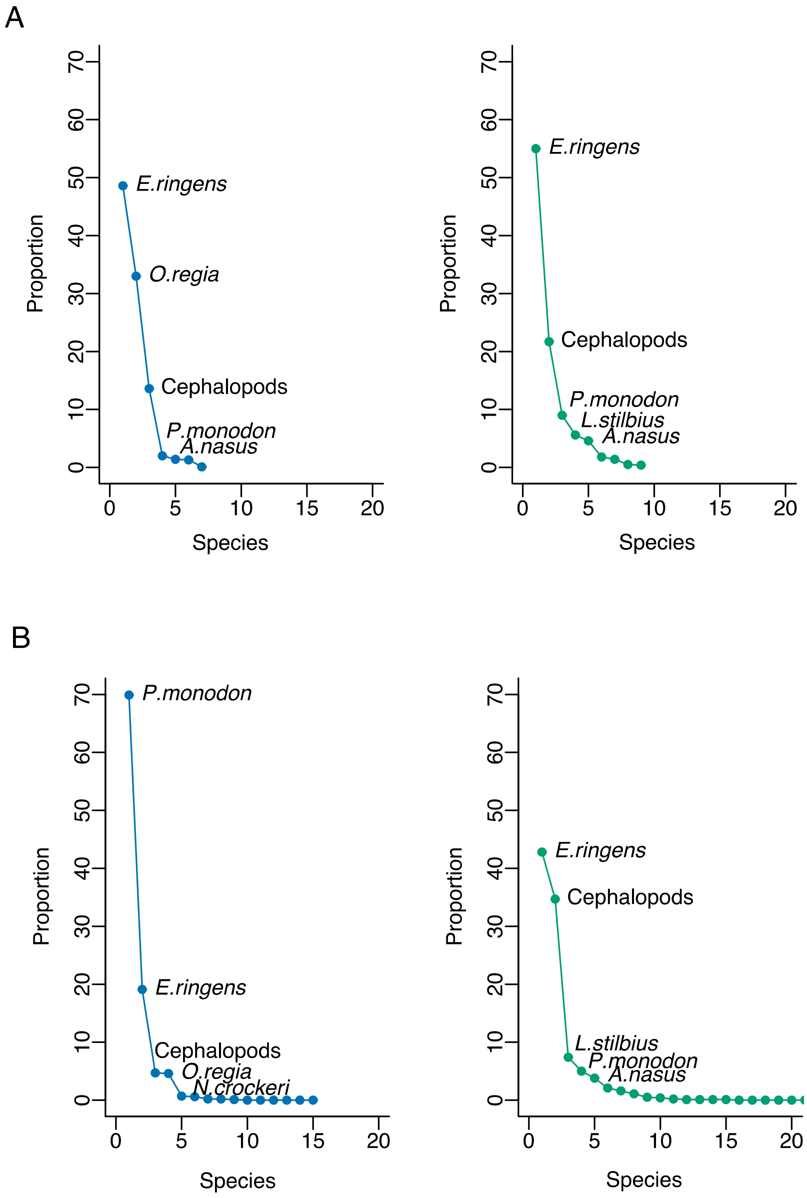

Figure 2. 6 Ranked abundance curves for prey items of South American sea lion (SASL, blue) and South American fur seal (SAFS, green) samples during A) seasons with trophic overlap (summer 2015 and fall 2015) and B) seasons without trophic overlap. Labels shown for top-five ranking prey items.

3.5 *Environmental conditions and trophic indices*

Throughout the entire study period, SST ranged between 13.20 and 17.70 °C. Mean SST throughout the study period was 16.06 ± 0.45 °C in summer, 15.52 ± 0.50 °C in fall, 14.28 ± 0.56 °C in winter and 14.56 ± 0.43 °C in spring. SSTA ranged between -1.00 to 1.44 °C. Mean SSTA during the study period was 0.21 ± 0.48 °C in summer, 0.54 ± 0.49 °C in fall, 0.30 ± 0.31°C in winter and 0.32 ± 0.31°C in spring. In general, SST was significantly different (ANOVA, F (1,15) = 9.54, p < 0.01), allowing to treat each season independently throughout the study period. However, Tukey multiple comparison of pairwise means showed that fall-summer (p = 0.38) and spring-winter (p = 0.84) were not significantly different to each other in some years (summer–fall 2015, 2017, 2018 and winter–spring 2017, 2018). Since the six months grouping could not be applied to the entire study period, we kept the 3-month seasonal sampling resolution to compare trophic indices and environmental conditions for all seasons and years (Appendix B3).

For SAFS (N = 16 seasons), significant correlations with scores > 0.50 were found between PN of cephalopods and TL (rs = 0.76); TL and Bi (rs = 0.64); Bi and mean SST (rs = 0.54); and between PN of cephalopods and PN of fish (rs = -0.74), PN of fish and TL (rs = -0.64), and PN cephalopods and crustaceans (rs = -0.55). For SASL (N = 15 seasons), significant correlations with scores >0.50 were found between PN of fish and Bi (rs = 0.93), PN crustaceans and TL (rs = 0.82), PN of fish and empty scats (rs = 0.72), and

proportion of empty scats and Bi (rs = 0.65); and between PN of crustaceans and PN of fish (rs = -0.96), TL and Bi (rs = -0.90), PN of crustaceans and Bi (rs = -0.90), PN of fish and TL (rs = -0.89), PN of crustaceans and proportion of empty scats (rs = -0.7), proportion of empty scats and TL (rs = -0.72), and Species Richness and Bi (rs = -0.63). For SASL, no significant correlations with scores > 0.50 were found between trophic and environmental indices (Appendix B4).

4. Discussion

This study demonstrates that trophic segregation exists between populations of sympatric SAFS and SASL at PSJ, Peru primarily due to the resource partitioning of three main shared prey items: Peruvian anchovy, cephalopods, and red squat lobster. Both otariids share Peruvian anchovy as an important prey item and complement their diets with two other important items: cephalopods in SAFS and red squat lobsters in SASL. The consumption of these prey items in different proportions by each otariid explains the trophic segregation detected through the hard part remains found in scats collected during the consecutive seasonal samplings in the 2015-2018 study period. As part of the study, we also detected that periods of higher trophic overlap can occur, when similar proportions of E. ringens and cephalopods were consumed by both species and interspecific competition could be exacerbated.

4.1 *Resource partitioning and trophic overlap*

In previous studies conducted in sympatric otariid colonies in Peru, Peruvian anchovy (*E. ringens*) made up 30 - 40% of the diet of both SAFS and SASL and was reported as the cause for interspecific trophic overlap between these sympatric otariids (Vásquez 1995, Arias-Schreiber 2003). As expected, *E. ringe*ns continues to be an important prey item that is widely available in the HCS system. However, in our study, SAFS consistently consumed anchovy and cephalopods, whereas SASL consumed anchovies and red squat lobsters. Increased in availability and consumption of red squat lobsters within the HCS system following the 1997-98 El Niño (Gutiérrez et al. 2008, Kiko et al. 2015) has made this item an important part of SASL diet (Espinoza et al. 2017).

During austral summer and fall of 2015 in which trophic overlap was detected, SASL did not consume P. monodon in the same proportions as other seasons, but instead increased consumption of E. ringens and included *O. regia*. This may be due to a reduced availability of *P. monodon* during months of the 2015/16 El Niño in the preferred habitat where sea lions forage as compared to SAFS. Oceanographic acoustic studies have shown that P. monodon have preference for cold coastal water masses, since they ensure good conditions for feeding, reproductive success and recruitment. However, during Extraordinary El Niño events such as in 2015-16, cold water contracts into the coast, decreasing the habitat for *P. monodon* and decreasing availability

of the resource (Yuffra et al. 2018). Therefore, it is possible that P. monodon was not available for SASL foraging range in the 2015 summer and fall seasons.

Foraging habitat of SAFS and SASL has been mostly studied in the Atlantic coast of South America and has found that SASL consumes demersal and benthic prey types while SAFS consumes pelagic prey (Riet-Sapriza et al. 2013, Baylis et al. 2016). In this study, ecological groups revealed that Demersal-Benthic species are not important in neither of the Peruvian otariids' diet composition (1-1.5%). SAFS diet is mostly composed of prey items from Pelagic (52.35%) and Demersal-Pelagic (47.25%) ecological groups. Meanwhile SASL's prey items are mostly Demersal-Pelagic (69.44%) and also include smaller amounts of Pelagic (23.88%) groups. This can be explained by the limited access to the benthic habitat for otariids i.e., in PSJ depth drops to >1000 m in <50km from shore. However, differences may also be attributed to sexual trophic segregation, as evidenced in SASL in Patagonia, where females have a more pelagic diet than males (Drago et al. 2009). Further studies using methods to explore intraspecific differences (e.g., stable isotopes) and depth (e.g., time depth recorders) are recommended in HCS.

4.2 *Empty scats*

In this study we found significant differences between the proportion of empty scats in SAFS compared to SASL. We also found a direct relationship

between empty scats and the proportion of fish consumed, which can be related with longer offshore foraging trips (Naya et al. 2002, Franco-Trecu et al. 2013, Baylis et al. 2014). We consider this an important indicator for differences foraging locations between fur seals (offshore) and sea lions (inshore), given that the three important prey items (*E. ringens, P. monodon* and Cephalopods) have pelagic ecological habits. This relation was also found in SAFS from the Atlantic coast of Uruguay, where the number of empty scats from females was related to longer foraging trips far away from the rookery (Franco-Trecu et al. 2013). An observational study at PSJ estimated that foraging trip duration of adult female SAFS attending new born pups was 3 - 4 days on average, within a range of 1 - 9 days (Ganoza 2016). Whereas studies in adult female SASL have reported foraging trips by adult females of 1-2 days (Soto et al. 2006). Thus, the high proportion of SAFS empty scats is possibly due the evacuation of otoliths in the ocean prior to returning to the colony.

4.3 *Previous research*

Due to the differences in the access to the benthic habitat for otariids in the Atlantic Ocean (extensive shelf with gradual decline) versus the Pacific Ocean (narrow shelf with steep decline), here we focus on comparing our study with previous research in sympatric sites in the Pacific Ocean conducted 2-3 decades earlier to analyse possible fluctuations in the availability of prey consumed over time. Vásquez (1995) evaluated samples from SAFS and

SASL in the same study location (PSJ) between 1986 - 1989. Back then red squat lobster was not identified as an important prey item for either of the otariids. However, Pacific Jack Mackerel (*Trachurus murphyi*, previously identified as *T. symmetricus*) was ranked as the second most frequent prey item after Peruvian anchovy with 17% and 15% occurrence in diets of SAFS and SASL, respectively. In our study, zero occurrence of *T. murphyi* was found. Also, Vásquez reported an occurrence of <1% in cephalopods for both SAFS and SASL diets and no occurrence of *P. monodon*. In contrast, we found cephalopods as an important prey item for SAFS and *P. monodon* as a dominating prey item for SASL. Overall, our findings suggest an increase in the availability of red squat lobsters and cephalopods in the HCS and a decrease in *T. murphyi* as a possible shifts in the diet composition of otariids over the past 25 years, that should be further explored.

Another important study for comparison is Arias-Schreiber (2003), that analysed samples from Punta Coles (17º42’S, 71º 23’W). The location of study sites undoubtedly can influence availability of prey resources; however, tagged SAFS and SASL from PSJ have been sighted in Punta Coles demonstrating animal dispersal between these sites (Arias-Schreiber 2000). Arias-Schreiber (2003) found that both otariids consumed mainly teleost fish, with no significant differences in fish diversity consumed. In total 61 fish species were identified, 41 fish species in SAFS and 51 in SASL. In our study, fish consumption was significantly higher in SAFS than in SASL; with 19 species in SAFS and 15 in SASL making a total of only 22 unique fish species

identified for both otariids. Arias-Schreiber (2003) found that 20% of SAFS and 32% of SASL samples contained cephalopod beaks, whereas in our study cephalopod consumption was significantly different between otariids, with 32% in SAFS in comparison to 1.6% in SASL. In regards to crustaceans, Arias-Schreiber (2003) found 8% of SAFS and 60% of SASL samples contained red squat lobster; similar to the 5% and 70% for SAFS and SASL respectively, found in our study. Overall, Arias-Schreiber (2003) results are similar to the current diet composition found in sympatric otariids in our study, suggesting long-term changes in trophic assemblages after the Extraordinary 1997-98 El Niño.

Trophic level did not reveal any significant differences between consumers. Similarity in the overall TL score is because the most abundant prey items have similar TL values (*E. ringens* TL = 2.9, *P. monodon* TL = 3.2 and cephalopods TL = 3.5). In terms of trophic niche breadth, we found that both species are categorized as specialists (Levin's Bi < 0.6), which contrasts with previous studies that classified species as generalists (Naya et al. 2002, Arias-Schreiber 2003, Sarmiento-Devia et al. 2020). This can be explained by the high proportions of 1-2 main prey items in each of the predator diets, in combination with the lower diversity of fish species found in our study. We also found higher trophic niche breadth for SAFS than SASL. This also differs from previous studies in the Peruvian HCS, that found that SASL consumed more fish species in previous years (Vásquez 1995, Arias-Schreiber 2003). Changes in the SASL diet coincides with higher variability and dietary shifts

reported in SASL Atlantic populations (Drago et al. 2009) in comparison to more stable diets in Atlantic SAFS (Vales et al. 2020).

4.4 *General limitations in methodology*

The analysis of hard remains in scats is one of the most widely used technique for estimating the diet of pinnipeds (Tollit et al., 2006, 1997). However, there are a number of recognized problems with this method, the main limitation are not being able to identify soft shell prey (e.g., crabs), variation in recovery rates and observation errors associated with structures used for identification (Tollit et al. 1997). In this study, we acknowledge that all these limitations are inherent to the study. However, we also consider this error is consistent between study species, location, and sampling season, making long-term temporospatial comparisons valid.

Previous studies in SAFS and SASL in HCS have identified cephalopod beaks belonging to the Teuthidae family (Majluf 1987, Vásquez 1995, Arias-Schreiber 2003, Sarmiento-Devia et al. 2020). However, other species, such as Octopus mimus have been detected in other locations (Sielfeld et al. 2018). Therefore, another limitation is the lack of species identification in the cephalopod prey item category. An additional mechanism for interspecific resource partitioning may also exist in prey sizes targeted. Thus, we recommend measuring hard parts to estimate differences in prey size consumed to determine if other measures of segregation in prey selection exist.

Low recovery of otoliths in otariid scats has been demonstrated through experimental feeding trials with captive otariids that measure the gut transit time of otoliths (Dellinger & Trillmich 1988, Tollit et al. 1997). In an experiment with captive SAFS and California sea lions (*Zalophus californianus*), Dellinger and Trillmich (1988) found mean recovery rates of 38.5% with high interindividual variation (1.25 - 87.3% in sea lions and 3.8 - 80% in fur seals), and a mean passage time in the gut of 22 hours (with initial defecation time of only 4 hours post feeding trial). How these data compare to free-ranging pinnipeds remains uncertain, but we acknowledge it as a limitation of our methods. Regardless, we consider the large sample size per season included in our study, along with the consecutive sampling over a four year period, strengthens our data as a reliable method to capture long term patterns and changes in the hard remains of prey items at a population scale.

4.5 *Environmental conditions and trophic indices*

Correlations between environmental condition indices (SST and SSTA) and trophic indices show that increases in SST and SSTA are related to wider trophic niche breadth in SAFS, elucidating that during warmer conditions there is inclusion of more prey pelagic / oceanic items, in agreement with previous studies conducted during ENSO conditions (Arias-Schreiber 2003). This suggests that a mechanism of SAFS to cope with warmer conditions is to increase the species richness as a response to the increase of tropical water species in the HCS (Majluf 1987, Paredes & Arias-Schreiber 1999, Arias-

Schreiber 2003). In SASL however, we did not find a clear relationship between changes in resource consumption in regard to SST or SSTA.

During February and March of 2015 El Niño conditions promoted the influx of superficial warm water masses towards coastal Peruvian waters, with the peak of positive SSTA extending from April to June 2015 in the El Niño +1.2 region (http://met.igp.gob.pe/datos/icen.txt). The 2015-16 El Niño was categorized as one of the most intense El Niño events in the historical record (L'Heureux et al. 2017). The metrics of the 2015-16 El Niño were based on the SSTA measured in the El Niño 3.4 region (5°N - 5°S, 170° - 120°W) that is ~1,800 km from the Punta San Juan (15°S, 72°W). Values for SST and SSTA used in this study were collected 5 km from PSJ. Seasonal SSTA values showed warming in the first quarter of 2016 and last 3 quarters of 2015. Thus, warming of the surface layer farther offshore could have already affected prey distribution earlier in 2015. Also in 2015 there were unusual reports of oceanic and tropical species found inshore, increased proportion of *E. ringens* juveniles in anchovy purse seine fisheries (IMARPE 2015) and decrease in available biomass of *P. monodon*, evidencing changes in coastal water masses (Yuffra et al. 2018). Although this does not completely explain the trophic overlap in summer and fall of 2015 between SAFS and SASL in the first semester of 2015, it reflects how oceanographic changes triggered by warm Kelvin waves can alter spatial and temporal food web composition, including prey base assemblages.

Increases in the population of *P. monodon* in Peru has occurred since mid-1990s, when the range of this species expanded from central Chile towards Peru taking advantage of the northern expansion of cold-water conditions (Gutiérrez et al. 2008). This, in combination with the shallow oxycline (< 100 m), has led authors to hypothesize a complete pelagic lifestyle for *P. monodon* in the Peruvian HCS takes place, making it available prey for otariids and seabirds (Espinoza et al. 2017). However, other studies state that vertical migration from the oxygenated surface waters towards the hypoxic to anoxic layer and back occur as well (Kiko et al. 2015). Therefore, further studies on day/night foraging in these otariids is recommended. From a predator perspective, the incidence of *P. monodon* in the diet of SASL proves that this prey item is accessible to sea lions in the oxygenated layer; supporting sea lion colonies in PSJ that range between 3,000 - 12,000 individuals and between 75 - 150,000 in Peru (Cárdenas-Alayza et al. 2021). This reveals the importance of the understudied red squat lobster in the fulfilling the energetic demands of SASL, the larger and most abundant of the two otariids in Peruvian HCS. In Falkland Islands (Malvinas), evidence of red lobster consumption are linked to nearshore feeding, due to nearby shoaling locations (Baylis et al. 2014). Furthermore, when predators feed on crustaceans, carapaces tend to dominate the scats evidencing consumption (Staniland 2002).

It has been well documented that the Peruvian HCS contains one of the world´s largest monospecific fisheries based on Peruvian anchovy, along with

other fisheries that target cephalopods and other small pelagic fish species. Many of these fisheries have been overcapitalized and are decreasing available biomass to dangerous levels for sustainability (Fréon et al. 2008, De la Puente et al. 2020). To present date, we are unaware of any large-scale exploitation of *P. monodon* in Peru that limits the availability of this prey item for predators. However, if this were to occur, it may severely affect the availability of this prey resource for SASL and could lead to further changes in the diet of this species, and increase competition between the two sympatric otariid species as evidenced in other regions (Drago et al. 2009, Szteren et al. 2018)

CHAPTER 3

Multiple strategies for segregation during foraging in sympatric otariids of the Peruvian upwelling Humboldt Current System

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Abstract

The principle of competitive exclusion predicts that species exhibit segregation mechanisms to coexist. In the Humboldt Current System, South American sea lions (SASL, *Otaria byronia*) coexist with South American fur seals (SAFS, *Arctocephalus australis*); however, temporal and spatial partitioning while foraging remains unknown. We analyzed locations of 35 adults (18 SASL, 17 SAFS; 12 females, 23 males) equipped with satellite tags in Punta San Juan, Peru (2013-2017) to determine their respective foraging strategies. We evaluated: 1) distance and duration of foraging trips; 2) 25, 50, 75 and 95% utilization distributions (UD); 3) foraging by hour of day and 4) association of environmental variables. Regular interval tracks (e/30min) were modeled using correlated random walk and residence time was estimated. Proportion overlap and analysis of similarity were used to discriminate locations in core areas (50%) and home ranges (95%). GAMMs were built to determine if hour of day had an effect on foraging events and to evaluate association with environmental conditions. Results show that duration and distance between species-sex groups are significantly different, except for trip duration between SASL sexes. All female UD overlap, while males UD overlap in 25% only. Effect of hour of day was significant for SAFS females and SASL males. In general, associated environmental variables suggest pelagic and coastal habitat features in female fur seals and sea lions, respectively. Males segregate in space and time; whereas females exhibit spatial overlap but have temporal segregation mechanisms. Results demonstrate how multiple foraging strategies at different scales aid resource partitioning.

Keywords: interspecific segregation, coexistence, fur seal, sea lion, Humboldt Current System

1. Introduction

Coexisting species that share similar morphological traits, may compete for resources (Hutchinson & MacArthur, 1959). Competition can compromise the fitness of the species involved and may ultimately lead to the competitive exclusion of one species, especially when resources are limited. The principal of competitive exclusion predicts that coexisting species will exhibit resource partitioning (spatial, temporal or dietary segregation) and occupy different ecological niches (Pianka, 1974; Schoener, 1974). However, the Lotka-Volterra model predicts that stable coexistence of competitors is possible when interspecific competition is, for both species, less significant than intraspecific competition (Begon et al., 2006). In these scenarios, niche differentiation will tend to concentrate competitive effects more within species than between them. The Lotka-Volterra model and the Competitive Exclusion Principle, therefore imply that any amount of niche differentiation will allow the stable coexistence of competitors. The ways in which species within ecological communities partition available resources among themselves is a major determinant of the diversity of coexisting species. A community with more resource sharing or greater niche overlap, will clearly support more species than one with lower niche overlap. Thus, coexisting species must differ in their ecological requirements by at least some minimal amount to avoid competitive exclusion (Pianka, 1974).

Among the sympatric marine mammal species with similar life-history traits and

foraging habits are the otariids: fur seals and sea lions. In general, where fur seals and sea lions live in sympatry, the fur seal population is typically larger and they appear to outcompete sea lions. Many studies in both northern and southern latitudes have examined potential competition between sympatric fur seal and sea lions, and their results are mixed. Some have found segregation with no trophic overlap (Antonelis et al., 1990; Aurioles-Gamboa & Camacho-Ríos, 2007; Dellinger & Trillmich, 1999; Franco-Trecu et al., 2012), some have determined spatial segregation (Baylis et al., 2016, 2018; Schwarz et al., 2021; Villegas-Amtmann & Costa, 2017) while others have found dietary overlap (Páez-Rosas & Aurioles-Gamboa, 2010; Page et al., 2005; Waite, Burkanov, et al., 2012).

In the southern Pacific Ocean, South American fur seals (SAFS) and South American sea lions (SASL) can be found in sympatry along Peru’s coastline. The present study is based in Punta San Juan, Peru, a protected area which supports important breeding colonies of both species in sympatry year round, making it a suitable location to study coexistence (Cárdenas-Alayza et al., 2021). South American fur seals and sea lions are sexually dimorphic otariid species, with differential parental care between the sexes. Reproductive roles can influence habitat selection and differential intraspecific foraging behavior in various ways. Foraging behavior of adult females (3-4+ years old) are constrained to provisioning for offspring, limiting the duration while searching for food. Whereas adult males are free to extend their foraging trips in terms of duration and distance; except during the breeding season, when territorial males are

competing for copulations, which may require a time of tenure on shore (Majluf, 1987; Soto & Trites, 2011). Furthermore, mass and size affect oxygen stores and metabolic rates which in turn have an impact on diving/foraging capabilities. Therefore, in our study species, sexual segregation plays a major role in obtaining nutritional demands.

Previous studies describe SAFS in Peru as epipelagic nocturnal foragers that dive in the range of 11-30m (Trillmich et al., 1987). However, at present, there are no published data on the spatial use patterns of SAFS in this ecosystem. Studies using depth sensors have reported that in many locations along their range, SASL feed on benthic resources on the continental shelf (Riet-Sapriza et al., 2013; Rodríguez et al., 2013; Thompson et al., 1998; Werner & Campagna, 1995). However, in the north of Chile pelagic foraging was reported by juvenile male SASL, with average dive depths of 30m (Hückstädt et al., 2014, 2016). Therefore, we consider it is possible that both species are partitioning resources in the pelagic domain. In a highly pelagic environment such as the south Peruvian coast of HCS, where the combination of a narrow continental shelf (80km from shore) and a shallow oxycline (50-80m) compress the habitat for potential prey (A. Bertrand et al., 2010, 2011) we hypothesize pelagic foraging strategies exist for both species combined with other forms of temporal and spatial segregation.

To determine how male and female SAFS and SASL segregate in the HCS, we compare feeding trips of 35 individuals (18 SASL, 17 SAFS) at Punta San Juan, Peru equipped with satellite transmission tags to determine interspecific and

intraspecific differences in the temporal, spatial, and environmental features associated to foraging events. Specific objectives include determination of interspecific and intraspecific differences in: 1) distance and duration of foraging trips; 2) utilization distributions for home range and core areas; 3) time of foraging by hour of day; and 4) environmental conditions associated with foraging events for each of the four species and sex groups.

We aim to determine if temporal and spatial segregation among species and sex groups is influenced by morphological (body mass), behavioral or environmental conditions during foraging. SASL are considerably larger in body size than fur seals and both species have a strong sexual dimorphism, with males being much larger than females (Ralls & Mesnick, 2002). We consequently expect that SASL will travel longer distances, forage for longer durations, and cover larger areas than SAFS. Furthermore, we anticipate that males of both species will travel longer distances, forage for longer durations, and cover larger areas in comparison to females. All females in this study were lactating pups when tagged. Due to energetic constraints linked to maternal attendance in both species, we expect females will have reduced ranges in terms of distance, duration and consequently, area covered compared to males. In terms of temporal segregation, based on Trillmich et al. (1991), we expect that fur seals will forage mostly in the night hours to capture superficial available prey during diel vertical migration of the most abundant prey item in HCS, Peruvian anchovy (*Engraulis ringens*), whereas we expect SASL to forage indifferently throughout the day or night hours as

shown in other sea lion species (Riet-Sapriza et al., 2013; Schwarz et al., 2021; Villegas-Amtmann et al., 2008). Due to the above mentioned energetic constraints linked to offspring survival, we also expect females of both species to be more coastal (inshore) and males more pelagic (offshore) as evidenced in other otariids (Page et al., 2006; Staniland & Robinson, 2008). In HCS, the coastal upwelling translates to lower sea surface temperatures (SST), higher productivity (assessed by higher concentrations of chlorophyll-a), less distance from coast, lower proximity to thermal fronts, and lower front gradients; and the opposite for pelagic habitats, which we expect to be more associated to male foraging behavior (Echevin et al., 2008; Gutiérrez et al., 2011).

2. Materials and Methods

2.1 *Data collection*

Satellite transmitting tags were deployed on 35 adult pinnipeds between 2013-2017 in Punta San Juan (PSJ), Peru (15°22'S, 75°12'W, Figure 3.1). Seventeen SAFS (8 females and 9 males) and eighteen SASL (4 females and 14 males) were captured and instrumented as part of this study. Adult females were nursing newborn pups prior to tagging and are therefore estimated to be 4+ years old. Adult male SAFS were selected from bulls holding tenure at territories and therefore are an estimated age of 9+ years old and their feeding trips reflect post-tenure feeding trips. Whereas SASL males were categorized in the field as sub-

adult males, which are reproductively mature individuals, but do not control female harems yet and are estimated to be within 5-8 years old. Adult females were instrumented during the peak of pupping during their respective breeding season: November for SAFS and February for SASL. Whereas males were all instrumented in November.

Anesthesia of individual SASL and male SAFS was induced using a combination of midazolam, butorphanol, and medetomidine administered via plastic dart as previously reported (Adkesson, Chinnadurai, Balko, Jankowski, Langan, et al., 2019; Adkesson, Chinnadurai, Balko, Jankowski, Meegan, et al., 2019). Female SAFS were captured using a hoop net and then anesthetized with isoflurane gas (1 - 5% to effect) mixed with oxygen as previously described (Jankowski *et al* 2015). Anesthesia was performed by a board-certified specialist in zoological medicine. Morphometrics and physiological parameters were recorded. Body weights were obtained using a tripod and field scale to the nearest 100 grams (Mini Crane Scale 300 kg, OCS-L). All animals were determined to be in good health by a veterinarian based on physical examination and veterinary assessment of routine blood parameters. Antagonist drugs (flumazenil, naltrexone, and atipamezole) were administered and all animals returned safely back into the colony or immediate surroundings.

All samples and methodology were approved by the Peruvian government under research permits Resolución Jefatural No. 09-2013, No. 024-2014, No. 008-2015- and 019-2016-SERNANP-RNSIIPG issued by the Peruvian National Service of

Natural Protected Areas (Spanish acronym SERNANP) and the Peruvian Ministry of the Environment (Spanish acronym MINAM). Procedures were approved by the Ethics Committee of Universidad Peruana Cayetano Heredia (Constancia #005-02-18). During restraint, each individual was instrumented with satellite transmitting tags (Spot 5, Spot 6 and Mk 110 from Wildlife Computers) that communicate with the Argos satellite system, programmed to relay 4-6 transmissions per day. Animal locations and associated errors were estimated by calculating the distance between tags and the satellites present during the time of message transmission. Geographically referenced sightings of satellite tagged individuals at the Punta San Juan site were added to each animal's location record.

2.2 *Track construction*

A range of possible locations were modelled using a forward particle correlated random walk method following Tremblay et al. (2009). Fifty particles were projected every 30 minutes based on animal speed and Argos location class quality to inform model. One average track and its associated error distribution were computed to describe each individual's track. Land locations were filtered out by using a combination of 5km circle buffers on known pinniped colonies along the coast of Peru (including islands), a bathymetry gridded map (GEBCO v. 2020) and a limit for a minimum number of 15 hours or more to consider a foraging trip at sea, based on previous findings (Ganoza, 2016; Hückstädt et al., 2014) (Figure 3.1). Individuals were tracked for 23-78 days. A summary of

individual identification, deployment date, weight, length, number of days, and number of trips for each individual is included in the Appendix C1.

2.3 *Foraging trips and events*

Total distance (km) and duration at sea (days) was estimated for each trip. Results are reported in mean ± SD obtained per each species and sex group. Interspecific and intraspecific differences were tested for each of these variables (Kruskal Wallis, $p<0.05$). We estimated residence time (RT) as a foraging index to understand the time spent (in hours) for area-restricted search by individuals in areas of radius “r” (in km) and maximum time (in hours) during which they actively explored or foraged, following Barraquand and Benhamou (2008). Individuals are presumed to be in “foraging” mode based on movements that include high tortuosity, slower speeds, and repeated entries in/out of an area. Whereas low tortuosity and high speeds are presumed to be in transit or commuting between foraging areas and/or haul-outs. To determine the best scale, multiple size radii and time thresholds were tested for each individual. Radii tested were in the range of 1km, and 5 - 45 each 5 km for each animal and maximum time of 3, 6, 8 and 12 hours were tested. An RT series was constructed for each animal and radii, resulting in 40 possible RT series per individual. The RT series with the highest contrast was selected and segments were categorized as either high (HRT) or low (LRT) time following Lavielle segmentation method (Lavielle, 2005), using the adehabitatLT package in R (Calenge, 2006).

3. Utilization distributions

We used kernel density estimations to calculate the utilization distribution (UD); 25%, 50%, 75% and 95% UD kernels (grid size =200) with R package adehabitatHR (Calenge, 2006). Proportion of overlap of the home range (95% UD) and core areas (50% UD) were estimated using adehabitatHR package and reported in ranges from 0 (no overlap) to 1 (complete overlap). Bhattacharyya´s affinity (BA) for all locations where presumed foraging activity took place was estimated. BA values were used to construct a dissimilarity matrix and analysis of similarity (ANOSIM) based on 999 permutations, to test the similarity between groups for each probable UD (25%, 50%, 75%, 95%) using package vegan in R. ANOSIM ranges from -1 to 1, with 0 indicating a random grouping. Finally, we tested for significant differences between populations according to UD based on ANOSIM statistic values ($p<0.05$).

4. Foraging by hour of day

We first explored the density of foraging events by hour of day to assess if there is interspecific segregation between the occurrence of foraging by hour of day for each sex. To test if there were different patterns per species and sex group, we constructed a general additive mixed-model (GAMM, mgcv R package) to determine if hour of day had a significant effect on the foraging events that occurred in 1 hour blocks according to each species and sex group (Wood, 2011). We used a binomial distribution, with a 1,0 response variable for foraging and

hour of day as the explanatory variable. Since the data is analyzed in 24, 1 hour cycles, we chose a cyclic penalized cubic regression spline as a smoother. Animal ID served to assign random effects and a continuous time index for each foraging trip was constructed and assigned to indicate a corAR1 temporal correlation structure. In the our study area and study period, changes in the time of sunrise and sunset are less than our sampling interval of 1 hour blocks, thus we did not include day length in our analysis.

5. Associated environmental conditions

We extracted five environmental variables for each location during feeding trips from remote sensor databases using R package raster. Environmental variables include: Distance to the Coast (DC, Source: NOAA ETOPO1, 1 arc minute), Sea Surface Temperature (SST, Source: MODIS, 4 km), Chl-a concentration (Source: MODIS-Aqua, 4 km), Proximity to thermal fronts (km) and Gradient of thermal fronts (°C/km) both in a 5x5 pixels range (4km/ pixel). Thermal fronts were constructed from daily composite SST maps (MODIS, 4 km) following Roa-Pascuali et al. (2015). Due to cloud coverage, some dates and locations do not have associated data. We extracted values during HRT locations (presumed foraging events) and compared significant differences between species (Wilcoxon, Test, $p<0.001$). Then, to explore the preferred environmental conditions during foraging, we fit univariate binomial General Additive Model (GAM) using cubic spline smoothers to estimate nonparametric functions for

HRT. Finally, to determine which variables best explained environmental conditions during foraging, we conducted a forward selection process for each species and sex group, constructing a GAMM model with binomial distribution (1,0 response variable) and cubic-splines smoothers to model non-parametric relationships. Animal id was set as random effect and a corAR1 error structure to account for temporal correlation. If more than 25% of locations lacked information, the covariate was not included in model selection. We then assessed for collinearity between remaining candidate explanatory variables and did not include covariates that had a Spearman rank correlation > 0.8 ($p < 0.05$). Finally, we only kept locations that had information for all environmental covariates included in the global model. To avoid overfitting, knots were set to 5. Model selection was done through a forward selection process which consisted of evaluating if the addition of a new covariate produced a significant improvement in the model, evaluated with ANOVA tests (Chi square , $p < 0.05$).

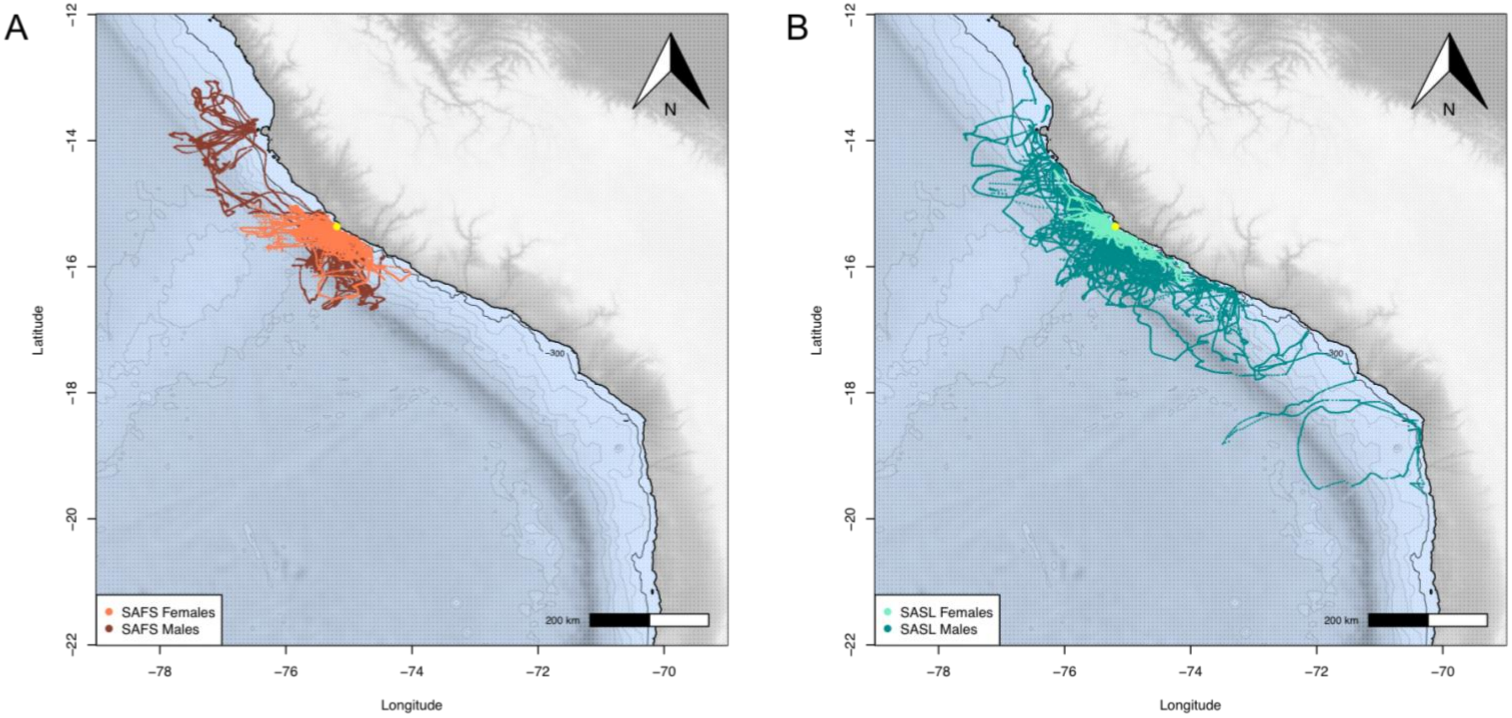

Figure 3. 1 Tracks for A) SAFS and B) SASL in the study area. SAFS females (orange), SASL females (aquamarine); SAFS males (brown) and SASL males (teal). Yellow circle indicates the Punta San Juan, Peru breeding colony, location of otariid instrumentation.

6. Results

6.1 *Body mass*

Body mass and length between all individuals have a strong positive linear relationship ($r^2 = 0.91$, $p<0.05$) with sizes scaling up in the following order: SAFS females < SASL females < SAFS males < SASL males. We therefore compared groups using only body mass and found that all species and sex groups are significantly different from each other, allowing us to make comparisons among the four groups (2-way ANOVA with Tukey post-hoc, $p<0.01$, Figure 3.2). Body mass of SASL males has the widest range since this age-class gathers sub adult males who are still growing at different rates with high interindividual variability, in contrast to the other groups that have less variable values between individuals in the group.

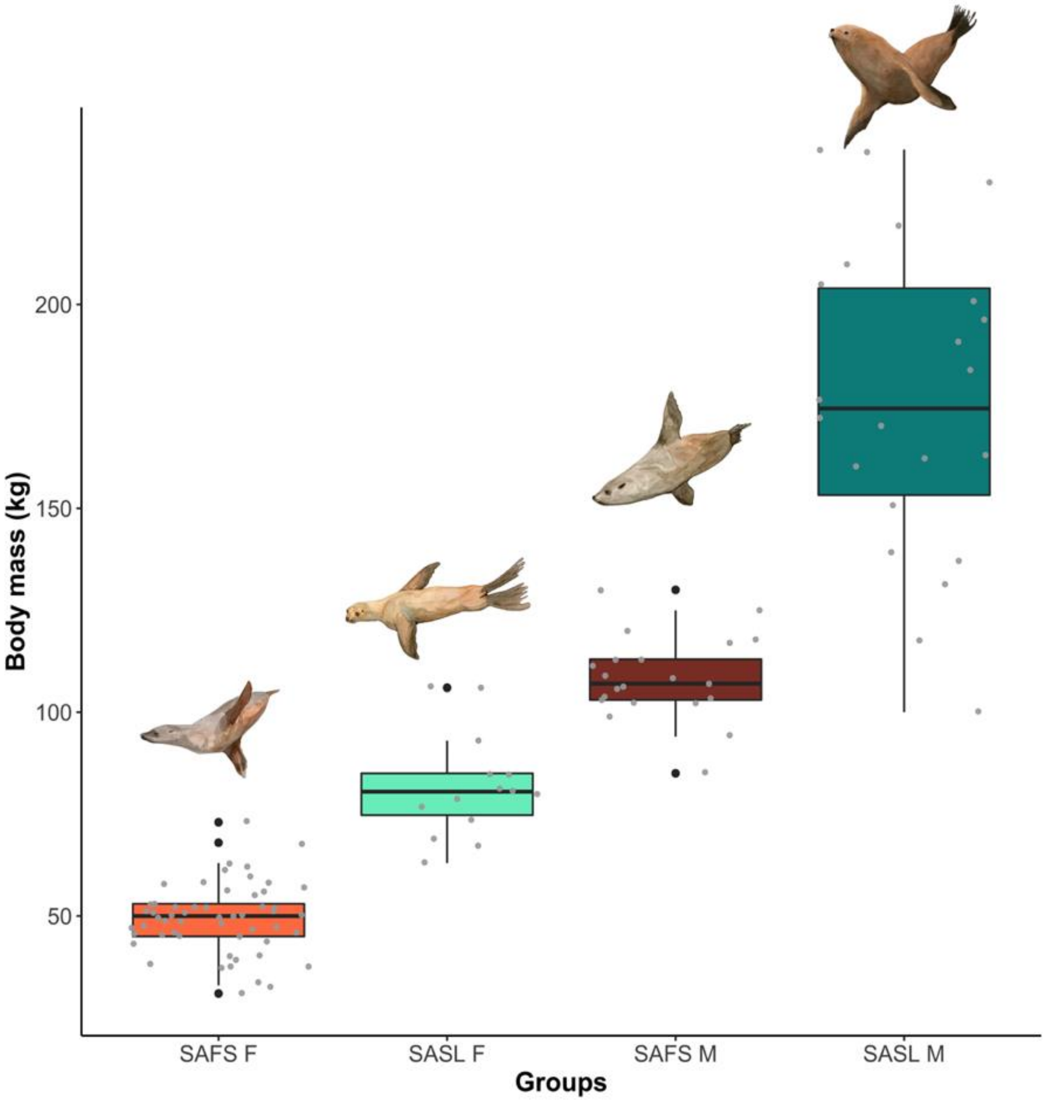

Figure 3. 2 Boxplot of body mass (kg) in y-axis according to species and sex groups in x-axis (ANOVA, p<0.05). SAFS females (orange), SASL females (aquamarine); SAFS males (brown) and SASL males (teal).

6.2 *Trip distance and duration*

SAFS travelled longer distances during trips at sea than SASL (Table 3.1, Figure 3.3). Interspecific differences were found in trip distance between adult females (Kruskal-Wallis, K-W = 14.8, n = 149, $p<0.01$) and adult males (Kruskal-Wallis, K-W = 8.8, n = 276, $p<0.01$). Intraspecific differences were found in trip distance between SAFS (Kruskal-Wallis, K-W = 4.1, n = 134, $p<0.05$) and SASL (Kruskal-Wallis, K-W = 19.5, n = 291, $p<0.01$). Mean trip duration was also longer in SAFS than SASL (Table 3.1, Figure 3.3). Interspecific differences exist in trip duration between adult females (Kruskal-Wallis, K-W = 8.5, n=149, $p<0.01$) and adult males (Kruskal-Wallis, K-W = 14.6, n=276 $p<0.01$). Intraspecific differences exist in trip duration between SAFS (Kruskal-Wallis, K-W = 4.6, n=134, $p<0.05$) but not between SASL trip duration (Kruskal-Wallis, K-W = 3.6, n=291, $p=0.0592$).

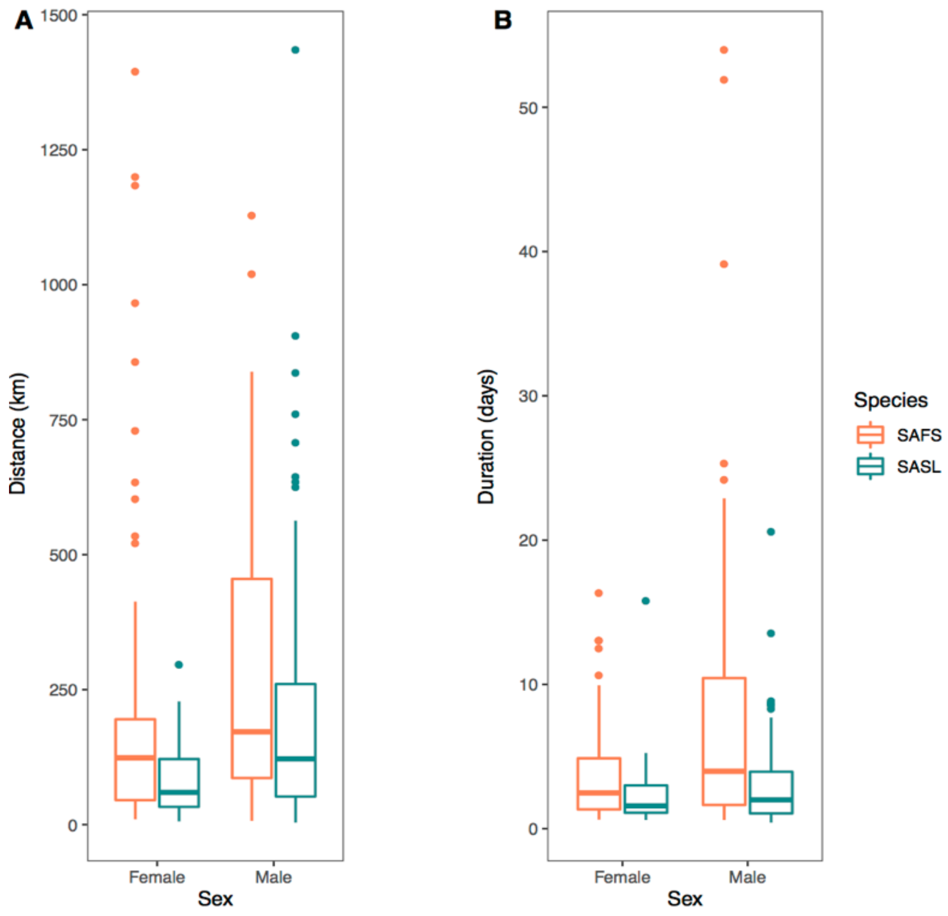

Figure 3. 3 Boxplots of A) distance (km) and B) duration (days) of foraging trips according to sex (x-axis). Colors represent species: SAFS (orange) and SASL (teal).

Table 3. 1 Number of individuals (N ind), number of trips (N trips), trip duration (days), and trip distance (km) for each species-sex group included in this study. Results reported as mean ± SD.

Group	***N* ind**	***N* trips**	**Trip Duration (days)**	**Trip Distance (km)**
SAFS Females	8	77	3.65 ± 3.38	221.81 ± 286.06
SASL Females	4	72	2.16 ± 2.02	81.76 ± 64.08
SAFS Males	9	57	8.32 ± 11.44	298.03 ± 277.97
SASL Males	14	219	2.87 ± 2.50	178.52 ± 184.09

6.3 *Utilization distributions*

In this study we consider Utilization Distribution at 95% as the home range and at 50% as the core area for foraging. SAFS home range area is smaller than SASL in both sexes, and female home range and core are is smaller than males in both species (Table 3.2). SAFS females home range and core area was overlapped in 0.43 - 0.50 by SASL females, whereas SASL females were overlapped 0.70 - 0.83 by SAFS females in 95% and 50 % UD, respectively. SAFS males home range and core area was overlapped in 0.85 - 0.71 by SASL males, whereas SASL males were overlapped 0.41 - 0.43 by SAFS males in 95% and 50 % UD, respectively (Table 3.3). In regards to intraspecific overlap, SAFS females were overlapped 0.83 - 1 by SAFS males, whereas SASL females were always completely overlapped by SASL males in 95% and 50 % UD, respectively (Table 3.3).

Table 3. 2 Area in km^2 of 25%, 50%, 75% and 95% Utilization Distributions (UD) for each species and sex group.

Group	UD 25%	UD 50%	UD 75%	UD 95%
SAFS Females	172.48	1,074.52	2,779.49	9,166.06
SASL Females	333.46	1,645.23	4,931.07	14,450.21
SAFS Males	2,430.72	7,806.89	20,616.80	55,537.99
SASL Males	1,786.86	10,894.50	33,211.20	106,615.05

No significant differences were detected between the distribution of SAFS and SASL females for all UD (25% to 95%), confirming that all female foraging grounds overlap in space and are considered similar by ANOSIM test. We found that SAFS and SASL males are only similar in the smallest UD area (25%), that is most proximate to the PSJ colony (Figure 3.4A-B). Between SAFS males and females, significant differences in UD occur at 75% and 95%; but 25% and 50% UD are not significantly different; suggesting sexual segregation in foraging grounds utilized at 75% and 95%. In contrast, in SASL males and females, only the home range (95% UD) is significantly different; meanwhile all other utilization distributions (25%-75%) overlap between the sexes (Figure 3.4C-D).

Table 3. 3 Proportion overlap for each group for core area (50% UD) and home range (95 % UD). Values represent the proportion overlap for the group in the rows by the group in the column. Proportion overlap > 0.70 in bold.

		SAFS F	SAFS M	SASL F	SASL M
95% UD	SAFS F	-	**0.83**	0.43	**1.00**
	SAFS M	0.20	-	0.13	**0.85**
	SASL F	**0.70**	**0.82**	-	**1.00**
	SASL M	0.12	0.41	0.07	-
50% UD	SAFS F	-	**1.00**	0.50	**1.00**
	SAFS M	0.18	-	0.11	**0.71**
	SASL F	**0.83**	**1.00**	-	**1.00**
	SASL M	0.11	0.43	0.07	-

6.4 *Foraging by hour of day*

Hour of day had a significant effect ($p < 0.01$) on the probability of foraging events in female SAFS and male SASL. Foraging events for female SAFS concentrates during night hours (0-5, 18 - 23 hours) and in SASL males in daylight hours (6 - 15 hours); whereas in the other groups the effect of hour of day was not identified as significant (Table 3.4, Figure 3.5, Appendix C2).

Table 3. 4 Results from the General Additive Mixed-Models to test for effect of Hour in the probability of foraging events in SAFS females, SASL females, SAFS males and SASL males. N represents the number of observations per group.

Group	*N*	Hour	p-value	Log-likelihood	df	Adj. R Sq.
SAFS Females	*24,818*	6.208	<0.01	-56037.49	3.12	0.000619
SASL Females	*22,650*	0.056	0.339	-53855.38	1.16	1.24e-06
SAFS Males	*60,927*	0	0.908	-148151.6	1	-5.31e-10
SASL Males	*91,209*	5.532	<0.01	-216553.8	3.08	0.000254

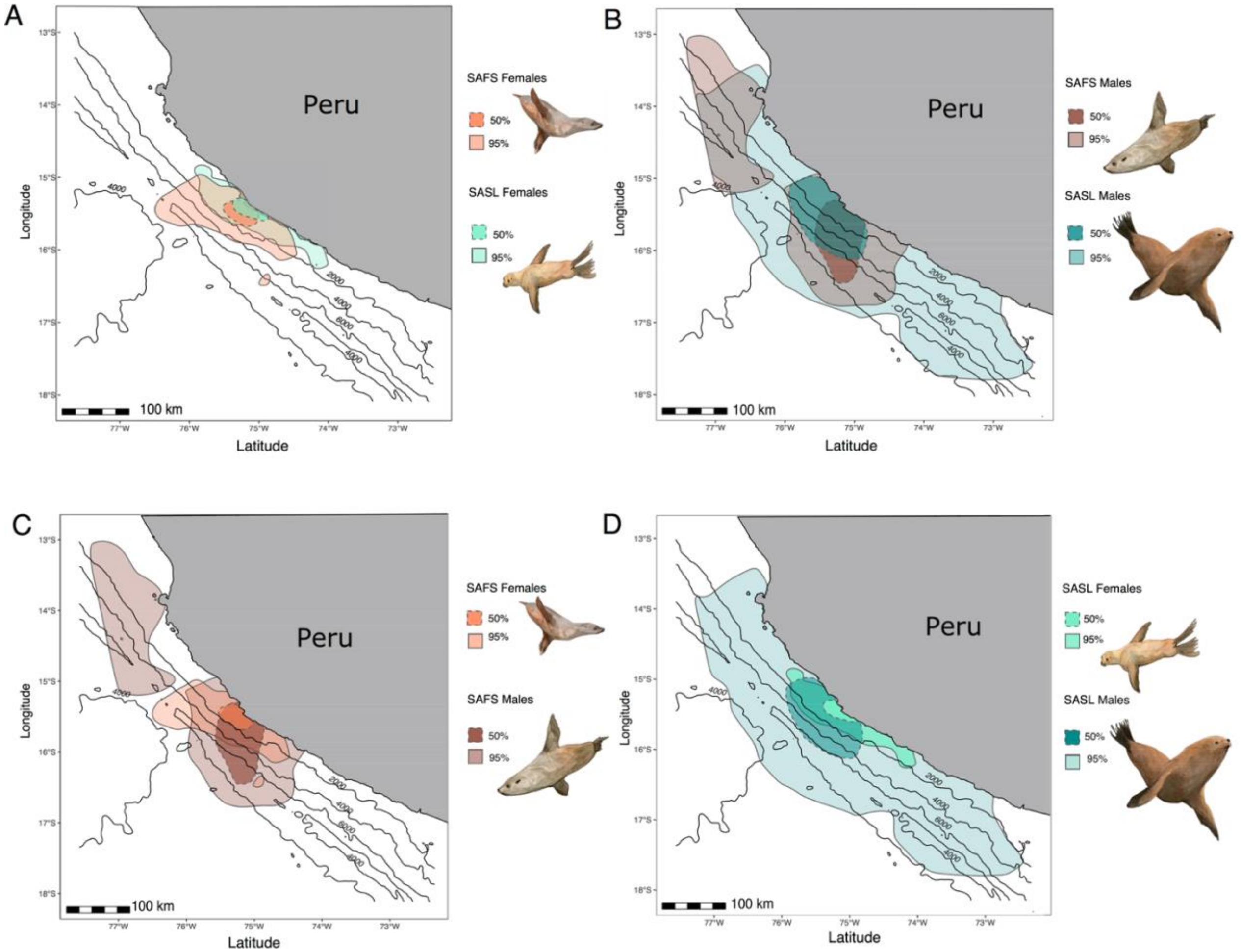

Figure 3. 4 Maps with filled contours of Utilization Distributions (UD) for 50% core foraging range (dotted line) and 95% home range (continuous line) for A) SAFS females (orange) and SASL females (aquamarine); B) SAFS males (brown) and SASL males (teal); C) SAFS females (orange) and SAFS males (brown); D) SASL females (aquamarine) and SASL males (teal). Black lines represent coastline and isobaths for depths of 2,000, 4,000 and 6,000 meters

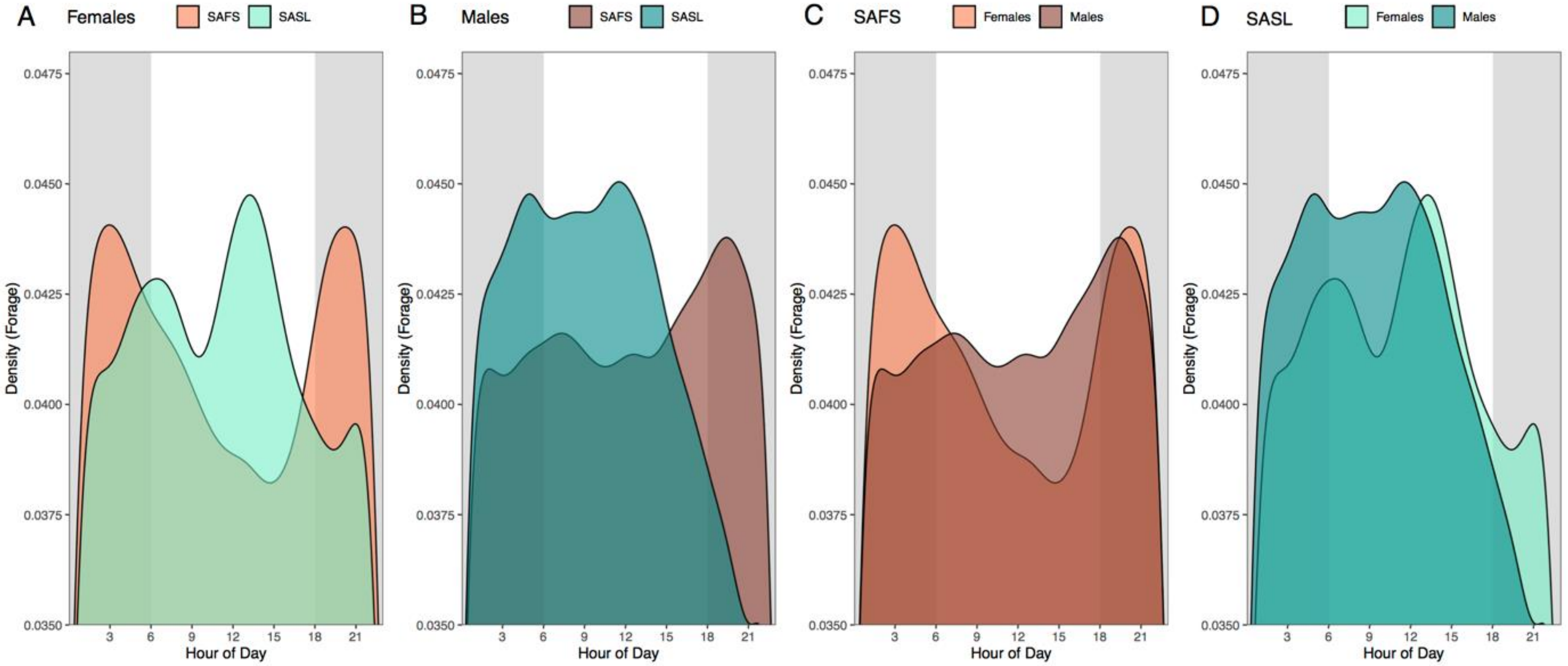

Figure 3. 5 Density plots of the foraging events (y-axis) by hour of day (x-axis) for A) SAFS females (orange) and SASL females (aquamarine); B) SAFS males (brown) and SASL males (teal); C) SAFS females (orange) and SAFS males (brown); D) SASL females (aquamarine) and SASL males (teal). Shaded areas indicate dark hours (0 - 5, 18 - 23 hours) in study area.

6.5 *Associated environmental conditions*

Mean values of environmental variables encountered while foraging are significantly different between species (Wilcoxon, Test, p<0.001), except for SST between females (ESM 2). Descriptive parameters of the environmental variable values (minimum, maximum, median, mean and SD) for locations where animals were presumed to be foraging are reported in the Appendix C3.

In HCS, higher DC (Distance to Coast), higher SST, lower Chl-a, increased Front Proximity and higher Front Gradient characterizes more oceanic waters and the opposite describes coastal waters. Univariate modelling of environmental variables shows that SAFS females are associated to higher SST, lower Chl-a, higher Front Proximity and higher Front Gradient and higher DC, characterizing more oceanic variables. In contrast, SASL females feature lower SST, higher Chl-a, lower Front Proximity and lower Front Gradient and lower DC. In females, SST, Front Proximity and Front Gradients showed inverse responses (Figure 3.6, Appendix C4). Among males, differences are not so evident. SAFS and SASL are positively and similarly associated to SST and Chl-a. However, SAFS males were associated to higher Front Proximity and Gradient and lower DC in comparison to SASL males (Figure 3.6, Appendix C4).

In preparation for the forward selection process, the only variable discarded was SST for SAFS female model, due to 39% missing information. All remaining covariates were checked for collinearity and had Spearman rank

rho<0.55 (Appendix C6). Throughout the GAMM forward selection process, in general, adding terms improved model performance (ANOVA, p <0.01, Table 3.5). Best fitting models for SAFS females included Chl-a, Front Proximity, Front Gradient and DC. Best fitting models for SASL females and SASL males included all covariates and best model for SAFS males included only SST, Chl-a and Proximity to Fronts (Table 3.5).

Table 3. 5 Results from the forward selection process of covariates that explain environment during foraging using a General Additive Mixed-Models. Bold indicates best fitting model and N represents the number of observations per group. Significant Chi square values have a (*) for p-values < 0.01 and (.) for p-values < 0.05. SST was not included in the SAFS females models due to missing values in 39% of foraging locations.

Group	SST	Chl-a	Proximity to Front	Gradient of Front	DC	Log-likelihood	df	Adj. R sq
SAFS Females ***N = 14,286***	-	432.8 (*)				-32,203.29	3.99	0.0494
	-	427.4 (*)	141.8 (*)			-32,328.98	6.98	0.0629
	-	608.2 (*)	138.9 (*)	231.6 (*)		-33,964.49	9.7	0.0932
	-	**580.1 (*)**	**174.3 (*)**	**282.8 (*)**	**608.1 (*)**	**-35,384.95**	**12.7**	**0.165**
SASL Females ***N = 18,423***	217.7 (*)					-43,395.54	3.98	0.0287
	153.4 (*)	265.4 (*)				-44,243.44	6.95	0.0815
	194.2 (*)	290.3 (*)	253.5 (*)			-45,400.05	9.93	0.113
	167.5 (*)	124.8 (*)	72.23 (*)	325.30 (*)		-46,215.19	12.77	0.154
	83.4 (*)	**111.3 (*)**	**22.6 (*)**	**497.9 (*)**	**7035.2 (*)**	**-56,823.42**	**15.43**	**0.279**
SAFS Males ***N = 51,849***	221.0 (*)					-126,784.5	3.96	0.0292
	220.1 (*)	1.3 (*)				-126,812.9	4.85	0.0291
	310.5 (*)	**2.5 (*)**	**1269.6 (*)**			**-133,128.4**	**8.06**	**0.124**
	224.3 (*)	0.0	1051.0 (*)	298.9 (*)		-131,095.6	9.96	0.104
	249.5 (*)	0.9 (.)	710.5 (*)	300.1 (*)	62.7 (*)	-133,079.6	13.59	0.103
SASL Males ***N = 65,040***	71.35 (*)					-159,739.4	3.58	-0.005
	31.5 (*)	261.9 (*)				-161,470.9	6.56	-0.001
	17.2 (*)	237.3 (*)	63.7 (*)			-161,359.8	9.35	0.006
	26.8 (*)	219.7 (*)	63.2 (*)	150.7 (*)		-164,919.2	12.17	0.009
	67.8 (*)	**161.8 (*)**	**245.4 (*)**	**597.0 (*)**	**2,111.3 (*)**	**-168,627.1**	**15.8**	**0.032**

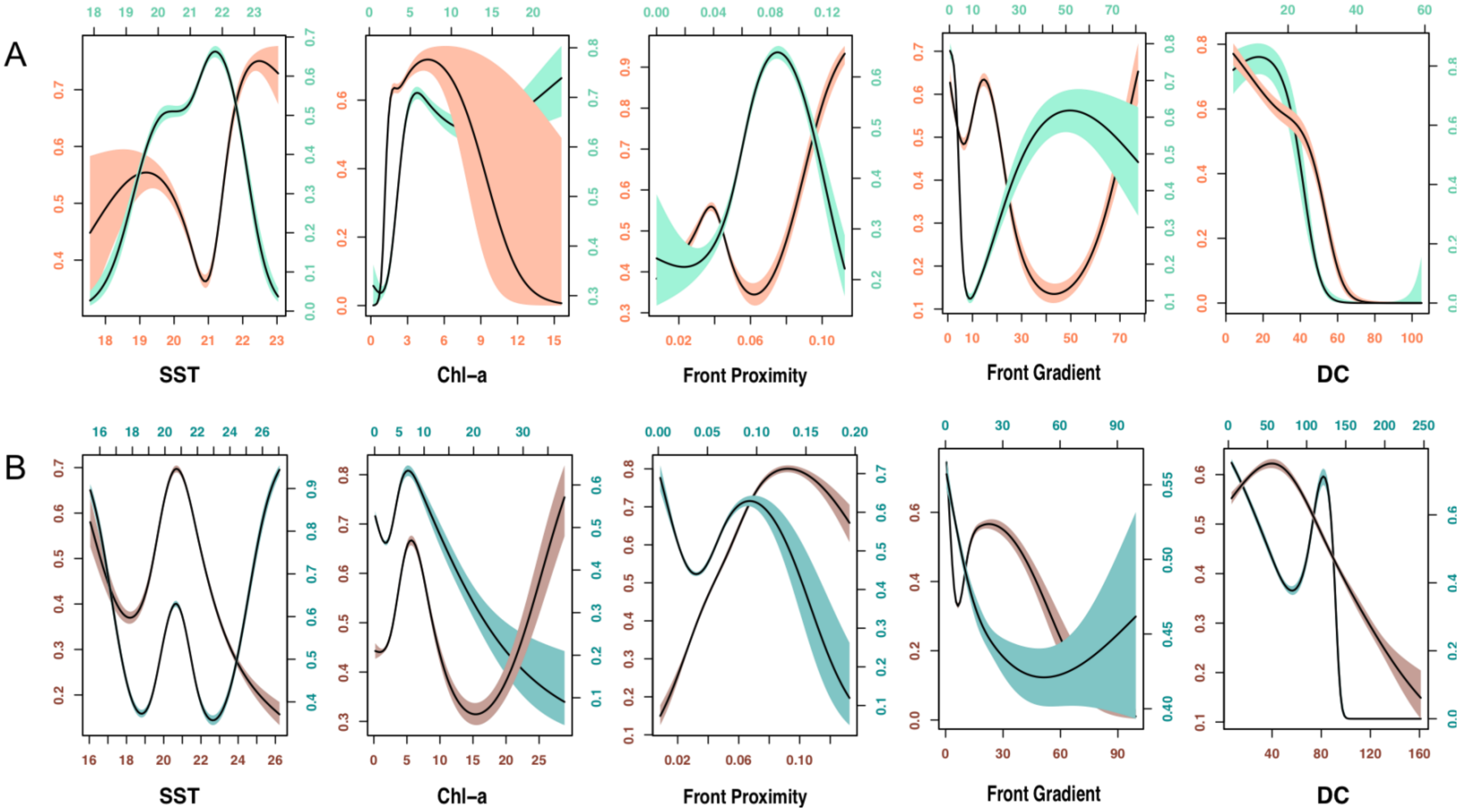

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Figure 3. 6 Probability of foraging events (y-axis 1 and 2) in relation to ranges of environmental variables (x-axis 1 and 2) for A) SAFS females (orange) and SASL females (aquamarine) and B) SAFS males (brown) and SASL males (teal). Colors of labels on x- and y-axis are indicative of values for each species and sex group.

7. Discussion

The results of our study show that sympatric otariids in the Humboldt Current System have multiple strategies to segregate while foraging in the pelagic environment and that body mass is not the sole driver for segregation in space and time, but rather a combination of energetic constraints according to sex, reproductive roles linked to specific dietary resources.

7.1 *Foraging tips and utilization distributions*

We found that although they are smaller in size, both SAFS females and males, make trips of longer distance and duration in comparison to both sexes of SASL, rejecting our hypothesis that larger animals make longer trips. In terms of area, SASL of both sexes cover larger areas, both in the home ranges and core areas, but do so with more consecutive shorter trips compared to SAFS. This reveals different use of the foraging grounds at interspecific level. SASL have larger home ranges as a group, covering a larger area parallel to the coastline that envelopes the SAFS home range. In contrast, SAFS travel farther offshore during feeding trips to specific areas (Figure 3.1A).

In agreement with our predictions based on previous studies focused on sexual segregation of otariids, females of both species show more constrained foraging trips in terms of distance traveled, home ranges and core areas in comparison to males of both species (Page et al., 2006; Staniland & Robinson, 2008). Interestingly, neither sex of SASL show a considerable significant

difference in the duration of their foraging trips (marginal p-value), albeit they are the species with the highest dimorphism. This result is in agreement with previous findings for this species in the Falkland Islands (Baylis et al., 2016). However, SASL sex-based differences should be further explored with the addition of tracking with depth recorders to better understand the foraging effort invested in diving while feeding.

In terms of spatial segregation, female locations are not significantly different throughout their home ranges or core areas. Among females, 0.70 - 0.83 of SASL UD was overlapped by SAFS; while 0.43 - 0.50 of SAFS UD was overlapped by SASL in 50 and 95% UD. These high proportions of overlap can be influenced by the main prey items reported for these species, red squat lobster (*Pleuroncodes monodon*) and Peruvian anchovy (*Engraulis ringens*). Red squat lobsters have been reported as a main prey for SASL based on identification of hard structures in scats (Cárdenas-Alayza et al., 2021; Sarmiento-Devia et al., 2020; Sielfeld et al., 2018). Distribution of red squat lobsters are associated to cold coastal waters and found in the first 30 km from the coast (Yuffra et al., 2018), explaining shorter trips within the coastal habitat covered by SASL. Red squat lobsters and anchovies have a high degree of spatial overlap in areas 50 km from the coastline. However, Peruvian anchovies, the preferred prey item by SAFS and second preferred by SASL, expand further offshore (Gutiérrez et al., 2008). Anchovies make dense aggregation sites, probably driving the preferred foraging grounds for SAFS as already reported in other regions (Baylis et al., 2014; Franco-Trecu

et al., 2013; Naya et al., 2002).

It is important to note that female fur seals and sea lions where not tracked simultaneously, or in the same calendar months/seasons. This study targeted females that were nursing recently newborn pups, and tracked SAFS females from November to January and SASL females from February to March. This is due to a two month difference in breeding seasons (SAFS breed during October-December and SASL breed during January-March). In Peru, these species have temporal segregation in their breeding seasons, contributing yet another mechanism for segregation known as allochrony to partition resources during energetically critical times, which has be postulated as one of the founding drivers behind speciation (Taylor & Friesen, 2017).

Also, in both species weaning of offspring is flexible and can be extended between 6 - 36 months, with high interannual variability (Majluf, 1987; Soto, 2004). Thus we consider that the spatial use patterns of lactating females in this study are representative of the most energetically constrained feeding trips during which the timing of feeding trips is critical towards the survival of small pups that do not withstand extended periods without provisions, compared to larger offspring (Campagna & Harcourt, 2021). Since trip duration, distance, and areas can change as offspring grow older, we recommend future studies to explore if female foraging behavior changes according to breeding season offspring number and age (Drago et al., 2010, 2015, 2021; Franco-Trecu et al., 2012).

In the spatial realm between males, the proportion of SAFS areas covered by the 50 and 95% UDs are overlapped in large proportions by SASL (0.85 - 0.71). However, because of the distributions of foraging locations in space, the similarity of distributions after 999 iterations was only significant for the 25% UD (e.g., close to the PSJ colony). In male SAFS, the focalized number of foraging locations and the bimodal distribution in Distance to Coast (Appendix C4) suggest a repetitive exploration of specific foraging areas within the wider and enveloping SASL male range. In contrast, SASL males make shorter and faster trips. Our results show that the varying lengths in distance and duration of foraging trips can be indicative of specialized foraging grounds, especially in SAFS males, suggesting potential foraging site fidelity in HCS. This has been reported in other locations and should be further explored for this study area (Baylis et al., 2017; Knox et al., 2018).

Since males are not constrained in their foraging trip distance and duration in comparison to females that have dependent offspring ashore, post-breeding dispersal is common in male pinnipeds. Regardless, this study shows that the South American otariids do not depart on a migration, but rather obtain their energetic demands in a local range of 55,000 - 106,000 km^2. These data are evidence that these sympatric species have evolved and adapted to obtain their resources locally in the nearby productive upwelling waters of HCS, occupying rookeries like PSJ year round.

When comparing sexes among sea lions, the analyses of similarity suggests that core areas and home ranges are significantly similar (25 - 95% UD). In SAFS similarity occurs in 25 - 50% UD, but remaining 75 - 95% UD are significantly different. This supports the theory that intraspecific competition within SASL can be enhancing stable coexistence with SAFS by decreasing interspecific competition pressures, as postulated by the Lotka-Volterra model (Schoener, 1974). On the contrary, reduced intraspecific competition in SAFS could negatively affect adaptation to current interspecific pressures. This may be one of the confounding reasons behind the current lack of population recovery and of decreasing SAFS in Peru, that also exists in this same study population (Cárdenas-Alayza et al., 2021).

7.2 *Foraging by hour of day*

In this study we found that the probability of foraging events incremented in the night hours for SAFS females and in the daytime for SASL males. Partly validating our hypothesis of nocturnal foraging patterns in SAFS and daylight foraging in SASL. Nocturnal foraging in SAFS females may be a synergistic effect between the energetic constraints to provision for their young and the vertical diel migration of prey items for SAFS such as Peruvian anchovies, squids and myctophids, making them more available in the night hours (Ayón et al., 2008). Since we did not find a significant effect for hour of day in male SAFS, we reject our hypothesis that this pattern holds for all SAFS. Since males do not have energetic constraints by offspring, daytime foraging segregation in SASL males may be a reflection of a reduction in competition with another otariid age-class, predator species or preference for a specific

prey (Chilvers & Wilkinson, 2009). Recent studies have found same age-class in Galapagos sea lions (*Zalophus wollebaeki*) have different foraging modes (pelagic, benthic and nocturnal divers, Schwarz et al. 2021). Thus, it is possible that there is individual specialization; or that individual can also switch between strategies according to prey availability. Thus, we recommend this is further explored in this ecosystem. Future studies involving depth recorders would again help refine estimation of foraging, since the present analyses may have associated errors in the identification of foraging events based on locations alone.

7.3 *Associated environmental conditions*

In general, environmental variables associated with foraging events show interspecific differences. When compared, environmental habitat features of SASL females are linked to the coastal habitat that is characterized by lower DC, less Proximity to Fronts and Gradients and higher Chl-a values. Whereas SAFS females are associated to a more pelagic environment characterized by lower Chl-a, higher Proximity and Front Gradients and higher DC values. It is important to note that the range in SST amongst female locations was wide and not significantly different. Thus, SST is not recommended as an explanatory environmental variable to compare these groups. Evidence from hard parts analysis in PSJ reports that SAFS consume Peruvian anchovy and squids (Arias-Schreiber, 2003) that are characteristic of the pelagic habitat

(Argüelles et al., 2012), in contrast to the more coastal red squat lobster (Yuffra et al., 2018), which is the primary prey item of SASL (Gutiérrez et al., 2008); lending support to the environmental variables associated with female foraging.

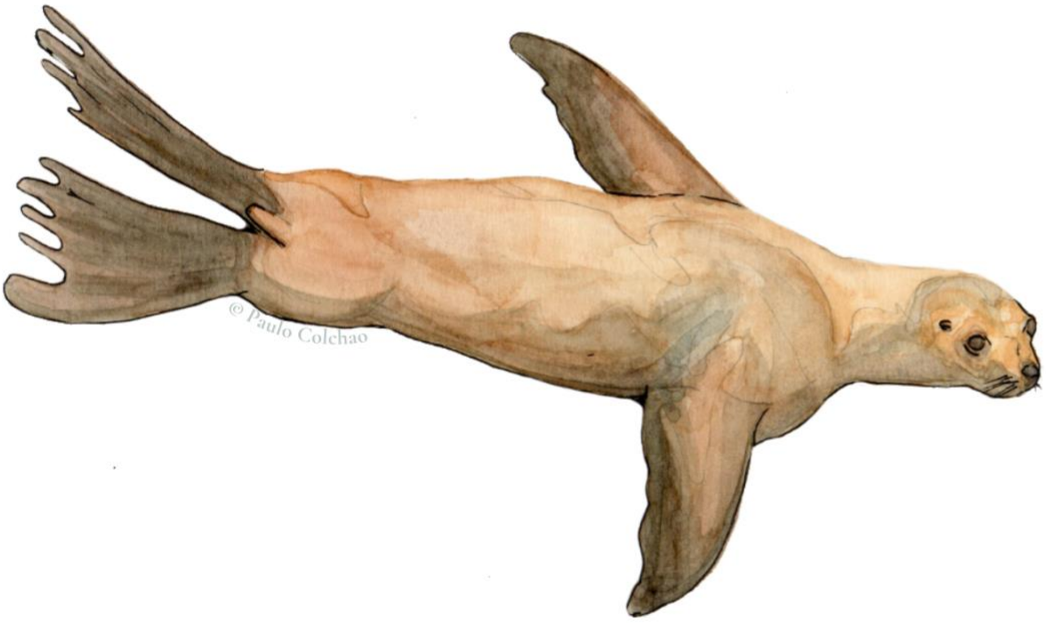
Among males, best fitting models for SAFS males included SST, Chl-a and Proximity to Fronts, whereas SASL males included all environmental covariates. SASL males have lower SST, lower Chl-a, lower Proximity to Fronts and lower DC, which could be a product of individual strategies. Ranges in the environmental variables targeted by SAFS and SASL males are highly overlapping; conclusions should be taken with caution and further studies exploring individual strategies should be conducted. We also suggest incorporating additional environmental variables to better explain male foraging environment, such as those related to the vertical structure of the water column.

Sympatric otariids in the Humboldt Current System show some level of segregation while foraging at sea, partly associated with reproductive role, body size and species. Whether these segregation mechanisms have changed or not in the recent years is unknown, but answering this question is key to understanding the recent trends in population sizes observed in both species after the 1997-1998 El Niño recovery (Cárdenas-Alayza et al., 2021). To tackle the beforementioned we recommend further studies using trophic signatures that archive information from 4-5 years to capture potential trophic shifts in individuals (e.g., stable isotopes and/or fatty acid analyses).

Segregation mechanisms only make sense if prey are partly limited and spatially partitioned. In the case of very high availability of prey, coexistence could occur without much need of segregation. However, in the case of food shortage, segregation mechanisms could sustain coexistence, by taking advantage of differential abilities to cope with such a situation. In the latter case, the differences observed in the foraging ecologies may depict a situation of one species outcompeting another, which couldn’t be considered as a coexistence mechanism. If the segregation we observed is stable in time and if both populations keep coexisting, it might indeed be induced by their ability to segregate. This raises the question of the dynamics of segregation mechanisms with respect to food availability, and calls for maintenance of the long term monitoring and research programs to compare theses indices over time.

CHAPTER 4

Sympatric otariids increase trophic segregation in response to warming ocean conditions in Peruvian Humboldt Current System



Cárdenas-Alayza S, Adkesson, Edwards, M.R., M.R., Hirons, A.C. Gutiérrez D, Tremblay Y, Franco-Trecu,V. Sympatric otariids increase trophic segregation in response to warming ocean conditions in Peruvian Humboldt Current System.

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Abstract

Determining trophic habits of predator communities is essential to measure interspecific interactions and response to environmental fluctuations. South American fur seals, *Arctocephalus australis* (SAFS) and sea lions *Otaria byronia* (SASL), coexist along the coasts of Peru. Recently, ocean warming events (2014 – 2017) that can decrease and impoverish prey biomass have occurred in the Peruvian Humboldt Current System (HCS). In this context, our aim was to assess the effect of warming events on long-term inter- and intra-specific niche segregation. We collected whisker from SAFS (55 females and 21 males) and SASL (14 females and 22 males) in Punta San Juan, Peru. We used $\delta^{13}C$ and $\delta^{15}N$ values serially archived in otariid whiskers to construct a monthly time series for 2005 – 2019. From the same time series we used sea level rise to determine different environmental conditions using a change point analysis. Ellipse areas (SIBER) estimated niche width of species-sex groups and their overlap. We detected a mean change in environmental conditions showing two distinct periods (P1: January 2005 - October 2013; P2: November 2013 - December 2019). Reduction in $\delta^{15}N$ in all groups during Period 2 suggests impoverished baseline values with bottom-up effects, a shift towards consuming lower trophic level prey, or both. Reduced overlap between all groups in P2 lends support of a more redundant assemblage during the colder P1 to a more trophically segregated assemblage during warmer P2. SASL females show the largest variation in response to the warming scenario (P2), reducing both ellipse area and $\delta^{15}N$ mean values. Plasticity to adapt to changing environments and feeding on a more available food source without fishing pressure can be more advantageous for female SASL, albeit temporary trophic bottom-up effects. This helps explain larger population size of SASL at Peru, in contrast to the smaller and declining SAFS population.

Keywords: isotopic niche, fur seals, sea lions, trophic shift

1. Introduction

Individual foraging behavior and trophic interactions determine the flow of energy along the food web, and ultimately these drive population dynamics, community structure, and most ecosystem processes (Arim et al., 2010). However, unpredictable and highly variable environments can also affect trophic behavior (Yurkowski et al., 2018). Top predators, such as pinniped species, are considered structural components of communities and ecosystem functioning (Pauly et al., 1998). Determining trophic habits of predators in a community is essential to measure the potential interspecific niche overlap and strength of interactions as well as the effects of environment changes (Layman et al., 2007).

Two otariid species breed in sympatry along the coast of South America: the South American fur seal, *Arctocephalus australis* (SAFS), and the South American sea lion, *Otaria byronia* (SASL). Information from areas where these otariids coexist serves as an interesting model to assess interspecific segregation (Franco-Trecu et al., 2014; Riverón et al., 2021; Szteren et al., 2018). However, the majority of research has focused on the Atlantic Ocean where SAFS are recognized as pelagic and SASL as benthic; little is known about their segregation in the upwelling ecosystem of the Humboldt Current System (HCS) in the Pacific Ocean. In contrast to the Atlantic coast that has a gradually declining offshore shelf, Peru's coast is characterized by a narrow continental shelf and shallow productive upwelling waters with a relatively shallow thermocline related to an upper minimum oxygen layer at depths of

approximately 50-80 m on average (Bertrand et al., 2010, 2011; Demarcq, 2009; Echevin et al., 2008). These features limit the potential habitat for otariid prey to be linked to the benthos (Hückstädt et al., 2014; Trillmich et al., 1987), making pelagic resources common for tertiary consumers in HCS (Arias-Schreiber, 2003; Sarmiento-Devia et al., 2020). Thus, in this productive, shallow environment foraging on highly patchy, dense prey resources near the surface may preclude the advantages of searching for more evenly distributed, but less dense, prey resources on the benthos (Arnould & Costa, 2006).

HCS is very dynamic since it is characterized by recurring El Niño Southern Oscillation (ENSO) events, which can vary in intensity and duration. ENSO is a coupled oceanic-atmospheric cycle of alternating warm El Niño and cold La Niña events, and it is the most prominent climate signal on Earth (McPhaden et al., 2006). When HCS is affected by an ENSO event, wind pressure drops, sea surface temperature rises, and reductions of primary productivity occur in the marine environment, altering distribution of habitats and associated prey biomass. ‘Extraordinary’ ENSO events that occurred 1982-83 and 1997-98 are well documented for dramatically altering species composition, reducing zooplankton and fish biomass, and causing mortality in higher trophic levels (Barber & Chavez, 1983; Tam et al., 2008; Tovar et al., 1985). However, the effects on trophic adaptation during weaker events that do not cause direct mortality, but impact reproduction, juvenile survival, and weaning have not been thoroughly investigated.

A warming climate is currently altering global ecosystem structure and driving species distributions to higher latitudes, thereby leading to altered interspecific interactions with unspecified consequences (du Pontavice et al., 2020; Walther et al., 2002). Climate driven shifts are more pronounced at the poles where deviations from long-term climatic variables are more striking (Kortsch et al., 2015; Parmesan & Yohe, 2003). However, in the past decade a series of warming events have taken place in the Pacific Ocean that may affect the organization of predator communities in the Peruvian HCS. Long-term warming climatic/oceanic events, or heatwaves known as “The Blob”, have impacted the Pacific Ocean in recent years (N. A. Bond et al., 2015). The Blob was first detected in the Gulf of Alaska in 2013-2014 and is a result of a persistent pattern of higher than normal rates of sea level pressure and weak coastal winds. In Peru, El Niño conditions occurred between 2014 and 2015 (Graco et al., 2016), and were followed by the strong El Niño event of 2015-2016 that affected the entire Pacific Ocean (Robinson, 2016). This event was then followed by the effects of ‘El Niño costero’ that was a more localized event detected in the El Niño 1+2 region between January and February of 2017 (Paulino et al., 2019). During these years, studies suggest that physical anomalies of these warming ocean events generated a biological response similar to those of El Niño (Espinoza-Morriberón et al., 2017). All the aforementioned events involve the rise of sea level forced by the passage of remotely generated and coastal trapped waves in response to heat expansion (Ryan & Noble, 2002). The thermocline, nearshore depth of

chlorophyll-a, and the nutricline deepened, decreasing nutrient enrichment in the euphotic zone. Weak winds caused the reduction in vertical nutrient fluxes to the depleted euphotic zone. A deeper concentration of chlorophyll-a decreased phytoplankton biomass, causing a shift in community structure toward smaller phytoplankton which can have bottom-up effects on food and energy availability at higher trophic levels (Zaba & Rudnick, 2016).

Upper trophic levels predators, like pinnipeds, act as sentinels to trophodynamic and species assemblage changes lower in the food web through their diet (Hazen et al., 2019). Stable isotopes analysis (SIA) of different tissues has emerged as a key method to investigate the differences in the foraging ecology of pinnipeds (Newsome et al., 2010). The $\delta^{15}N$ value is used to estimate the trophic position (Post et al., 2002) and $\delta^{13}C$ values predict the carbon sources used by the predators (Bearhop et al., 2004; DeNiro & Epstein, 1978) at different temporal scales, depending on the moment of production and the turnover rate of the tissue analyzed (Dalerum & Angerbjörn, 2005). The SIA of metabolically inert tissues, such as tooth dentine and whisker keratin with continuous growth, represents sequential archives that allow inference of foraging strategies at the individual level over long periods of time (Franco-Trecu et al., 2014; Kernaléguen et al., 2012). Based on previous studies that estimated whisker growth rates in this species (Lima et al., 2019), each whisker gives information for up to 4.8 years (Edwards, 2018). In our study, long-term niche differentiation in individuals was investigated by examining the isotopic signature in whiskers of male and

female South American fur seals and South American sea lions. We aim to understand how niche segregation between species is affected by changing environmental, morphological, and/or behavioral traits.

Several authors have reported relationships showing that larger animals tend to consume higher trophic level prey (Barnes et al., 2010; Segura et al., 2015). South American sea lions are considerably larger in body size than fur seals and both species have a strong sexual dimorphism, with males being much larger than females (Ralls & Mesnick, 2002); thus we expect that SASL males have highest values of δ^{15}N and that SAFS males have higher values than SAFS females. In terms of δ^{13}C, we expect groups to follow the inshore-offshore δ^{13}C gradient already reported in northern HCS (Espinoza et al., 2017). Since otariid females perform feeding trips during lactation, which usually last ~11 months (Schulz & Bowen, 2005), we suspect they are restricted to foraging grounds close to the breeding colony compared to males (Le Boeuf et al., 2000; Meynier et al., 2008). Thus, we expect both otariid females to show more enriched ^{13}C values, indicative of higher productivity since they remain constrained closer to the land-based colony. In contrast, we expect males to have a wider range of δ^{13}C from foraging more “freely” between coastal and pelagic zones. As reported, the Peruvian coast has been affected by a decrease in the biomass of local prey and an impoverishment in lower trophic levels during 2014 - 2017 warming ocean events (Espinoza-Morriberón et al., 2017; Graco et al., 2016). On a long-term timescale, we expect to find a reduction in the trophic position of otariids and a higher

overlap in isotopic niche space during warmer events when pelagic (cold-water) resources are less available. Finally, due to the beforementioned energetic constraints linked to maternal attendance, we expect females will reflect a narrow range of isotopic signatures compared to males and therefore be less flexible to adapt to changes in the environment.

2. Materials and Methods

2.1 *Study site and sample collection*

Whiskers were collected from lactating females and adult males chosen at random during pinniped health assessment campaigns between 2010 and 2019 at Punta San Juan (PSJ), a marine protected area located along the southern coast of Peru (15° 22’ S, 75° 11’ W). Whiskers were collected from 76 SAFS (55 females and 21 males) and 36 SASL (14 females and 22 males). Anesthesia of individual SASL and male SAFS was induced using a combination of midazolam, butorphanol, and medetomidine administered via plastic dart as previously reported (Adkesson, Chinnadurai, Balko, Jankowski, Langan, et al., 2019; Adkesson, Chinnadurai, Balko, Jankowski, Meegan, et al., 2019). Female SAFS were captured using a hoop net and then anesthetized with isoflurane gas (1 - 5% to effect) mixed with oxygen as previously reported (Jankowski et al. 2015). Anesthesia was performed by a board-certified specialist in zoological medicine. Morphometrics and physiological parameters were recorded. Body weights were obtained using a

tripod and field scale to the nearest 100 grams (Mini Crane Scale 300 kg, OCS-L). Whiskers, including the follicle, were removed manually. All animals were determined to be in good health by a veterinarian based on physical examination findings and veterinary assessment of routine blood parameters.

2.2 *Sample analysis*

Each whisker was scrubbed with an abrasive plastic pad and rinsed with deionized water to remove surface contaminants. Whiskers were thoroughly dried at 60° C for a minimum of 24 hours and then cut into 2.5 mm fragments from base (proximal) to tip (distal), obtaining between 10 and 62 fragments according to the total length of the whisker. Every other fragment was prepared for stable isotope analysis while the remaining segments were reserved. We then subsampled each portion to obtain 0.6 - 0.8 mg (high precision microbalance Mettler Toledo MX5, precision=1µg). Fragments were placed in individual tin capsules, pelletized, and then sent for stable isotope analysis.

Samples were combusted and analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the Smithsonian Institution's Museum Conservation Institute (Suitland, MD) using a Thermo Delta V Advantage mass spectrometer in continuous flow mode coupled to a Costech 4010 Elemental Analyzer (EA) via a Thermo Conflo IV (CF-IRMS) to determine natural carbon and nitrogen abundance and their isotopic ratios with an analytical precision of ± 0.2 ‰ for both isotopes. A set of standards

were run for every 10-12 samples. The standards included USGS40 and USGS41 (L-glutamic acid) as well as Costech acetanilide. All samples and standards were run with the same parameters; this included an expected reproducibility of the standards < 0.2 ‰ (1σ) for both $\delta^{13}C$ and $\delta^{15}N$. Stable isotope values were expressed in terms of δ and were reported relative to the standard reference material, Vienna Pee Dee Belemnite (VPDB) standard for $\delta^{13}C$ and atmospheric air (N_2) for $\delta^{15}N$. The resulting isotope ratios for each whisker segment were converted and reported to the conventional values delta (δ) in parts per thousand (‰), according to: $\delta X = (R_{sam} / R_{st}) - 1$, where X stands for ^{13}C or ^{15}N, R for $^{13}C/^{12}C$ or $^{15}N/^{14}N$, R_{sam} for isotope ratio of the sample, and R_{st} for isotope ratio of the standard.

2.3 *Data analysis*

The most recent growth is located at the base of the whisker, and an individual whisker can represent several years' growth (Ginter et al., 2012; Hirons, 2001; Hirons et al., 2001). Based on an otariid whisker growth rate of 0.08 mm/day (Lima et al. 2019), each 2.5 mm segment represented approximately 30 days.

2.4 *Environment: sea level and sea temperature*

Monthly records for sea level (cm) for latitude 15° South, location of our study area between January 2005 to December 2019, were extracted from the Copernicus ocean products repository (https://marine.copernicus.eu/). Monthly sea surface temperature (SST) records collected by the naval base at

San Juan de Marcona bay (Dirección de Hidrografía y Navegación, DHN), located less than 5 km from the sampling site during the study period. We constructed a time series of SST for each month during the fifteen-year period. Since sea level and SST were correlated during the study period (Spearman, $r=0.74$, $p<0.001$), to avoid redundancy, we selected sea level as our environmental variable because it reflects longer term processes caused by heat expansion in the water column. In contrast, due to the large scale atmospheric forcing SST is not good indicator of changes in upwelling intensity in a warming context (Demarcq, 2009). Change point analysis was applied to the sea level monthly time series to distinguish between different consecutive and consistent periods of environmental conditions in the 2005-2019 time series using R package changepoint (Killick & Eckley, 2014).

2.5 *Study groups*

Principal components analysis (PCA) of six morphometric measures (skull girth, axillary girth, snout to tail base, brachial girth, axilla to fore flipper, tail base to hind flipper) collected for SAFS and SASL (N=98) between 2010 - 2019 were accessed and grouped by species and sex groups. Measures were standardized and PCA was built to determine significant clusters based on the morphometric differences between groups.

2.6 *Isotopic signatures*

By analyzing monthly means of individual seals' isotopic signatures, a mean

for both $\delta^{13}C$ and $\delta^{15}N$ was acquired per individual (i.e. month, year). Across the 2,941 fragments from 112 whisker samples, a total of 14 years of stable isotope data were recorded.

2.7 *Influence of the environment, species and sex on isotopic composition*

First, we used Linear Mixed-Effects Models (LMM) (Pinheiro & Bates, 2000) to examine the effect of body mass on the $\delta^{13}C$ and $\delta^{15}N$ values from each sex group, using individual ID as random effect. Since body mass at the time of whisker collection is affected by feeding habits during recent months, in the LMM we included values from the last three fragments analyzed from each individual, integrating feeding information about the last six months. Second, we used LMM to examine the differences on the average $\delta^{13}C$ and $\delta^{15}N$ values between groups (species and sex), periods, and their interactions as fixed effects. Models included individual identity as a random effect to account for repeated measures of each response variable on the different fragments of each whisker. We used a continuous autocorrelation function (Pinheiro & Bates, 2000) to model the serial correlation of the set of values of the response variables at the individual level. We compared the global model (all fixed effects and their interactions) with models without interaction with the Akaike Information Criterion (AIC) using the $\Delta AIC > 2$ criterion (Bolker, 2008). Selected models were subject to the customary residual analyses (results not shown) and were found to have a satisfactory fit.

3. Isotopic niche

Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al., 2011) were estimated to measure the isotopic niche width at 75% for SAFS and SASL. Mean isotopic values for each individual were used to estimate the ellipses since whisker fragments are temporally correlated and do not comply with sample independence. This method is a Bayesian version of Layman metrics (Layman et al., 2007) that can incorporate uncertainties such as sampling biases and small sample sizes into niche metrics (Jackson et al., 2011). Based on Markov-Chain Monte Carlo simulation, the SIBER approach obtains measures of uncertainty to construct parameters of ellipses in a way similar to the bootstrap. Standard ellipse areas corrected for small sample size (SEA$_C$) were used to compare the different sex-species groups (SAFS females, SASL females, SAFS males, SASL males) in the isotopic space in both periods and estimated the area of overlap of their isotopic niche using Maximum Likelihood standard ellipse areas (SEA$_C$). Values estimated for the overlap of each group is expressed in percentage.

Then, Layman metrics were estimated for the otariid community (the four species-sex groups) by period. Layman metrics are δ^{13}C range, δ^{15}N range, total area of convex hull (TA), mean distance to centroid from means (CD), mean nearest neighbor distance of the means, (MNND),, and the standard deviation of the nearest neighbor distance (SDNND) following Layman et al. (2007).

4. Results

4.1 *Study groups*

PCA results show that horizontal axis 1 explains 87.9% of all variation, forming four different groups for SAFS females, SAFS males, SASL females and SASL males. Vertical axis reveals that 4.7% of variation is explained by similar morphometrics between SAFS males and SASL females (Figure 4.1). Since the majority of variation is explained for each species and sex, four species-sex groups (SAFS females, SASL females, SAFS males and SASL males) are compared throughout our study. LMM from females indicate that there is a positive correlation between body mass and $\delta^{15}N$ values, but only at intraspecific level (p-value < 0.001 in both cases). While SASL females are twice the size of SAFS, the former had 2.22 ‰ lower in $\delta^{15}N$ values (p-value < 0.001). In the male LMM, no body mass effect on $\delta^{15}N$ was detected for either of the two species (p-values > 0.05 in both cases).

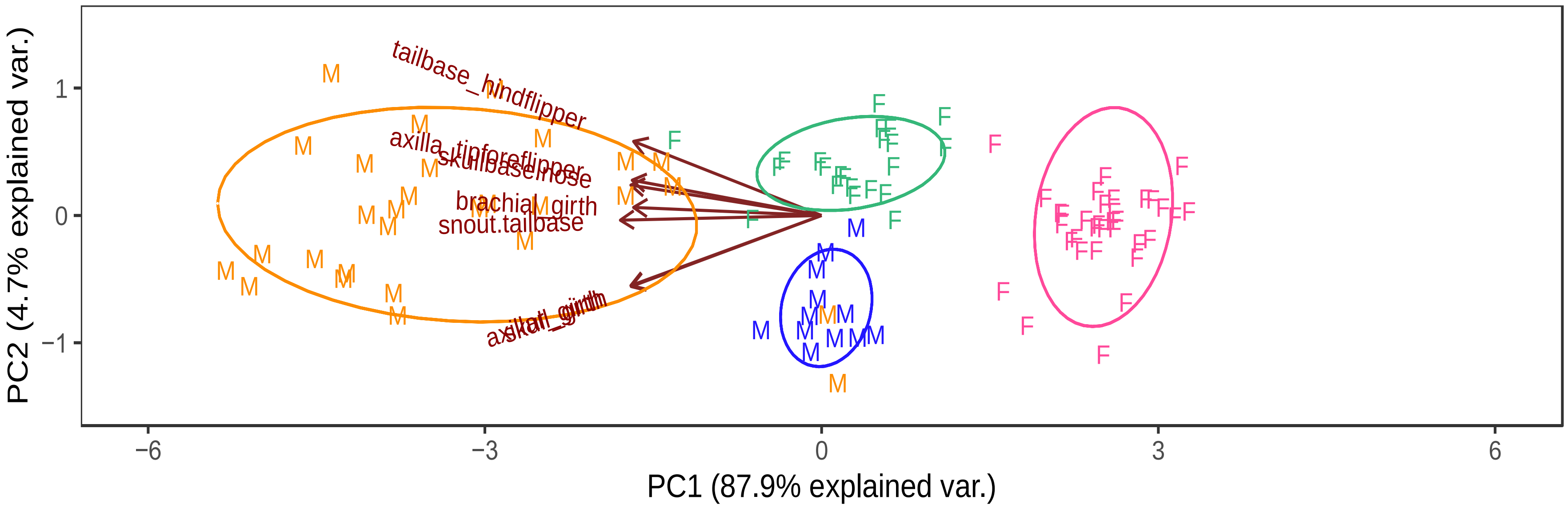

Figure 4. 1 Principal components analysis of six morphometric measures (skull girth, axillary girth, snout to tail base, brachial girth, axilla to fore flipper, tail base to hind flipper) for each of the groups. SAFS females (pink, N = 35), SASL females (green, N= 22), SAFS males (blue, N=12) and SASL males (orange, N=29)

4.2 *Influence of environment on isotopic composition*

The average lengths of the whiskers analyzed were 123.97 ± 11.72 mm and 175.63 ± 325.23 mm for SAFS and SASL, respectively. Mean isotopic values by group, sample size, and fragments number analyzed are shown in Table 4.1. We found significant change points in the sea level time series, dividing it into two periods: Period 1, from January 2005 – October 2013 with a mean of 3.42 cm, and Period 2, from November 2013 – December 2019 with a mean of 8.06 cm (Figure 4.2A). A similar change point was found for SST, with only 1 month difference, giving support to period breakdown. There were significant differences in the mean whisker $\delta^{13}C$ content among species-sex groups in both periods analyzed (see interaction terms in Table 4.2). In Period 1 the average $\delta^{13}C$ was significantly lower for SAFS females compared with SAFS males and SASL males and females. However, this difference is even greater in Period 2 due to the change in opposite direction of mean $\delta^{13}C$ isotopic value of SAFS females in comparison to the other three groups (Figure 4.2, Table 4.2). Mean $\delta^{15}N$ values significantly differed between species-sex group and periods, but without interaction. SASL females had the lowest values and showed the greatest change in Period 2, being the only species-sex group that decreases the N mean value (Figure 4.2, Table 4.2).

Table 4. 1 Isotopic signatures of Peruvian otariid whiskers according to periods investigated in present study. Number of whiskers (N), mean length (mm) by species and sex. Mean ± SD of the stable isotope values (δ13C and δ15N) during two periods according to sea level. N fragments: sample size for species and sex.

Species	**Sex**	***N***	**Length (mm)**	**Period 1**			**Period 2**		
				δ^{13}C	**δ^{15}N**	***N* fragments**	**δ^{13}C**	**δ^{15}N**	***N* fragments**
SAFS	F	55	115.68 ± 26.78	-14.32 ± 0.39	19.03 ± 0.94	1,002	-14.87 ± 0.47	17.99 ± 1.01	182
SASL	F	14	150.71 ± 32.61	-13.58 ± 0.50	19.05 ± 1.13	71	-13.72 ± 0.73	16.66 ± 1.60	322
SAFS	M	21	132.26 ± 40.34	-13.91 ± 0.35	20.20 ± 0.83	406	-14.27 ± 0.36	18.71 ± 1.30	125
SASL	M	22	200.54 ± 60.23	-13.45 ± 0.43	20.04 ± 1.54	719	-13.36 ± 0.58	18.58 ± 1.84	114
		112				2,198			743

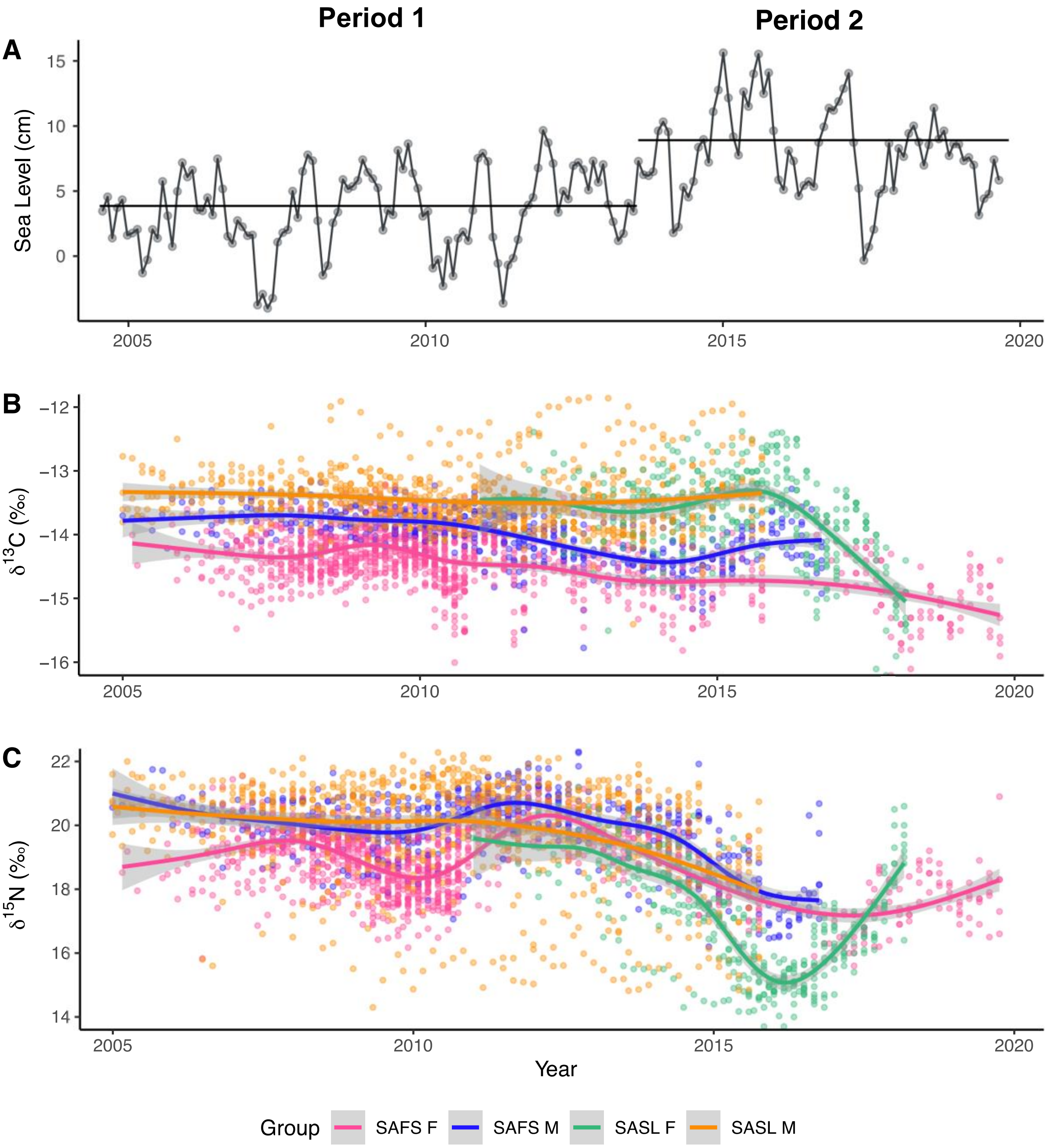

Figure 4. 2 Time series for A) monthly sea level records from San Juan de Marcona bay, horizontal lines show Period 1 (P1, mean = 3.42 cm) and Period 2 (P2, mean = 8.06 cm), B) δ13C and C) δ15N isotopic signatures for all otariid groups.

Table 4. 2 Linear Mixed-Effects Models (LMM) for δ13C and δ15N values. LMM for δ13Ccor and δ15Ncor whisker values including group (sex-species), period and their interactions as fixed effects and identity and whisker portion as random effect (continuous autocorrelation function). Estimates and p-values (in brackets) are shown for each variable. In bold we show the selected model by the Akaike Information Criterion (AIC). (***) denotes p<0.01

Model	Intercept	SAFS M	SASL F	SASL M	Period 2	SAFS M *Period2	SASL F *Period2	SASL M *Period2	AIC
δ^{13}C~SpecieSex*Period	**-14.40 (***)**	**0.35 (***)**	**0.47 (***)**	**0.88 (***)**	**-0.34 (***)**	**0.17 (0.14)**	**0.40 (***)**	**0.39 (***)**	**1300**
δ^{13}C~SpecieSex+Period	-14.44 (***)	0.37 (***)	0.69 (***)	0.96 (***)	-0.11 (***)	-	-	-	1311
δ^{15}N~SpecieSex*Period	18.91 (***)	1.14 (***)	-1.02 (***)	0.86 (***)	-0.56 (0.0034)	-0.0008 (0.99)	-0.03 (0.92)	0.34 (0.21)	6291
δ^{15}N~SpecieSex+Period	**18.89 (***)**	**1.13 (***)**	**-1.10 (***)**	**0.94 (***)**	**-047 (***)**	**-**	**-**	**-**	**6287**

4.3 *Isotopic niche size, overlap and community metrics according to period*

Standard ellipse areas (SEAc) increased in male groups of both species between Period 1 and Period 2 (11.03% in SAFS M and 16.27% in SASL M). In females, SEAc remained stable in SAFS and decreased for SASL by 72.75% (Figure 4.3, Table 4.3). In Period 1, SASL female SEAc overlaps with all groups (66.37 - 92.99%) followed by SASL male SEAc that overlap with SASL females (30.90%) and SAFS males (22.63%) and SEAc of SAFS males and SAFS females that overlap in range of 12.85 - 24.58% and 10.85 - 15.48%, respectively. In Period 2 only two cases of overlap of $\leq 1\%$ were detected (Table 4.4). All ellipses segregate in the isotopic space in Period 2, evidenced by expansion of Layman metrics, including δ^{15}N range, δ^{13}C range, TA, CD, MNND and SDNND (Table 4.5).

Table 4. 3 Corrected Standard Ellipse Area (SEAc) for each period and group estimated with 75% maximum likelihood.

Group	SEAc Period 1	SEAc Period 2
SAFS F	0.94	0.95
SAFS M	1.29	1.45
SASL F	4.88	1.33
SASL M	2.27	2.64

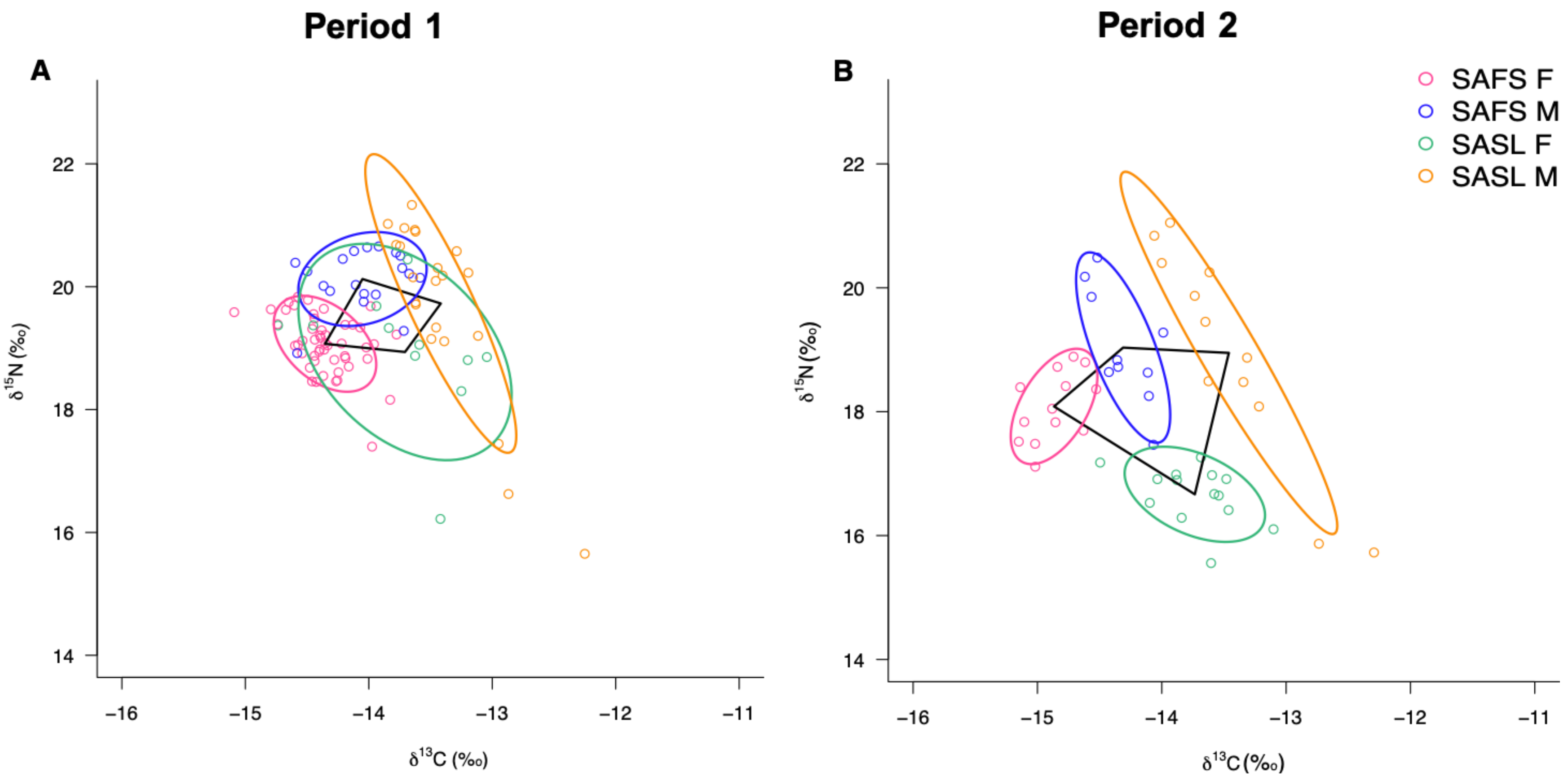

Figure 4. 3 Standard Ellipse Area (75%) for A) Period 1 and B) Period 2. Black lines delineate community convex hull between centroids of each group.

Table 4. 4 Percent overlap between Peruvian otariid groups according to period. Values indicate the percent overlap for the group in the row.

		SAFS F	SAFS M	SASL F	SASL M
Period 1	**SAFS F**	-	14.94	80.67	0
	SAFS M	10.85	-	92.99	22.63
	SASL F	15.48	24.58	-	30.90
	SASL M	0	12.85	66.37	-
Period 2	**SAFS F**	-	1.03	0	0
	SAFS M	0.67	-	0	0
	SASL F	0	0	-	0
	SASL M	0	0	0	-

Table 4. 5 Layman metrics estimated according to period. δ13C range = distance range of δ13C values, δ15N range = distance range of δ15N values, TA = Total area of convex hull, CD = the mean distance to centroid from means, MNND = mean nearest neighbor distance of the means, SDNND = standard deviation of the nearest neighbor distance.

Layman Metrics	Period 1	Period 2
δ^{13}C range	0.94	1.41
δ^{15}N range	1.18	2.36
TA	0.67	1.91
CD	0.60	1.05
MNND	0.71	1.16
SDNND	0.05	0.45

5. Discussion

In this study, long-term niche differentiation in individuals was investigated by examining the isotopic signatures serially archived in whiskers of male and female South American fur seals and South American sea lions during 2005-2019 in the HCS. We found a reorganization of our four otariid study groups in the isotopic space as a response to the increase in average sea level and warmer sea surface temperatures from November 2013 onwards (Period 2). Groups expanded their niche width (except SASL females), segregated in isotopic space, and reduced the $\delta^{15}N$ signal during the warmer period. Overall decline in otariid $\delta^{15}N$ suggests impoverished baseline values of $\delta^{15}N$ with bottom-up effects impacting tertiary consumers, a shift in diet towards lower trophic prey, or both. Overlap reduced between all otariid groups in Period 2, providing support of a temporal shift from a more redundant assemblage (similar isotopic niches) during the colder period to a more trophically diverse assemblage (divergent isotopic niches) during the warmer period.

Although we did find significant differences to compare the four species-sex groups according to morphometrics, size was not a driver for higher $\delta^{15}N$ as hypothesized. In our study, differences in the isotopic signatures in both species are driven by environmental conditions and behavioral traits according to sex. Different behavioral constraints between sexes in both otariid species, may allow larger male individuals to invest more time and energy foraging at sea, possibly being more selective hunters to capture higher level prey, as evidenced in reports of diverse hunting strategies in male and

subadult male Galapagos sea lions (*Zalophus wollebaeki*) (De Roy et al., 2021; Páez-Rosas et al., 2020). Interestingly, sexual differences are generally maintained, but all δ^{15}N signatures decrease in Period 2, with female SASL showing the largest drop in δ^{15}N of 2.4, while male groups δ^{15}N values drop in 1.5 and female SAFS decrease slightly in δ^{15}N by 1.0. We consider that the change in δ^{15}N in Period 2 reflects a bottom-up effect in the trophic food web, linked to the dietary habits of each species and sex group, in response to changes in the environment.

In November 2013 an elevation in the average sea level time series was detected, giving rise to a second period of higher sea level and warmer sea surface temperatures. This change is in agreement with the propagation of physical anomalies that started in the North Pacific Ocean that forced a biological response in the vertical distribution of nutrients and the abundance of chlorophyll-a (Zaba & Rudnick, 2016). Concurrently, in mid-2014 off the coast of Peru, a moderate, coastal El Niño was reported and then followed by an Extraordinary El Niño in 2015-2016 (L'Heureux et al., 2017) and subsequently followed by a costal El Niño in 2017, continuing to promote warm water assemblage. Warm water Kelvin waves that travel north-south, during which cold water gets "trapped" under, depresses upwelling and decreasing productivity in the euphotic zone (Graco et al., 2007). Arrival of these warm water waves changed oceanographic conditions in April 2014, deepening the thermocline, increasing nearshore depth of chlorophyll-a, and decreasing the nutricline which negatively impacted nutrient enrichment in

the system (Graco et al., 2016). In the California Current, another upwelling eastern boundary current marine ecosystem, deeper chlorophyll-a decreased phytoplankton biomass and caused a shift in community structure towards a smaller phytoplankton species, which caused bottom-up effects on food and energy availability at higher trophic levels, that resulted in high mortality rates of red tuna crabs (*Pleuroncodes planipes*) and California sea lions (*Zalophus calfornianus*) (Zaba & Rudnick, 2016). Based on the long-term changes of the δ^{15}N signal captured in otariid whiskers, we suggest similar effects occurred in the HCS off the coast of Peru.

The red squat lobster (*Pleuroncodes monodon*) inhabits the northern HCS and has been abundant since the mid-1990s (Gutiérrez et al., 2008). It is an important prey item for seabirds, mammals, and coastal fish (Jahncke & Goya, 1997; Zavalaga et al., 1998). This crustacean has been identified as the dominant prey item in SASL diet composition (~70%) based on scat analysis. Whereas, SAFS have been reported to consume mostly Peruvian anchovy (49%) and squids (30%), with red squat lobsters contributing only a minor amount (6%) to the diet (Arias-Schreiber, 2003; Sarmiento-Devia et al., 2020; Sielfeld et al., 2018; Vásquez, 1995). Due to inherent limitations in the methodology, trophic studies based on scat samples rely on manually collected samples from colonies, resulting in sampling from individuals of unknown sex and age class. When samples are collected at breeding sites, researchers commonly assume that these belong to adult females given they alone represent 40-60% of the colony abundance and spend considerable time

onshore while nursing their pups, while males are fasting on land (García-Rodríguez & Aurioles-Gamboa, 2004; Páez-Rosas & Aurioles-Gamboa, 2010; Porras-Peters et al., 2008). Having mentioned this, the steeper drop in $\delta^{15}N$ signal during Period 2 in SASL females compared to SAFS females agrees with a higher consumption of a lower trophic prey item (crustaceans) in the former. Furthermore, during El Niño events, diatoms, the dominant phytoplankton in the HCS, are greatly impacted by the less enriched conditions, with a reported decrease of 25-60% of their biomass during these events, while less nutritious species (e.g. dinoflagellates) can temporarily occupy their niche (Espinoza-Morriberón et al., 2017). *P. monodon* has a similar trophic position as anchovies, with phytoplankton, eggs, and larvae (and not anchovies) being the main source of their diet (Espinoza et al., 2017). Meanwhile, zooplankton is the main prey item of anchovies (Espinoza & Bertrand, 2008) and enforces bottom-up control (Ayón et al., 2008). Squids feed on mesopelagic fish (Argüelles et al., 2012). Thus, since SASL females are feeding directly on red squat lobsters aggregated on the coastal habitat, their $\delta^{15}N$ signal can be more directly reduced in comparison to SAFS females feeding on anchovies and squid in the pelagic realm. Thus, the less pronounced bottom-up effect in the latter can be partly explained by the trophic food web interactions. However, we cannot rule out partial prey switching or variations in the proportions of resources consumed, which can also impact the $\delta^{15}N$ and $\delta^{13}C$ signals.

The $\delta^{13}C$ isotopic signature serves as a proxy for the inshore /offshore location

of the foraging grounds. We found interspecific differences in $\delta^{13}C$ were more accentuated during the warmer period, with lower $\delta^{13}C$ values in SAFS compared to SASL, independent of period. We did not find differences in $\delta^{13}C$ explained by sex but followed the inshore-offshore gradient reported by Espinoza et al. (2017), with decreasing values in the gradient of coastal >neritic >oceanic zones. Therefore, trophic resource acquisition by SAFS is linked to more offshore location items in comparison to SASL. Furthermore, in the warming period, SAFS exhibit decreases in the $\delta^{13}C$ signal towards offshore waters, while SASL remains in the same range. This agrees with the association of the biomass of the main prey item of SASL the red squat lobster with cold coastal waters that contract further inshore during warming events (Yuffra et al., 2018). Studies using hydro acoustic surveys along the coast of Peru found that distribution of Peruvian anchovy and red squat lobsters spatially overlap, with both prey species distributed close to the coast, but red squat lobsters concentrate closer towards shore, in the first 40 km (Gutiérrez et al., 2008). Whereas, Peruvian anchovies, the main prey item for SAFS, show larger range in $\delta^{13}C$ values, indicative of a wider use of the pelagic habitat in comparison to red squat lobsters (Espinoza et al., 2017). Between sexes, males have higher $\delta^{13}C$ than females, which may reflect inclusion of coastal/benthic foraging in males. The latter can be related to the requirement in females for homogenous prey patches that are available in the offshore environment in HCS to more efficiently optimize milk production to nurse pups, whereas males have more possibilities of exploring different foraging

grounds and strategies (Krüger et al., 2014).

The reduction in overlap of the isotopic niches between the two periods suggests that the response to warmer anomalies promoted trophic segregation between otariid predator communities, contrary to what we hypothesized. When using Layman metrics, we found that the ranges of both isotopic signatures (δ^{15}N and δ^{13}C ranges) and the total area occupied (TA) expanded in response to warmer conditions in Period 2 (Figure 4.3, Appendix D1). Furthermore, the lower levels of the trophic position in the otariid community during Period 2 was predominantly driven by a niche shift in all groups, with a significant contribution from SASL females. This supports the theory that a new basal resource with a more depleted δ^{15}N took place in Period 2, as reported in other studies showing temporal niche shifts in marine predators (Amador-Capitanachi et al., 2020; Yurkowski et al., 2018).

In general, populations can be separated into specialists when they have narrower niches or into generalists when they have broader niches (Begon et al., 2006). Generalist populations with broader niches are likely favored in heterogeneous and stable environments, whereas specialist populations with narrower niches are favored in highly dynamic ecosystems and homogeneous environments (Kassen, 2002). Thus, during the warmer period, it is possible that prey assemblages are more diverse in contrast with dense prey aggregations favored by nutrient rich, cold-water in HCS. Since TA serves as a proxy for the extent of trophic diversity within the community, its expansion (along with CD, NND and SDNND) reflects a more generalist community

with looser packing of individuals in the isotopic niche space during Period 2 (Layman et al. 2007). Of all the groups, female SASL show the largest variation in response to the warming scenario, reducing both ellipse area and δ^{15}N values. This suggests that this group has higher plasticity to adapt to changing environmental conditions, as reported in other otariids (Amador-Capitanachi et al., 2020). This helps explain current, larger population biomass of SASL reported for PSJ and Peru, in contrast to the smaller and steeper declining SAFS population (Cárdenas-Alayza et al., 2021). Plasticity and feeding on a more available food source that lacks commercial fishing pressure can be currently more advantageous for SASL.

In the Atlantic Ocean SAFS forage in pelagic environments with abundant, but similar, prey. They are identified as a specialist population composed of generalist individuals. Whereas, benthic SASL forage in habitats with diverse, but less abundant prey, with more generalist populations composed of highly specialized individuals (Franco-Trecu et al., 2014; Riverón et al., 2021). However, this marine ecosystem is relatively stable compared to the dynamic upwelling HCS. In the Galapagos Islands, an upwelling system with more similarities to the HCS environment, segregation with low overlap exists between sympatric fur seals and sea lions. Galapagos fur seals (*Arctocephalus galapagoensis*) forage in the pelagic zone with a smaller population isotopic niche compared to benthic foraging Galapagos sea lions (*Zalophus wollebaeki*) with larger isotopic niche (Páez-Rosas & Aurioles-Gamboa, 2014). However, in our study site in the Peruvian HCS, the bathymetry

deepens very rapidly, reaching over 1000 m in less than 50 km offshore, leaving a much-reduced area for benthic foraging; this reason is why the contribution of specialized individuals employing benthic strategies is still put in question. Thus, individual specialization and the capacity to adapt different foraging strategies can be playing an important role in the variability between our study groups. We recommend future research explore individual specialization to understand exploitation mechanisms by individual otariids in the HCS and how individuals respond to changing environmental conditions.

DISCUSSION

> "FOR WHATEVER WE LOSE
> (LIKE A YOU OR A ME).
> IT'S ALWAYS OUR SELF
> WE FIND IN THE SEA."
> *- E.E. Cummings*

The main goal of this thesis is to describe and compare the ecological niches of sympatric otariid species South American fur seal (SAFS, *Arctocephalus australis*) and South American sea lion (SASL, *Otaria byronia*) that coexist in Punta San Juan; and determine intraspecific and interspecific niche differentiation/overlap. In the data chapters of this thesis I explore different dimensions of trophic ecology and surrounding environmental conditions to explain the current divergent population trends of sympatric otariids in Punta San Juan, reported in Chapter 1. In Chapter 1 analyzed trends of abundance for a 20 year period and found that on average, 83% of all otariid biomass is composed by SASL and 17% by SAFS; making SASL the current 'dominating' species in the study site (SASL is currently 89% of total otariid biomass). Furthermore, results from the population assessment reveal a current decline in both populations, suggesting a resource limitation in the marine environment, which started in November of 2014 in SAFS and in March 2017 in SASL.

1. Interspecific and intraspecific segregation of the trophic niche (diet composition and isotopic signals)

To describe and compare the trophic ecology of sympatric pinnipeds, I assess the degree of interspecific and intraspecific trophic niche segregation, through

the analysis of diet composition and isotopic signals between the sympatric pinnipeds SAFS and SASL in relation to environmental conditions. My main hypotheses was that larger body size relates to foraging strategies that facilitates consumption of larger prey items, linked to the benthos. Being SASL overall 1.5 times larger than SAFS in all age-sex classes, I hypothesized that SASL would be foraging in more coastally restrained areas to access the benthos to find larger prey, and SAFS would forage in pelagic locations (Chapter 3). I also expected that consumption of higher trophic level prey would be related to body size. This was assessed through the trophic levels of prey items consumed (Chapter 2) and through the trophic position of each species-sex group determined through the $\delta^{15}N$ isotopic signature in individual whisker samples (Chapter 4).

Due to the dimorphism in otariids, I expected to find sexual segregation, when sample collection from individuals permitted this evaluation (Chapter 3 and Chapter 4). In this case, the hypotheses was that lactating female foraging grounds should be more proximate to the colony in comparison to males, reflecting a reduction in the distance, time and area invested in the search for prey, to ensure pup survival on land (Chapter 3). In the isotopic signals, this would reflect on $\delta^{13}C$ values of females closer to zero (more coastal) with a narrower range, indicative of more restricted area search for prey in comparison to males. I expected males could be have more negative $\delta^{13}C$ values wither a broader range of values, reflecting wider search for food in

the pelagic domain (Chapter 4).

For this objective, results have shown that trophic interspecific segregation exists at different levels. In Chapter 2 I determined that dietary interspecific segregation exists due to resource partitioning of three main shared prey items: Peruvian anchovy, cephalopods, and red squat lobster. The consumption of these prey items in different proportions by each otariid segregates into two clusters containing the combinations the prey resources consumed during consecutive seasonal samplings in the 2015-2018 study period. In general, SAFS consistently consumed Peruvian anchovy (42.8%) and cephalopods (34.7%); with smaller components of myctophids (7.4%), red squat lobsters (5%), and eleven other fish species. SASL diet is mainly composed of red squat lobster (69.9%) and Peruvian anchovy (19.1%); with smaller amounts of cephalopods (4.7%), silversides (4.6%), and five other fish species. The classification of prey items into ecological groups, based on published literature on habits of prey items, showed that SAFS prey items are from Pelagic (52.35%) and Demersal-Pelagic (47.25%) ecological groups. Meanwhile SASL’s prey items are from Demersal-Pelagic (69.44%) and of Pelagic (23.88%) groups. Meanwhile, Demersal-Benthic species are not important in neither of the Peruvian otariids’ diet composition (1-1.5%). This suggests that majority of prey items come from the pelagic zone, but more refined methods are required to understand the vertical or temporal use of foraging grounds of otariids (i.e., time depth recorders).

Average trophic level values of the prey items alone did not reveal any significant differences between trophic positions for SAFS (4.31 ± 0.15) and SASL (4.55 ± 0.11). This can be due to the variability in the sources of information from the literature and the wide range of study locations. However, isotopic signatures for δ^{15}N for recent years (December 2014 - December 2019), did reveal a higher trophic position in males compared to females for both species. In females, a higher δ^{15}N signal was found in SAFS compared to SASL, albeit the interspecific difference in body size (SAFS females:17.9; SAFS males:18.7 and SASL females: 16.6; SASL males: 18.5, Chapter 4). In Chapter 2, an important significant difference was found between niche breadth based on identification of hard parts, with SAFS (0.26 ± 0.13) reaching double Levin's B_i than SASL (0.14 ± 0.16). In general, SAFS diet also tended to show higher species richness compared to SASL (Chapter 2). When comparing the species consumed, although SAFS diet composition concentrated on anchovy and cephalopod consumption, during many seasons it added new species to the diet, explaining the broadening of niche breadth; in contrast to a less variable species richness in SASL diet, based consistently on large quantities of red squat lobsters and anchovy.

The increase in unique species to SAFS were of pelagic domain (e.g,, King gar (*Scomberesox saurus scombroides*), Pelican barracuda (*Sphyraena idiastes*), California needlefish (*Strongylura exilis*), Sharpchin flyingfish (*Fodiator rostratus*), Appendix B2) in diet confirms that SAFS forage

commonly further offshore. Whereas in SASL's unique species pertain to the coastal domain (e.g., Chameleon wrasse (*Haliocheres dispilus*), Banded toadfish (*Aphos prosus*), Appendix B2). In the isotopic realm, dietary segregation of a more offshore diet on anchovy and cephalopods in SAFS and a more inshore diet based on red squat lobsters and anchovy is backed up by the interspecific δ^{13}C signals found (Chapter 4). The δ^{13}C signal SAFS has a more negative (e.g. offshore) signal in comparison to SASL (e.g., inshore) in both sexes (SAFS females: -14.87± 0.47, males: -14.27 ± 0.36; SASL females: -13.72 ± 0.73, males: -13.36 ± 0.58).

2. Foraging strategies (spatial and temporal dimensions)

To respond to my objective focused on determination of distinct foraging strategies (spatial and temporal dimensions) employed by sympatric pinnipeds SAFS and SASL in relation to environmental conditions. To address this objective, my hypothesis was also based on body size. Since SASL are considerably larger in body size than SAFS, and both species have a strong sexual dimorphism, with males being much larger than females (Ralls & Mesnick, 2002). In Chapter 3, I expected that SASL will travel longer distances, forage for longer durations, and cover larger areas than SAFS. Also, in terms of temporal segregation, based on Trillmich et al. (1991), I predicted that fur seals will forage mostly in the night hours to capture

superficial available prey during diel vertical migration of the most abundant prey item in HCS, Peruvian anchovy (*Engraulis ringens*). In contrast, I expected SASL to forage indifferently throughout the day or night hours as shown in other sea lion species (Riet-Sapriza et al., 2013; Schwarz et al., 2021; Villegas-Amtmann et al., 2008).

Due to the energetic constraints linked to parental roles and offspring survival, in Chapter 3 I expected females of both species to be more coastal (inshore) and males more pelagic (offshore) as evidenced in other otariids (Page et al., 2006; Staniland & Robinson, 2008). Since in HCS, cool coastal upwelling translates to lower sea surface temperatures (SST), higher productivity (assessed by higher concentrations of chlorophyll-a), lower proximity to fronts, and lower front gradients in reduced distance from coast (Echevin et al., 2008; Gutiérrez et al., 2011) I expect this pattern to be related to female foraging habitat. Whereas the opposite features, that characterize pelagic habitats, I envisioned would be associated to male foraging. Furthermore, in Chapter 4, in terms of isotopic space I hypothesized that both otariid females will show $\delta^{13}C$ values closer to zero indicative of higher productivity since they remain constrained closer to the land-based colony, where chlorophyll-a is higher. In contrast, males would have a wider range of $\delta^{13}C$ from foraging more “freely” between coastal and pelagic zones.

Two scales are explored and discussed for segregation in the temporal dimension in Chapter 3. Peruvian otariids have a 1-3 month temporal

segregation in their breeding seasons (SAFS breeds from October to December and SASL from January to March). This contributes yet another mechanism for segregation known as allochrony to partition resources during energetically critical times, which has be postulated as one of the founding drivers behind speciation (Taylor & Friesen, 2017). Since lactation is extended in temperate latitude species and time of weaning is flexible (reported to occur between 6-36 months), we consider it valuable to explore segregation mechanisms while lactating females are foraging to nurse their pups. In a smaller foraging trip scale, I found nocturnal foraging in SAFS females (incremental peak in dusk hours) and daytime foraging in SASL males (incremental peak in dawn hours). Nocturnal foraging in SAFS females may be a synergistic effect between the energetic constraints to provision for their young and the vertical diel migration of prey items for SAFS such as Peruvian anchovies, squids and myctophids, that are more available in the dusk to night hours (Ayón et al., 2008). Since we did not find a significant effect for hour of day in male SAFS, we reject our hypothesis that this pattern holds for all SAFS. Since males do not have energetic constraints linked to parental care, daytime foraging segregation in SASL males may be a reflection of a reduction in competition with another otariid age-class, predator species or preference for a specific prey (Chilvers & Wilkinson, 2009). In Chapter 2 we report a high consumption of red squat lobsters in SASL, therefore we consider this could be a preferred targeted prey for this

temporal segregation. Studies on diel migration of Peruvian anchovies and red squat lobsters show a high degree of overlap. However at hours of dawn, squat lobsters congregate in more dense aggregations closer to the surface in comparison to anchovies (Gutierrez et al., 2005), suggesting it can be the best time to increase the capturability of these prey patches. Studies in other sea lion species have found individuals in the same age-class in have different foraging modes (pelagic, benthic and nocturnal divers, Schwarz et al. 2021). Thus, it is possible that also in SASL there are individual specialization mechanisms; or that individuals can also switch between strategies according to surrounding prey availability. Thus, we recommend these scenarios are further explored in this ecosystem. Future studies involving depth recorders coupled with availability of local biomass of prey items would help refine validation of foraging along the water column, since present analyses may have associated errors in the identification of foraging events based on locations alone.

The results of Chapter 3 show that sympatric otariids in the HCS have multiple strategies to segregate while foraging in the pelagic environment and that body mass is not the sole driver for segregation in space and time, but rather a combination of energetic constraints according to sex, reproductive roles linked to specific dietary resources. We found that although they are smaller in size, both SAFS females and males, make trips of longer distance and duration in comparison to both sexes of SASL, rejecting our hypothesis

that larger animals would make longer trips. In terms of area, SASL cover larger home ranges and core areas, but do so with more consecutive shorter trips compared to SAFS. This reveals different use of the foraging grounds at interspecific level. SASL have larger home ranges as a group, covering a larger area parallel to the coastline that envelopes the SAFS home range. In contrast, SAFS travel farther offshore during feeding trips to specific areas. In agreement with our predictions based on previous studies focused on sexual segregation of otariids, females of both species show more constrained foraging trips in terms of distance traveled, home ranges and core areas in comparison to males in both species (Page et al., 2006; Staniland & Robinson, 2008). Finally, although post-breeding dispersal is common in male pinnipeds this study shows that the South American otariids do not depart on a migration, but rather obtain their energetic demands in a local range of 55,000 - 106,000 km^2. These data are evidence that these sympatric species have evolved and adapted to obtain their resources locally in the nearby productive upwelling waters of HCS, occupying rookeries like PSJ year round.

3. Environmental conditions associated to foraging

The environmental variables associated with foraging events evaluated in sympatric pinnipeds in Chapter 3 revealed interspecific and intraspecific

differences. When compared, environmental habitat features of SASL females are linked to the coastal habitat that is characterized by lower distance to coast (DC), lower sea surface temperature (SST), lower Proximity to Fronts and higher chlorophyll-a (Chl-a) values. Whereas SAFS females are associated to a more pelagic domain characterized by higher SST, more proximity to fronts, higher front gradients and of course, higher DC values. Among males, best fitting models for SAFS males included SST, Chl-a and Proximity to Fronts, whereas SASL males included all environmental covariates. SASL males have lower SST, lower Chl-a, lower Proximity to Fronts and lower DC, which could be a product of individual strategies. Ranges in the environmental variables targeted by SAFS and SASL males are highly overlapping; thus conclusions should be taken with caution and further studies exploring individual strategies should be conducted. We also suggest incorporating additional environmental variables to better explain male foraging environment, such as those related to the vertical structure of the water column.

In Chapter 4, I set up a framework to explore $\delta^{13}C$ and $\delta^{15}N$ isotopic niche differentiation along longitudinal samples in whiskers, permitting to compare a fifteen year period (2005-2019), during which a change in environmental conditions were found. In this study I found a reorganization of our four otariid study groups in the isotopic space as a response to the increase in average sea level and warmer sea surface temperatures from November 2013

onwards (Period 2). Groups expanded their niche width (except SASL females), segregated in isotopic space, and reduced the $\delta^{15}N$ signal during the warmer period. A decline in otariid $\delta^{15}N$ suggests impoverished baseline values of $\delta^{15}N$ with bottom-up effects impacted tertiary consumers, a shift in diet towards lower trophic prey, or both. Niche overlap was reduced between all otariid groups in Period 2, providing support of a temporal shift from a more redundant assemblage (similar isotopic niches) during the colder period (Period 1) to a more trophically diverse assemblage (divergent isotopic niches) during the warmer period (Period 2). Results from Chapter 4 are in agreement with other findings in stable isotope signals in SAFS whiskers that suggest having captured ENSO signals (Edwards et al., 2021).

The analyses of this long term dataset depicts a shift in the trophic organization that is aligned temporally with the decline of the Punta San Juan otariid populations detected in Chapter 1. Furthermore, the break into two periods of varying environmental conditions explains the changes in the trophic reorganization in the otariid community. During Period 2, female SASL show the largest drop in $\delta^{15}N$ of 2.4, while male groups $\delta^{15}N$ values drop in 1.5 and female SAFS decrease slightly in $\delta^{15}N$ by 1.0. We consider that the change in $\delta^{15}N$ in Period 2 reflects a bottom-up effect in the trophic food web, linked to the dietary habits of each species and sex group, in response to changes in the environment.

In November 2013 an elevation in the average sea level time series for the

study area was detected, giving rise to a second period of higher sea level and warmer sea surface temperatures. This change is in agreement with the propagation of physical anomalies that started in the North Pacific Ocean that forced a biological response in the vertical distribution of nutrients and the abundance of chlorophyll-a (Zaba & Rudnick, 2016). Concurrently, in mid-2014 off the coast of Peru, a moderate, coastal El Niño was reported and then followed by an Extraordinary El Niño in 2015-2016 (L’Heureux et al., 2017) and subsequently followed by a costal El Niño in 2017, continuing to promote a warm assemblage. During these years, studies suggest that physical anomalies of these warming ocean events generated a biological response similar to those of El Niño (Espinoza-Morriberón et al., 2017). All the beforementioned events involve the rise of sea level forced by the passage of remotely generated and coastal trapped waves in response to heat expansion (Ryan & Noble, 2002). The thermocline, nearshore depth of chlorophyll-a, and the nutricline deepened, decreasing nutrient enrichment in the euphotic zone. Weak winds caused the reduction in vertical nutrient fluxes to the depleted euphotic zone. A deeper concentration of chlorophyll-a decreased phytoplankton biomass, causing a shift in community structure toward smaller phytoplankton which can have bottom-up effects on food and energy availability at higher trophic levels (Zaba & Rudnick, 2016).

Given these results and those of Edwards et al. (2021), we propose that there is a pattern in the response of otariid communities towards different climatic

scenarios in HCS. In cold scenarios with low SST and low sea level there will be higher prey available of higher quality. This will promote population growth in otariids, with higher recruitment of females and juveniles, and the opposite during warm regimes. Due to more prey available, dietary segregation, spatial overlap, temporal segregation and segregation in isotopic space will be reduced, in comparison to an opposite warm scenario (Figure D.1).

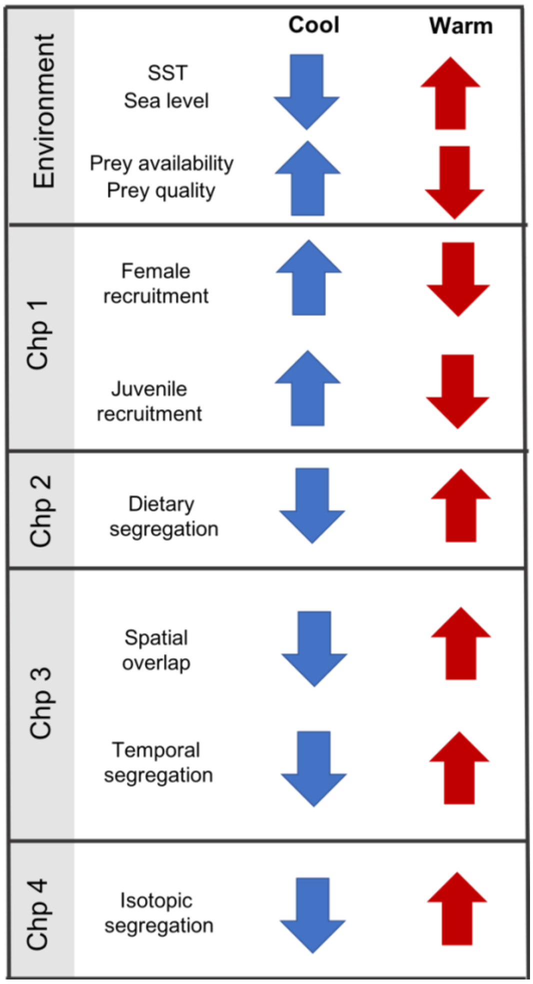

Figure D. 1 Diagram summarizing main findings to explain current population decline in Peruvian otariids in context of two contrasting environmental scenarios: cool (blue) and warm (red) conditions.

4. Final remarks

Populations can be separated into specialists when they have narrower niches or into generalists when they have broader niches (Begon et al., 2006). Generalist populations with broader niches are likely favored in heterogeneous and stable environments, whereas specialist populations with narrower niches are favored in highly dynamic ecosystems and homogeneous environments (Kassen, 2002). Thus, during the warmer period, results suggest that prey assemblages are more diverse in contrast with dense prey aggregations favored by nutrient rich, cold-water in HCS. Since total ellipse area serves as a proxy for the extent of trophic diversity within the community, its expansion during Period 2 reflects a more generalist community with looser packing of individuals in the isotopic niche space (Layman et al., 2007). From all the species and sex groups, female SASL show the largest variation in response to the warming scenario, reducing both isotopic niche width and $\delta^{15}N$ values. This suggests that this group has higher plasticity to adapt to changing environmental conditions, as reported in other otariids (Amador-Capitanachi et al., 2020). Knowing that SASL is the dominating species in Peru, higher plasticity in adult females helps explain current, larger population biomass of SASL reported for PSJ and Peru, in contrast to the smaller and steeper declining SAFS population (Cárdenas-Alayza et al., 2021). Thus, trophic plasticity, enhanced by feeding primarily on a more available food source (*P. monodon*) that lacks commercial fishing

pressure can be currently more advantageous for SASL population growth.

Results show that sympatric otariids in the HCS currently show some level of segregation through trophic indices and while foraging at sea, partly associated with reproductive role, body size and species. Based on our long term stable isotopes time series, trophic segregation mechanisms have changed after November 2014. Segregation mechanisms only make sense if prey are partly limited and spatially partitioned. In the case of very high availability of prey, coexistence could occur without much need of segregation. This could be the case in the previous colder Period 1, January 2005 – October 2014. However, in the case of food shortages, segregation mechanisms could sustain coexistence, by taking advantage of differential abilities to cope with such a situation, which could be the case of Period 2. In the latter case, the differences observed in the foraging ecologies may depict a situation of one species outcompeting another, which couldn’t be considered as a coexistence mechanism. In this context, the plasticity in SASL females in contrast to the less flexible SAFS female group, can help explain SASL as the dominating of the two sympatric species in HCS, albeit environmental changes. This continues to raise the question of the dynamics of segregation mechanisms with respect to food availability in dynamic marine environments like HCS, and calls for maintenance of the long term monitoring and research programs.

In general, empirical understanding of competitive networks is limited by the

absence of detailed information on the extent of resource partitioning and competition at a community scale, and the effects of interactions among species that do not come into direct contact (Eurich et al., 2018). Thus, other potential competitors in HCS can also be contributing to reduced SAFS population. For example, many other predatory fish species have been reported to be feeding red squat lobsters, after the increase in its availability in the cold water regime. Species like dolphinfish (*Coryphaena hippurus*), Jack mackerel (*Trachurus murphyi*), bonito (*Sarda chilensis*) and several shark species could be a source of competition for items targeted by SASL (Alegre, 2015; Gonzalez-Pestana et al., 2021). This will increase in cases of shortage of this currently abundant prey item that is sustaining many predators.

Research on Jumbo squid (*Dosidicus gigas*) show how this voracious short-lived cephalopod with diel migration has increased its population biomass in the cold regime during the 2000s off the coast of Peru incrementing the size at maturity (Argüelles et al., 2008). Investigations on trophic ecology of this species report that the main contribution to diet composition is based on other cephalopods along with mesopelagic fishes, euphasiids and some cannibalistic feeding on smaller age-classes of *D. gigas*. Larger sized Jumbo squid consume larger prey items such as cephalopods, while smaller *D. gigas* consume lower trophic level prey (Alegre et al., 2014). Thus, the successful population growth of Jumbo squid in the past 20 years can be a new source of

competition for species like SAFS, based on the similarities in their diet composition and offshore nocturnal habits. Potential competition between SAFS and *D. gigas* should be further explored to determine if recent changes in predator guilds can help explain reduced population abundance of SAFS.

It has been well documented that the Peruvian HCS contains one of the world´s largest monospecific fisheries based on Peruvian anchovy, along with other fisheries that target cephalopods and other small pelagic fish species. Many of these fisheries have been overcapitalized and are decreasing available biomass to dangerous levels for sustainability, both at industrial and artisanal level (De la Puente et al., 2020; Fréon et al., 2008). To present date, it is well documented that Peruvian anchovy (*E. ringens*) is heavily exploited and is a source of competition for several predators in HCS. However, we are unaware of any large-scale exploitation of red squat lobsters (*P. monodon*) in Peru that limits the availability of this prey item for predators. However, if this were to occur, it may severely affect the availability of this prey resource for SASL and could lead to further changes in the diet of this species, and increase competition between the two sympatric otariid species as evidenced in other regions (Drago et al., 2009; Szteren et al., 2018). Thus, we recommend the incorporation of trophic ecology studies of top predators to further inform the generation of quotas to improve the level of biomass left available in the oceans for the predator populations to recover from decline.

5. Future Recommendations

As part of this study, we would like to offer a series of recommendations for future research to continue to disentangle sources of segregation to explain the coexistence of Peruvian otariids, as follows:

- First, there is a need to continue to update resource partitioning information by identifying cephalopods to species level to determine how cephalopod species diversity impacts niche breadth. Furthermore, estimation of the size of fish and cephalopods consumed by otariids is recommended to determine if there is interspecific resource partitioning in prey sizes targeted by SAFS or SASL.

- In the realm of foraging strategies, I recommend to determine if female foraging behavior changes according to breeding or non-breeding season as well as offspring number and age (Drago et al., 2010, 2015, 2021; Franco-Trecu et al., 2012). This could help finetuning the critical time of energetic constraint in females according to species.

- Findings show varying lengths in distance duration of foraging trips according to species-sex groups. This can be indicative of the use of specialized foraging grounds in some groups, suggesting potential site fidelity to foraging grounds. This has been reported in other locations and

should be further explored in HCS (Baylis et al., 2017; Knox et al., 2018).

- Ranges in the environmental variables targeted by SAFS and SASL males are highly overlapping and ranges are hard to interpret as a specific habitat selection. Further analyses that explore individual and/or group strategies is recommended.

- Given the dynamic environment in HCS and the differences observed in the foraging ecologies of one species outcompeting another, the question of the dynamics of segregation mechanisms with respect to food availability persists and calls for maintenance of the long term monitoring and research programs to compare theses indices over time. Monitoring programs on top predators should continue to collect information on diet composition, foraging behavior and populations dynamics.

- Given the variation in some groups (e.g., males) contribution of specialized individuals employing benthic strategies close to shore is still put in question. Thus, individual specialization and the capacity to adapt different foraging strategies can be playing an important role in the variability between study groups. I recommend future research to explore individual specialization to understand exploitation mechanisms into how individuals respond to changing environmental conditions. Deployment of time-depth

recorders and collection of tissue samples that archive long term signals such as stable isotopes and fatty acid signatures should be prioritized.

- Ecological theory has progressed from a focus of pairwise interactions to a multifactorial perspective of mechanisms that drive competition at community level. To get a bigger picture of the interactions of SAFS and SASL in HCS, further studies that compare trophic ecologies with other potential predators in HCS (e.g., seabirds, squids, large predatory fish, elasmobranchs and cetaceans) are recommended to further establish roles and interactions between potential competing predators in HCS.

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GRAPHIC REFERENCES

Ilustraciones de las lobos marinos dibujadas por Paulo Colchao Claux; entregadas para uso con autorización para fines de esta tesis.

Diseño de las carátulas de los capítulos realizados en www.canva.com/design

APPENDIX

APPENDIX A1

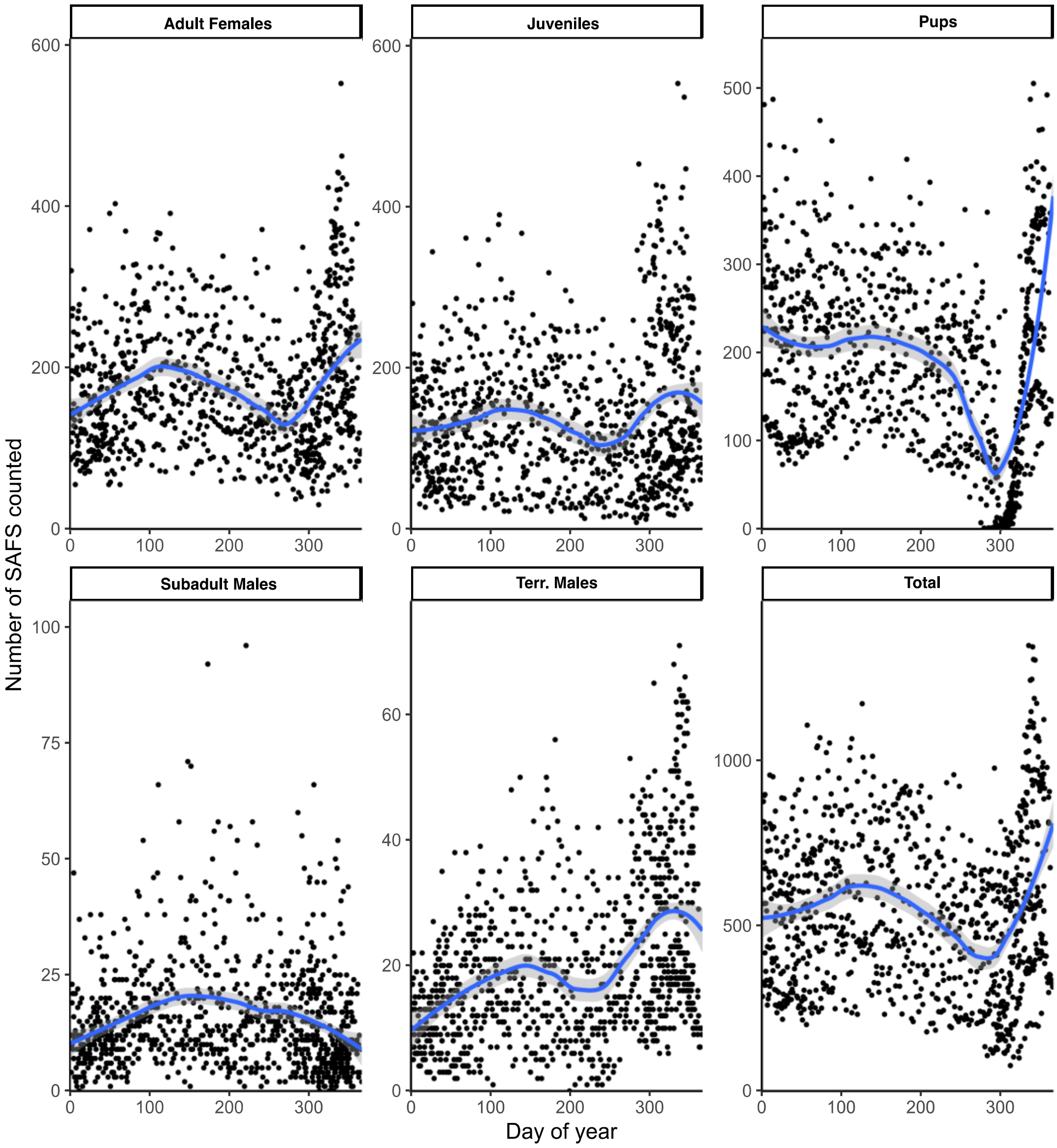

Figure A. 1 Multi-panel plot of South American fur seals counts by age-class according to day of year collected at the main breeding site S3 in Punta San Juan, Peru. Classes include: Adult Females, Juveniles, Pups, Subadult Males and Territorial Males. Total is the sum of all the age-classes. Blue line is a fitted loess model to depict the trend in abundance throughout the year. Data points include all study years available for site.

APPENDIX A2

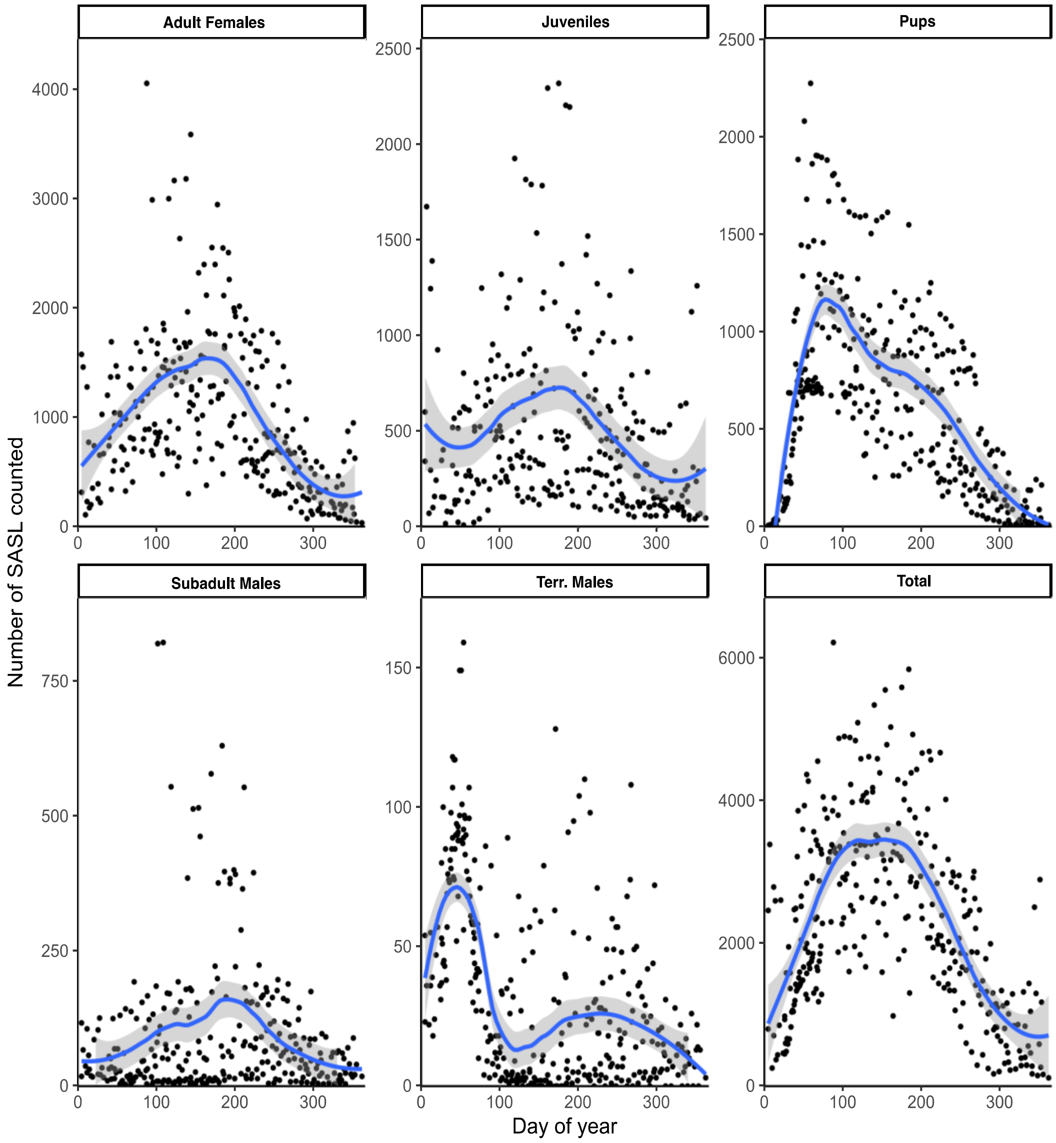

Figure A. 2 Multi-panel plot of South American sea lions counts by age-class according to day of year collected at the main breeding site N7 in Punta San Juan, Peru. Classes include: Adult Females, Juveniles, Pups, Subadult Males and Territorial Males. Total is the sum of all the age-classes. Blue line is a fitted loess model to depict the trend in abundance throughout the year. Data points include all study years available for site

APPENDIX B1

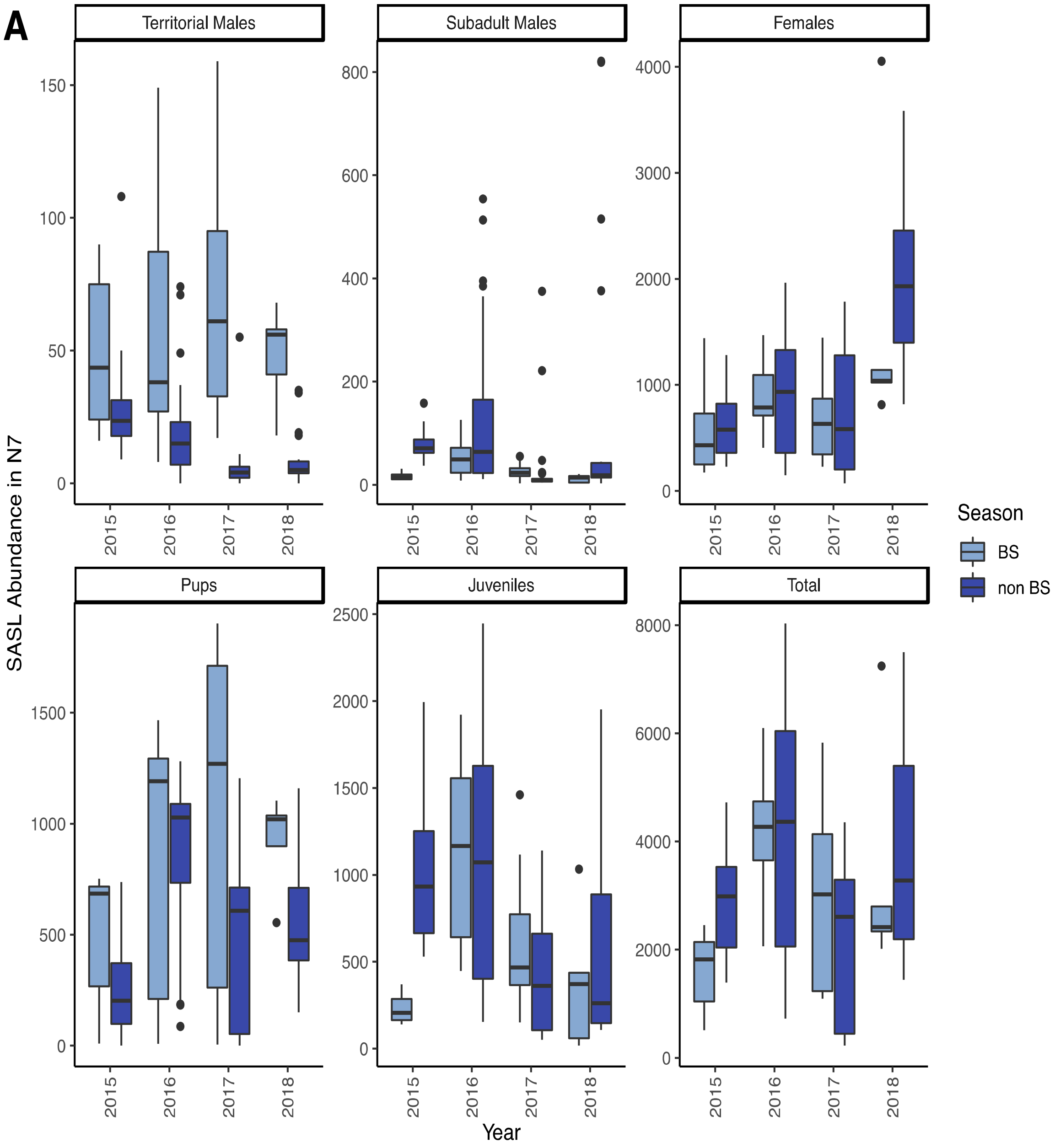

Figure B1. 1 Boxplots of abundance of South American sea lions (SASL) in site N7 (2015-2018) according to age class during breeding (BS, January -March) and non breeding months (non BS, April – December) according to age class.

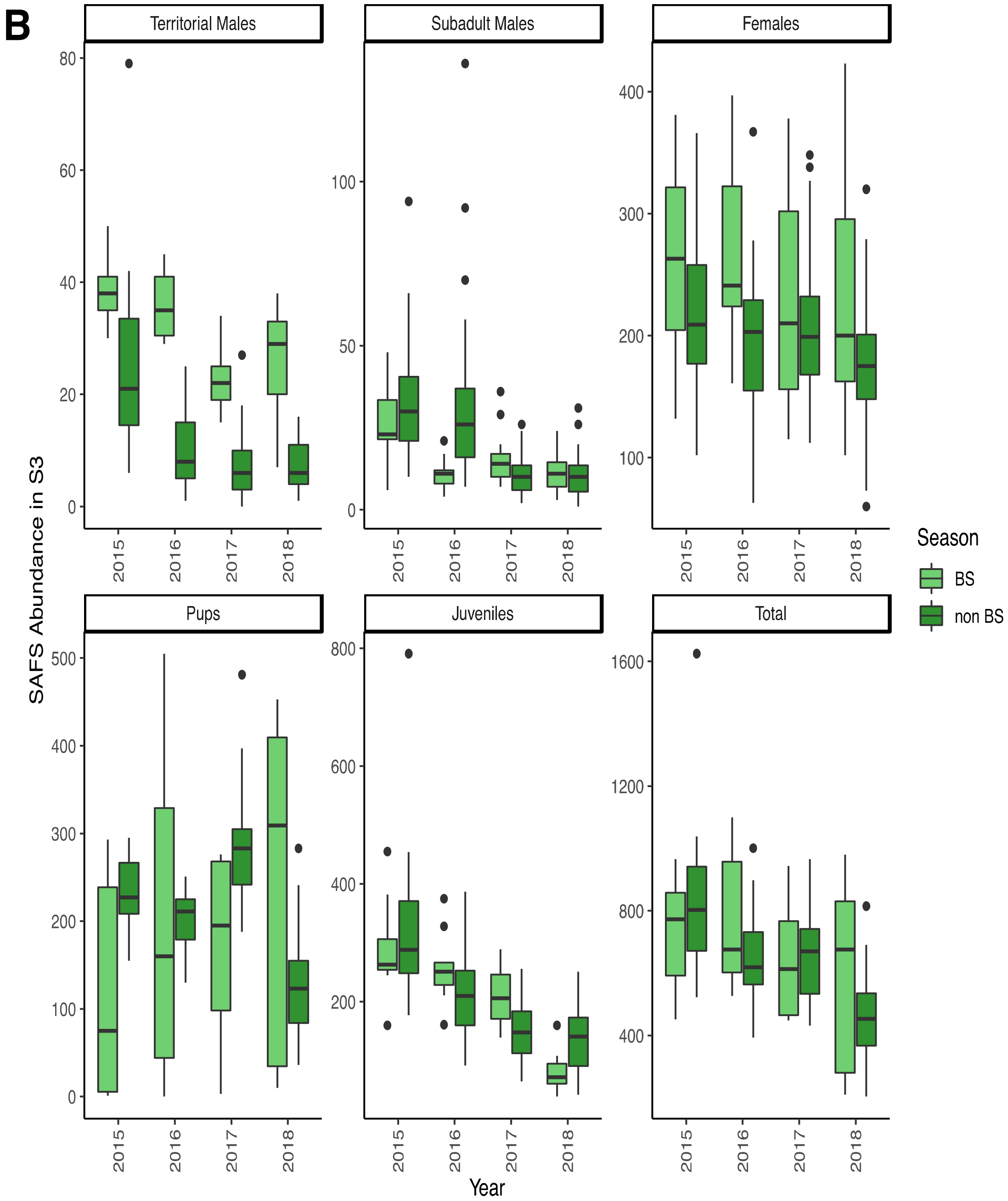

Figure B1. 2 Boxplots of abundance of South American fur seals (SAFS) in site S3 (2015-2018) according to age class according to age class during breeding (BS, October - December) and non breeding months (non BS, January – September).

APPENDIX B2

Table B2. 1 List of prey items identified in the samples of South American fur seals (SAFS) and South American sea lions (SASL) and the habitat group category assigned.

	Scientific name	English common name	Habitat	SAFS	SASL
1		Cephalopods	Demersal-Pelagic	X	X
2	*Anchoa nasus*	Longnose anchovy	Pelagic	X	X
3	*Aphos prosus*	Banded toadfish	Demersal-Benthic		X
4	*Engraulis ringens*	Peruvian anchovy	Pelagic	X	X
5	*Fodiator rostratus*	Sharpchin flyingfish	Pelagic	X	
6	*Haliocheres dispilus*	Chameleon wrasse	Demersal-Benthic	X	
7	*Isacia conceptionis*	Cabinza grunt	Demersal-Pelagic	X	X
8	*Lampanyctus parvicauda*	Slimtail lampfish	Demersal-Pelagic	X	
9	*Leuroglossus stilbius*	California smoothtongue	Demersal-Pelagic	X	X
10	*Merluccius gayi*	South Pacific hake	Demersal-Benthic	X	X
11	*Mugil cephalus*	Flathead grey mullet	Pelagic		X
12	*Normanichthys crockeri*	Mote sculpin	Demersal-Benthic	X	X
13	*Odontesthes regia*	Chilean silverside	Pelagic	X	X
14	*Paralabrax humeralis*	Peruvian rock seabass	Demersal-Pelagic	X	X
15	*Pleuroncodes monodon*	Red squat lobster	Demersal-Pelagic	X	X
16	*Prionotus stephanophris*	Lumptail searobin	Demersal-Benthic		X
17	*Sardinops sagax sagax*	South American pilchard	Pelagic	X	
18	*Sciacena deliciosa*	Lorna drum	Demersal-Benthic	X	X
19	*Scomberesox saurus scombroides*	King gar	Pelagic	X	
20	*Scomber japonicus*	Chub mackerel	Pelagic	X	X
21	*Sphyraena idiastes*	Pelican barracuda	Pelagic	X	
22	*Strongylura exilis*	California needlefish	Pelagic	X	

APPENDIX B3

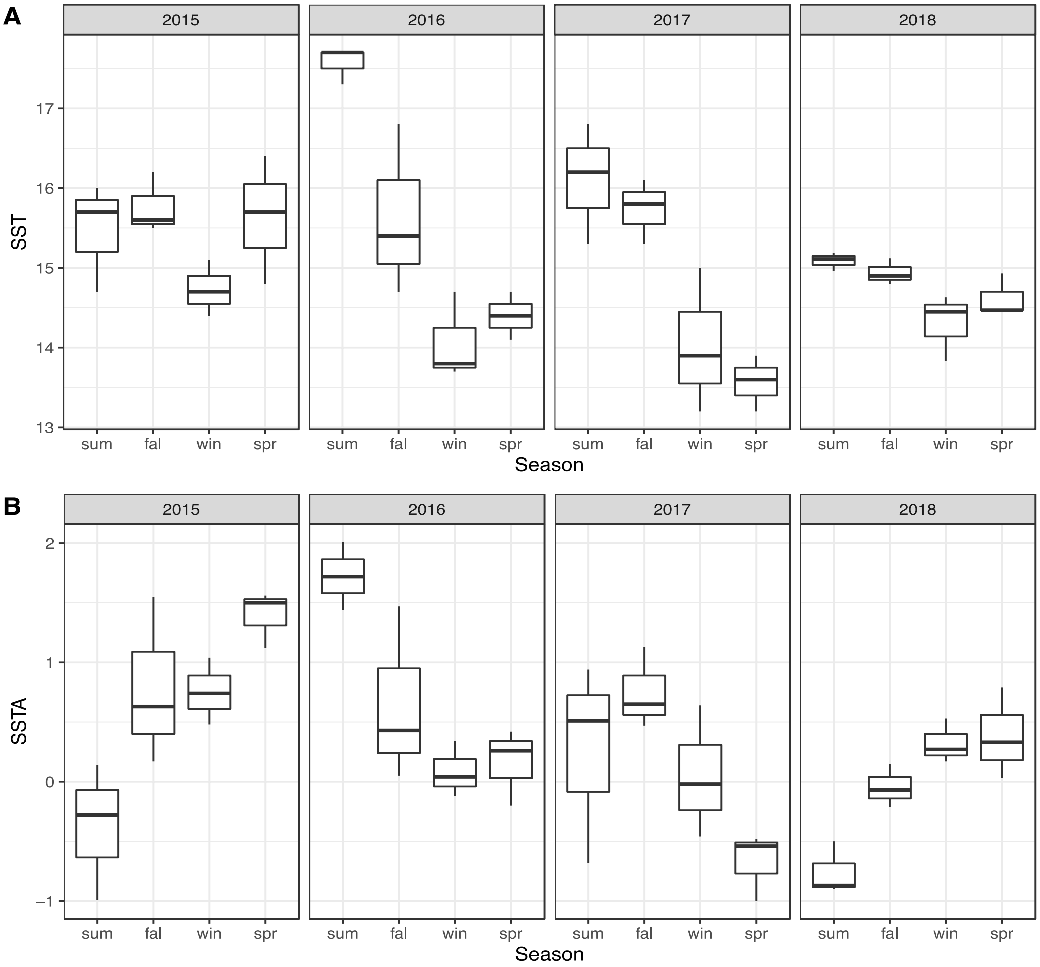

Figure B3. 1 Boxplots of the seasonal A) SST and B) SSTA for study period 2015-2018 collected in San Juan de Marcona, source: DHN - Peru.

APPENDIX B4

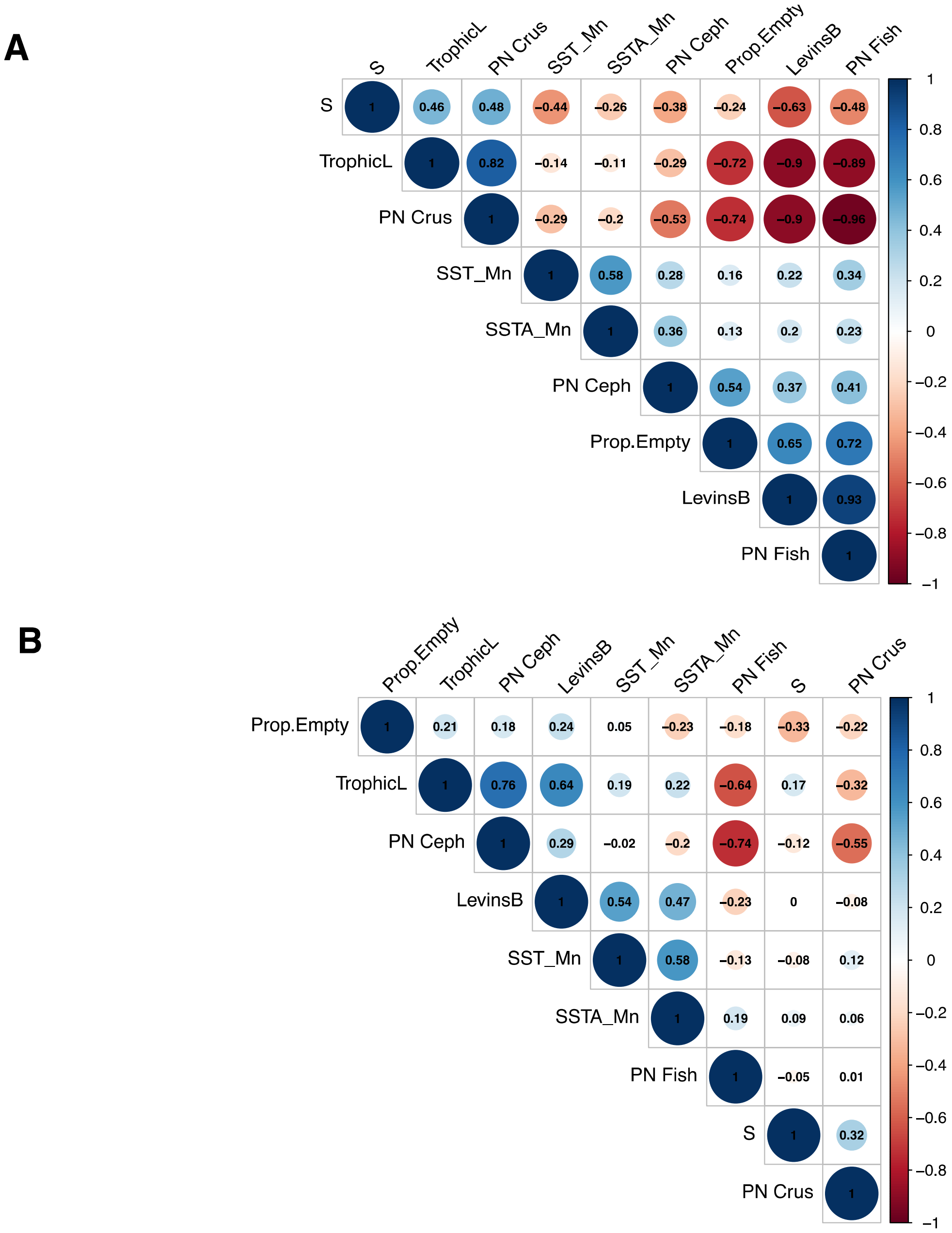

Figure B4. 1 Spearman correlation charts ($p< 0.05$) for trophic and environmental indices for A) South American sea lions, SASL and B) South American fur seals, SAFS. Positive correlation scores in shades of blue and negative in shades of red.

APPENDIX C1

Table C1. 1 Species, sex, individual identification (ID) deployment date, weight (kg), length (cm), number of days tracked and number of trips recorded for each individual.

No.	Species	Sex	ID	Date Deployment	Weight	Length	# Days	# Trips
1	SAFS	F	A00_157689	November 19, 2015	38.00	114.0	57.69	16
2	SAFS	F	A02_157694	November 19, 2015	47.80	124.0	23.19	6
3	SAFS	F	A03_157695	November 19, 2015	52.20	125.0	53.83	9
4	SAFS	F	A04_157696	November 19, 2015	56.00	131.0	75.38	11
5	SAFS	F	A05_157697	November 19, 2015	40.10	115.0	45.38	9
6	SAFS	F	A06_157698	November 20, 2015	47.60	121.0	49.40	15
7	SAFS	F	A07right_8	November 20, 2015	33.70	111.0	34.50	8
8	SAFS	F	44Y_157700	November 20, 2015	48.80	127.0	26.44	4
9	SASL	F	F01_157689	February 24, 2017	74.50	146.0	72.77	23
10	SASL	F	F02_157697	February 25, 2017	63.30	135.0	78.02	29
11	SASL	F	F04_157699	February 25, 2017	85.00	143.0	76.31	23
12	SASL	F	F05_157700	February 25, 2017	86.00	148.5	48.85	19
13	SAFS	M	36Y_143666	November 15, 2014	118.80	158.0	56.19	5
14	SAFS	M	39Y_143667	November 15, 2014	117.30	151.0	43.68	12
15	SAFS	M	41Y_143663	November 15, 2014	107.20	150.0	66.19	10
16	SAFS	M	C55_143664	November 13, 2016	113.30	148.0	60.15	3
17	SAFS	M	C56_143665	November 13, 2016	99.20	151.0	70.38	9
18	SAFS	M	C57_157694	November 13, 2016	106.60	147.0	50.40	3
19	SAFS	M	C58_157695	November 14, 2016	103.40	159.5	46.88	9
20	SAFS	M	C59_157697	November 14, 2016	102.40	158.0	40.87	3
21	SAFS	M	C60_157699	November 14, 2016	94.10	153.5	70.87	4
22	SASL	M	03V_134432	November 15, 2013	151.40	174.5	73.75	22
23	SASL	M	04V_134430	November 15, 2013	237.20	205.0	70.79	14
24	SASL	M	05V_134433	November 15, 2013	219.40	198.0	72.29	18
25	SASL	M	06V_134429	November 16, 2013	238.60	203.0	73.75	16
26	SASL	M	12V_134431	November 19, 2013	184.10	183.0	67.40	14
27	SASL	M	13V_141850	November 13, 2014	196.60	196.5	36.75	11
28	SASL	M	15V_141852	November 13, 2014	201.60	200.0	70.58	7
29	SASL	M	17V_141853	November 14, 2014	162.40	190.0	73.71	14
30	SASL	M	19V_157686	November 17, 2015	160.60	196.0	61.90	12
31	SASL	M	20V_157685	November 17, 2015	139.30	189.0	60.88	14
32	SASL	M	22V_157688	November 17, 2015	191.90	191.0	67.42	25
33	SASL	M	23V_157693	November 17, 2015	131.60	170.5	71.96	21
34	SASL	M	25V_157690	November 18, 2015	137.80	185.0	72.92	13
35	SASL	M	27V_157692	November 18, 2015	172.00	191.1	69.50	20

APPENDIX C2

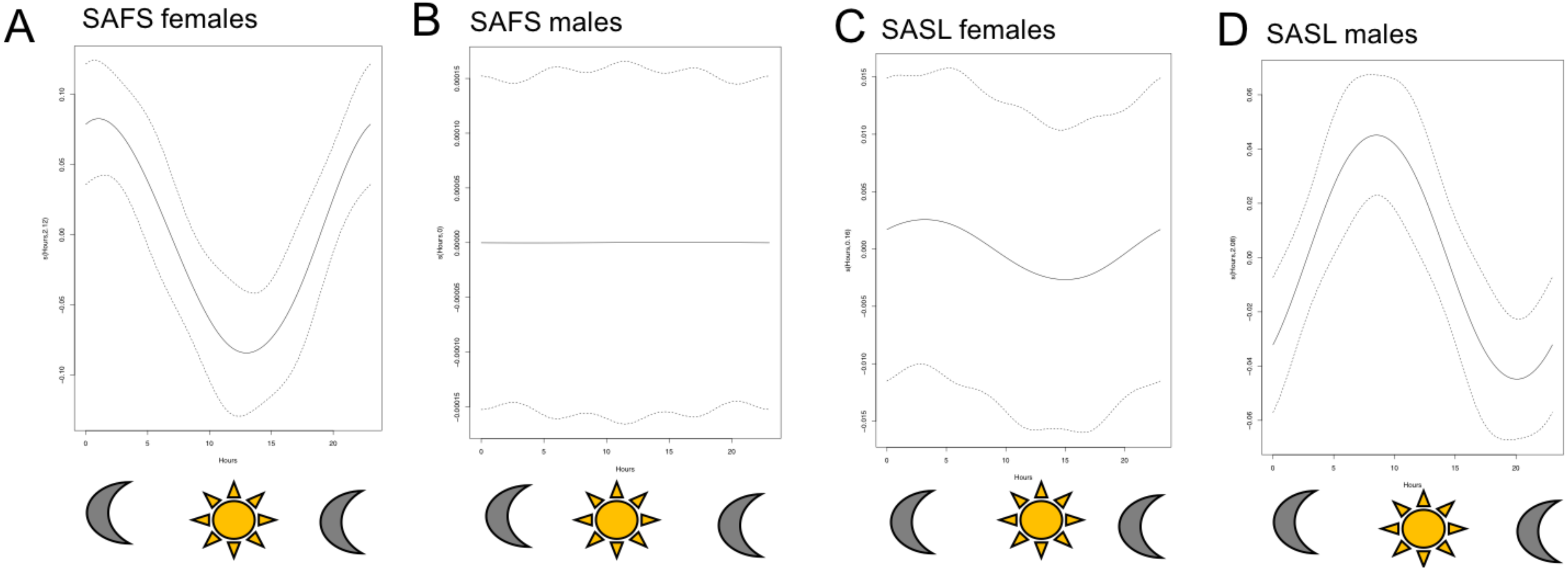

Figure C2. 1 Smoother response for probability of foraging (y-axis) according to hour of day (x-axis) for A) SAFS females, B) SAFS males, C) SASL females and D) SASL males from General Additive Mixed-Models. Significant relationships (p < 0.01) were found for A) SAFS females and B) SASL males. Icons represent daylight (sun) and dark hours (moon).

APPENDIX C3

Table C3. 1 Descriptive statistics for the environmental covariates extracted for foraging event locations for each species and sex group.

Group	Environmental covariate	SST	Chl-a	Proximity to Front	Gradient of Front	Distance from Coast
SAFS Females	*N obs*	*4,408*	*6,294*	*5,852*	*5,862*	*6,348*
	Min	19.28	0.71	0.01	1.28	4.00
	Max	23.03	5.92	0.11	93.50	57.00
	Median	21.29	2.15	0.04	9.88	19.00
	Mean	21.16	2.27	0.04	14.29	22.47
	SD	0.92	0.84	0.01	16.30	11.09
SASL Females	*N obs*	*4,269*	*4,392*	*4,356*	*4,356*	*4,170*
	Min	19.07	0.63	0.01	0.57	9.00
	Max	23.33	20.20	0.11	50.00	26.00
	Median	21.26	4.58	0.07	1.94	15.00
	Mean	21.12	5.85	0.07	3.69	13.93
	SD	0.84	3.88	0.01	7.00	4.16
SAFS Males	*N obs*	*12,264*	*12,474*	*13,197*	*13,197*	*12,996*
	Min	16.11	0.22	0.01	0.48	7.00
	Max	25.22	23.47	0.13	39.13	148.00
	Median	21.08	3.26	0.05	3.55	42.00
	Mean	20.97	3.95	0.05	7.48	51.20
	SD	1.39	3.38	0.02	8.30	34.27
SASL Males	*N obs*	*14,223*	*17,367*	*18,036*	*18,075*	*18,345*
	Min	15.41	0.18	0.00	0.64	4.00
	Max	26.11	25.23	0.11	98.57	147.00
	Median	20.71	2.05	0.03	8.92	23.00
	Mean	20.48	3.05	0.04	13.88	40.46
	SD	1.89	3.10	0.02	14.69	36.11

APPENDIX C4

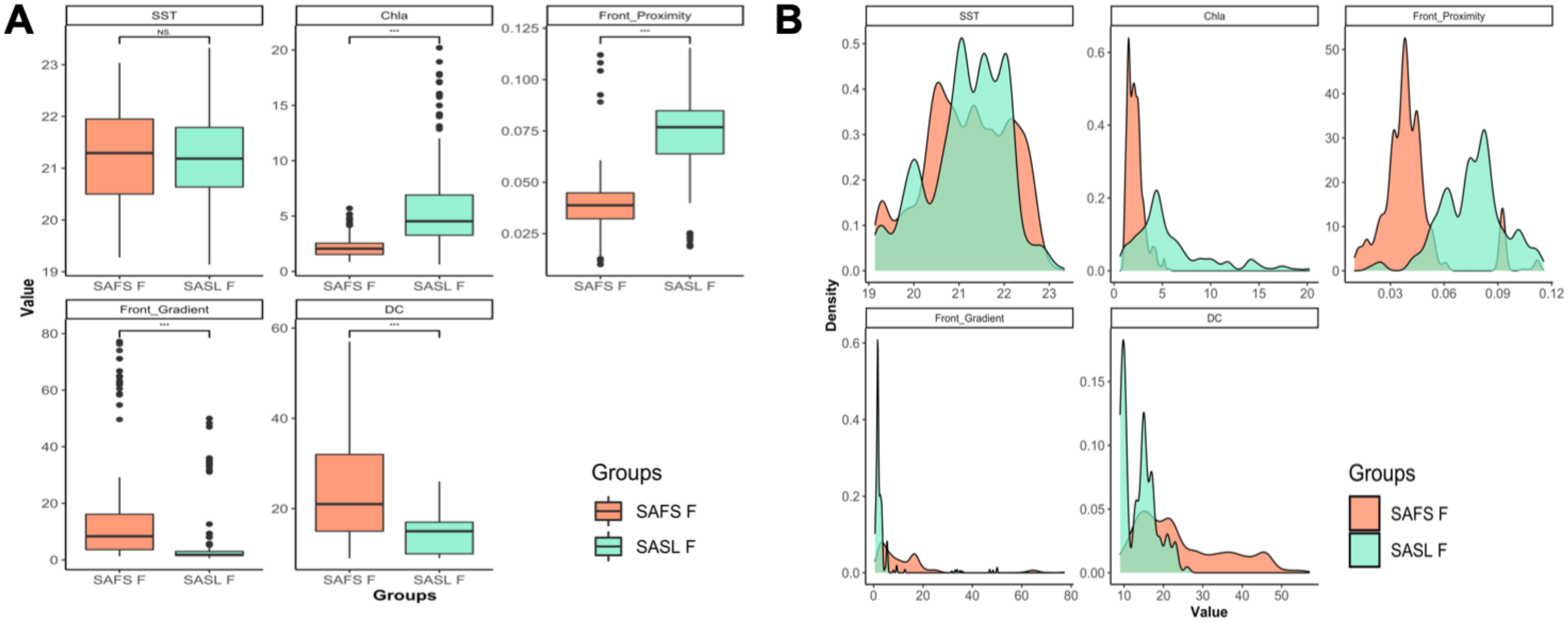

Figure C4. 1 Environmental conditions (SST, Chl-a, Front Proximity, Front Gradient and DC) associated to female SAFS (orange) and SASL (aquamarine) foraging events. A) Boxplots depicting significant differences (***) indicates $p < 0.01$. B) Density curves show distribution of frequencies. SST between SAFS and SASL is not significantly different (N.S.).

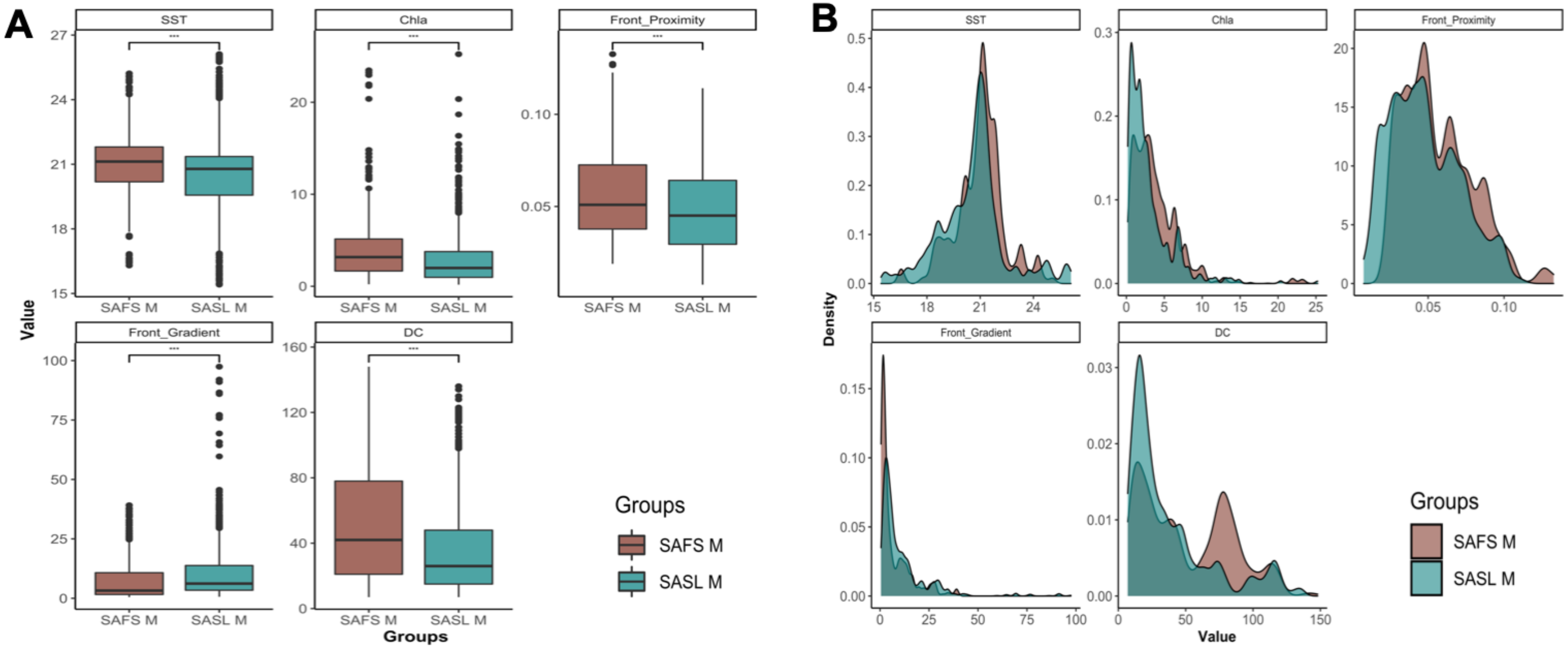

Figure C4. 2 Environmental conditions (SST, Chl-a, Front Proximity, Front Gradient and DC) associated to male SAFS (brown) and SASL (teal) foraging events. A) Boxplots depicting significant differences (***) indicates p < 0.01. B) Density curves showing distribution of frequencies.

APPENDIX C5

Table C5. 1 Deviance explained by univariate General Additive Models (GAM) of each environmental covariate explored in response to foraging events. N = number of observations included in each group.

Group	Environmental covariate	% Deviance
SAFS Females *N = 14,286*	SST	5.37%
	Chl-a	7.31%
	Proximity to Front	1.90%
	Gradient of Front	3.72%
	DC	6.37%
SASL Females *N = 18,423*	SST	3.95 %
	Chl-a	6.60 %
	Proximity to Front	4.29 %
	Gradient of Front	12.50 %
	DC	11.20 %
SAFS Males *N = 51,849*	SST	5.21 %
	Chl-a	2.02 %
	Proximity to Front	7.49 %
	Gradient of Front	3.82 %
	DC	2.75 %
SASL Males *N = 65,040*	SST	3.17%
	Chl-a	0.76 %
	Proximity to Front	0.98 %
	Gradient of Front	0.39 %
	DC	4.05 %

APPENDIX C6

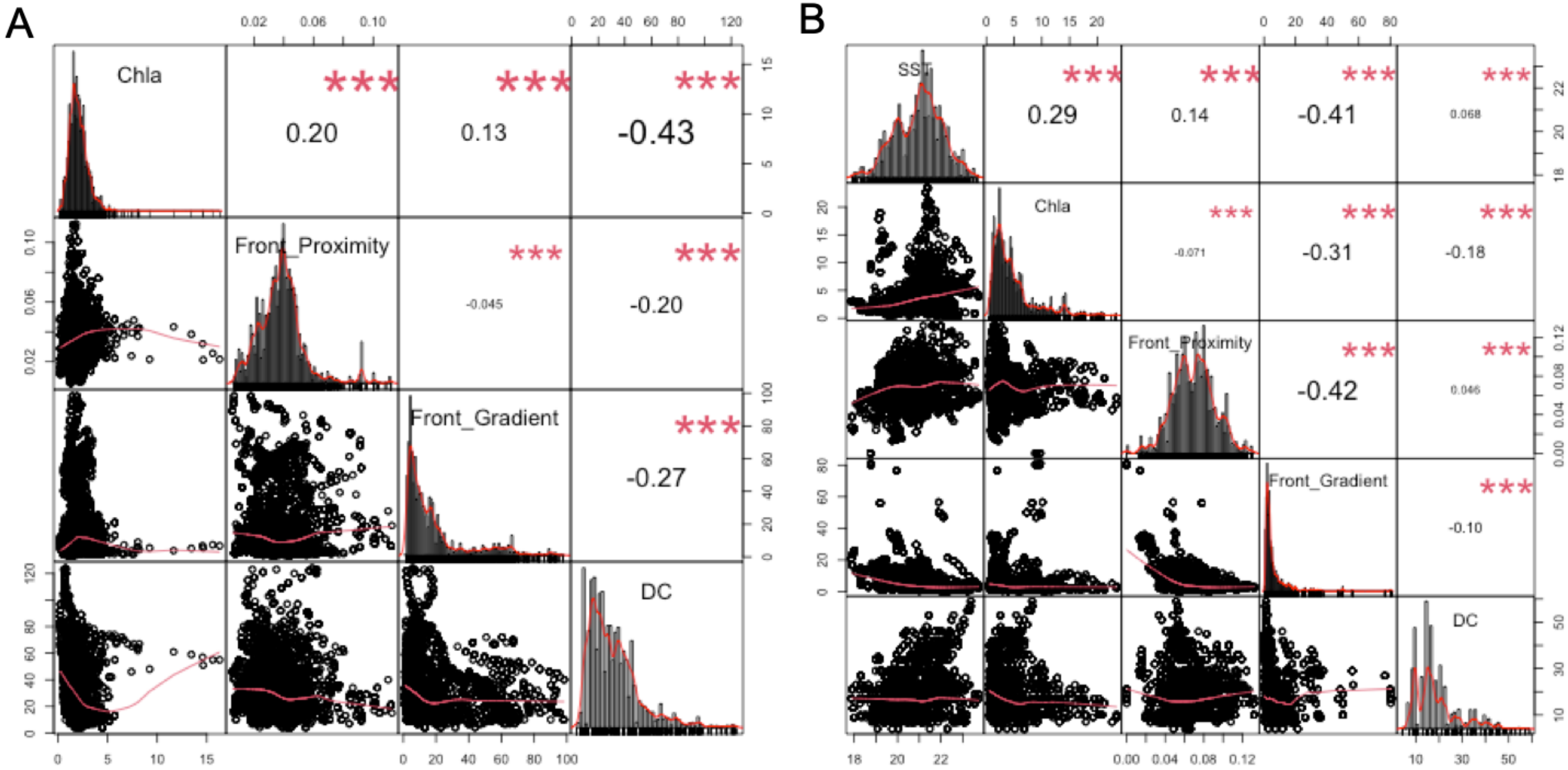

Figure C6. 1 Correlation chart (Spearman rho, p=0.05) between the environmental covariates (SST, Chl-a, Front Proximity, Front Gradient, Distance to Coast) for A) SAFS females and B) SASL females. SST not included in for SAFS females due to 39% missing values.

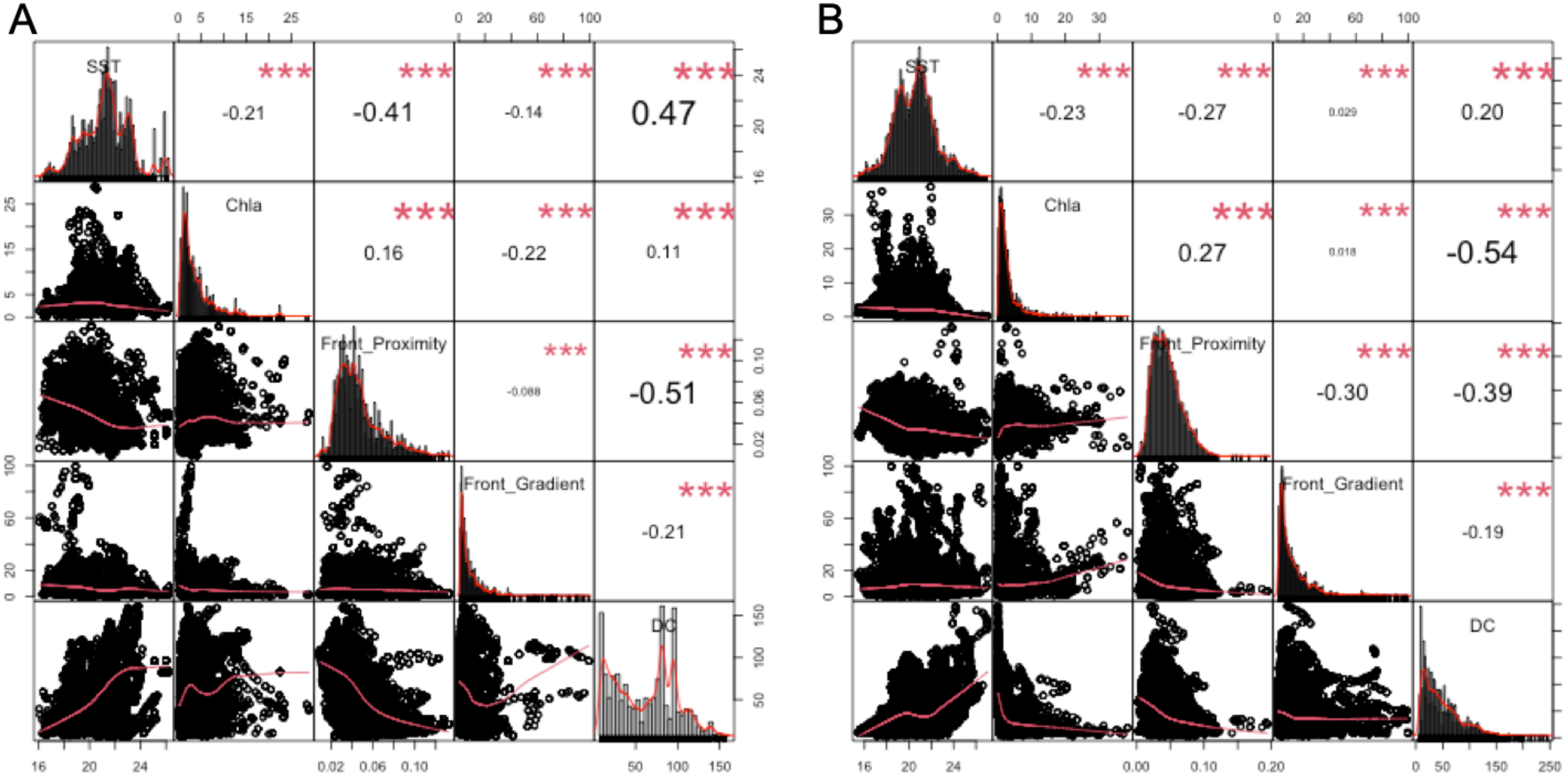

Figure C6. 2 Correlation chart (Spearman rho, p=0.05) between the environmental covariates (SST, Chl-a, Front Proximity, Front Gradient, Distance to Coast) for A) SAFS males and B) SASL males

APPENDIX D1

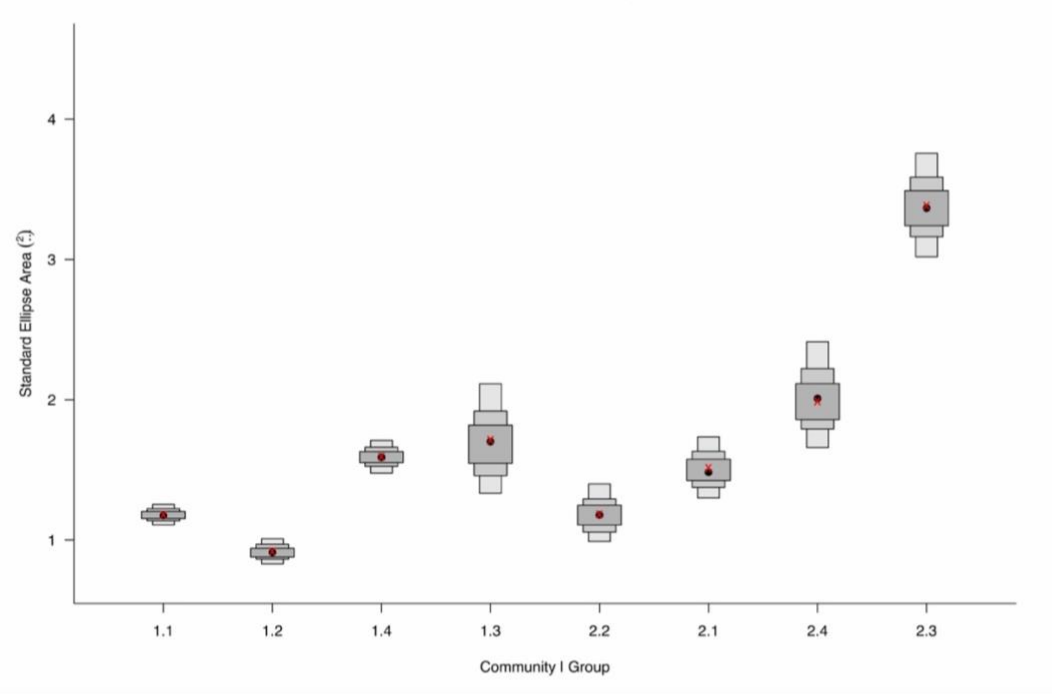

Figure D1. 1 Standard Ellipse Area estimated for each group. Labels represent Community (Period 1 and 2) and Group (1 = SAFS females, 2 = SAFS males, 3 = SASL females, 4 = SASL males). The black points correspond to the mean standard ellipse area for each group, red cross is the standard ellipse area corrected for small sample size. Grey and white boxed areas reflect the 95, 75 and 50% confidence intervals.

APPENDIX D2

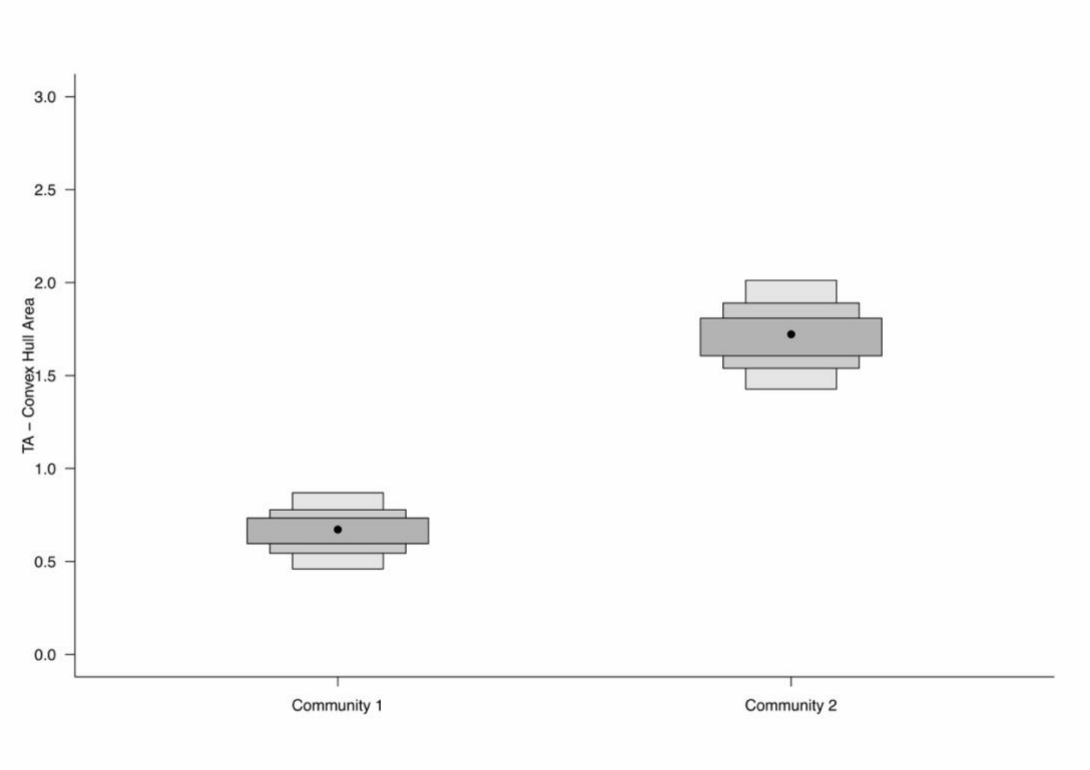

Figure D2. 1 Total area of convex hull estimated for each community or period. Community 1 = Period 1, Community 2 = Period 2. The black points correspond to the mean standard ellipse area for each group while the grey and white boxed areas reflect the 95, 75 and 50% confidence intervals.

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Trends in sympatric otariid populations suggest resource limitations in the Peruvian Humboldt Current System

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Otaria byronia
Arctocephalus australis

ABSTRACT

Sympatric species evolve mechanisms to avoid competition and coexist. In the Humboldt Current System (HCS), populations of South American sea lions (SASL, *Otaria byronia*) and South American fur seals (SAFS, *Arctocephalus australis*) fluctuate mostly due to ENSO events and prey availability. We evaluate population trajectories of Peruvian sympatric otariids and discuss mechanisms for competition and/or resource limitation. For this purpose, we analyzed population trajectories of SASL and SAFS in a sympatric breeding site in Punta San Juan, Peru between 2001 and 2019. Wavelet analysis was used to extract trends and derivatives to estimate rates and turning points. Age-class proportions and biomass times series were constructed from weekly counts and evaluated. Both populations show a growth phase and subsequent decline. SAFS started to decline ~2.25 years before and at a rate 1.5 times faster than SASL. Decrease in juvenile age-class suggests that resource limitation is the main contributing factor for current population decline.

1. Introduction

Understanding how species coexist is an important theme in ecology. Coexistence theory is a framework to understand how competitor traits can maintain species diversity and prevent competitive exclusion, even among similar species in ecologically similar habitats (Chesson and Kuang, 2008). Competition can compromise the fitness of one of the species involved, and may ultimately lead to its exclusion (Pacala and Roughgarden, 1985). Under the resource-utilization niche concept, two species cannot occupy the same ecological niche without exerting strong competition on each other (Schoener, 1974). The Lotka–Volterra competition model states that coexistence of two species is possible when the competitive effect that a species has on another species (interspecific competition) is less than the competitive effect that it has on its own species (intraspecific competition) (Chase et al., 2002; Chesson and Warner, 1981; Schoener, 1983). Furthermore, competitive interactions are known to be stronger between morphologically and phylogenetically closely related sympatric species (Di Bitetti et al., 2009; Loveridge and Macdonald, 2003; Schoener, 1983).

Otariids, composed of fur seals and sea lions, occur in sympatry in a number of upwelling regions in the world and have many similar life-history traits and foraging habits (Bailleul et al., 2005; Dellinger and Trillmich, 1999; Franco-Trecu et al., 2012; Jeglinski et al., 2013; Page et al., 2005; Villegas-Amtmann et al., 2013; Waite et al., 2012). Coexisting species are expected to develop strategies for niche differentiation when resources become scarce, to mitigate the reduction in population attributes, such as growth, survival or fecundity (Begon et al., 2006). The duration of coexistence in sympatric otariid seals is not known, and it is possible that sympatry has resulted from recent population recoveries posterior to the period of commercial sealing (Arnould and Costa, 2006). If sympatry is a result of recent events, it is possible that divergence is not yet evident or that competitive exclusion is now occurring.

In sympatric fur seals and sea lions, past research have found mixed results with regards to competition and segregation. Contrary to the situation in Peru, in many locations fur seal populations are typically larger and they appear to outcompete sea lions (Wickens and York, 1997). Researchers studying sympatric otariids have found trophic segregation, differing foraging strategies and contrasting population trends as mechanisms that explain coexistence (Franco-Trecu et al., 2014; Pablo-Rodríguez et al., 2016; Páez-Rosas et al., 2012). More recent studies demonstrate that intraspecific segregation, driven by

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Peruvian Fur Seals as Archivists of El Niño Southern Oscillation Effects

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Peru's coastal waters are characterized by significant environmental fluctuation due to periodic El Niño- La Niña- Southern Oscillation (ENSO) events. This variability results in ecosystem-wide food web changes which are reflected in the tissues of the Peruvian fur seal (*Arctocephalus australis*). Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) in Peruvian fur seal vibrissae (whiskers) are used to infer temporal primary production and dietary variations in individuals. Sea surface temperature anomaly (SSTA) recordings from the Niño 1+2 Index region captured corresponding ENSO conditions. Fluctuations in $\delta^{15}N$ values were correlated to SSTA records, indicating that ENSO conditions likely impact the diet of these apex predators over time. Anomalous warm phase temperatures corresponded to decreased $\delta^{15}N$ values, whereas cold phase anomalous conditions corresponded to increased $\delta^{15}N$ values, potentially from upwelled, nutrient-rich water. Vibrissae $\delta^{13}C$ values revealed general stability from 2004 to 2012, a moderate decline during 2013 (La Niña conditions) followed by a period of increased values concurrent with the 2014–2016 El Niño event. Both $\delta^{13}C$ and $\delta^{15}N$ values were inversely correlated to each other during the strongest El Niño Southern Oscillation event on record (2014–2016), possibly indicating a decline in production leading to an increase in food web complexity. Lower $\delta^{13}C$ and $\delta^{15}N$ values were exhibited in female compared to male fur seal vibrissae. Findings suggest ENSO conditions influence resource availability, possibly eliciting changes in pinniped foraging behavior as well as food web of the endangered Peruvian fur seal.

Keywords: Peruvian fur seal, stable isotope ratio, El Niño Southern Oscillation (ENSO), $\delta^{13}C$ and $\delta^{15}N$, sea surface temperature anomalies, SECLER

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INTRODUCTION

Large-scale climatic anomalies associated with periodic, alternating El Niño- La Niña-Southern Oscillation (ENSO) conditions are recorded globally through a combination of atmospheric and oceanic teleconnections, resulting in significant, ecosystem-wide impacts (Ropelewski and Halpert, 1987; Trenberth et al., 1998; McPhaden et al., 2006; Sulca et al., 2017). ENSOs are alternating cycles of warm and cold sea surface temperature (SST) in the tropical central and eastern Pacific