Title
Illuminating the Twilight Zone: Diet and Foraging Strategies of a Deep-Sea Predator, the Northern Elephant Seal

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ILLUMINATING THE TWILIGHT ZONE: DIET AND FORAGING STRATEGIES OF A DEEP-SEA PREDATOR, THE NORTHERN ELEPHANT SEAL

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

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in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Chandra Goetsch

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ABSTRACT

Illuminating the twilight zone: Diet and foraging strategies of a deep-sea predator, the northern elephant seal

by

Chandra Goetsch

Marine top predators are often keystone species, having a considerable impact on community structure and ecosystem function due to their large population sizes, wide-ranging behavior, and high energy requirements. To effectively evaluate the susceptibility of marine predators and ecosystems to changing environmental conditions, whether natural or anthropogenic in origin, it is critical to understand predator diet and foraging behavior over space and time. Moreover, intraspecific variation in foraging behavior, including diet specialization and individual foraging strategies, may influence the ability of predator populations to respond to environmental change and may safeguard species during conditions when preferred prey are scarce or unavailable. However, in marine systems, especially the deep ocean, predator trophic dynamics, such as diet, food web interconnections, and predator-prey interactions, are poorly understood and logistically challenging to study. Studies on the diet and foraging strategies for wide-ranging marine predators are often highly localized in space and time and limited to small subsets of the total population. Advances in biologging technology have enabled the documentation of *in situ* foraging behavior, using animal-borne still and video cameras to obtain snap-shots of the diet for marine predators. Yet, while this approach provides invaluable

data on the diet composition for a few individuals over short time-spans, it does not provide comprehensive diet information over broader spatiotemporal scales. In contrast, biochemical methods of diet determination, like fatty acid analysis, allow for the quantification of population diet trends over long time periods, while overcoming well-known biases of traditional methods, like stomach contents and fecal analyses. Combining diet composition data derived from biochemical analysis with concurrent movement and diving data collected by biologging instruments allows for a comprehensive approach in assessing the foraging ecology of deep ocean predators.

My dissertation is an extensive analysis of the diet and foraging behavior, from population-level to individual, of a deep ocean predator, the northern elephant seal (*Mirounga angustirostris*). Female northern elephant seals range across the entire eastern North Pacific, diving deeply into mesopelagic (200-1000 m) and bathpelagic (> 1000 m) zones to forage on prey in the deep acoustic scattering layers. While much is known about elephant seal physiology, diving behavior, and movement patterns, comprehensive information on their at-sea diet has been frustratingly difficult to obtain. In Chapter 1, I used quantitative fatty acid signature analysis (QFASA) to quantify the diet composition of 155 adult female northern elephant seals over five years. This is the first study to show that deep-sea fishes, particularly energy-rich myctophids, are a critical prey resource for northern elephant seals, refuting the long-held view that elephant seals are squid specialists. Moreover, I was able extend the applicability of the QFASA method for species with scant a priori diet data and large variety of potential prey available in their foraging habitat. In Chapter 2, using the

QFASA-derived diet data, I tested for spatiotemporal differences in diet composition. I found evidence of seasonal, spatial, and interannual diet differences for female seals and that these differences are likely driven by the spatiotemporal dynamics of the oxygen minimum zone in the eastern north Pacific and interannual variation in climate phenomena. Finally, in Chapter 3, I quantified vertical foraging strategies for female elephant seals and tested whether those foraging strategies were correlated with diet composition or diet specialization. I found that female seals are generalists in both their vertical foraging behavior and individual diet composition. Further, their flexibility in foraging tactics appears to be tied to in to broad-scale spatiotemporal variation in their deep ocean habitat, reflecting differences in the distribution and availability of their prey. Overall, my dissertation provides critical insights to the trophodynamics of a deep-diving top predator in the North Pacific deep-sea ecosystem.

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When I came to the University of California, Santa Cruz to begin my PhD program, I had no idea what I was getting myself into. It was both a time of endings and beginnings for me. Two months previously, my dad died of lung cancer. He was the one who made this entire journey possible, and he wasn't even able to see me start it. At the same time that I was coping with that loss, my new adventure began in sunny California, pulling me through my grief and into the world of elephant seals, fieldwork, research, and scientific collaboration. As I move forward now, transitioning from graduate student to professional, I would like to reflect upon my journey and thank those who helped me along the way.

I would not have been a graduate student at UCSC, if not for two things: Dr. Dan Costa and the NSF Predoctoral Fellowship. Dan, thank you so much for allowing me to join your lab. You took me on as a student, knowing that I was still green when it came to science. I had little field experience and most of it was working on plants, far different from the northern elephant seals that became my study species. You have taught me many important lessons during my graduate career, both about being a scientist and about life. I learned how to answer big, but testable, questions, how to get people excited about science, and how to write more concisely (still difficult for this English-major!). You gave me the opportunity to pursue an ambitious project, providing resources for me to collect samples in the North Pacific, meet with collaborators in Japan and Canada, attend conferences in Australia, New Zealand, and Europe, and live for four months conducting research in Halifax, Nova Scotia. You never gave up on me, even when I was dealing with severe health issues and dissertation setbacks. You are an incredible mentor and have taught me how to be a better scientist by not allowing my focus on details to overwhelm the “big picture”. Thank you for your guidance and for your unwavering support.

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* * *

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This work was original research by Chandra Goetsch, with contributions from co-authors as minor revisions of text or statistical advice. Supplementary materials from this published material from Goetsch et al. (2018) were integrated into Chapter 1.

DEDICATION

"Somewhere, something incredible is waiting to be known."
— Carl Sagan

To my dad,
who taught me to reach for the stars and never fear uncharted waters

***

"You cannot swim for new horizons until you have
courage to lose sight of the shore."
— William Faulkner

To Mary,
whose strength of spirit taught me to smile through
the ups *and* downs of life's rollercoaster

INTRODUCTION

Broad Context

Many populations of large marine vertebrates are threatened due to fisheries exploitation, incidental take, and habitat degradation (Myers & Worm 2003, Estes et al. 2009, Ferretti et al. 2010, Croxall et al. 2012), which can have cascading effects on ecosystem structure and function (Heithaus et al. 2008, Baum & Worm 2009, Estes et al. 2011, 2016). Our ability to predict how predator populations may respond to environmental change (bottom-up processes) and how population declines may affect ecosystems (top-down processes), is dependent upon understanding predator diet composition and how it changes across individuals, space, and time (Bradshaw et al. 2003, Young et al. 2015). Further, knowledge of individual specialization in diet and foraging strategy is necessary to understand the susceptibility of species to changes in their environment whether such changes are driven by anthropogenic stressors or natural variation (Bolnick *et al.* 2003; Pistevos *et al.* 2011). However, the logistics of characterizing diet for elusive, wide-ranging marine predators are challenging, leading to large data gaps for deep-diving predators that exploit the deep ocean.

The deep ocean, which encompasses the mesopelagic “twilight” (200-1000 m) and bathypelagic “midnight” (> 1000 m) zones, is the earth’s largest ecosystem, an immense volume of over a billion cubic kilometers (Robison 2004, Webb et al. 2010, Ramirez-Llodra et al. 2010). In many ways, we know more about Mars, 54.6 million kilometers from Earth, than we do about the deep ocean. Little is known about the trophic ecology and food web interactions in these remote, hard-to-access depths; yet, with mesopelagic biomass estimated at over 10 billion tons (Irigoien et al. 2014, Rogers 2015), it represents a critical gap in our understanding of these systems. Many top marine predators have large population sizes, wide-ranging migratory behavior, and high energy requirements (Block et al. 2011, Hazen et al 2012, Young et al. 2015). Further, deep ocean predators often demonstrate large vertical excursions, regularly diving more than a kilometer deep and contributing to nutrient and carbon cycling between the surface and the depths (Sutton 2013). Thus, these predators can have a high impact on community structure and function (Estes et al. 2016). Yet, in many cases, we lack even basic knowledge of the spatiotemporal dynamics of population-level diet and predator-prey interactions in the deep ocean, and studies on these issues are often limited to a few individuals and highly localized in space and time (Young et al. 2015).

Recent advances in biologging technology have made it possible to obtain snap-shots of diet and foraging behavior using still and video cameras (Davis et al. 1999, Hooker et al. 2002, Naito et al. 2013, Krause et al. 2015, Volpov et al. 2015). While this approach provides invaluable glimpses of the diet for a few individuals over short time-spans, it does not provide comprehensive diet information over broader spatiotemporal scales (Young et al. 2015). Advances in biochemical techniques of diet determination, including fatty acid analysis, stable isotope analysis, and DNA barcoding, have increased our ability to describe population-level diet and identify consumption trends over longer time periods (Iverson and Bowen 2013, Young

2015). The power of biochemical techniques increases when they are used in conjunction with more traditional methods for determining diet, such as stomach contents and scat analyses, and any available videography data to provide a more nuanced understanding of trophic dynamics at small and large scales (Iverson and Bowen 2013, McInnes et al. 2016, Goetsch et al. 2018).

Biochemical methods also create opportunities to investigate more nuanced questions of foraging behavior within populations, such as individual diet specialization. Ecological research on populations has traditionally focused on 'average' behavior, treating individuals as ecologically equivalent (Roughgarden 1972; Grant & Price 1981; Bolnick *et al.* 2011). However, recently there has been recognition of the prevalence individual variation and its effects on ecosystem dynamics (Bolnick et al. 2003, 2011, Araujo et al. 2011, Tinker et al. 2012, Ceia and Ramos 2015, Rosenblatt et al. 2016). Individual variation in foraging strategy, including diet specialization, may influence a population's ability to adapt (behaviorally or evolutionarily) to changing conditions and increase a population's resilience to environmental change (Bolnick *et al.* 2003; Pistevos *et al.* 2011). Increasing our understanding of individual diet specialization, particularly the trophodynamics of deep ocean predators, is necessary to quantify behavior and prey variability within populations. When combined with predator movement data collected using satellite tags, time depth recorders, and accelerometers, it becomes possible to explore specialization in the foraging strategies of individuals within the population.

Foraging behavior of marine predators is a function of the diverse behaviors and life histories of their prey. Consequently, successful capture of different prey may require different pursuit and capture techniques, resulting in individual foraging strategies for animals that focus on different prey types. Multiple foraging strategies are particularly important for populations of long-lived marine predators, because variability in foraging strategies within the population may serve to buffer the population during periods in which preferred prey are scarce or unavailable (Bolnick *et al.* 2011; Villegas-Amtmann *et al.* 2011). Species with low variability in foraging strategies may be more vulnerable to environmental changes because certain strategies may be differentially affected by changing conditions (Williams *et al.* 2008). Individual specialization in diet and foraging behavior may be expected in populations with high intraspecific competition, since conspecifics foraging on similar prey may decrease the availability in preferred prey, forcing dietary niche expansion (i.e. resource partitioning) (Bolnick *et al.* 2003; Araújo, Bolnick & Layman 2011). Likewise, variability in individual strategies can be expected in populations that feed on patchy prey across a dynamic environment, such as the deep ocean (Levin & Whitfield 1994; Medvinsky *et al.* 2001). Since the foraging behavior of marine predators tracks the abundance and distribution of their prey, which, in turn, are linked to spatiotemporally dynamic oceanographic features like currents and frontal system which aggregate those prey, foraging strategies within a predator population are likely to vary spatially and temporally as well, particularly for wide-ranging predators.

Dissertation Summary

For my dissertation, I described the spatial and temporal diet composition of a deep-diving marine predator, the northern elephant seal (*Mirounga angustirostris*) and quantified the prevalence of foraging strategies within the population. Northern elephant seals exemplify the characteristics that define deep-diving marine predators. Their foraging range encompasses the entire eastern North Pacific basin, spanning 3 distinct mesopelagic biogeographic provinces: the California Current, the North Central Pacific and the Subarctic Pacific (Sutton et al. 2017). In addition, female seals undertake two annual foraging trips: a short trip after breeding during the winter-spring and a long trip after molting during the summer-fall. On these foraging trips, seals dive nearly continuously into the mesopelagic zone (typically > 300-400 m) (LeBoeuf et al. 2000, Robinson et al. 2012), likely targeting the deep scattering layers, where dense aggregations of fishes, squids, and other micronekton (organisms 2-20 cm) provide an abundant prey resource (Robinson et al. 2012, Naito et al. 2013). However, unlike most deep ocean predators, they are accessible to researchers at terrestrial colonies when they haul-out to breed and molt. As endothermic mammals with a high metabolic rate, large body size (300-2000 kg), and large population (~240,000), elephant seals should consume a significant amount of mesopelagic prey and are likely to have top-down influences on the mesopelagic community. Further, movement patterns suggest evidence of individual foraging strategies with regard to their migration route with some females foraging primarily in the Subarctic Pacific or the North Central Pacific, while others remain in the California Current (Simmons *et* *al.* 2007; 2010; Robinson *et al.* 2012). Individual northern elephant seals also demonstrate strong year-to-year route fidelity which may indicate a degree of spatiotemporal stability to these foraging strategies (Simmons 2008; Block *et al.* 2011; Maxwell *et al.* 2012). Multiple studies on the Southern Ocean congener of northern elephant seals, the southern elephant seal (*Mirounga leonina*) have found evidence of individual dietary specialization and foraging strategies (Martin et al. 2011, Huckstadt et al. 2012). While these species forage in vastly different oceanic regions, they have similar morphology, physiology, and life history, so they also may exhibit similar foraging ecology. However, no quantitative analysis has been done for northern elephant seals to identify foraging strategies that are defined by both diet composition and foraging behavior.

In Chapter 1, I used quantitative fatty acid signature analysis (QFASA) to quantify the population-level diet composition and variability of female northern elephant seals and examine the relative importance both proportionally and energetically of mesopelagic fishes and squids in the diet. To accomplish this, I developed a novel application of the QFASA method for cases in which little *a priori* diet data are available for predators that may potentially forage on many prey species. In Chapter 2, I investigated spatiotemporal variability in diet for female elephant seals and related those patterns to oceanographic variability over biogeographic regions and interannual climate phenomena. In Chapter 3, I evaluated whether spatiotemporal variability in diet composition and the environment correlates with specific foraging dive behaviors, and I investigated the prevalence of individual diet specialization within the population. Collectively, my dissertation is a multifaceted investigation of diet and foraging strategies for a deep ocean predator, providing data and insight that is critical for understanding both the overall functioning of deep ocean ecosystems and possible responses of those ecosystems to current and future environmental change.

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CHAPTER 1:

Energy-Rich Mesopelagic Fishes Revealed as a Critical Prey Resource for a Deep-Diving Predator using Quantitative Fatty Acid Signature Analysis

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1.1 Abstract

Understanding the diet of deep-diving predators can provide essential insight to the trophic structure of the mesopelagic ecosystem. Comprehensive population-level diet estimates are exceptionally difficult to obtain for elusive marine predators due to the logistical challenges involved in observing their feeding behavior and collecting samples for traditional stomach content or fecal analyses. We used quantitative fatty acid signature analysis (QFASA) to estimate the diet composition of a wide-ranging mesopelagic predator, the northern elephant seal (*Mirounga angustirostris*) across five years. To implement QFASA, we first compiled a library of prey fatty acid (FA) profiles from the mesopelagic eastern North Pacific. Given the scarcity of *a priori* diet data for northern elephant seals, our prey library was necessarily large to encompass the range of potential prey in their foraging habitat. However, statistical constraints limit the number of prey species that can be included in the prey library to the number of dietary FAs in the analysis. Exceeding that limit could produce non-unique diet estimates (i.e. multiple diet estimates fit the data equally well). Consequently, we developed a novel *ad-hoc* method to identify which prey were

unlikely to contribute to diet and could, therefore, be excluded from the final QFASA model. The model results suggest that seals predominantly consumed small mesopelagic fishes, including myctophids (lanternfishes) and bathylagids (deep sea smelts), while non-migrating mesopelagic squids comprised a third of their diet, substantially less than suggested by previous studies. Our results revealed that mesopelagic fishes, particularly energy-rich myctophids, were a critical prey resource, refuting the long-held view that elephant seals are squid specialists.

1.2 Introduction

The deep-sea ecosystem is the largest on the planet with an estimated biomass between 7 and 10 billion metric tons (Kaartvedt et al., 2012, Irigoien et al., 2014). The main contributor to this biomass is found in the deep scattering layers of the mesopelagic (200-1,000 m) and the bathypelagic (1,000-4,000 m) depth zones (Sutton, 2013; Davison et al., 2015). The deep scattering layers are composed of dense aggregations of fishes, squids, and other micronekton (organisms 2-20 cm) that provide an abundant prey resource to those deep-diving predators able to access them (MacLeod et al., 2003; Harvey et al., 2013; Howey et al., 2016). Despite the ecological significance of the deep ocean, it has been understudied, with scant information for many species, communities, and life histories, as well as limited understanding of the complex trophic interactions occurring therein (Webb et al., 2010; St. John et al., 2016;). In many cases, the only information available for deep-sea species are reports of their existence (e.g. *Stemonosudis rothschildi*, a deep sea barracudina) with little to no description of their biology, let alone their position or importance in the food web (Drazen and Sutton, 2017; Priede, 2017).

Understanding the diet of mesopelagic predators like the northern elephant seal (*Mirounga angustirostris*) can provide valuable insights into the deep ocean food web (Benoit-Bird and Lawson, 2016; Benoit-Bird et al., 2016). Yet, obtaining dietary information on these elusive predators is notoriously difficult, limiting our knowledge to that gained from stomach contents (from dead seals or stomach lavage) and fecal studies (from enemas or scat) (Antonelis et al., 1987; Staniland et al., 2003). Further, samples obtained from elephant seals on shore are biased toward hard parts that resist digestion and toward their last meal, as these animals may have been fasting for days or weeks since leaving their primary foraging areas. Improved technology in the form of animal-borne biologging cameras have provided tantalizing glimpses of feeding behavior and diet of marine predators but are limited to a few individuals over short timescales (Davis et al., 1999; Naito et al., 2013; Krause et al., 2015; Volpov et al., 2015). Diet studies on other mesopelagic predators, such as sperm whales (*Physeter macrocephalus*) and beaked whales (F. Ziphiidae), have been limited to a few stranded individuals or those taken either in commercial whaling or as fishery by-catch (Walker et al., 2002; Ohizumi et al., 2003; Harvey et al., 2013)

Northern elephant seals utilize the entire eastern North Pacific Ocean, foraging for nine to ten months of the year and diving continuously into the mesopelagic zone (LeBoeuf et al., 2000; Robinson et al., 2012), where they feed almost exclusively below 400 m (Naito et al., 2013). Stomach content analyses have suggested that adult elephant seal diet is dominated by pelagic squids (Huey, 1930; Condit and Le Boeuf, 1984; Antonelis et al., 1987; 1994). In contrast, juvenile elephant seals appear to have a more diverse diet, mostly feeding over the continental shelf on a range of intertidal and neritic organisms (Sinclair, 1994). Recent studies using jaw motion analysis and videography suggest that small mesopelagic nekton, such as lanternfishes (F. Myctophidae), could be an important component of adult seal diet (Naito et al., 2013; 2017), but such studies are either indirect (i.e. jaw motion event frequency as a proxy for prey size) or subject to the same biases as stomach content analyses. Though mesopelagic fishes have not been confirmed in the diet of northern elephant seals, multiple lines of evidence indicate that their Southern Ocean congeners, southern elephant seals (*Mirounga leonina*), feed predominately on deep ocean fishes (Bradshaw et al., 2003; Cherel et al., 2008; Banks et al., 2014). Since northern and southern elephant seals display similar morphology, life histories, foraging dive behavior, and migration strategies, it is reasonable to hypothesize that northern elephant seals may also consume more fishes than indicated by stomach contents studies.

Biomolecular techniques, such as fatty acid (FA) analysis, stable isotope analysis, and DNA barcoding, have become standard in determining the diet of cryptic marine predators (Boecklen et al., 2011; Bowen and Iverson, 2012; Ramos and González-Solís, 2012). These techniques complement traditional methods of diet determination (i.e. stomach content and fecal analyses) by overcoming the well-known biases of those methods toward prey with indigestible hard parts and against small, soft-bodied prey (Harvey and Antonelis, 1994; Bowen, 2011). Stomach contents and fecal analyses are also limited in that they only provide a snapshot of the most recent meal. However, biochemical methods also have constraints. Stable isotope analysis is excellent for determining the trophic position of both prey and predators, but obtaining species-level estimates of trophic level and diet composition has been problematic due to difficulties with prey signature resolution, baseline isotopic values, and trophic discrimination factors (Hobson et al., 1996; Newsome et al., 2010). Conversely, DNA barcoding provides diet estimates that are highly resolved to species level since it is not dependent on undigested remains; yet, it is limited by what is in the digestive tract at the time of sample collection (Tollit et al., 2009; Bowen and Iverson, 2012). FA analysis is able to provide diet information that is resolved to species level and is integrated over longer timescales of weeks to months (Budge et al., 2004; 2006; Iverson et al., 2004; Bowen and Iverson, 2012).

Quantitative fatty acid signature analysis (QFASA) has become a widespread method of diet determination for diverse marine predators, such as sea birds, seals, sea lions, fish, and polar bears (Thiemann et al., 2008; Tucker et al., 2009; Meynier et al., 2010; Budge et al., 2012; Conners et al., 2018). The basic concept of FA analysis is that, molecularly speaking, “you are what you eat,” albeit with some predictable metabolic processing. Reliable species-specific calibration coefficients that quantify the metabolic changes in FAs from ingestion to tissue deposition are crucial for accurate QFASA diet estimates (Rosen and Tollit, 2012; Bromaghin et al., 2016a). Using calibration coefficients and a subset of dietary FAs common to both predator and prey, the QFASA model finds which combination of prey minimizes the distance between prey and predator FA signatures (Iverson et al., 2004; Budge et al., 2006). Typically, studies utilizing QFASA have used small to moderate prey libraries (<30 prey species); however, QFASA can effectively differentiate among larger numbers (~30-50) of potential prey species (Piché et al., 2010; Conners et al., 2018). This capability is important for determining the diets of mesopelagic predators, because the deep scattering layer is a highly interconnected food web where many prey species exploit similar resources.

Our study evaluated the efficacy of QFASA to quantify the diet of free-ranging northern elephant seals. Limited knowledge of elephant seal diet necessitated the use of a large library of potential prey species. However, having more prey species in the library than FAs in the analysis produces non-unique diet estimates, so we developed a novel method to reduce our prey library. We estimated the diets of adult female northern elephant seals resolved to prey species and functional groups, using the QFASA model and the reduced prey library. Furthermore, we used a combination of diagnostic analyses to evaluate QFASA model performance and quantify model error. Ultimately, we used our diet results to examine the hypothesis that mesopelagic fishes contribute significantly to northern elephant seal diet at the population-level, based on inferences from their diving behavior during their foraging migrations and recent video data.

1.3 Materials and Methods

1.3.1 Ethics Statement

The protocol for animal use was approved by the Institutional Animal Care and Use Committee (IACUC) of the University of California Santa Cruz and the Japan Ministry of Agriculture, Forestry and Fisheries. Elephant seal sampling was authorized by National Marine Fisheries Service permits 14636 and 14535 and conducted in accordance with the guidelines set forth by the ethics committee of the Society of Marine Mammalogy and the Canadian Council for Animal Care. Prey sampling on the vessel T/S Oshoro-maru was conducted under the United States Department of State, Bureau of Oceans and International Environmental and Scientific Affairs permit U2012-013.

1.3.2 Field Methods

Elephant seal sampling

Adult female northern elephant seals (n = 155) were instrumented with Argos or GPS satellite transmitters (Wildlife Computers, Redmond, WA; SPOT4, SPOT5, MK10-AF) at Año Nuevo State Reserve, San Mateo, CA, USA (37°59’N, 122°169’W) during January-March for the short (post-breeding) and May-June for the long (post-molt) foraging trips in 2005-2006 and 2009-2012. Seals were sedated for instrument attachment and recovery using established protocols (see Robinson et al., 2012). During handling, we collected a full depth blubber biopsy (5-7 days after the seal’s return) from the seal’s lateral side, approximately 13 cm anterior of the hip, using a 6mm biopsy punch. Female seals typically lose up to 40% of their body mass, mainly fat stores, when they fast on land during breeding and molting (Crocker et al., 2014). When they return to sea for their foraging migrations, they gain mass consistently and rapidly to replenish fat stores in the blubber, so blubber sampled upon their return should be reflective of diet. The blubber samples were divided into inner and outer halves with each half placed into a glass vial with a Teflon-lined cap with 3 ml of 2:1 chloroform:methanol (v/v) and 0.01% BHT. Previous studies have shown that elephant seal blubber is stratified with the outer layer being more structural in nature for streamlining and thermoregulation, whereas the inner layer is more metabolically active and, thus, a better indicator of diet (Best et al., 2003; Strandberg et al., 2008; Crocker et al., 2014). Vials were kept frozen at -20°C until analysis.

Collecting the prey library

We collected mesopelagic fish and squid from onboard the research vessel T/S Oshoro-maru (Hokkaido University) along a north-south transect through the Subarctic Pacific and North Central Pacific (also called the Transition Zone) mesopelagic biogeographic regions (Sutton et al., 2017). This transect was determined at sea by the real-time Argos locations of 16 concurrently tracked female elephant seals (Figure 1.1), and sampling was conducted at depths where elephant seals routinely forage (Robinson et al., 2012). Potential prey samples were collected during four midwater trawls (10 mm mesh at the cod end, 314 m^2 net mouth, and tow speed of 3.5-4 knots; Saijo et al., 2017), two during the day (maximum depths of 730 and 720 m) and two at night (both at 650 m). Automatic squid jigs (surface to 650 m, Towa-denki Seisakusho Co. Ltd) were also used to collect samples of active, vertically migrating squids. Additionally, one *Stigmatoteuthis dofleini*, a mesopelagic squid, was sampled opportunistically (May 22, 2014) from a commercial fishery vessel off the coast of Oregon-Washington. All samples were identified to the lowest possible taxonomic level (Food Habits Lab, National Marine Mammal Laboratory, Seattle, WA) and measurements of mass and length (standard length for fishes, dorsal mantle length for squids) were recorded (Tables 1.1 and 1.2). In total, we collected 865 samples, representing 62 mesopelagic genera (50 fish and 12 squid species). Prey samples were kept whole at -20°C until analysis.

1.3.3 Prey Classification

We compiled information on prey distribution, behavior, and physiology from existing literature (Supplemental Table 1), and, subsequently, classified prey by taxonomic group, behavioral and ecological traits, and primary distribution. We defined 11 functional groups (2 squid groups and 9 fish groups; Tables 1.1, 1.2, and Supplemental Table 1).

The two squid functional groups were classified by diel migration behavior, body composition, and hunting strategy: (1) vertically migrating, muscular squids (hereafter migrating squids) and (2) meso-bathypelagic, neutrally buoyant squids (hereafter non-migrating squids). The migrating squids show strong diel migration from the mesopelagic or bathypelagic zone during the day into the epipelagic at night in pursuit of prey. They are active hunters with a thick, muscular mantle and include commercially important species, such as *Ommastrephes bartramii*, *Onychoteuthis borealijaponica*, and *Gonatopsis borealis*. Other species in this functional group are

Gonatus berryi, *Abraliopsis felis* and *Berryteuthis anonychus*; the latter two form dense schools in the upper epipelagic zone at night. The non-migrating squids are neutrally buoyant, sit-and-wait hunters with no mantle musculature (*Chiroteuthis* c.f. *calyx*, *Galiteuthis phyllura*, *Taonius borealis*) to weak mantle musculature (*S. dofleini* and *Octopoteuthis deletron*). They remain in the meso- and bathypelagic depths and are rarely, if ever, found in the epipelagic zone. A possible exception to this is *C. calyx* which has been classified in some studies as a midwater migrator (Roper and Young, 1975), since it undergoes ontogenic migration (i.e. depth distribution becomes deeper with age). However, adult *C. calyx* typically do not migrate into the epipelagic zone (Burford et al., 2014).

The largest component of our prey library consisted of fishes from the mesopelagic deep scattering layers. We grouped fishes based on diel migratory strategy and diet (Supplemental Table 1). Vertical migrator categories included surface migrators (species that migrate within 20 m of the surface at night), midwater migrators (migrate at night to the epipelagic, but remain below 20 m), bathy-midwater migrators (migrate from the bathypelagic into the mesopelagic at night), and non-migrators (no diel pattern, but can be vertically mobile, and typically remain in the same depth zone). Diet guilds included zooplanktivores, gelativores, piscivorous micronektivores (hereafter piscivores), macro-crustacean micronektivores (hereafter crustacivores), and generalists (Drazen and Sutton, 2017). The zooplanktivore guild consumes mainly tiny crustaceans like nauplii, copepods, ostracods, and euphausids, and includes the families Myctophidae (lanternfishes), Sternoptychidae (hatchet fishes), Melamphidae (bigscales) and Notosudidae (wary fishes). The gelativore guild feeds primarily on medusae, ctenophores, salps, and other gelatinous species. Gelativores include the Bathylagidae (deep sea smelts), Opisthoproctidae (barreleyes and spookfishes), and Platytroctidae (tubeshoulders) families. The piscivore guild includes the Paralepididae (barracudinas), Stomiidae (dragonfishes), Gempylidae (snake mackerels) and Scopelarchidae (pearleyes). Crustacivores mainly feed on midwater shrimps and larger mysids and are represented by the Howellidae (oceanic basslets), Melanonidae, and Nemichthyidae (snipe eels). Our final reduced prey library (see Prey Library Reduction section) had fish species representing nine functional groups: (1) surface migrating zooplanktivores, (2) surface migrating piscivores, (3) midwater migrating zooplanktivores, (4) midwater migrating piscivores, (5) bathy-midwater migrating gelativores, (6) non-migrating zooplanktivores, (7) non-migrating gelativores, (8) non-migrating piscivores, and (9) non-migrating generalists.

1.3.4 Lipid Analysis

Lipid extraction

Given that small, fragile otoliths from mesopelagic fish species would not be preserved in elephant seal digestive tracts, we had limited *a priori* evidence to determine which fish species to retain in our final prey library. Analyzing all our collected fish samples for lipids was not possible; thus, we limited our analysis to species with 3 or more intact individuals (n = 39, table 1.2). In contrast, squid beaks, being indigestible, are well-preserved in elephant seal stomachs (Harvey and

Antonelis, 1994). Since mesopelagic squid are notoriously difficult to obtain (Hoving et al., 2014), all intact squids (n = 11, Table 1.1) reported in previous stomach content studies were retained, regardless of sample size. Elephant seals use suction feeding to consume prey whole, so we homogenized each whole prey item separately, then combined mass-specific aliquots from each individual into a species-homogenate (n = 3-15 individuals/homogenate). Three to five 1.5 g subsamples (replicates) were taken from each prey-homogenate, except when there was a single representative individual (Conners et al., 2018). Using a prey-homogenate gives an average prey FA profile but eliminates data on within-species variation between individuals in FA composition; however, within-species variability is likely small compared to between-species variation (Budge et al., 2002). Following a modified Folch extraction method, we isolated lipids from the prey-homogenates and blubber (n = 155 seals), using 2:1 chloroform:methanol (v/v; Folch et al., 1957; Budge et al., 2006).

Gas chromatography and FA profiles

We used an acidic methanol (H_2SO_4/MeOH) transesterification process (Hilditch method) to transform lipids to fatty acid methyl esters (FAME), increasing their volatility for gas chromatography (details in Budge et al., 2006). FAME composition was quantified using a Scion 436 gas chromatograph (GC) on a split injection setting with a silica column coated with 50% cyanopropyl polysiloxane (0.25 μm film thickness; J&W DB-23, Agilent Technologies, Folsom, CA, USA, operational setting details in Budge et al. 2006). Peaks in the output chromatographs were identified using standard FA mixtures (Nu-Check Prep, Elysian, MN, USA) and integration software (Varian Galaxie Workstation). When necessary, we used gas chromatography mass spectrometry (GC-MS) with electron ionization and identical GC conditions to determine FA structures. To account for small shifts in retention time, each chromatograph was manually adjusted for accuracy in peak identification and integration of peak areas. To generate a FA profile, peak areas of constituent FAs (n = 76) were reported as mass percent of total FAs and a mean was taken of replicate injections (2 per sample). We eliminated extremely low FAs (< 0.2%), unless that FA was at least partially sourced from diet (i.e. minimally biosynthesized; Budge et al., 2006), giving a FA profile of 55 FAs.

Fatty acid subset

We defined the dietary FA subset to only include FAs that are sourced from diet (n = 46). In addition, we excluded 3 FAs that have been included as dietary FAs in previous QFASA studies for other species. FA 16:4n-3 was excluded because its calibration coefficient was zero, meaning it was not present in the captive seal. FAs 18:1n-11 and 20:1n-11 had calibration coefficients indicating likely *in vivo* short-chaining of 22:1n-11, making them unreliable as dietary tracers in this study (Cooper et al., 2006). This provided a final dietary subset of 43 FAs (Table 1.3). The 43 FA proportions in each profile were then rescaled (i.e. normalized) to sum to one (Iverson et al., 2004; Budge et al., 2006).

1.3.5 QFASA Diagnostics

Unless otherwise stated, all analyses were conducted in R v.3.4.1 (R Core Team, www.R-project.org). All QFASA modeling and diagnostics were done with the

QFASAR package v.1.2.0 (Bromaghin, 2017). For all model runs, we converted prey FA values to the predator optimization space (Bromaghin et al., 2015), and used the Aitchison distance measure (Bromaghin et al., 2015; 2016b).

Calculation of calibration coefficients

We calculated calibration coefficients to account for *in vivo* fatty acid modification due to predator metabolism (Iverson et al., 2004; Budge et al., 2006), using data from a captive adult female elephant seal and her known diet. We collected a blubber sample and a random selection of prey from her long-term diet, 18 individuals each of capelin and herring. The captive seal's diet proportions of ~70% herring and 30% capelin for the year prior to sampling were used as weights to calculate combined diet FA values. For each FA, $k = 1, \ldots, 55$, we calculated every possible combination of herring FA proportion ($\boldsymbol{H}_i$), $i = 1, \ldots, 18$, and capelin FA proportion ($\boldsymbol{C}_j$), $j = 1, \ldots, 18$, resulting in 324 combinations. The ratio of the FA proportion from the captive seal blubber to the corresponding FA proportion from each of the 324 diet combinations was calculated, and the 10% trimmed mean of those ratios was taken as the estimated calibration coefficient for that FA (Table 1.3):

$$c^k = \ trimmed\ mean\left(\frac{[\text{FA proportion of seal}]_k}{\left[(0.7\boldsymbol{H}_i +\ 0.3\boldsymbol{C}_j)\right]_k}\right)$$

We compared our elephant seal calibration coefficients to those reported from formal captive feeding trials of four other phocids: monk seals (*Neomonachus schauinslandi*), grey seals (*Halichoerus grypus*), harbor seals (*Phoca vitulina*), and harp seals (*Pagophilus groenlandicus*).

Predator FA values outside the range of the prey

If seal FA values fall outside the range of prey FA values after converting the prey values to the predator optimization space, this may indicate incorrect calibration coefficients and/or an incomplete prey library (Bromaghin et al., 2016b). We explored our data for indications of these problems using the function pred_beyond_prey (R package QFASAR) to find the proportion of seal FA values that were outside the range of the prey values (Bromaghin, 2017).

Prey library reduction

QFASA requires that the number of FAs in the analysis equal or exceed the number of potential prey in the prey library. Including more prey than FAs generates diet estimates that are non-unique (i.e. multiple diet estimates provide an equally good fit to the predator profile data; Bromaghin et al., 2013; Phillips et al., 2014). Most previous studies have dealt with this problem by pooling prey species with similar FA profiles into a common prey type prior to QFASA, reducing the number of prey types in the model to below the number of dietary FAs (Piché et al., 2010; Iverson et al., 2011; Bromaghin et al., 2013; Haynes et al., 2015). Conversely, Meynier et al. (2010) took a *post-hoc* approach, estimating diet using each individual prey animal as a distinct prey type and subsequently pooling those prey type estimates into their respective species groups. Neither approach is ideal: the *a priori* approach could potentially result in pooled prey types with mean FA profiles that do not resemble actual prey, while the *post-hoc* approach does not guarantee that the pooled diet estimates will be unique. Since we had more prey in the library (n = 51) than dietary FAs (n = 43), we needed either to select one of these approaches or find an alternate method to decrease the number of prey types prior to modeling.

All the squid in our library, except for *B. anonychus*, were previously documented in seal stomach contents (Condit and Le Boeuf, 1984; Antonelis et al., 1987; 1994) and were retained in the prey library, but we had no previous elephant seal diet data to justify excluding any mesopelagic fish species. The *a priori* pooling approach was a viable option, since it would avoid the problem of non-unique diet estimates. However, we only considered the Meynier et al. (2010) *post-hoc* approach as a last resort because there does not appear to be an accepted method of testing the uniqueness of the pooled diets. To assess whether we could justifiably use the *a priori* approach, we analyzed the prey FA profiles with non-metric dimensional scaling (NMDS) and leave-one-prey-out (LOPO) analysis.

Non-metric dimensional scaling

To visualize the similarity/dissimilarity among the FA profiles of prey species, we used a 3-dimensional NMDS with the Aitchison distance measure for compositional data (Aitchison, 1986). We looked for the presence of natural clusters that would allow us to combine fish species into a smaller number of prey types. We found a clear separation between fish and squid FA profiles (Figure 1.2). However, since we lacked data on within-species variation in prey FA profiles, we were unable to assess the degree of overlap among species or ecological groups (i.e. migrator type, diet guild, and mesopelagic biogeographic region). Although there were some species that were close to each other within ecological groups, there were no distinct, clearly defined clusters based on ecological characteristics (Figure A2.1). Thus, we were not confident that the degree of similarity within ecological groups was enough to justify pooling those species.

LOPO analysis

Leave-one-prey-out (LOPO) analysis is a cross-validation technique used to assess the ability of the QFASA model to distinguish between prey profiles (i.e. degree of "prey confounding"). When prey FA profiles are highly similar (high prey confounding), model performance is decreased and there is less certainty in the diet estimates (Bromaghin et al., 2015; 2016b). Also, high prey confounding may indicate potential clusters of prey that could be grouped, allowing us to reduce the prey library. In our study, the LOPO results may be somewhat biased toward the removed prey profile, since, by design, there is low variation between the homogenate FA profiles. However, any consequential misidentifications would still be evident and informative. While two prey species (subadult *O. borealijaponica* and *W. telescopa*) showed some degree of confounding, no other prey species did (Figure A2.2). Thus, based on both the NMDS and LOPO analyses, we determined that pooling species into a smaller number of prey types prior to QFASA was not justified.

Drop core prey (DCP) analysis

To solve our "more prey than FAs" problem, we developed a novel method to exclude non-contributing prey species and create a reduced prey library. We could not simply exclude prey species that were not present in the original diet estimates generated with the complete prey library (51 species), because those prey might have had larger contributions to diet in other equally viable estimates. Hence, excluding them could have resulted in removing prey from the library that actually were present in elephant seal diet. We reasoned that if we dropped apparently important core prey from the library (DCP) and forced the model to generate new diet estimates, any prey that were never present in any of the DCP diet estimates would (1) truly be absent from the diet and (2) be isolated from the non-uniqueness problem and, therefore, could justifiably be excluded permanently.

We identified 36 core prey (present in at least one seal's diet at proportions > 0.001) in the original diet estimates. Each core prey was then iteratively removed from the library (50 prey) and the QFASA model was rerun. We compared the objective functions, or the values of the minimized Aitchison distance, between the new DCP diet estimates and the original diet estimates, and we considered the DCP estimates equally valid if the objective functions were less than or equal to those from the complete prey library. The majority of the DCP diet estimates fit the data as well as or better than the original diet estimates, confirming that the results using the full prey library were not unique. Finally, we identified 10 prey species that were never present in the diet across all the DCP diet estimates (36 core prey × 155 seals = 5,580 diet estimates): *A. felis*, *Abraliopsis infans*, *Howella sherborni*, *Ichthyococcus elongatus*, *Lampadena yaquinae*, *Melanonus zugmayeri*, *Nannobrachium regale*, *O. deletron*, *Pseudobathylagus milleri*, and *Sigmops gracilis*. We excluded these prey from the library, resulting in a final reduced prey library of 41 prey, which numbers less than the 43 dietary FAs.

1.3.6 Quantitative Fatty Acid Signature Analysis

Final diet estimation

Final diets were estimated for each elephant seal (n = 155) with the dietary FA subset and the reduced prey library. The raw diet output (% lipid mass from each prey type) was then adjusted for the lipid content of the prey (Supplemental Table 2) to give the final diet estimates (% biomass of each prey species). To quantify generalized elephant seal diet and the relative importance of specific prey, we calculated three traditional diet metrics: (1) mean occurrence (%) of prey *i* in the population-level diet with standard deviation, (2) maximum occurrence (%) that prey *i* occurred in any individual seal's diet, and (3) frequency of occurrence (%) of prey *i* across all seal diets (number of diets with prey *i* > 0.01% divided by the total number of seal diets).

Quantifying QFASA model error: Diet simulations

To further assess QFASA model performance, we employed a strategy utilizing simulated diets. We used a semi-random, partially supervised method to construct 550 simulated diets per prey species, p_i (n = 41), using the Dirichlet distribution, the multivariate case of the beta distribution (0-1) for compositional data. To ensure that we had a sample of simulated diets representing the range of all possible seal diets, we assigned prey *i* a vector of proportional values with the sequence $p_{i(1\text{-}11)}$ (0.01, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and 0.99). The composition of the remainder of each simulated diet (1 - *p*) was randomly generated from the Dirichlet distribution (α = 0.25). The simulated diets (n = 22,550) were used to generate pseudo-predator FA profiles (Bromaghin, 2015), which were then evaluated by the QFASA model to determine an estimated diet for each simulated diet. For each prey species, we plotted the prey proportion in the known simulated diet against the proportion in the model-generated estimated diet (Figure A2.3). We also calculated the difference between the simulated diet proportion of prey *i* and its corresponding estimated diet proportion as a measure of model error. Due to the lack of variation in the homogenized diet replicates for each species, we had no basis on which to simulate variance in the pseudo-predator FA profiles. Consequently, our simulations likely underestimated the model error, giving results for a best case scenario. Regardless, the simulations provided a comparison of how well the model estimates the presence of each prey item in the diet relative to the others.

1.4 Results

We report the mean FA profile (mass percent of total FAs) from 155 female elephant seals (± SD) with respective calibration coefficients in Table 1.3. The mean FA profiles of the complete prey library (51 species) with prey lipid content (percent of wet weight) is provided in Supplemental Table 2.

1.4.1 QFASA Diagnostics

Reliability of the calibration coefficients

The elephant seal calibration coefficients fell within the range reported for other phocids (Figure 1.3). The FA 20:1n-11 had a calibration coefficient (8.06) that was higher than other phocids (grey seal: 3.42, harbor seal: 1.87, harp seal: 2.83, and monk seal: 3.36). Also, the calibration coefficient of FA 18:1n-11 (12.98) was higher for the elephant seal than all other phocids except for grey seals (15.04). Our captive elephant seal was likely chain shortening FA 22:1n-11, resulting in elevated levels of 18:1n-11 and 20:1n-11 which were not attributed to diet alone (Cooper et al. 2006). However, we could not be certain if our calibration coefficients accurately reflect chain shortening. For this reason, we did not use these FAs as dietary tracers and excluded them from the dietary FA set. Overall, only 1.5% of seals had any FA values beyond the range of prey FA values (Figure 4). For most of the dietary FAs, we found only a low number of seals had FA values outside the range of the prey values (Figure 1.4). Only four dietary FAs, 16:0 (10.8%), 17:1a (21.2%), 16:3n-4 (13.5%), and 18:1n-7 (8.3%), resulted in more than 5% of all seals having FA proportions that fell outside the range of the prey.

Degree of prey confounding

The LOPO analysis showed good discrimination among prey FA profiles by the QFASA model (i.e. a low degree of prey confounding). Most species that were eventually dropped from the model (*A. felis*, *A. infans*, *H. sherborni*, *I. elongatus*, *L. yaquinae*, *M. zugmayeri*, *P. milleri*, and *S. gracilis*) were almost never misidentified as other species, with nearly 100% of their diet estimate attributed to themselves (Figure A2.2). The remaining two dropped prey, *N. regale* and *O. deletron*, still had high proportions correctly attributed: 77% and 84%, respectively. The myctophid, *N. regale*, was most often misattributed to *A. infans* (7%), which was also dropped from the model, and *M. lugubris* (5%). *O. deletron* was most often misassigned to other squids (gonatid squid species: *B. anonychus*, *G. berryi*, and *G. borealis*, and the mesopelagic squid *S. dofleini*), all < 3%. Only two species besides *N. regale* were self-attributed < 80%: subadult *O. borealijaponica* (54%) and *W. telescopa* (77%). Subadult *O. borealijaponica* was most often misidentified as the squid species *O. bartramii* (27%), *T. borealis* (7%), *O. deletron* (5%), and adult *O. borealijaponica* (3%). The spookfish *W. telescopa* was most often misidentified as the gelativore, *M. bericoides* (6%), or the two barracudinas, *S. rothschildi* (4%) and *L. ringens* (4%).

Simulations and prey-specific error

Diet simulations confirmed that the QFASA model reliably estimated the simulated diets (Figure 1.5A and Figure A2.3). The highest underestimation error was found in the piscivorous fishes *Benthalbella dentata* (0.8%) and *Diplospinus multistriatus* (0.6%) across the range of possible proportions in the diet (0-100%). The highest overestimation error was for the squids *B. anonychus* and *S. dofleini* (both 0.5%). The variation in error for all species was also low (range -0.27% to 2.6% with the aforementioned species having the highest variation in error (*B. dentata*: -2.6 to 0.9%, *D. multistriatus*: -2.1 to 0.8%, *B. anonychus* and *S. dofleini*: -0.8 to 1.7%) Several species were estimated nearly perfectly with error close to 0% (*G. borealis*, *C.* c.f. *calyx*, *T. borealis*, and *T. macropus*). *C.* c.f. *calyx* and *G. borealis* also had the lowest variation in error (both -0.3%). The two functional groups with the highest average simulation error were the non-migrating piscivore group (underestimated by 1.4%) and the migrating squid group (overestimated by 1%). The functional group with the lowest simulation error was the bathy-midwater migrating gelativore group (underestimated by 0.08%). The other functional groups were over- or underestimated by less than 0.9%.

1.4.2 Diet Characterization

Of the 41 species in our reduced prey library, 33 (25 fishes and 8 squids, Figure 1.5B) were present in the diet of at least one seal. Combined mesopelagic fishes dominated the population-level diet of elephant seals at 63.7%; although the average diet had a high proportion of non-migrating squids, total squids only had a mean occurrence of 36.3% (Table 1.4, Figure 1.5B). Surface migrating zooplanktivores were the most common fish group (24.5% mean occurrence and 98.7% of diets), followed by the non-migrating piscivore group (17.8% mean occurrence and 93.5% of diets), and the non-migrating gelativore group (11.7% mean occurrence and 82.6% of diets). Within the surface migrating fish group, *Tarletonbeania taylori* and *Electrona risso*, both myctophids, were the most common species (9.8% and 5.9% mean occurrence), but *E. risso* was present in more seal diets than *T. taylori* (83.2% vs. 70.3%). Nearly all the species of myctophids represented in the average diet were in the surface migrating zooplanktivore group. The non-migrating zooplanktivore and bathy-midwater migrating gelativore groups had low mean occurrences (2.5% and 4%, respectively), but they were both present in a large proportion of seal diets (91.6% and 86.5%)

The most common species from the non-migrating piscivore group were *S. rothschildi* and *Chauliodus macouni*, (9.9% and 6.5% occurrence, respectively). *S. rothschildi* was present in 87.7% of all diets and *C. macouni* in 56.8% of diets.

Gelativores, both migrating and non-migrating, were important prey (15.7% combined mean occurrence). Of these, the Bathylagidae (*Melanolagus bericoides, Lipolagus ochotensis*, and *Bathylagus pacificus*, combined mean occurrence 13.9%) was the most common family. In the non-migrating gelativore group, *M. bericoides* was the most common species (9.9% occurrence in 73.5% of diets). *L.s ochotensis* (bathy-midwater gelativore) and *Melamphaes lugubris* (non-migrating zooplanktivore) only occurred in low mean proportions (3% and 2.5% occurrence, respectively), but were present a high number of diets (82.6% and 91.6% of diets, respectively). Some species were only important in a few seals' diets: *W. telescopa* (non-migrating gelativore), adult *O. borealijaponica* (migrating squid), and *B. pacificus* (midwater migrating gelativore) had maximum occurrences of 34%, 28.6%, and 24.8% respectively.

Meso-bathypelagic non-migrating squid was the most represented functional group (33.2%) in mean population-level diet, occurring in 100% of seal diets (Table 1.4, Figure 1.5B). The maximum occurrence of this group in a single diet was 59%. *C.* c. f. *calyx* was the dominant representative of the non-migrating squid group and was also the most frequently occurring species in the population-level diet (26.6% mean occurrence in 99.4% of diets). *S. dofleini* was the next most common non-migrating squid species (6.2% mean occurrence and 41.3% of diets). The maximum occurrences of *C.* c. f. *calyx* and *S. dofleini* were 45.8% and 43.8%, respectively. Vertically migrating squids only occurred in small proportions (3.1%) but were present in over half of the seals' diets and one seal had just under 30% of its diet as this functional group.

1.5 Discussion

1.5.1 Diet of Female Northern Elephant Seals

Female northern elephant seals overwhelmingly consumed energy-dense, meso- and bathypelagic fishes contrary to previous stomach content studies which determined squids to be the dominant prey (Antonelis et al., 1987; 1994). Moreover, these fishes comprised a substantial proportion of their diet over long time periods of months to years. Further, our findings are consistent with recent observations from head-mounted cameras showing that northern elephant seals more frequently feed on fishes than squids (Naito et al., 2017). In addition, our diet estimates for northern elephant seals now align with similar results from multiple studies showing the importance of mesopelagic fishes in the diets of their Antarctic congener, the southern elephant seal (Bradshaw et al., 2003; Cherel, 2008; Banks et al., 2014). Our study highlights the importance of using complementary methods of diet determination like QFASA to reveal critical "hidden" prey species that cannot be adequately detected by traditional stomach contents analysis alone.

The two fish groups which dominated the diet were surface migrating zooplanktivores and non-migrating piscivores. Surface migrating zooplanktivores were the largest fish component accounting for a quarter of the average diet for elephant seals, and were represented by 5 species from the family Myctophidae

(*Diaphus perspicillatus, Diaphus theta, E. risso, Symbolophorus californiensis, T. taylori*), the most abundant family in the deep scattering layers (Catul et al. 2011; Irigoien et al., 2014). These myctophids have high lipid content, making them one of the most energetically-rich prey resources (i.e. *E. risso* ~ 12,100 kJ kg^{-1}) available to elephant seals (Sinclair et al., 2015). Within the non-migrating piscivores, the viperfish *C. macouni* and the barracudina *S. rothschildi* were the most commonly consumed. The family Stomiidae is the most abundant group of fish predators in the mesopelagic (Choy et al., 2013), with *C. macouni* being the most abundant species of this group caught in our trawls (Saijo et al., 2017). *C. macouni* is energetically-rich (~4,500 kJ kg^{-1}), but still only has around half as much energy as most myctophids (Sinclair et al., 2015). *C. macouni* employs a sit-and-wait hunting strategy (Drazen and Sutton, 2017), which may make them easier to capture. In contrast, barracudinas are small, fast-moving hunters, with a lower gross energy content than Stomiidae due to their smaller size (Spitz et al., 2010). This suggests they would be an unfavorable prey item for elephant seals, since chasing and capturing a single barracudina would be energetically expensive. However, it is hypothesized that barracudinas form large, dense schools (Harry, 1953; Fukui and Ozawa, 2004). Given that elephant seals employ suction feeding and rapid jaw movements, they can likely capture many barracudinas at a time, increasing net energy gain compared to capturing one alone.

Gelativores of the family Bathylagidae (deep-sea smelts), both in the bathy-midwater migrating and the non-migrating gelativore groups, were also important prey species for elephant seals. This was especially true for some individuals, for whom bathylagids represented over a third of their total diet. In addition, bathylagids were identified in recent video footage from free-ranging feeding female elephant seals (Naito et al., 2013; 2017). Despite being less energy-dense than myctophids (Sinclair et al., 2015), bathylagids are the second most abundant group of mesopelagic fishes in the eastern North Pacific (Brodeur and Yamamura, 2005), which supports their prevalence in elephant seal diet. The non-migrating gelativore, *Icosteus aenigmaticus*, has been identified in video footage as a species consumed on particularly deep dives (>900 m, Naito et al., 2017). However, this species was not included in our prey library, so we cannot comment on the hypothesis of Naito et al. (2017) that it may be an important dietary item for larger, deeper diving females.

Although female northern elephant seals predominately consumed fishes, non-migrating squids were still a key component in the diet of nearly all seals. Non-migrating squids are less energy dense (~2,000 and 4,000 kJ kg^{-1}) than the other functional groups in our study (Sinclair et al., 2015); however, they are generally slow moving, sit-and-wait hunters which may make them easy targets for seals. In contrast to previous studies, we found that *C.* c.f. *calyx* was the most dominant species followed by *S. dofleini*. Antonelis et al. (1987, 1994) found that *O. deletron* was the most common squid in the diet of adult females, followed by two histioteuthid squids, *Histioteuthis heteropsis* and *S. dofleini*. The discrepancies between our results and those of Antonelis et al. (1987, 1994) may be due to seals foraging in the California Current as they return to the rookery, since *O. deletron* is more associated with the California Current than *C. calyx,* and squid beak retention in the stomach is biased toward more recently consumed squids. Another possibility could be interannual differences in the distribution and abundance of squid species between their study period and ours.

Vertically migrating squids, while highly abundant in the eastern North Pacific, were not a major contributor to the diet of elephant seals, similar to the findings of Antonelis et al. (1987, 1994). Chasing and capturing these fast-moving, agile squids would increase energy expenditure of foraging seals, considerably reducing the net energy gain from this prey type. Since vertically migrating squids are less energy-dense (~3,000 – 6,000 kJ kg^{-1}) than many mesopelagic fishes (~10,000 – 15,000 kJ kg^{-1}, Sinclair et al. 2015), they may be less favorable prey despite their larger size, explaining their relative infrequency in elephant seal diet. However, there were a few individual seals that consumed higher proportions of migrating squids (e.g. ~30%), suggesting some individuals may specialize on this prey type.

According to optimal foraging theory, predators should prefer prey items that maximize their net energy gain (Charnov, 1976; Pyke, 1984; Stephens and Krebs, 1986), accounting for both prey energy content as well as the energy and time expended while foraging. Mesopelagic fishes have an average energy content (gram/wet weight) up to an order of magnitude higher than that of squids (Sinclair et al., 2015), so there may be an energetic advantage to this prey type, if seals can capture them efficiently. In addition, mesopelagic squids can be distributed more sparsely compared to fishes (Hoving et al., 2011), potentially making them difficult to catch frequently or in large numbers. Jaw motion analysis provides additional evidence that elephant seals often feed on many, small prey rather than single, large prey, despite the differences in gross energy content (Naito et al., 2013, Y. Naito & H. Louis, unpublished data).

The estimated diets in this study, with seals consuming both migrating and non-migrating fishes, are also consistent with the documented foraging behavior of female northern elephant seals observed with time depth recorders. Female seals display a marked day/night pattern in their foraging dives (mean day: ~620 m, mean night: ~450 m), as well as a diurnal bimodal dive distribution (modes, 385 m and 641 m; Robinson et al., 2012; Naito et al., 2017), which mirrors the vertical distribution of the deep scattering layers elephant seals forage upon (Frost and McCrone, 1979; Klevjer et al., 2016; Proud et al., 2018). Migrating mesopelagic fishes, like myctophids, rise from depths of approximately 300 to 700 m during the day to less than 20 m at night (Brodeur and Yamamura, 2005; Watanabe et al., 1999). Since adult northern elephant seals typically do not feed at depths shallower than 400 m (Naito et al., 2013), it is likely that they are consuming these myctophids at deeper depths during the day and during twilight as they move upward in the water column. Yet, even at night many seals exhibit deep foraging dives that range from 650 m to greater than 1,000 m (Naito et al., 2013; 2017), which is consistent with the presence of non-migrating species in their diets.

As a large endothermic predator with high prey requirements, northern elephant seals may exert top-down effects on the mesopelagic ecosystem. Thus, determining the diet of this top predator is a critical first step to unraveling complex food web interactions in the mesopelagic community of the North Pacific. Recent energetic studies using doubly-labeled water have shown that, on average, an adult female ingests approximately 64-141 MJ per day (Maresh et al., 2015). Based on the energetic content of a mesopelagic squid (*Octopoteuthis deletron*, 3.08 MJ kg^{-1}) and myctophid fish (Myctophidae, 0.02 kg, 11.88 MJ kg^{-1}) and assuming a simple monophagus diet, Maresh (2014) calculated that a single female elephant seal would need to consume ~5,600 kg of squids or 1,600 kg of fishes per year from the North Pacific mesopelagic ecosystem. The current population estimate for northern elephant seals is ~240,000 (Lowry et al., 2014), with adult females representing around 22% of the population or ~53,000 individuals (Lowry et al., 2014). Scaled up to the population level, female seals are likely extracting ~286 million kg (286 thousand metric tons) of squids or 82 million kg (82 thousand metric tons) of fishes per year, and that may be a conservative estimate. However, the paucity of data on the standing biomass of mesopelagic fauna makes it difficult to assess whether this level of prey extraction by elephant seals would result in any appreciable top-down effects on the North Pacific mesopelagic ecosystem.

Our prey library did not include two species, Pacific hake (*Merluccius productus* or Pacific whiting) and pelagic red crab (*Pleuroncodes planipes*), that have previously been reported as important prey items for elephant seals (Antonelis et al., 1987). Pacific hake is most likely not a significant component of diet of most female seals, as its distribution is confined largely to the demersal regions of the continental shelf and slope (Agostini et al., 2006). Female seals do not spend a significant portion of their foraging trips utilizing the continental shelf and slope regions (Robinson et al., 2012; Naito et al., 2013), so it is more likely that they opportunistically feed on hake near shore as they return to the rookery for breeding or molting (Sinclair, 1994). Pelagic red crab was only observed in the diet of seals during the 1984 El Niño (Antonelis et al., 1987; 1994) and was likely a unique event. Future diet analyses could focus on expanding the prey library to include species from the California Current biogeographic province and from the coastal shelf regions, which would facilitate diet estimation for seals that exclusively forage in those areas.

1.5.2 Evaluating QFASA

We developed a novel method, the drop core prey (DCP) analysis, to exclude prey species from the library based on quantitative criteria in order to resolve the problem of non-unique diet estimates. A non-arbitrary method of decreasing the number of prey was critical, as we lacked *a priori* information on which mesopelagic fish were likely to be in the elephant seal diet. Our method iteratively eliminated core prey species from the complete prey library, and subsequently identified whether QFASA could estimate equally-valid diets with the reduced prey library. From this, we inferred that any prey species that failed to appear in any of DCP diets, was truly absent from the diet. We permanently removed those absent prey species to obtain a final reduced prey library. The DCP analysis extends the applicability of QFASA to predators with access to many potential prey, where available data are insufficient to narrow those options.

NMDS ordination allowed us to see the relations of prey species in FA space, and, importantly, showed distinct separation between fish and squid FA profiles. Squids can be problematic in QFASA models (Conners et al., 2018), because most of their lipids are found in the large digestive gland, rather than other tissues like the mantle (Phillips et al., 2002). This results in a FA profile that may strongly resemble that of recently consumed prey present in the digestive gland. Since squids consume deep scattering layer fishes and other squids, they are more prone to be misidentified as their own prey. This problem is not limited to QFASA, but also occurs in stomach contents analyses, where it cannot be verified whether some prey remains were eaten by the predator of interest or if they were in the stomach of one of the prey items (Harvey and Antonelis, 1994; Bowen and Iverson, 2012). However, the separation between fishes and squids in the NMDS analysis combined with low error in the diet simulations suggests that this may not be a major source of error in our model.

The LOPO analysis and the diet simulations provided complementary information, which, when used together, allowed us to evaluate the ability of QFASA to distinguish among the species in our prey library. Several species (e.g. *G. borealis* and *T. macropus*) that had nearly zero estimated error in the simulations were occasionally misidentified as other species in the LOPO analysis. *G. borealis* was misidentified, though rarely, as *C. calyx* and *O. deletron*, whereas *T. macropus* was occasionally misidentified as *B. dentata* and *M. lugubris*. Consequently, we are confident that while the QFASA error for these species is likely not zero, it is still very low. Furthermore, the two species that had the highest rates of misidentification in the LOPO analysis (subadult *O. borealijaponica* and *W. telescopa*) had low error in the simulations, increasing our confidence in their estimates. No species with extremely low error in the simulations was self-attributed at < 87% in the LOPO analysis. When examined separately these methods were both likely to underestimate model error; however, interpreting them together allowed us to more accurately assess model performance in the absence of within-species variation in FA profiles.

Care must be taken in the selection of calibration coefficients because they represent the highest source of error and bias in QFASA modeling (Rosen and Tollit, 2012; Bromaghin et al., 2016b). Fortunately, we had access to a single captive adult female elephant seal and were able to compare her known diet to her FA profile. This provided a non-traditional method of calculating the elephant seal calibration coefficients. We found that our calibration coefficients were comparable to those of other phocids in formal captive feeding studies (Iverson et al., 2004; 2011; Rosen and Tollit, 2012). Therefore, while not a substitute for the traditional method, ours is a reasonable alternative for obtaining species-specific calibration coefficients when conducting a full captive feeding trial is not an option.

1.5.3 Conclusions

Using QFASA, we obtained the first quantitative estimates of the population-level diet of adult northern elephant seals, one of the top predators in the eastern North Pacific. Our findings change the prevalent view of northern elephant seals as specializing on squids, and, instead, confirm a broad diet dominated by deep-sea fishes. Myctophids and bathylagids are both critical prey groups that elephant seals exploit on their deep foraging dives into the deep scattering layers of the mesopelagic zone. Additionally, though still undeniably an important prey type, non-migrating mesopelagic squids only account for about a third of the population-level diet, far less than previously thought. Since non-migrating squids are also common prey items for sperm whales, fur seals, and beaked whales feeding in the eastern North Pacific (MacLeod et al., 2003; Gallo-Reynoso and Esperón-Rodríguez, 2013; Harvey et al., 2013), our study provides further evidence that these squids play an important role in the mesopelagic food web. Given the magnitude of mesopelagic biomass consumed by northern elephant seals, this study provides essential information on food web structure and function for the difficult to observe deep-ocean ecosystem of the North Pacific.

1.6 References

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Table 1.1 Squid species (n = 11; 1 species has 2 age classes) in complete prey library. Mean mantle length ± standard deviation (cm ± SD) and mean mass (g ± SD) for the individual prey items (n) in the homogenate sample. Whole prey were homogenized and mass-specific aliquots of each individual were combined into a species-homogenate.

Family *Species*	n	Mantle Length (cm) mean ± SD	Mass (g) mean ± SD	Homogenate replicates	Functional Group
Chiroteuthidae - Swordtail squids					
Chiroteuthis c. f. *calyx*	2	19.25 ± 14.64	48.65 ± 38.68	1	Non-migrating
Cranchiidae - Glass squids					
Galiteuthis phyllura	3	43.27 ± 11.7	86.83 ± 61.15	3	Non-migrating
Taonius borealis	2	38.8 ± 7.5	168.45 ± 43.77	1	Non-migrating
Enoploteuthidae - Armed squids					
Abraliopsis felis	14	4.51 ± 0.72	4.37 ± 1.11	1	Vertically migrating
Gonatidae - Armhook squids					
Berryteuthis anonychus	6	9.32 ± 0.48	25.47 ± 4.5	3	Vertically migrating
Gonatopsis borealis	15	23.62 ± 2.23	424.52 ± 126.17	3	Vertically migrating
Gonatus berryi	1	19.7	102.9	1	Vertically migrating
Histioteuthidae - Cock-eyed squids					
Stigmatoteuthis dofleini	1	12.0	565.0	2	Non-migrating
Octopoteuthidae - Octopus squids					
Octopoteuthis deletron	3	14.2 ± 0.7	128.2 ± 7.26	3	Non-migrating
Ommastrephidae - Flying squids					
Ommastrephes bartramii	9	41.4 ± 2.85	2,104 ± 669.11	3	Vertically migrating
Onychoteuthidae – Hooked squids					
Onychoteuthis borealijaponica (adult)	10	30.98 ± 2.12	679.6 ± 123.95	3	Vertically migrating
Onychoteuthis borealijaponica (subadult)	10	21.94 ± 2.86	264.07 ± 95.04	3	Vertically migrating

Table 1.2 Fish species (n = 39) in complete prey library. Mean standard length ± standard deviation (cm ± SD) and mean mass (g ± SD) for the individual prey items (n) in the homogenate sample. Whole prey were homogenized and mass-specific aliquots of each individual were combined into a species-homogenate.

Family *Species*	n	Standard Length (cm) mean ± SD	Mass (g) mean ± SD	Homogenate replicates	Functional Group
Anoplogastridae - Fangtooths					
Anoplogaster cornuta	5	10.6 ± 2.34	42.63 ± 25.47	3	Non-migrating generalist
Bathylagidae - Deep Sea Smelts					
Bathylagus pacificus	15	14.36 ± 1.11	20.67 ± 4.49	3	Bathy-midwater gelativore
Lipolagus ochotensis	15	7.74 ± 0.88	3.85 ± 1.36	3	Bathy-midwater gelativore
Melanolagus bericoides	5	13 ± 1.87	12.46 ± 5.78	3	Non-migrating gelativore
Pseudobathylagus milleri	8	13.55 ± 1.65	22.49 ± 6.71	5	Bathy-midwater gelativore
Gempylidae - Snake Mackerels					
Diplospinus multistriatus	7	46.37 ± 8.13	59.47 ± 54.05	3	Midwater migrating piscivore
Gonostomatidae - Bristlemouths					
Sigmops gracilis	15	10.71 ± 0.82	3.34 ± 1.02	3	Non-migrating zooplanktivore
Howellidae - Oceanic basslets					
Howella sherborni	5	7.78 ± 0.59	10.1 ± 3.39	3	Bathy-midwater crustacivore
Melamphaidae - Bigscales					
Melamphaes lugubris	8	8.16 ± 0.68	16.86 ± 3.91	3	Non-migrating zooplanktivore
Poromitra crassiceps	3	10.37 ± 1.02	21.13 ± 6.96	3	Non-migrating gelativore
Melanonidae - Melanonids					
Melanonus zugmayeri	5	16.46 ± 1.63	25.96 ± 5.76	3	Non-migrating crustacivore
Myctophidae - Lanternfishes					
Diaphus theta	15	7.54 ± 0.6	8.43 ± 2.1	3	Surface migrating zooplanktivore
Diaphus gigas	5	8.62 ± 0.36	10.28 ± 1.47	3	Midwater migrating zooplanktivore
Diaphus perspicillatus	15	7.73 ± 0.62	7.83 ± 2.47	3	Surface migrating zooplanktivore
Electrona risso	15	6.91 ± 0.47	7.68 ± 0.97	3	Surface migrating zooplanktivore
Lampadena urophaos	2	10.6 ± 0.28	16.25 ± 7.42	3	Midwater migrating zooplanktivore
Lampadena yaquinae	8	12.16 ± 1.02	24.81 ± 6.92	3	Bathy-midwater zooplanktivore
Lampanyctus jordani	15	9.11 ± 0.37	8.9 ± 1.1	3	Non-migrating zooplanktivore
Nannobrachium regale	4	17.78 ± 2.18	54.58 ± 16.16	3	Non-migrating piscivore
Stenobrachius leucopsarus	15	9.93 ± 0.37	14.78 ± 1.64	3	Midwater migrating zooplanktivore
Stenobrachius nannochir	15	10.18 ± 0.52	11.34 ± 1.4	3	Non-migrating zooplanktivore

Table 1.2 (*Continued*) Fish species (n = 39) in complete prey library. Mean standard length ± standard deviation (cm ± SD) and mean mass (g ± SD) for the individual prey items (n) in the homogenate sample. Whole prey were homogenized and mass-specific aliquots of each individual were combined into a species-homogenate.

Family *Species*	n	Standard Length (cm) mean ± SD	Mass (g) mean ± SD	Homogenate replicates	Functional Group
Myctophidae - Lanternfishes					
Symbolophorus californiensis	4	7.43 ± 0.5	5.15 ± 0.87	3	Surface migrating zooplanktivore
Tarletonbeania taylori	15	4.29 ± 0.28	0.85 ± 0.16	3	Surface migrating zooplanktivore
Nemichthyidae - Snipe Eels					
Avocettina infans	14	47.57 ± 9.14	9.61 ± 4.99	5	Non-migrating crustacivore
Notosudidae -Waryfishes					
Scopelosaurus harryi	4	13.55 ± 3.24	10.55 ± 7.97	4	Non-migrating zooplanktivore
Opisthoproctidae - Barreleyes/Spookfishes					
Macropinna microstoma	3	12.7 ± 1.13	40.1 ± 9.53	3	Non-migrating gelativore
Winteria telescopa	4	8.68 ± 0.61	17.63 ± 3.64	3	Non-migrating gelativore
Paralepididae - Barracudinas					
Lestidiops ringes	3	18 ± 0.42	5.55 ± 0.07	5	Non-migrating piscivore
Stemonosudis rothschildi	5	11.14 ± 0.93	1.98 ± 0.63	3	Non-migrating piscivore
Phosichthyidae - Lightfish					
Ichthyococcus elongatus	7	7.79 ± 0.99	5.19 ± 2.26	3	Midwater migrating zooplanktivore
Platytroctidae - Tubeshoulders					
Sagamichthys abei	15	19.57 ± 3.1	70.08 ± 27.41	5	Non-migrating gelativore
Scopelarchidae - Pearleyes					
Benthabella dentata	15	19.83 ± 1.91	52.8 ± 17.31	3	Non-migrating piscivore
Sternoptychidae - Hatchetfish					
Argyropelecus aculeatus	11	4.56 ± 0.61	2.65 ± 0.9	5	Midwater migrating zooplanktivore
Argyropelecus sladeni	15	3.95 ± 0.44	1.83 ± 0.6	5	Midwater migrating zooplanktivore
Stomiidae - Barbeled Dragonfish					
Aristostomias scintillans	3	38.03 ± 2.71	91.87 ± 23.91	3	Midwater migrating piscivore
Chauliodus macouni	15	22.78 ± 1.31	49.1 ± 10.34	3	Non-migrating piscivore
Idiacanthes antrostomas	5	32.7 ± 3.22	10.74 ± 3.66	3	Non-migrating piscivore
Opostomias mitsuii	5	24.74 ± 5.84	78.82 ± 51.18	3	Non-migrating piscivore
Tactostoma macropus	10	31.52 ± 3.09	49.33 ± 15.5	3	Surface migrating piscivore

Table 1.3 Mean fatty acid values ± standard deviation (% ± SD) and calibration coefficients for female northern elephant seals (n = 155).

Fatty Acid	Percent ± SD	Calibration coefficient	Fatty Acid	Percent ± SD	Calibration coefficient
14:0*	2.88 ± 0.49	0.96	**18:3n-6***	0.1 ± 0.02	1.21
14:1n-5*	0.11 ± 0.03	5.74	**18:3n-4***	0.23 ± 0.03	2.51
***i*-15:0**	0.14 ± 0.02	0.99	**18:3n-3***	0.39 ± 0.07	0.83
15:0*	0.33 ± 0.04	0.68	**18:3n-1***	0.21 ± 0.02	0.6
16:0*	10.41 ± 1.48	0.53	**18:4n-3***	0.27 ± 0.09	0.44
16:1n-11	0.39 ± 0.06	0.82	**18:4n-1***	0.02 ± 0.02	0.72
16:1n-9	0.35 ± 0.04	1.93	**20:0**	0.21 ± 0.03	1.23
16:1n-7*	4.04 ± 0.79	0.98	**20:1n-11**	11.69 ± 2.1	8.06
16:1n-5*	0.2 ± 0.03	0.51	**20:1n-9***	7.03 ± 0.78	1.53
17:1a*[†]	0.12 ± 0.03	0.45	**20:1n-7***	0.49 ± 0.2	1.51
***i*-17:0**	0.19 ± 0.05	0.68	**20:2n-9**	0.16 ± 0.03	1.82
16:2n-6*	0.01 ± 0.01	0.65	**20:2n-6***	0.42 ± 0.04	1.35
17:1b*[†]	0.57 ± 0.07	0.97	**20:3n-6***	0.1 ± 0.01	1.77
16:2n-4*	0.08 ± 0.04	0.71	**20:4n-6***	0.56 ± 0.07	0.52
17:0*	0.32 ± 0.04	0.9	**20:3n-3***	0.15 ± 0.02	1.18
Phytanic Acid	0.05 ± 0.04	0.7	**20:4n-3***	0.45 ± 0.08	1.22
16:3n-4*	0.03 ± 0.01	0.47	**20:5n-3***	1.53 ± 0.62	0.23
17:1*	0.45 ± 0.07	1.08	**22:1n-11***	9.56 ± 2.51	0.59
16:4n-3	0.08 ± 0.11	0	**22:1n-9***	1.17 ± 0.26	0.88
16:4n-1*	0.01 ± 0.02	0.33	**22:1n-7***	0.15 ± 0.04	0.59
18:0*	2.82 ± 0.29	1.14	**21:5n-3***	0.11 ± 0.03	0.82
18:1n-13	0.4 ± 0.15	1.28	**22:4n-6***	0.18 ± 0.05	2.42
18:1n-11	1.81 ± 0.69	12.98	**22:5n-6***	0.18 ± 0.03	0.93
18:1n-9*	26.93 ± 3.63	2.31	**22:4n-3***	0.07 ± 0.02	1.57
18:1n-7*	3.17 ± 0.66	1.26	**22:5n-3**	1.33 ± 0.34	3.44
18:1n-5*	0.45 ± 0.05	0.77	**22:6n-3***	4.87 ± 0.81	0.42
18:2n-6*	1.25 ± 0.17	1.57	**24:1***	0.69 ± 0.19	0.42
18:2n-4*	0.06 ± 0.02	0.75			

* Dietary fatty acid

† 17 C fatty acids with one double bond and a methyl branch; locations of the double bond and methyl branch are unknown, but differ between 17:1a and 17:1b.

Table 1.4 Mean dietary composition for northern elephant seals as determined by QFASA using the reduced prey library (n = 41 prey types): occurrence (% ± SD) in the population-level elephant seal diet, maximum occurrence (%) in any individual seal's diet, and frequency of occurrence (%) across all seal diets (n = 155).

Reduced Prey Library	Occurrence in Diet (%) mean ± SD	Occurrence in Diet (%) individual maximum	Frequency of Occurrence (%) across all seal diets
Non-migrating Squids	**33.2 ± 9.6**	**59**	**100**
C. c. f. calyx	26.6 ± 7.6	45.8	99.4
G. phyllura	0.4 ± 1.5	9.9	9
T. borealis	0 ± 0	0	0
S. dofleini	6.2 ± 10.2	43.8	41.3
Vertically Migrating Squids	**3.1 ± 5.1**	**29**	**52.9**
B. anonychus	0.9 ± 2	11.8	29
G. berryi	0 ± 0	0	0
G. borealis	0 ± 0.4	4.7	0.6
O. bartramii	0.5 ± 1.7	13.1	14.2
Adult *O. borealijaponica*	1.6 ± 4.1	28.6	27.1
Subadult *O. borealijaponica*	0.1 ± 1.2	15.4	0.6
Surface Migrating Zooplanktivores	**24.5 ± 13**	**59.5**	**98.7**
D. perspicillatus	4.4 ± 6.9	30.8	43.2
D. theta	4.3 ± 7.7	41.2	36.1
E. risso	5.9 ± 9.6	59.5	83.2
S. californiensis	0.1 ± 0.6	6.4	5.2
T. taylori	9.8 ± 9.8	38.2	70.3
Surface Migrating Piscivores	**0 ± 0.2**	**1.6**	**1.3**
T. macropus	0 ± 0.2	1.6	1.3
Midwater Migrating Zooplanktivores	**0 ± 0.5**	**6.5**	**1.3**
D. gigas	0 ± 0	0	0
L. urophaos	0 ± 0.5	6.5	0.6
S. leucopsarus	0 ± 0	0	0
A. aculeatus	0 ± 0	0	0
A. sladeni	0 ± 0	0.6	0.6

Table 1.4 (*Continued*) Mean dietary composition for northern elephant seals as determined by QFASA using the reduced prey library (n = 41 prey types): occurrence (% ± SD) in the population-level elephant seal diet, maximum occurrence (%) in any individual seal's diet, and frequency of occurrence (%) across all seal diets (n = 155).

Reduced Prey Library	Occurrence in Diet (%) mean ± SD	Occurrence in Diet (%) individual maximum	Frequency of Occurrence (%) across all seal diets
Midwater Migrating Piscivores	**3 ± 5.3**	**23.7**	**36.8**
A. scintillans	3 ± 5.3	23.7	36.8
D. multistriatus	0 ± 0	0	0
Bathy-Midwater Migrating Gelativores	**4 ± 4.5**	**27.5**	**86.5**
B. pacificus	1 ± 3.9	24.8	9.7
L. ochotensis	3 ± 2.5	9.2	82.6
Non-migrating Zooplanktivores	**2.5 ± 1.7**	**7.2**	**91.6**
L. jordani	0 ± 0	0	0
S. nannochir	0 ± 0.5	5.9	0.6
M. lugubris	2.5 ± 1.7	7	91.6
S. harryi	0 ± 0.2	2.6	1.3
Non-migrating Gelativores	**11.7 ± 9.7**	**42.4**	**82.6**
M. bericoides	9.9 ± 9.6	42.4	73.5
P. crassiceps	0 ± 0	0	0
M. microstoma	0.1 ± 0.8	10.1	1.9
W. telescopa	1.7 ± 5.4	34	14.8
S. abei	0 ± 0.4	5.2	0.6
Non-migrating Piscivores	**17.8 ± 12.6**	**72.3**	**93.5**
L. ringens	0.2 ± 1.3	8.4	3.2
S. rothschildi	9.9 ± 6.5	26.6	87.7
B. dentata	0 ± 0.2	1.6	3.9
C. macouni	6.5 ± 10.2	52.1	56.8
I. antrostomas	1.1 ± 2.4	14	29
O. mitsuii	0 ± 0.3	4.2	0.6
Non-migrating Generalist	**0 ± 0.4**	**5.1**	**0.6**
A. cornuta	0 ± 0.4	5.1	0.6

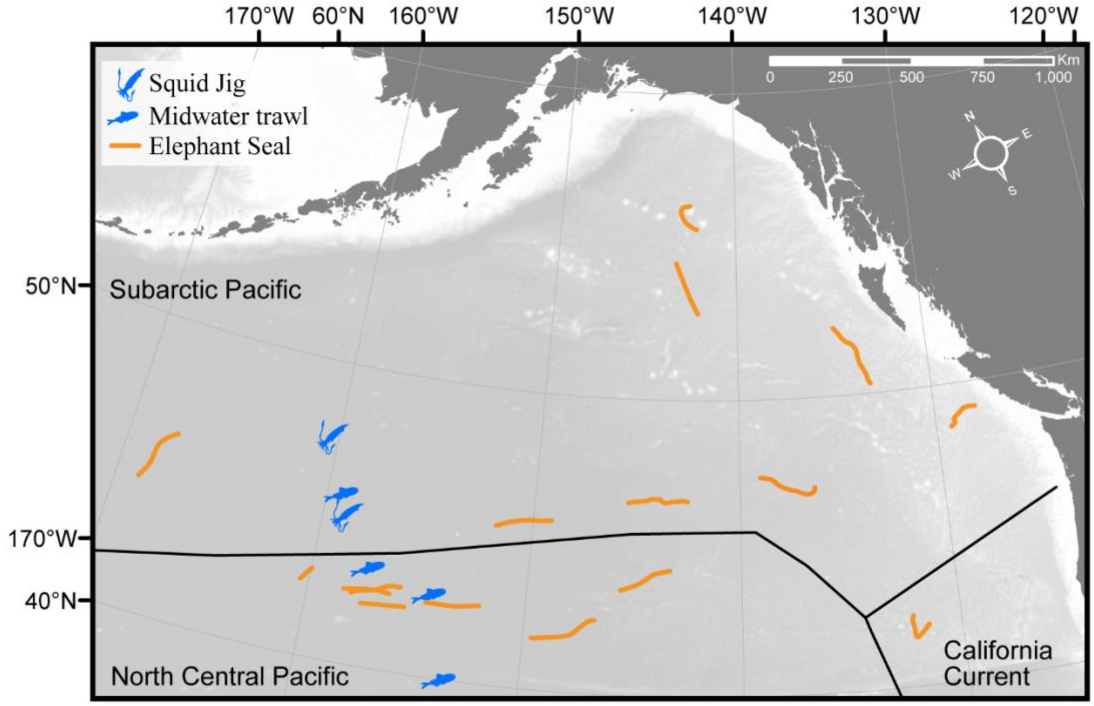

Figure 1.1 Locations of the midwater trawls (4) and squid jigs (2) where samples were collected to establish the prey library during July 7-9, 2012. Sampling locations span the boundary between the Subarctic Pacific and North Central Pacific mesopelagic biogeographic provinces and overlap with the concurrent foraging paths (orange lines) of 16 satellite-tagged, free-ranging female northern elephant seals (tracks shown are a subset of the 155 total seals analyzed for diet composition).

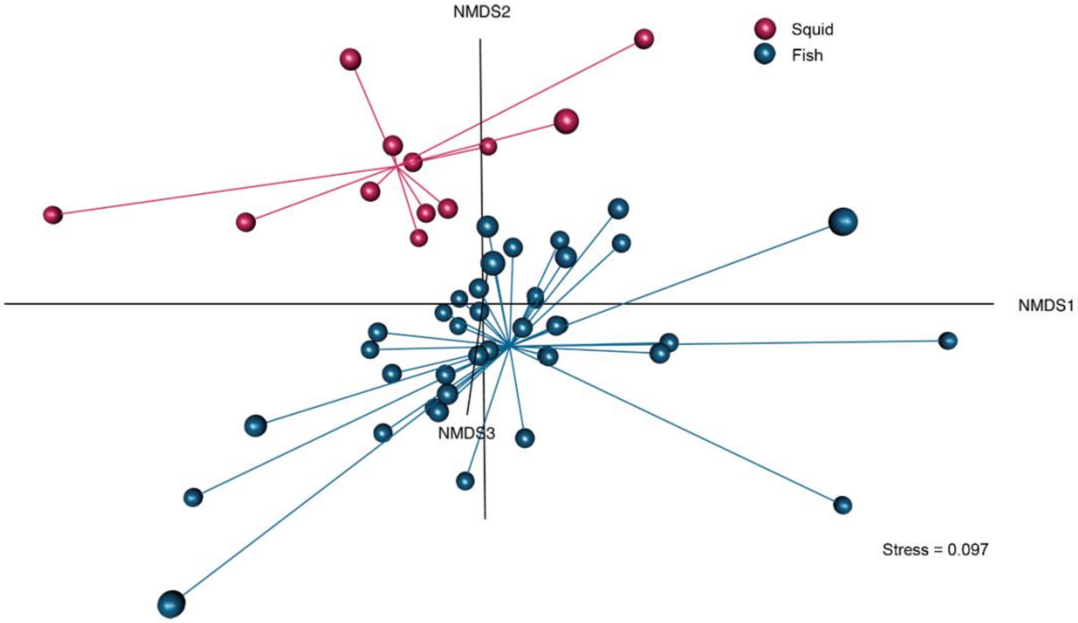

Figure 1.2 Three-dimensional NMDS analysis of prey dietary fatty acid profiles using the complete prey library (n = 51 prey types). Red spheres are squids (n = 12), while blue spheres are fishes (n = 39). Squid fatty acid profiles cluster distinctly from fish fatty acid profiles. Size of the sphere indicates position on the z-axis (NMDS3), larger spheres are closer and smaller spheres are farther away.

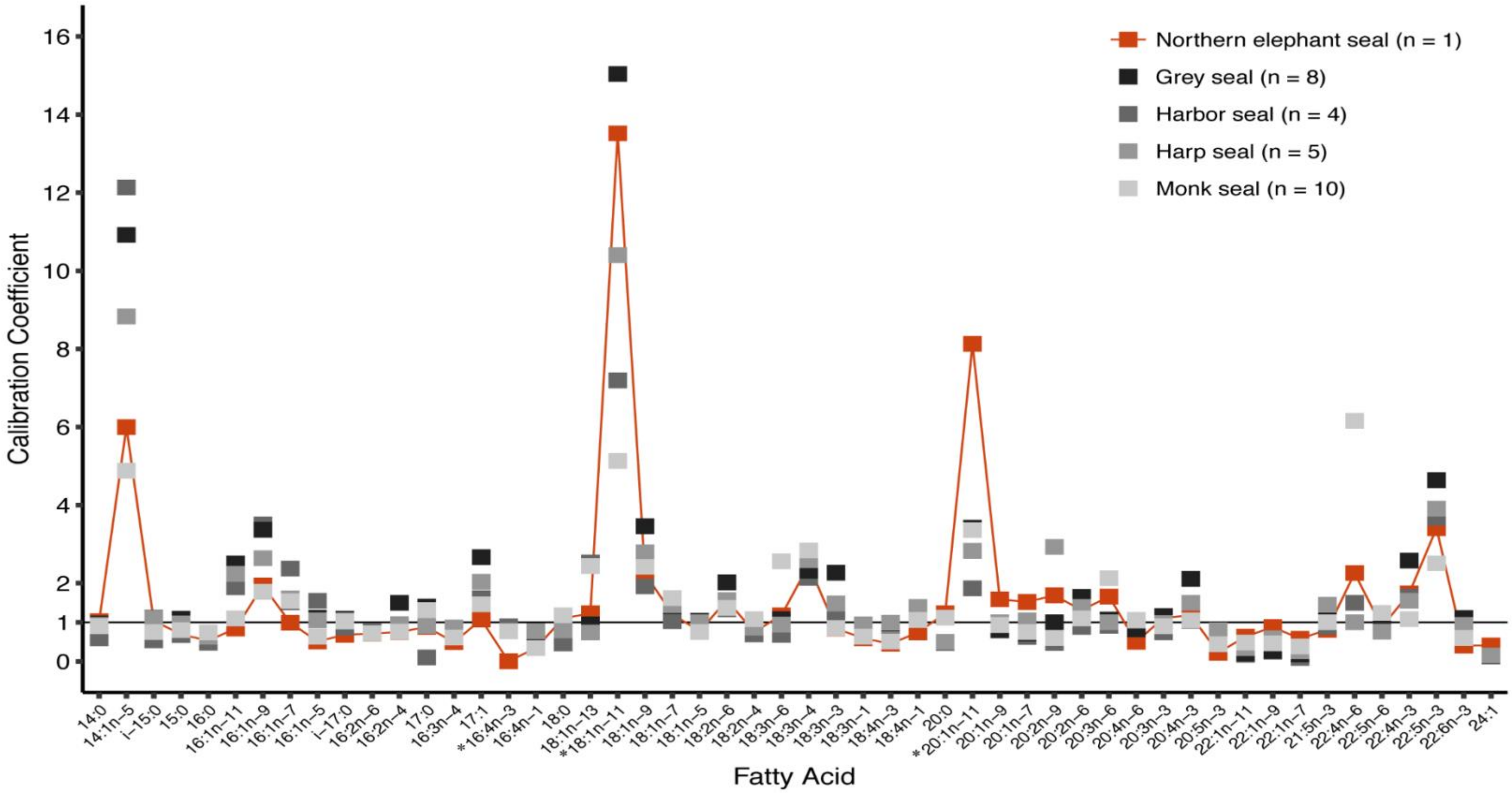

Figure 1.3 Calibration coefficients for an adult female northern elephant seal (n = 1, this study) compared with those reported for four other phocid seals. FAs 16:4n-3, 18:1n-11, and 20:1n-11 (*) were not designated as dietary fatty acids in this study. Values for 16:4n-3 were only available for northern elephant seals, harbor seals, and monk seals. Values for 24:1 were only available for northern elephant seals, grey seals, and harp seals. Data for grey seals and harbor seals taken from Rosen and Tollit (2012). Data for harp seals taken from Iverson et al. (2004). Data for monk seals provided by S. Iverson and first reported in Iverson et al. (2011). Figure modified with permission from Iverson et al. 2004 and 2011.

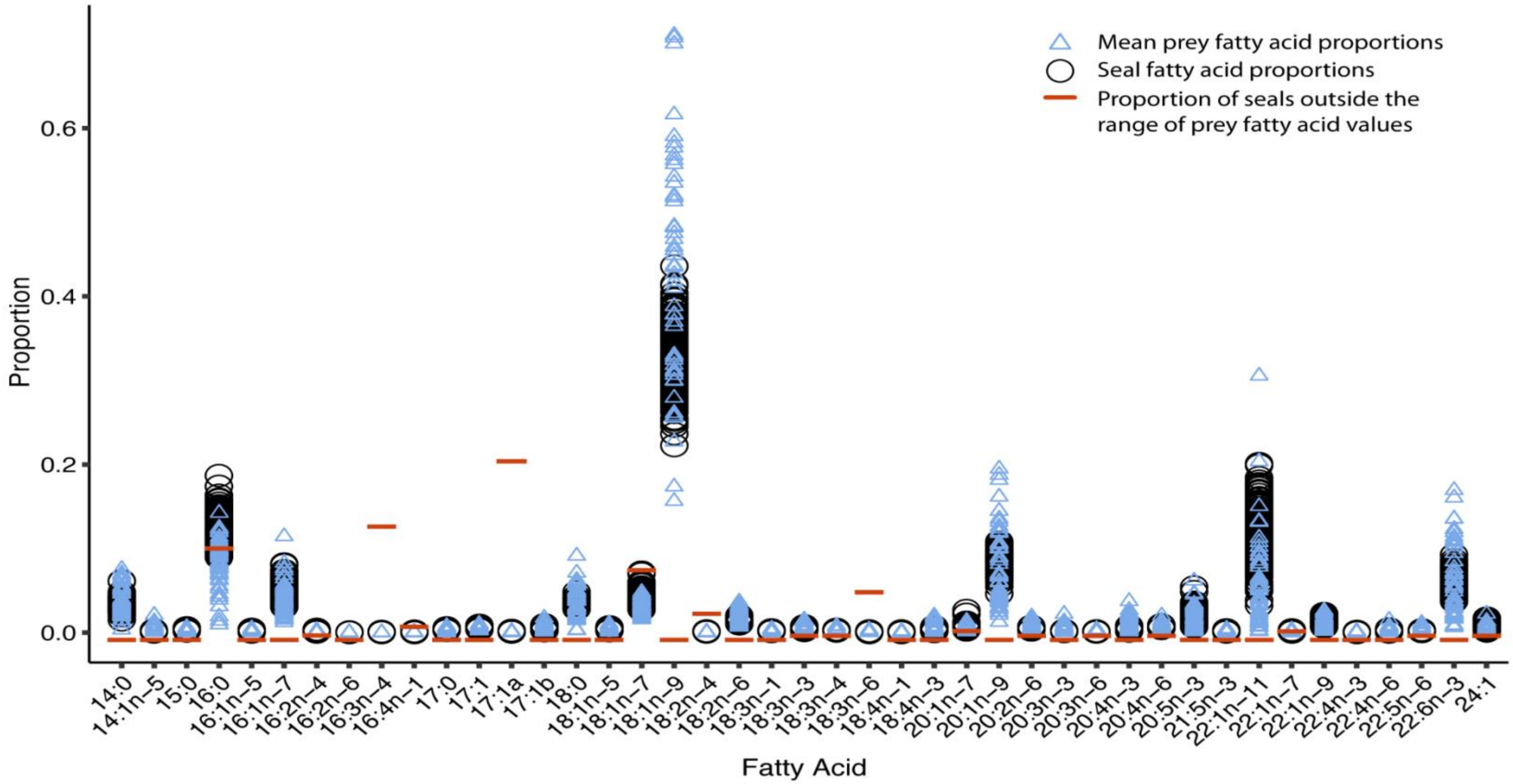

Figure 1.4 Overlap of elephant seal fatty acid (FA) values with the range of mean prey FA values indicates that the calibration coefficients are consistent with the prey library. Blue triangles indicate dietary FA proportions for prey (one mean value per species, n = 51 for each FA). Prey values have been transformed to predator FA optimization space with the calibration coefficients. Black circles indicate FA proportions for individual elephant seals (one value per individual, n = 155 for each FA). Orange lines indicate the proportion of individual seals that fall outside the range of prey values for each FA. Less than 5% of seals (proportion <0.05) have FA values outside the range of the prey.

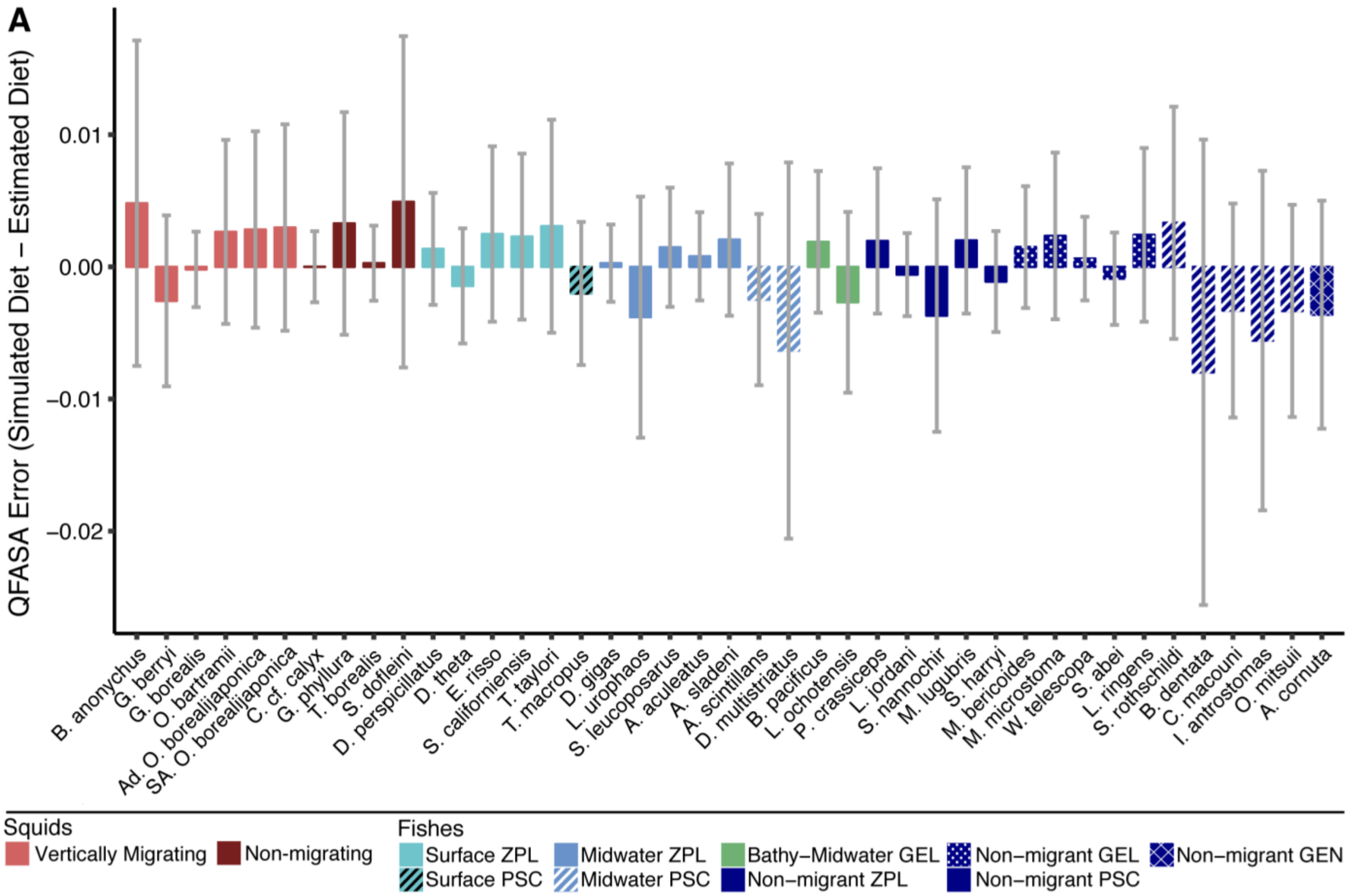

Figure 1.5 (A) Mean error and standard deviation (SD) of QFASA model, calculated as the difference between the proportion of each prey species in the simulated diets (i.e., truth) and the respective proportion in the QFASA estimated diets. Prey with model error > 0 were overestimated by the QFASA model while prey with model error < 0 were underestimated. Gray bars indicate SD. ZPL, zooplanktivore; GEL, gelativore; PSC, piscivore; GEN, generalist.

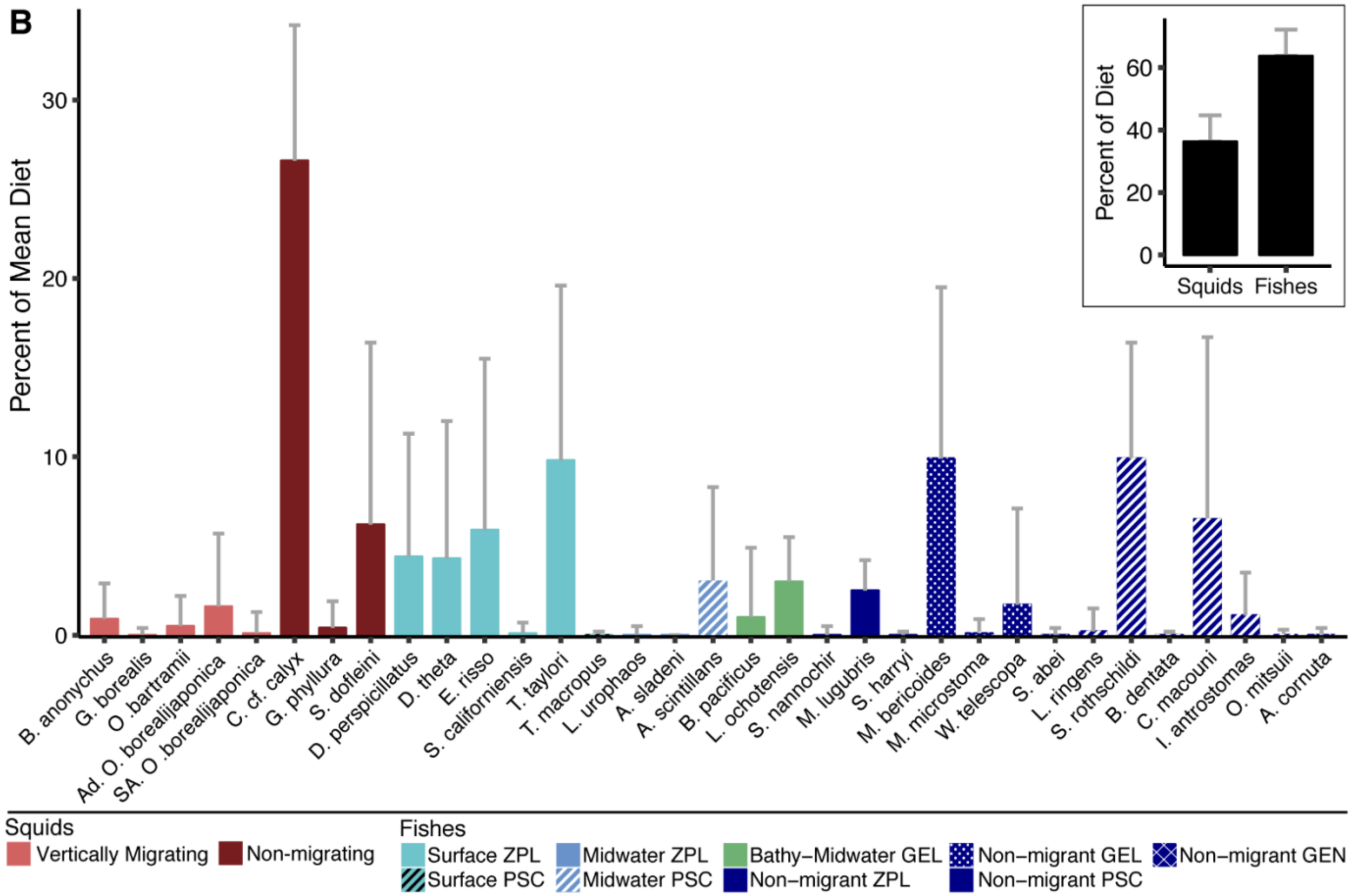

Figure 1.5 (B) Average diet for female northern elephant seals (n = 155) determined by QFASA. Thirty-three prey from 11 functional groups are represented in the overall diet. The prey represented are a subset of the reduced prey library that were present in at least one seal's diet. The inset highlights the finding that fishes (63.7%), rather than squids (36.3%), dominate the mean population-level diet of elephant seals. Refer to Table 4 for exact percentages and absent species. Gray bars indicate SD. ZPL, zooplanktivore; GEL, gelativore; PSC, piscivore; GEN, generalist.

CHAPTER 2

Spatial, Seasonal, and Interannual Diet Differences Revealed for a Deep-Diving Ocean Predator

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2.1 Abstract

Predator-prey interactions in pelagic deep ocean ecosystems are still largely an uncharted frontier in ecology due to the logistical challenges involved in its study and the elusive nature of many deep-sea predators. Marine mammals that depend upon the deep ocean for survival provide an insight into this environment, some transiting over a thousand meters to forage on deep prey, then back to the surface to breathe, on each dive. Characterizing the trophodynamics of deep-diving northern elephant seals (*Mirounga angustirostris*) that forage in the mesopelagic zone and range across the entire eastern North Pacific basin can increase our understanding of deep-sea food web interactions across space and time. The vertical structure and faunal composition of the organisms that make up the deep-scattering layers (the prey base of elephant seals), changes in 3-dimensional space across seasonal and inter-annual timescales, governed by underlying oceanographic features at both fine and broad scales. To characterize the spatiotemporal feeding ecology of elephant seals, we used quantitative fatty acid signature analysis (QFASA) to estimate the diets of 131 adult female seals whose foraging trips were tracked with bio-logging transmitters. Diet composition differed across years and was associated with the oceanographic province in which the seals primarily foraged. Both spatial and interannual differences in diet were influenced by season and may be governed by intrinsic physiological constraints on foraging behavior. Spatial differences in diet composition may be related to regional variation in the location and thickness of the oxygen minimums zones, whereas interannual differences may be driven by large-scale climate phenomena, such as the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO). This study provides further evidence that the deep ocean ecosystem is more responsive to changing environmental conditions than conventionally thought. Furthermore, we demonstrate that long-term trophic data of deep-ocean predators that forage at these depths can provide critical insights to the predator-prey interactions within the under-studied deep ocean.

2.2 Introduction

Trophic interactions, especially spatial and temporal dynamics, are still relatively unknown for most deep ocean predators and represent a critical gap in our understanding of deep-sea ecosystems (Webb et al. 2010, St John et al. 2016, but see Benoit-Bird and Lawson, 2016). Until recently, the deep ocean has been assumed to be a stable, relatively stable ecosystem isolated from the environmental issues facing the surface and coastal oceans (Halpern et al. 2008, Ramirez-Llodra et al. 2011, Rogers 2015). However, it is increasingly apparent that deep ocean ecosystems are impacted by external processes (Levitus 2000, Lyman et al. 2010, Hoegh-Guldberg and Bruno 2010, Doney et al. 2012, Choy and Drazen 2013, Rogers 2015). Environmental changes resulting from natural variation and anthropogenic forces can have cascading effects on top predators in addition to disrupting overall ecosystem structure and function (Heithaus et al. 2008, Baum and Worm 2009, Estes et al. 2011, 2016). Thus, we need to better understand similar ecological interactions in the deep sea to effectively predict how predator populations will respond to environmental change (bottom-up processes) and how declining predator populations may affect ecosystems (top-down processes), it is critical to understand how not just the diet composition of a predator, but how diet changes among individuals, over space, and across time (Bradshaw et al. 2003, Young et al. 2015).

Together the mesopelagic (200-1000 m) and bathypelagic (> 1000 m) regions represent the earth's largest biome with an immense volume of over a billion cubic kilometers and an estimated biomass of approximated 10 billion tons (Robison 2004, Webb et al. 2010, Ramirez-Llodra et al. 2010, Kaartvedt et al. 2012, Irigoien et al. 2014, Rogers 2015). The majority of this biomass is contained within deep scattering layers, dense aggregations of micronekton (organisms 2-20 cm), including crustaceans, fishes, squids, and jellyfishes. Many organisms from the deep scattering layers undertake daily vertical migrations into the epipelagic zone at night to feed, comprising on of the greatest migrations on earth (Hays 2003, Ramirez-Llodra et al. 2010, Klevjer et al. 2016). The species composition and spatial distribution of this region is influenced by oxygen content, light level, vertical mixing, and primary production at the surface (Rogers 2015, St John et al. 2016, Sutton et al. 2017, Aksnes et al. 2017), but the mechanisms of these linkages are not well understood. These abiotic factors differ geographically and change temporally on daily to decadal scales, affecting the abundance and distribution of species and, hence, the diet composition of deep-sea predators (Robison 2004, Robinson, Steinberg, et al. 2010, Koslow et al. 2014, Klevjer et al. 2016, Urmy and Horne 2016, Sommer et al. 2017). These oceanographic characteristics and associated faunal assemblages have been used to delineate the mesopelagic zone into similar biogeographic provinces (*sensu* Longhurst 2006; Proud et al. 2017, Sutton et al. 2017, Reygondeau et al. 2018). The large spatial extent coupled with the difficult logistics and high costs make studying the deep ocean challenging (Benoit-Bird and Lawson 2016). Thus, little is known about the predator-prey interactions occurring in these remote, hard-to-access depths, and even less is known about how those interactions vary in space and time (Webb et al. 2010, St John et al. 2016).

Northern elephant seals (*Mirounga angustirostris*) are deep ocean predators that dive nearly continuously to feed on the wealth of prey resources in the deep scattering layers, while migrating thousands of kilometers from their haul-out sites into the productive waters of the eastern North Pacific (LeBoeuf et al. 2000, Robinson et al. 2012). Their vast foraging range encompasses the entirety of eastern North Pacific from the California Current to the Transition Zone, which straddles the boundary between the Subarctic and Subtropical Gyres (LeBoeuf et al. 2000, Robinson et al. 2012, Figure 2.1A). Though the population forages throughout the eastern North Pacific, most individual females forage in one of three mesopelagic biogeographic provinces (the Subarctic Pacific, the North Central Pacific, or the California Current), while a few forage across all three provinces (Robinson et al. 2012, Peterson et al.

2015, Sutton et al. 2017). Female seals have two seasonal foraging migrations: a short, post-breeding trip (~2.5 months) during the winter and spring seasons (hereafter, winter-spring trip), and a longer, post-molting trip (~7-8 months) during the summer and fall (hereafter, summer-fall trip). Female seals have shown decreased foraging reproductive success in response to positive phases of the El Nino Southern Oscillation (ENSO), known as El Niño, and the Pacific Decadal Oscillation (PDO), two major drivers of oceanographic variability in this region (LeBoeuf and Crocker 2005, Crocker et al. 2006, Trillmich and Ono 2012, Abrahms et al. 2018). Thus, shifts in the diet composition of female northern elephant seals can provide a window into the dynamics of the deep scattering layers in the eastern North Pacific, a region where data on the trophodynamics over broad spatial and temporal scales are nonexistent.

Diet information for northern elephant seals has been limited to the analysis of stomach contents and photographs from animal-borne cameras, (Condit and Le Boeuf 1984, Antonelis et al. 1987, 1994, Naito et al. 2013). Although valuable, stomach contents are biased toward prey items with undigestible hard parts (e.g. squid beaks) and only represent the most recent meal consumed (Harvey and Antonelis 1994, Bowen and Iverson 2012). Further, photographs and video are limited by the resolution of prey identification and memory constraints on biologging instruments. In recent years, well-established biochemical techniques, such as quantitative fatty acid signature analysis (QFASA), can provide species-level diet estimates integrated across time scales of two to three months (Iverson et al. 2004, Budge et al. 2006, Bowen and Iverson 2012). QFASA provides a quantitative estimate of diet by comparing the fatty acid (FA) profiles of the predator to a library of FA profiles from potential prey, after accounting for predator metabolic processes (Iverson et al. 2004, Budge et al. 2006, Parrish 2009). Recently, QFASA has shown that the diet of female elephant seals consists of diel migrating myctophids (i.e. lanternfishes) and non-migrating species such as stomiids and bathylagids (i.e. dragonfishes and deep-sea smelts, Goetsch et al. 2018). This is in marked contrast to earlier stomach content analysis which was unable to record the occurrence of mesopelagic fishes (Goetsch et al. 2018). However, elephant seals foraging on myctophids has been observed by animal-borne camera tags (Naito et al. 2017).

We examined the spatiotemporal patterns in the diets of free-ranging female northern elephant seals using diet data derived from QFASA coupled with concurrent movement data collected over multiple years and seasons. We classified individual seals relative to their primary spatial patterns, based on where they spent the majority of their time foraging, and examined the variability in their diet relative to foraging habitat, year, and season. Finally, we explored how spatial patterns in the vertical structure of the deep ocean and temporal patterns in ocean climate, such as ENSO, may influence the variability in diet composition of this mesopelagic predator, in turn, providing unique insight to the trophic dynamics of the deep ocean ecosystem.

2.3 Materials and Methods

2.3.1 Sample Collection

We instrumented 131 adult female northern elephant seals at Año Nuevo State Reserve, San Mateo, CA, USA (37° 59′ N, 122° 169′ W) with ARGOS or GPS satellite transmitters (Wildlife Computers, Redmond, WA; SPOT4, SPOT5, MK10-AF). We deployed tags in 2005-2006 and 2010-2012 during January-March prior to the winter-spring foraging migration and in May-June before the summer-fall foraging migration. We recovered the bio-logging instruments and collected a blubber biopsy from the lateral side of each seal, anterior to the hip upon their return to the colony (Goetsch et al., 2018). We used established procedures for sedation and instrumentation (Robinson et al. 2012). Blubber biopsies were stored in non-reactive vials and immersed in 2:1 chloroform:methanol (v/v) with 0.01% BHT to prevent oxidation (Iverson et al. 2004, Budge et al. 2006, Goetsch et al. 2018)

To compile the requisite prey library for QFASA, we collected potential prey samples during four midwater trawls (T/S Oshoro-maru, Hokkaido University,) along a north-south transect spanning the Subarctic Pacific and North Central Pacific mesopelagic biogeographic provinces (Sutton et al. 2017, Saijo et al. 2017, Figure 2.1A). Trawl locations were determined by real-time tracking locations of foraging female elephant seals. Maximum trawling depths were based upon typical foraging depths for female seals (Robinson et al. 2012, Naito et al. 2017): two night trawls at 650 m and two day trawls at 730 m and 720 m, respectively. We also collected vertically migrating squid using automatic squid jigs, and we opportunistically obtained one specimen of the mesopelagic squid *Stigmatoteuthis dofleini* from a commercial hake fishery vessel off the coast of Washington in 2014.

2.3.2 Lipid Analysis and QFASA

Methods of blubber processing and lipid analysis are described thoroughly in Goetsch et al. 2018. Whole prey individuals were homogenized and combined into a species-homogenate for lipid analysis (Goetsch et al. 2018). Lipids were extracted from prey-homogenates and elephant seal blubber biopsies using a modified Folch extraction (2:1 chloroform:methanol, Folch et al. 1957, Budge et al. 2006). Resulting lipids were converted to fatty acid methyl esters (FAME) using an acidic methanol transesterification process as described in Budge et al. (2006). FAME were analyzed with a Scion 436 gas chromatograph (GC) using split injection (silica column with 50% cyanopropyl polysiloxane, 0.25 µm, J & W DB-23, Agilent Technologies, Folsom, CA., for detailed settings see Budge et al. 2006). Peaks were identified with FA standards and, when necessary, FA structures were determined using gas chromatography mass spectrometry (GC-MS, Goetsch et al. 2018).

To account for lipid metabolism and differential deposition of fatty acids in seal blubber, we used calibration coefficients calculated using the FA profiles of one captive adult female elephant seal and samples of her diet which consisted of capelin and herring (n = 18 per species, Goetsch et al. 2018). The calibration coefficients were used to adjust the free-ranging elephant seal FA profiles to account for *in vivo* physiological alterations (Iverson et al. 2004, Budge et al. 2006, Rosen and Tollit 2012). The corrected dietary FA profiles of the elephant seals and the prey FA profiles (n = 43) were analyzed using the QFASA model (Bromaghin 2017). The model minimizes the distance between the corrected predator FA profile to a series of estimated diets containing different proportions of prey, which are adjusted for the lipid content of the prey (Iverson et al. 2004, Budge et al. 2006), resulting in a final diet estimates reported as proportion of biomass consumed of each prey species. We used Aitchison distance for proportional data and traditional scaling to parameterize the model (Goetsch et al. 2018) and converted prey FA signatures to predator optimization space following Bromaghin et al. (2015). For model details and performance diagnostics see Goetsch et al. 2018). All prey species that were not present in any individual's diet were removed from further analyses.

2.3.3 Prey Functional Groups

We classified prey species (n=41, 29 fishes and 11 squids) into 11 functional groups based on diel migration behavior and diet (Table 2.1). Squid functional groups were vertically migrating muscular squids and non-migrating gelatinous squids. Fish functional groups were surface migrating zooplanktivores, surface migrating piscivores, midwater migrating zooplanktivores, midwater migrating piscivores, bathy-midwater migrating gelativores, non-migrating zooplanktivores, non-migrating gelativores, non-migrating piscivores and non-migrating generalists. See Table 2.1 for families and species represented in each functional group and species' spatial distribution, vertical range, and energy content.

A limitation of our study was that we only collected prey samples from the Subarctic Pacific and the North Central Pacific mesopelagic biogeographic provinces (Figure 2.1A). We focused on prey from those provinces, because the majority of females forage there and it is where female seals have the greatest foraging success (LeBoeuf et al. 2000, Robinson et al. 2012). However, 22 of the 41 prey species in our study are found in all three biogeographical provinces, so the California Current province was adequately represented.

2.3.4 Spatial Strategy Classification

Tracking data were analyzed using standard filtering and interpolation techniques, including a continuous time-correlated random walk model (Johnson et al. 2008, R Core Team) for track smoothing (Johnson et al. 2008, Robinson et al. 2012) All tracks were interpolated to one position every four hours (6 locations per day) using a custom linear interpolation function in Matlab® (IKNOS package, Y. Tremblay, unpublished). Each position was assigned to one of three mesopelagic biogeographic provinces in the eastern North Pacific (Sutton et al. 2017): the North Central Pacific, the Subarctic Pacific, the California Current, and positions < the 200 m isobath were assigned to the continental shelf (ArcGIS, v.10.4.1, ESRI Inc.). Time spent in a province was used as a proxy of foraging success, since transit rate is a consistent predictor of foraging success for northern elephant seals (Robinson et al. 2010, Simmons, et al. 2010). Each animal was classified to a primary foraging province if they spent greater than 50% of their time in that province. Animals that did not spend over 50% of their time in a single province were classified as having a mixed province strategy.

2.3.5 Statistical Analyses

We tested for differences in FA profiles and diet composition between provinces, years, and seasons (for sample sizes see Table 2.2), using a three factor permutational multivariate analysis of variance (per-MANOVA) with interactions (Primer 6.1.12 with Permanova+ 1.0.2, Primer-E, Ivybridge, United Kingdom, http://www.primer-e.com/). FA profiles were tested to validate the general patterns seen in diet estimates, since we were unable to comprehensively sample prey in all biogeographic provinces. Similarity matrices were calculated using Aitchison distance for FA profiles and Bray-Curtis distance for diet composition. Per-MANOVA results were conducted with 999 permutations and considered significant if p-values were < 0.05. Post-hoc pairwise comparisons were conducted for significant factors to determine which groups differed ($p < 0.05$, unless otherwise indicated). To visualize differences in diet composition between groups, we used canonical analysis of principle coordinates (CAP), a constrained ordination method (Primer 6.1.12 with Permanova+ 1.0.2), which allows for specific hypothesis testing, as opposed to unconstrained ordination methods, such as principal component analysis (PCA) and nonmetric multidimensional scaling (NMDS), which merely reduce data dimensions but do not use *a priori* hypotheses (Anderson 2001, Anderson and Willis 2003). Pearson's correlation coefficients (r) were calculated to determine which functional groups were significant drivers ($r > 0.3$) of the differences between groups (i.e. provinces and years). To examine how each functional group contributed broadly to the diets of elephant seals, we calculated the ratio of fishes:squids for provinces and years by season.

2.4 Results

In general, the ratio of fishes to squids in elephant seals diets ranged from 1.5:1 to 2:1, both spatially and interannually (Tables 2.3 and 2.4). Among biogeographic provinces, the range of fishes:squids diet values was similar between seasons. However, interannually, the fishes:squids ratio for seal diets was more variable during the winter-spring foraging trip (1.5:1 to 2:1) than during the summer-fall trip (1.6:1 to 1.7:1). The variation between diets, both spatially and interannually, was primarily due to changes in the relative proportions of the fish functional groups; whereas the representation of the two squid functional groups was more consistent.

2.4.1 Spatial Variability in Diet

The majority of seals primarily foraged in the Subarctic Pacific (44.7%) or the North Central Pacific (37.9%) mesopelagic biogeographic provinces during winter-spring and summer-fall foraging trips (Figure 2.1). The remaining seals primarily foraged in the California Current (6.8%) or mixed provinces (9.8%). Only one seal foraged primarily over the continental shelf, and she was removed from subsequent analyses. Diet differences were observed among seals foraging in different provinces and were dependent on season (year × season interaction: pseudo-F = 2.46, p = 0.001, Table 2.3 and Figure 2.2A and B). Seal FA profiles were similarly influenced by foraging strategy and season (pseudo-F = 2.77, p = 0.001). During the winter-spring trip, six of the eleven functional groups were significant drivers of the spatial differences in diet ($r > 0.3$): surface migrating zooplanktivores, non-migrating zooplanktivores, non-migrating gelativores, non-migrating piscivores, vertically migrating squids, and non-migrating squids (Figure 2.2A). During the summer-fall trip, only three functional groups significantly accounted for spatial differences: non-migrating piscivores, non-migrating generalists, and non-migrating squids (Figure 2.2B). Within-province variability was minimal: only seals that foraged in North Central Pacific had diets that differed between seasons ($p = 0.001$, Figure 2.3A and B). The ratio of fishes to squids was approximately the same for seals that foraged in North Central Pacific between seasons (2:1 fishes:squids), but the types of fishes consumed differed: during the winter-spring trip, seals consumed 1.5 times more surface migrating zooplanktivores, > 3 times more non-migrating gelativores, and 1.5 times less non-migrating zooplanktivores than North Central Pacific foragers during the summer-fall migration (Table 2.3, Figure 2.3A and B).

Between-province variability: Winter-Spring

Diets of seals that foraged in the Subarctic Pacific during the winter-spring differed from those that foraged in the North Central Pacific ($p = 0.001$) and multiple provinces ($p < 0.01$, Table 2.3, Figure 2.2A). North Central Pacific foragers also had diets that differed from seals that foraged in multiple provinces ($p = 0.001$, Table 2.3, Figure 2.2A). Squid consumption was highest (40.4% of diet) in the Subarctic Pacific (North Central Pacific: 32.8% and Mixed: 33.8%, Table 2.3, Figure 2.3A), while, consequently, fish consumption was lowest (59.6%). Though seals in the Subarctic Pacific consumed the least amount of fishes, they did consume the highest percentage of surface migrating zooplanktivores (30.0%), > 10% more than North Central Pacific foragers (18.2%) and multiple province foragers (20.2%, Table 2.3 and Figure 2.2A). However, they consumed the lowest percentage of non-migrating piscivores (9.1%) compared to seals foraging North Central Pacific (16.6%) and multiple provinces (24.6%). Also, seals that foraged in the Subarctic Pacific consumed half as many non-migrating gelativores (9.8%) as seals that foraged in the North Central Pacific (19.9%), though Subarctic foraging seals consumed a similar percentage as seals that foraged in multiple provinces (9.8%). North Central Pacific foraging seals consumed the highest percentage of fishes (67.2%), dominated by non-migrating functional groups: zooplanktivores (3.9%), gelativores (19.9%), and piscivores (16.6%). Seals that foraged in multiple provinces also consumed diets with a high percentage of non-migrating fishes, driven by the extremely high percentage of non-migrating piscivores (24.6%). Seals that foraged in the California Current had diets that were similar to seals in the Subarctic Pacific but differed from seals that foraged in the North Central Pacific and multiple provinces ($p < 0.05$, Table 2.3, Figures 2.2Aand 2.3A). California Current foragers consumed a lower percentage of vertically migrating squids (< 0.05%) and non-migrating piscivores (12%), but a higher percentage of non-migrating gelativores (21.6%).

Between-province variability: Summer-Fall

During the summer-fall foraging trip, the diets Subarctic Pacific, North Central Pacific and California Current foragers differed from each other (Subarctic Pacific vs North Central Pacific and California Current: $p < 0.05$ for both; North Central Pacific vs. California Current: p = 0.001), but none of these groups had diets that differed from seals with a mixed province strategy (Table 2.3 and Figure 2.2B). Seals that foraged in the North Central Pacific greater percentage of fishes (65.1%) compared to seals from the Subarctic Pacific (59.2%) and the California Current (55.9%). This trend was driven by the high percentage of non-migrating piscivores in the diet of North Central Pacific foragers (25.9%), which was over twice as much as in the diet of California Current foragers (12.2%). The diet of seals that foraged in the North Central Pacific had the lowest percentage of squids (34.9%) with non-migrating squids driving this difference (31.1%). Conversely, seals that foraged in the California Current consumed a lower percentage of fishes (55.9%) than the seals that foraged in the other two provinces.

2.4.2 Temporal Variability in Diet

Elephant seal diets differed by year and season (year × season interaction, pseudo-F = 5.19, p = 0.001, Table 2.4 and Figures 2.2C and D). Interannual differences in elephant seal diet during the winter-spring foraging trip were accounted for by seven out of the eleven functional groups: surface migrating zooplanktivores, midwater migrating piscivores, bathy-midwater migrating gelativores, non-migrating zooplanktivores, non-migrating gelativores, vertically migrating squids, and non-migrating squids (Figure 2.3C). During the summer-fall foraging trip, surface migrating zooplanktivores, midwater migrating piscivores, non-migrating zooplanktivores, non-migrating gelativores, and vertically migrating squids remained significant drivers for diet differences between years; however, midwater migrating zooplanktivores and non-migrating piscivores replaced bathy-midwater migrating gelativores and non-migrating squid as significant functional groups during this season (Figure 2.3D). Intra-annual diet variation (i.e. between seasons within the same year) was only observed during 2005 and 2012 ($p < 0.05$ and $p = 0.001$, respectively, Figure 2.3C and D). In 2005 during the winter-spring trip, seals consumed more than twice the amount of non-migrating gelativores (14.2%) than during the summer-fall trip (5.4%, Table 2.4, Figure 2.3C and D). However, in the summer-fall, seals consumed 10% more surface migrating zooplanktivores than in the winter-spring (34.2% vs. 23.0%). During the winter-spring of 2012, seals consumed 15% more surface migrating zooplanktivores, 8 times more midwater migrating piscivores, and over twice as many non-migrating gelativores than during the summer-fall foraging trip; whereas during the summer-fall, seals consumed over 3 times more non-migrating piscivores than during the winter-spring foraging trip.

Interannual variability: Winter-Spring

Interannual differences in elephant seal diets were evident for the winter-spring foraging trip. Seal diets during 2010 were the most distinct, differing from all other years (2005: $p < 0.01$; 2006: $p = 0.001$; 2011: $p = 0.059$, marginal difference; 2012: $p = 0.001$; Table 2.4, Figure 2.2C). In 2010, seals consumed the least squids (33.0%) and the most fishes (67.0%) compared to other years. Though squid consumption was low overall in 2010, seals consumed the most vertically migrating squids (4.1%) than in other years (Table 2.4 and Figure 2.3C). In addition, during the winter-spring trip in 2010, seals consumed more non-migrating gelativores (22.7%) than in other years.

Seals foraging during 2010 had diets that were most similar to those foraging during 2011 (Table 2.4, Figure 2.3C) with the biggest difference that seals in 2011 consumed more midwater migrating piscivores (6.5%) than in 2010 (0.4%) and around 6% less non-migrating gelativores. Diets of seals foraging in 2005 and 2006 were similar, but differed diets of foraging in 2010 ($p < 0.01$ and 0.001, respectively), 2011 ($p < 0.05$, both), and 2012 ($p < 0.001$ and 0.01, respectively; Table 2.4, Figure 2.2C). In 2005 and 2006, seals consumed the most bathy-midwater migrating gelativores (6.2% and 9.2%, respectively) than during 2010 (4.5%), 2011 (3.4%), and 2012 (4.1%; Table 2.4, Figure 2.3C). No seals consumed midwater migrating piscivores during either 2005 or 2006. Seals foraging during 2011 and 2012 also had similar diets, and both differed from the diets of seals during 2005, 2006, and 2010. Seals during 2011 and 2012 consumed the greatest amount of midwater migrating piscivores (6.5% and 8.0%, respectively) and least amount of bathy-midwater migrating gelativores and non-migrating zooplanktivores (Table 2.4, Figure 2.3C).

Interannual variability: Summer-Fall

For the summer-fall foraging trip, diets in 2010 were also different than in all other years (2005: $p < 0.01$, 2011: $p < 0.05$, and 2012: $p = 0.001$). Similar to the 2010 winter-spring trip, seals foraging during the 2010 summer-fall consumed the least squids (37.0%) and the most fishes (63.0%) compared to the other years (Table 2.4, Figure 2.3D), yet they ate the most vertically migrating squids (6%). Furthermore, seals in the summer-fall of 2010 consumed 2-3 times more non-migrating gelativores (14.1%) than in other years. Seal diets in 2012 were also distinct from all other years for the summer-fall trip (2005, 2010, 2011: p = 0.001 for all). The fish portion of seal diets in 2012 was dominated by non-migrating piscivores (41.3%), over 2.5 times as much as in other years (Table 2.4, Figure 2.3D). Seals in 2012 also consumed less than half the quantity of surface migrating zooplanktivores than they did in other years (Table 2.4, Figure 2.3C). During the summer-fall foraging trip in 2005 and 2011, seal diets were mostly similar. In both years, seals consumed more than 30% surface migrating zooplanktivores and less than 2% vertically migrating squids. One notable difference between 2005 and 2011 was that seals in 2011 consumed more midwater migrating piscivores (8.1% vs. 1.3%), and seals in 2011 consumed more of this functional group than any other year.

2.5 Discussion

The faunal composition and distribution of prey in the ocean's deep scattering layers are influenced by large-scale patterns of circulation, vertical gradients of abiotic environmental factors, and annual to decadal patterns of ocean climate (Robison 2004, Robinson 2010, Steinberg, et al. 2010, Klevjer et al. 2016). Female northern elephant seals must respond to the spatial and temporal variability in the environment, since it governs the dynamics of the prey they rely upon. Understanding variability in elephant seal diet across time and space provides insight to predator-prey interactions in the deep ocean and how those interactions change in response to changes in the deep-sea habitat. The average diet of an adult female elephant seal is approximately 64% fishes and 36% squids, and, in general, diet is dominated by surface migrating zooplanktivores (25%), non-migrating piscivores (18%), non-migrating gelativores (12%), and mesopelagic squids (33%; Goetsch et al. 2018). We found that province, season, and year all influenced diet composition and varied, considerably in some cases, from the overall population-level diet. While the total proportions of fishes and squids remained remarkably consistent among provinces and years in both seasons (proportion of fishes 1.3-2 times that of squids), spatiotemporal differences in seal diets were associated with changes in the prey functional groups consumed. The spatiotemporal variation we observed in diet is likely due to synergistic effects among three interacting factors: 1) intrinsic physiological time and energy constraints, 2) extrinsic influences of physical variables, such as the oxygen minimum zone, and 3) extrinsic broad-scale influences of interannual variation in ocean climate.

2.5.1 Influence of Intrinsic Physiological Constraints

Due to their annual life history cycles of breeding and molting, female elephant seals experience different physiological constraints during the shorter winter-spring foraging trip than the longer summer-fall trip. These physiological constraints may play a role in the seasonal effects on diet composition seen in our results by influencing the degree of prey selectivity and foraging efficiency. Female elephant seals typically lose up to 40% of their body mass during the annual breeding season while ashore, transferring a substantial portion of their energy reserves to their pup via lipid-rich milk (~50% milk-fat; Costa et al. 1986, Crocker et al. 2014). Female seals are constrained by the 2.5-month period during which they must travel to their preferred foraging areas, recover as much energy as possible, and then return to the rookery to molt (Simmons et al. 2010, Robinson et al. 2012). Optimal diet theory predicts that predators should select prey types that maximize net energy gain (Pulliam 1974, Stephens and Krebs 1986). However, for predators foraging under a time constraint, there is a trade-off between consumption rate and selectivity for optimal prey, such that as time available for foraging decreases, predators should be less selective in their diet choices (Lucas 1985, Lucas et al. 1993, Grieco 2002). We found that elephant seals had a more variable diet during the winter-spring trip with greater spatiotemporal differences, suggesting that female seals were less selective in their prey choice and were consuming most of the prey encountered regardless of its net energetic value. Diet composition should reflect the abundance and distribution of prey in the environment and, thus, be more likely to change in response to environmental variability, whether spatial or temporal. Following Ashmole’s halo, the time-constraint of the winter-spring foraging migration likely restricts the seals’ foraging range that, in turn, may increase intraspecific competition, leading to diet diversification (Figure 2.1B and C; Jovani et al., 2015; Robinson et al., 2012; Svanbäck and Bolnick, 2007). For example, both sea otters (*Enhydra lutris*) and sea lions exhibit more diverse diets when there is more competition for resources (Watt et al. 2000, Estes et al. 2003, Villegas-Amtmann et al. 2008, 2011, 2013). While the degree of intraspecific competition is unknown for female elephant seals, it is more likely to be a factor during the winter-spring trip than during the summer-fall. Conversely, during the longer summer-fall trip, female seals are at sea nearly three times longer. Since the time-constraint on foraging is eased and intraspecific competition decreases as they can travel further from the rookery, female seals may become more selective in their diet choices possibly accounting for why there were less differences between diets of seals during the summer-fall trip. Also, female seals are pregnant during the summer-fall trip and changing nutritional demands due to gestation may lead to further selectivity in their diet choices (Pyke 1984, Kohl et al. 2015).

2.5.2 Influence of the Oxygen Minimum Zone (OMZ)

A primary influence on the vertical distribution of elephant seal prey in the deep scattering layers is dissolved oxygen concentration (Bianchi et al. 2013, Netburn and Koslow 2015, Klevjer et al. 2016). Oxygen minimum zones (OMZ) are relatively stable oxygen-deficient midwater expanses within the water-column which can vary regionally in depth, thickness, and degree of oxygen depletion (Paulmier and Ruiz-Pino 2009, Gilly et al. 2013, Moffitt et al. 2015). The upper boundary of the OMZ is defined by a steep oxycline which separates the well-oxygenated mixed layer from a core region of extremely low oxygen concentration (Bertrand et al. 2010, Gilly et al. 2013, Gallo and Levin 2016) and serves as a physical barrier to hypoxia intolerant species (Rogers 2000). The lower boundary of the OMZ is typified by a more gradual gradient as dissolved oxygen again in deeper waters (Gilly et al. 2013, Galloway et al. 2014). Exceptionally anoxic or thick OMZs can partition a single scattering layer into several based on vertical microhabitats of oxygen concentration with shallower layers composed of vertically migrating species, such as myctophids, and deeper layers of primarily non-migrating species (Gilly et al. 2013, Maas et al. 2014, Netburn and Koslow 2015, Gallo and Levin 2016).

The differences in diet composition among seals with differing spatial strategies are likely due to the differences in the vertical distribution on prey in the deep scattering layers which varies predictably between mesopelagic provinces (Klevjer et al. 2016, Proud et al. 2017, Sutton et al. 2017, Reygondeau et al. 2018). The Subarctic Pacific is a seasonally productive region with an intense, seasonal OMZ that is relatively shallow (~ 300 m) and exceptionally thick (~ 1000 m), especially at higher latitudes (Paulmier and Ruiz-Pino 2009, Moffitt et al. 2015, Gallo and Levin 2016, Priede 2017, Sutton et al. 2017, Breitburg et al. 2018). During the winter-spring when the Subarctic OMZ is strongest (Paulmier and Ruiz-Pino 2009), we found that Subarctic foraging seals consumed more surface migrating zooplanktivores and less non-migrating fishes. Due to the shallowness of the upper OMZ boundary, migrating prey species may be constrained by daylight from above (i.e. risk from visual predators) and hypoxic water below to a narrow band of refuge where they can escape from visual predators with higher oxygen requirements but still meet their own oxygen needs (Whitney et al. 2007, Koslow et al. 2011, Gilly et al. 2013). For air-breathing deep divers like northern elephant seals that are not constrained by dissolved oxygen concentrations, focusing on the densely-packed layer of surface migrators may increase foraging efficiency in the Subarctic province. Conversely, non-migrating prey are typically found at the lower boundary of the OMZ (Wishner et al. 2013, Koslow et al. 2014, Maas et al. 2014), which is much deeper in the

Subarctic Pacific (> 1300 m) due to the thickness of the OMZ (Moffitt et al. 2015, Gallo and Levin 2016). Since this is over twice as deep as the average daytime diving depth (~600 m) of female seals (Robinson et al. 2012), it may be less profitable for seals to consume non-migrating species in this province, especially since non-migrating species also tend to be less energy dense (Goetsch et al. 2018, Sinclair et al. 2015).

In contrast to the Subarctic Pacific, the OMZ in the North Central Pacific is deeper in the water column and corresponds with a deeper migrating scattering layer (~550 m for both) (Paulmier and Ruiz-Pino 2009, Gallo and Levin 2016). Indeed, female seals consistently dive deeper in the North Central Pacific than in other regions (Peterson et al. 2015). Due to the deeper OMZ, surface light attenuation plays a less important role in concentrating the vertically migrating fish species in the upper layer of the OMZ during the day, resulting in a wider, but more diffuse distribution of these fishes in the North Central Pacific province (Bianchi et al. 2013). Additionally, relative to provinces with shallower OMZs, diel migration rates increase for vertically migrating species (Bianchi and Mislan 2015). These conditions may make it less energetically efficient for seals foraging in the North Central Pacific to focus on this functional group and may explain the decreased consumption of surface migrating zooplanktivores in their diets compared to seals foraging in the Subarctic province during the winter-spring. Furthermore, the North Central Pacific OMZ is narrower than in the Subarctic (Moffitt et al. 2015), making the lower boundary of the OMZ more accessible to foraging elephant seals and may explain why North Central Pacific seals consumed more non-migrating fishes than seals in the Subarctic Pacific during both seasons.

Seals that primarily foraged within the California Current were rare for both seasons, as were seals that exhibited a mixed province strategy. The mesopelagic zone of the California Current includes fauna that are a combination of those in the Subarctic Pacific and the North Central Pacific, and is subject to nearshore processes that are not a factor for the two pelagic provinces (Bograd et al. 2008, Checkley and Barth 2009, Koslow et al. 2014, Netburn and Koslow 2018). In the winter-spring, the California Current foragers had different diets from North Central Pacific and mixed strategy foragers, but their diets were similar to Subarctic Pacific foragers. The California Current has a shallow OMZ (~300-400 m), similar to the Subarctic Pacific province, due to upwelling typical of eastern boundary currents (Bograd et al. 2008, Klevjer et al. 2016, Urmy and Horne 2016). In the winter-spring foraging trip, when upwelling intensifies (Chan et al. 2008), the OMZ shoals and the non-migrating scattering layer associated with the lower OMZ boundary disappears (Urmy and Horne 2016). Similarity in the foraging conditions of the California Current and the Subarctic Pacific during the winter-spring may account for the similarity we found in diets of seals foraging in these provinces. In the summer-fall, we found that diet compositions differed among seals foraging in these two provinces which we hypothesize was due to redistribution of the deep scattering layers as upwelling subsides the California Current and the OMZ in the Subarctic Pacific diminishes.

2.5.3 Influence of Ocean Climate Variability

The El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) have both been found to affect the dynamics of OMZ and the deep scattering layers (Whitney et al. 2007, Koslow et al. 2011, Gilly et al. 2013, Gallo and Levin 2016). Previous studies have found a correlation between the primary foraging areas of seals and subsurface chlorophyll maxima and thermal inversion layers (Robinson et al. 2012, Saijo et al. 2017), which can also be altered by changing climate conditions (Masuda et al. 2006); however, there is a paucity of data on how thermal inversions affect the deep scattering layers. The interannual differences in diet composition for elephant seals during the winter-spring foraging trip may relate to interdecadal fluctuations in these climate indices. In 2010, there was a strong, yet brief, Central Pacific El Niño event that coincided with a positive PDO phase which are both associated with cooler than normal surface temperatures in the North Central and Subarctic Pacific provinces and warmer than normal temperatures with decreased upwelling in the California Current (Di Lorenzo et al. 2010, Abrahms et al. 2018). Seals during the 2010 winter-spring trip consumed less squids and more fishes than seals during the winter-spring for all other years, including a La Niña in 2011. While seals during the 2010 El Niño ate less squids overall, this was primarily due to a decreased consumption of mesopelagic squids which was 5% less than average for female seals and the lowest of any year or season in our study. Instead, seals consumed more vertically migrating squids than average which, despite their larger size, are faster and less energy-dense making them less energetically favorable prey (Goetsch et al 2018). This suggests that El Niño may influence the mesopelagic prey base in the eastern North Pacific, causing seals to alter their feeding habits to include less preferable prey. Though the strong El Niño during the winter-spring foraging trip swiftly transitioned to a strong La Niña during the subsequent foraging trip (2010 summer-fall), there was no corresponding change in diet between the foraging trips within that year. Furthermore, despite the strong La Niña continuing into the winter-spring of 2011, seal diets were only marginally different from those of seals during the El Niño the previous year. Seals again consumed less non-migrating squids and nearly twice the amount vertically migrating squids than average. This trend suggests a possible lag effect of El Niño. Also, during the 2010 El Niño, seals began consuming greater quantities of midwater migrating piscivores which are typically only a small component of seal diet (< 2%). This functional group remained elevated in the diet through the end of the La Niña conditions, also indicating a lag effect. Conversely, since the midwater migrating piscivores are at their highest in the diet beginning in the winter-spring 2011 and remain that way until winter-spring 2012, this could suggest a lag effect due to the La Niña of 2010-2011. Interestingly, the only times when seal diets differed between seasons of the same year were 2005 and 2012, that had neutral ENSO conditions. This suggests that strong interannual variability, including ENSO conditions, may swamp out any normal intra-annual diet differences.

Seals compensated for changes in their environment by changing their diet as evidenced by seals in 2010 winter-spring having average foraging success (Robinson et al. 2012). Since female seals had decreased foraging success during the 1998 super-El Niño (Crocker et al. 2006), it is possible that there is a threshold for northern elephant seals beyond which they can no longer compensate for adverse conditions by merely changing their diet. Further evidence of a compensatory threshold, is demonstrated by the differential foraging success of female seals that foraged during positive phases of the PDO. Females that had high foraging site fidelity had decreased foraging success, while seals that were more plastic in their foraging location showed more success (Abrahms et al. 2018). During 2014, there were abnormally warm conditions in the eastern North Pacific Transition Zone, referred to as the Blob, (Whitney 2015, Di Lorenzo and Mantua 2016), followed by an extremely strong El Nino in 2015 (Jacox et al. 2016). We hypothesize that during these conditions female seals would most likely exhibit both a change in diet composition and a decrease in foraging and/or reproductive success, yet additional data are needed to test these hypotheses.

2.5.4 Conclusions

Our results show that both intrinsic physiological factors and extrinsic environmental factors affect the diet composition of female northern elephant seals both spatially and temporally. The interactions among intra-annual seasonal changes, large-scale spatial patterns in the deep ocean environment, and interannual climate variability result in complex intraspecific variability in female elephant seal foraging behavior, especially diet. Furthermore, we suggest that the spatiotemporal dynamics of the OMZ in the eastern north Pacific is a primary driver of this behavioral variability, supporting similar findings by Naito et al. (2017). The northward extension of North Central Pacific province (Polovina et al. 2011) coupled with the expansion and shoaling of the OMZ (Bograd et al. 2008, Gilly et al. 2013, Breitburg et al. 2018), predicted under climate change have serious implications for deep ocean ecosystems and the predators, like elephant seals, that rely upon them. The northward retreat of the Subarctic province may negatively impact seals, especially during the time-limited winter-spring trip, by increasing the distance seals must travel to reach their primary foraging areas. This may negatively impact female seals by increasing energy expenditure for seals already swimming at an increased transit rate (Simmons et al. 2010). Furthermore, increased energy expenditures during the summer-fall migration when female seals are gestating a pup could have consequences on reproductive success. Foraging may become less efficient if prey species in the deep scattering layer are more dispersed as a result of a thickening of the OMZ. Conversely, shoaling of the OMZ in other areas compress the migrating scattering layer the upper OMZ boundary, resulting in increased foraging success for some seals. In a changing climate, predators that are more flexible in their foraging behavior and diet choices may have an advantage since they can respond more quickly to changing environmental conditions and foraging cues. This study presents unprecedented and much needed information on the interactions within the deep-sea food web which are critical to future management and conservation of these systems under continued climate change.

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Table 2.1 Core distributions and primary depth zones for deep-sea fishes and squids occurring in adult female northern elephant seal diet as determined from QFASA. Prey species are classified by functional group and further divided by family. Modified from Goetsch et al., 2018.

Functional Group* *Family*	**Species**	**Biogeographic Province**[†]	**Vertical Range**[‡]	**Energy Content**[§] (kJ kg^{-1} wet wt.)
Surface Migrating Zooplanktivores				
Myctophidae	*Diaphus perspicillatus*	NCP	Epi-Mesopelagic	-
	Diaphus theta	SAP, NCP, CC	Epi-Mesopelagic	12,108 - 12,108
	Electrona risso	SAP, NCP, CC	Epi-Mesopelagic	-
	Symbolophorus californiensis	NCP, CC	Epi-Mesopelagic	-
	Tarletonbeania taylori	SAP, NCP	Epi-Mesopelagic	-
Surface Migrating Piscivores				
Stomiidae	*Tactostoma macropus*	SAP, NCP, CC	Epi-Mesopelagic	6,556
Midwater Migrating Zooplanktivores				
Myctophidae	*Lampadena urophaos*	NCP, CC	Mesopelagic	-
Sternoptychidae	*Argyropelecus sladeni*	SAP[†], NCP, CC	Epi-Mesopelagic	-
Midwater Migrating Piscivores				
Stomiidae	*Aristostomias scintillens*	SAP, NCP, CC	Epi-Bathypelagic	-
Bathy-midwater Migrating Gelativores				
Bathylagidae	*Bathylagus pacificus*	SAP, NCP, CC	Meso-Bathypelagic	-
	Lipolagus ochotensis	SAP, NCP, CC	Meso-Bathypelagic	2,394 - 5,149
Non-migrating Zooplanktivores				
Myctophidae	*Stenobracchius nannochir*	SAP, NCP, CC	Mesopelagic	8,925 - 10,252
Melamphaidae	*Melamphaes lugubris*	SAP, NCP, CC	Mesopelagic	15,052 - 15,788
Notosudidae	*Scopelosaurus harryi*	SAP, NCP, CC	Mesopelagic	5,670
Non-migrating Gelativores				
Bathylagidae	*Melanolagus bericoides*	NCP, CC	Mesopelagic	-
Opisthoproctidae	*Macropinna microstoma*	SAP, CC	Mesopelagic	4,192
	Winteria telescopa	NCP[†]	Meso-Bathypelagic	-
Platytroctidae	*Sagamichthys abei*	SAP, NCP[†], CC	Mesopelagic	-

Table 2.1 (*Continued*) Core distributions and primary depth zones for deep-sea fishes and squids occurring in adult female northern elephant seal diet as determined from QFASA. Prey species are classified by functional group and further divided by family. Modified from Goetsch et al., 2018.

Functional Group* *Family*	**Species**	**Biogeographic Province**†	**Vertical Range**‡	**Energy Content**§ (kJ kg^{-1} wet wt.)
Non-migrating Piscivores				
Paralepididae	*Lestidiops ringens*	SAP, NCP, CC	Meso-Bathypelagic	-
	Stemonosudis rothschildi	NCP	Meso-Bathypelagic	-
Scopelarchidae	*Benthalbella dentata*	SAP, NCP, CC	Mesopelagic	10,609
Stomiidae	*Chauliodus macouni*	SAP, NCP, CC	Mesopelagic	5,434 - 5,485
	Idiacanthes antrostoma	SAP, NCP, CC	Mesopelagic	-
	Opostomias mitsuii	SAP, NCP, CC	Meso-Bathypelagic	-
Non-migrating Generalist				
Anoplogastridae	*Anoplogaster cornuta*	SAP, NCP, CC		
Vertically Migrating Squids				
Gonatidae	*Berryteuthis anonychus*	SAP, NCP	Epi-Mesopelagic	4,242
	Gonatopsis borealis	SAP, NCP, CC	Epi-Mesopelagic	3,284 - 5,830
	Ommastrephes bartramii	SAP†, NCP	Epi-Bathypelagic	6,552
Onychoteuthidae	Adult. *Onychoteuthis borealijaponica*	SAP, NCP, CC	Epi-Bathypelagic	5,400
	Subadult *O. borealijaponica*	SAP, NCP, CC	Epi-Mesopelagic	-
Non-migrating Squids				
Chiroteuthidae	*Chiroteuthis* c. f. *calyx*	SAP, NCP, CC	Meso-Bathypelagic	2,801 - 4,162
Cranchiidae	*Galiteuthis phyllura*	SAP, NCP	Meso-Bathypelagic	3,528
Histioteuthidae	*Stigmatoteuthis dofleini*	SAP, NCP, CC	Meso-Bathypelagic	2,650

* **Migratory pattern**: **Surface** – migrates to < 20 m at night; **Midwater** – migrates at night, but remains > 20 m from surface; **Bathy-midwater** – remains < 1000 m during day, migrates into mesopelagic at night; **Non-migrating** – vertically mobile but no diel pattern, generally stays within same depth zone; **Diet Guild**: **Piscivores** – mostly fishes, but some shrimps, larger mysids, and cephalopods; **Gelativores** – medusae, ctenophores, salps, etc.; **Zooplanktivores** – diverse zooplankton like copepods, and euphausids; **Generalists** – diverse zooplankton and micronekton (Drazen et al. 2017)

† **Biogeographic province**: **SAP** – Subarctic Pacific, **NCP** – North Central Pacific; **CC** – California Current (Sutton et al. 2017)

‡ **Vertical Range**: **Epi-mesopelagic** – mesopelagic zone during the day, migrates into epipelagic zone at night; **Mesopelagic** – primarily stays within mesopelagic zone, even if species is a diel migrator; **Epi-bathypelagic** – migrates from the bathypelagic zone into the epipelagic zone at night; **Meso-bathpelagic** – species vertical range extends > 1000 m into the bathypelagic zone

§ Perez and Bigg 1986, Perez 1994, Sinclair et al. 2015

Table 2.2 Sample sizes of female northern elephant seals with paired tracking and diet data for mesopelagic biogeographic province and year by season. Abbreviations: NCP – North Central Pacific, SAP – Subarctic Pacific, CC – California Current.

a. Biogeographic Province

Season	NCP	SAP	CC	Mixed	Total
Winter-Spring	31	30	6	9	76
Summer-Fall	19	29	3	4	55
Total	50	59	9	13	131

b. Year

Season	2005	2006	2010	2011	2012	Total
Winter-Spring	14	12	17	15	18	76
Summer-Fall	16	-	12	12	15	55
Total	30	12	29	27	33	131

Table 2.3 Mean occurrence (% biomass) of functional groups represented in the diet of female northern elephant seals by biogeographic province during the winter-spring and summer-fall foraging trips, respectively. Significant differences in seal diet between provinces were determined by post-hoc pairwise comparisons. The functional groups shown are significant drivers of the differences in seal diet (*r* > 0.3). For percent occurrence of all functional groups and prey species occurring in seal diet by province, see Tables A1.1 and A1.2.

Season Functional Group	**Mean occurrence in diet (%)**			
Winter-Spring Trip[1]	**SAP**[a]	**NCP**[b]	**CC**[c]	**Mixed**[d]
Fishes	**59.6**	**67.2**	**64.6**	**66.2**
Surface migrating zooplanktivores	30.0	18.2	22.4	20.2
Non-migrating zooplanktivores	2.6	3.9	2.1	2.7
Non-migrating gelativores	9.4	19.9	21.6	9.8
Non-migrating piscivores	9.1	16.6	12.0	24.6
Squids	**40.4**	**32.8**	**35.4**	**33.8**
Vertically migrating	2.2	3.8	0.4	3.2
Non-migrating	38.2	29.0	35.0	30.7
Fishes:Squids Ratio	1.5:1	2:1	1.8:1	2:1
Summer-Fall Trip[2]	**SAP**[a]	**NCP**[b]	**CC**[c]	**Mixed**
Fishes	**59.2**	**65.1**	**55.9**	**67.8**
Non-migrating piscivores	19.1	25.9	12.2	27.5
Non-migrating generalists	0.0	0.0	1.7	0.0
Squids	**40.8**	**34.9**	**44.1**	**32.2**
Non-migrating	37.1	31.1	43.5	29.5
Fishes:Squids Ratio	1.5:1	1.9:1	1.3:1	2.1:1

1. Winter-Spring
    a. SAP differed from NCP ($p = 0.001$) and Mixed ($p < 0.01$).
    b. NCP differed from all other provinces ($p < 0.01$).
    c. CC differed from the NCP ($p < 0.01$) and Mixed ($p < 0.05$).
    d. Mixed differed from all other provinces ($p < 0.05$).
2. Summer-Fall
    a. SAP differed from the NCP and CC ($p < 0.05$).
    b. NCP differed from the SAP ($p < 0.05$) and CC ($p = 0.001$).
    c. CC differed from the SAP ($p < 0.05$) and NCP ($p = 0.001$).

Table 2.4 Mean occurrence (% biomass) of functional groups represented in the diet of female northern elephant seals by year during the winter-spring and summer-fall foraging trips, respectively. Significant differences in seal diet between years were determined by post-hoc pairwise comparisons. The functional groups shown are significant drivers of the differences in seal diet ($r > 0.3$). For percent occurrence of all functional groups and prey species occurring in seal diet by year, see Table A1.3 and A1.4.

Season **Functional Group**	**Mean occurrence in diet (%)**				
Winter-Spring Trip^{1}	**2005^{a}**	**2006^{b}**	**2010^{c}**	**2011^{d}**	**2012^{ae}**
Fishes	**60.2**	**62.6**	**67.0**	**65.0**	**63.6**
Surface migrating zooplanktivores	23.0	25.8	20.8	19.5	27.9
Midwater migrating piscivores	0.0	0.0	0.4	6.5	8.0
Bathy-midwater migrating gelativores	6.2	9.2	4.5	3.8	3.0
Non-migrating zooplanktivores	3.4	4.1	3.5	2.5	2.3
Non-migrating gelativores	14.2	9.2	22.7	16.4	9.8
Squids	**39.8**	**37.4**	**33.0**	**34.9**	**36.3**
Vertically migrating	2.0	2.6	4.1	3.9	1.4
Non-migrating	37.8	34.8	28.9	31.0	34.9
Fishes:Squids Ratio	1.5:1	1.6:1	2:1	1.9:1	1.8:1
Summer-Fall Trip	**2005^{a}**	**2006**	**2010^{b}**	**2011^{c}**	**2012^{d}**
Fishes	**61.8**	**-**	**63.0**	**61.1**	**61.0**
Surface migrating zooplanktivores	34.2	-	25.2	33.8	12.2
Midwater migrating zooplanktivores	0.0	-	0.0	0.0	0.04
Midwater migrating piscivores	1.3	-	1.7	8.2	0.3
Non-migrating zooplanktivores	2.1	-	2.5	1.2	1.1
Non-migrating gelativores	5.4	-	14.1	5.2	3.6
Non-migrating piscivores	15.2	-	16.2	11.3	41.3
Squids	**38.2**	**-**	**37.0**	**38.9**	**39.0**
Vertically migrating	1.7	-	6.0	1.9	4.6
Fishes:Squids Ratio	1.6:1	-	1.7:1	1.6:1	1.6:1

1. Winter-Spring
   a. 2005 differed from 2010 ($p = 0.01$), 2011 ($p < 0.05$), and 2012 ($p = 0.001$).
   b. 2006 differed from 2010 ($p = 0.001$), 2011 ($p < 0.05$, and 2012 ($p < 0.01$).
   c. 2010 differed from all years: 2005 ($p < 0.01$), 2006, 2012 ($p = 0.001$), 2011 ($p = 0.59$, marginal).
   d. 2011 differed from 2005, 2006 ($p < 0.05$), and 2010 ($p = 0.59$, marginal)
e. 2012 differed from 2005 and 2010 ($p = 0.001$) and 2006 ($p < 0.01$).
2. Summer-Fall
   a. 2005 differed from 2010 ($p < 0.01$) and 2012 ($p = 0.001$).
   b. 2010 differed from all other years: 2005 ($p < 0.01$), 2011 ($p < 0.05$), and 2012 ($p = 0.001$).
   c. 2011 differed from 2010 ($p < 0.05$) and 2012 ($p = 0.001$).
   d. 2012 differed from all other years: 2005, 2010, and 2011 ($p = 0.001$ for all)

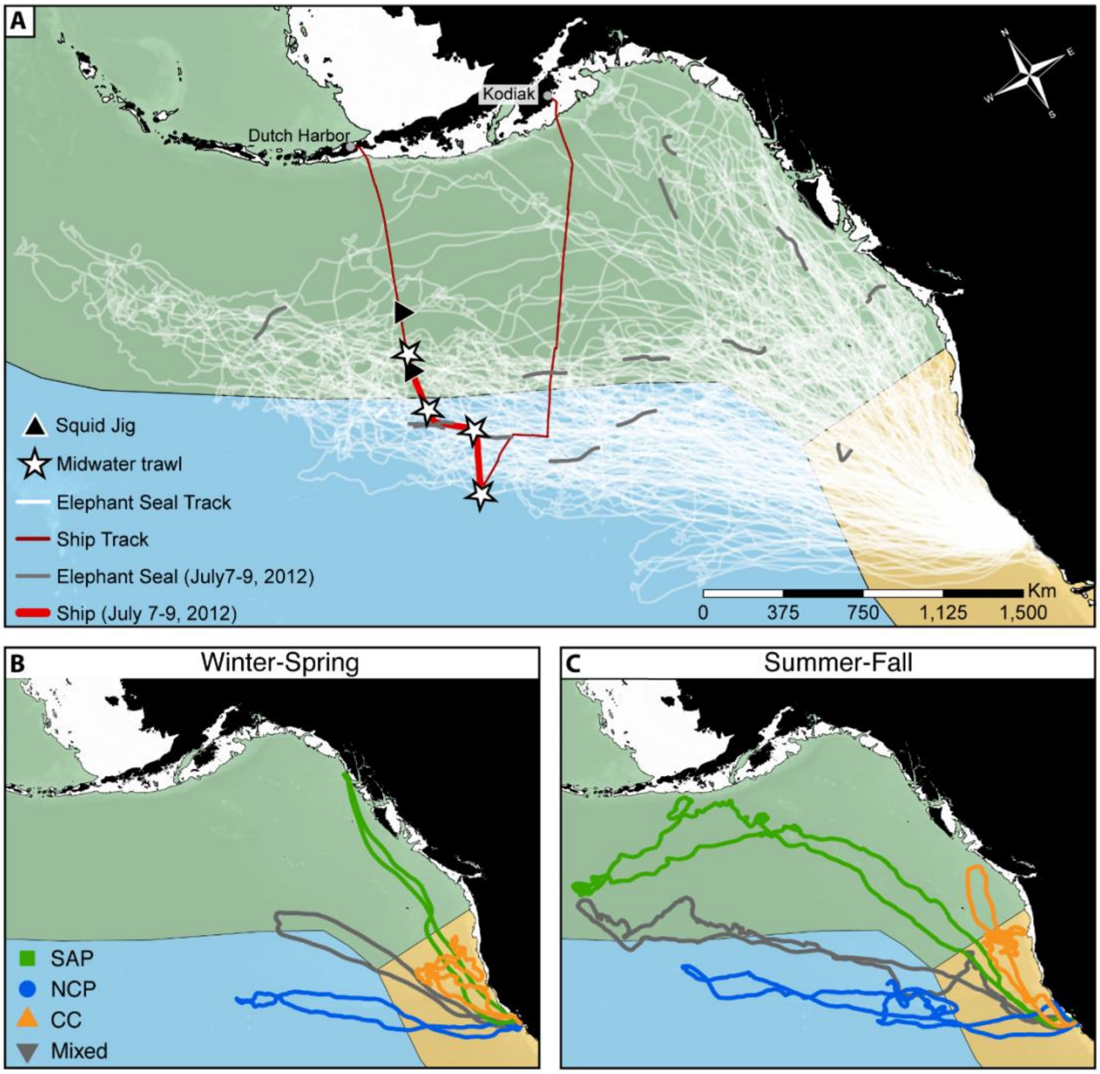

Figure 2.1 (A) Locations of midwater trawls (4) and squid jigs (2) where prey samples were collected for the QFASA prey library and transect the Subarctic Pacific (green) and North Central Pacific (blue) biogeographic provinces (California Current province: orange). The period of July 7-9, 2012, during which trawls were conducted, is shown for the ship track (thick red line) and concurrently tagged female northern elephant seals (grey lines). Tracks of study seals (n = 131; 2005-2006, 2010-2012) depict their foraging range across the eastern North Pacific. Representative tracks depicting the spatial foraging strategies of female seals: Subarctic Pacific (SAP); North Central Pacific (NPC), California Current (CC), and Mixed for the **(B)** Winter-spring and **(C)** Summer-fall foraging trips.

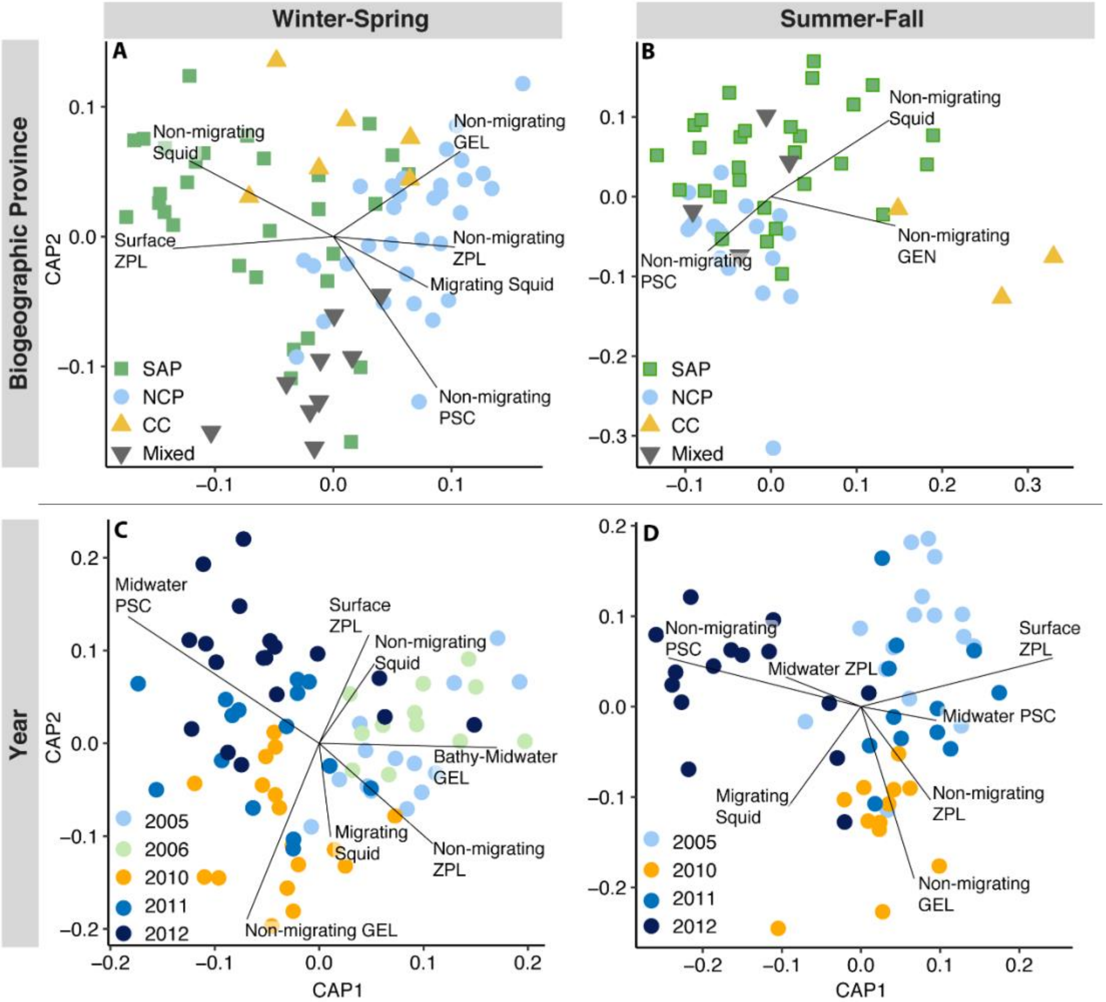

Figure 2.2 Canonical analysis of principle coordinates (CAP) of female northern elephant seal diets during the winter-spring and summer-fall foraging migrations by biogeographic province (**A** and **B**) and year (**C** and **D**). Black lines show the prey functional groups that significantly drive (r > 0.3, Pearson's correlation) diet differences between seals and are scaled to fit the range of the CAP values. For example, in panel A, Subarctic Pacific foragers (SAP, green squares) consumed greater amounts of non-migrating squids and surface migrating zooplanktivores (ZPL) than North Central Pacific foragers (NCP, blue squares) during the winter-spring foraging trip. For exact percentages of significant function groups contributing to the diet differences of seals foraging in different provinces and years, refer to Tables 3 and 4, respectively. Prey abbreviations: ZPL – zooplanktivore, GEL – gelativore, PSC – piscivore, GEN – generalist.

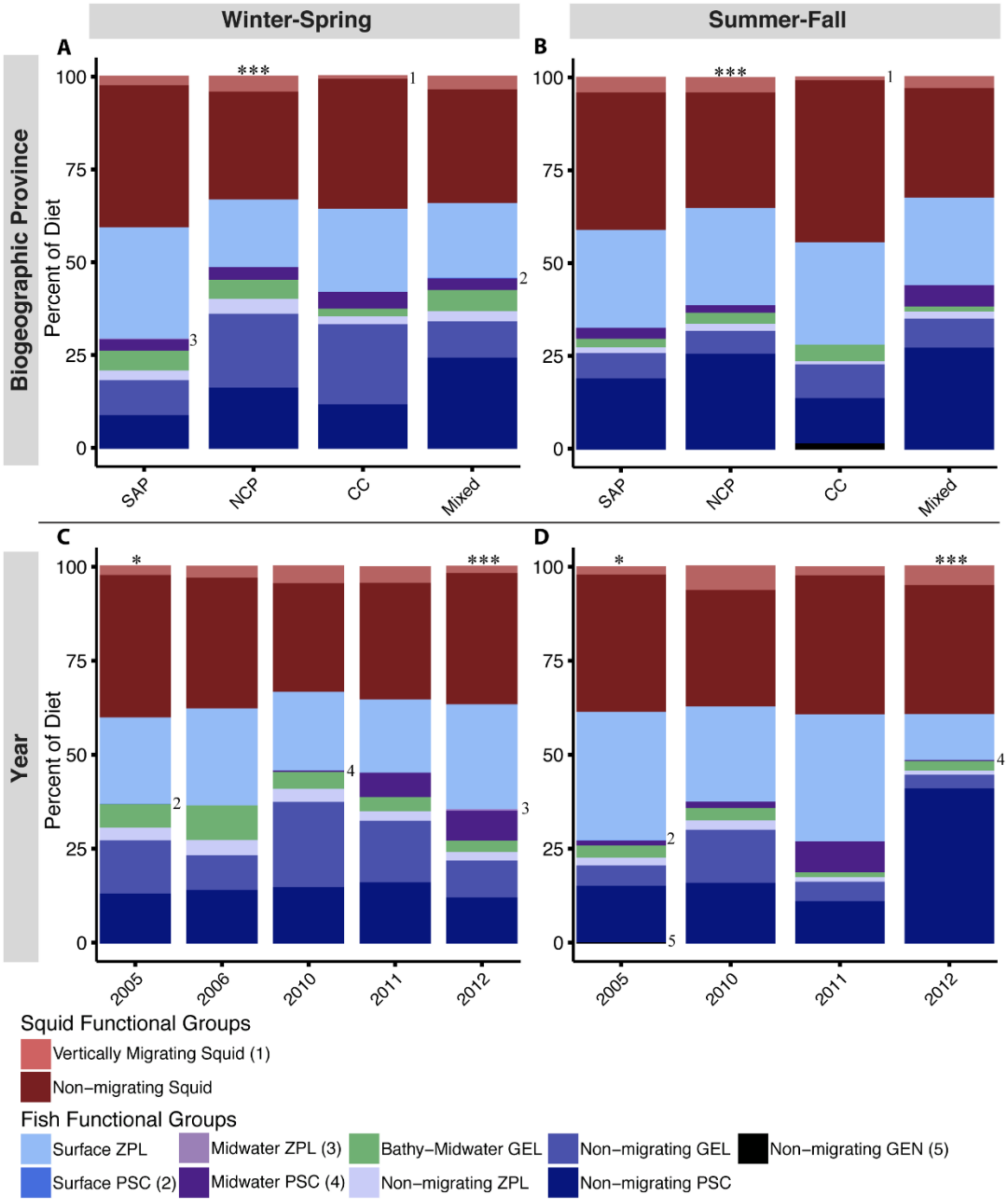

Figure 2.3 Diet composition by functional group as determined by QFASA of adult female northern elephant seals during the winter-spring and summer-fall foraging migrations by biogeographic province (**A** and **B**) and year (**C** and **D**). Numbers identify functional groups present in small quantities (see legend for cross-reference). Asterisks refer to significant differences in diet between foraging trips within the same province or year (* $p < 0.05$, *** $p < 0.001$). Refer to Tables 2.3 and 2.4, respectively, for percentages of functional groups that significantly contributed to diet differences between groups of seals. For percent occurrence of all functional groups and prey species in seal diet by province and year see Tables A1.1-A1.4.

CHAPTER 3

Vertical Foraging Strategies Reflect Spatiotemporal Differences in Diet for a Mesopelagic Predator

Chandra Goetsch, Elliott L. Hazen, Melinda G. Conners, and Daniel P. Costa

3.1 Abstract

Intraspecific foraging niche partitioning is a well-documented ecological pattern that can serve to reduce competition among conspecifics as well as buffer populations against environmental change. Furthermore, individual variation in foraging strategies may be particularly important for long-lived top predators, allowing populations to respond when adverse or atypical conditions result in decreases in the abundance or availability of preferred prey. Studies evaluating foraging strategies of wide-ranging predators tend to be highly localized on a small subset of the population and rarely include data on foraging behavior and diet composition that encompasses the entirety of their foraging range. Northern elephant seals (*Mirounga angustirostris*), wide-ranging marine predators, displays intraspecific niche partitioning in foraging behavior that is to spatiotemporal variation in their horizontal and vertical foraging habitat. To define horizontal and vertical foraging strategies for female elephant seals, we analyzed diving and movement behavior from biologging instruments. Using diet estimates for northern elephant seals derived from quantitative fatty acid signature analysis (QFASA), we tested whether individual foraging strategies were correlated with diet composition or diet specialization. We found northern elephant seals were foraging generalists, displaying individual flexibility in both vertical foraging

behavior and diet composition. The flexibility in foraging tactics of elephant seals is likely linked to broad-scale spatiotemporal variation in the deep ocean environment, especially the oxygen minimum zone (OMZ). This high level of foraging plasticity may increase the resilience of seals to changes in environmental conditions and is likely one of the factors that facilitated the recovery of northern elephant seals from near extinction.

3.2 Introduction

Intraspecific competition occurs when individuals within a population vie for the same resources in both time and space. However, competition can be reduced if groups within a population specialize with regard to resource use or resource acquisition (e.g. diet or foraging behavior) in order to maximize foraging success (Gause, 1934). Partitioning of resources, or niche partitioning, may occur via differences in prey selection, habitat use, and patterns in the timing of foraging events (Bolnick et al., 2003; Cristescu et al., 2013; Kronfeld-Schor and Dayan, 2003; Schoener, 1974). This phenomenon is frequently observed highly sexual dimorphic species and across ontogeny (LeBoeuf et al., 2000; Ruckstuhl, 2007; Selander, 1966; Shine, 1989; Werner and Gilliam, 1984). Likewise, niche partitioning is also expected in populations that forage in dynamic environments where prey tend to be patchily distributed, such as seen in marine ecosystems (Levin and Whitfield, 1994; Medvinsky et al., 2001). From this perspective, specialization of individuals within a population is merely a fine-scale extension of intraspecific niche partitioning (Araújo et al., 2011; Bolnick et al., 2003; Turcotte and Levine, 2016; Violle et al., 2012).

Even generalist species with a broad population-level foraging niches may be composed of many individuals with non-overlapping niches, each using only a portion of the population's available niche (Bolnick et al., 2003; 2007; Newsome et al., 2012). A combination of parameters including diet composition, vertical and horizontal habitat, and diel patterns in foraging bouts has been used to define intraspecific niches and detect the presence of multiple foraging strategies within populations of generalist species (Baylis et al., 2015; Hückstädt et al., 2012; Jeglinski et al., 2013; Kernaléguen et al., 2015a; 2015b; Tinker et al., 2008; Villegas-Amtmann et al., 2008; Weimerskirch et al., 1997).

Ecological research has typically focused on population-level behavior, ignoring differences among individuals (Bolnick et al., 2011; Grant and Price, 1981; Roughgarden, 1972). Yet, individual variation in diet and foraging behavior has implications for individual survival and reproductive fitness, as well as more accurately representing the population and community dynamics (Bolnick et al., 2011; Johnson et al., 2009; Schreiber et al., 2011; Sherratt and MacDougall, 2008)Intraspecific variation in foraging niches may influence a population's ability to adapt behaviorally or evolutionarily to changing environmental conditions and may increase resilience to environmental perturbations (Davidson et al., 2012). Species that are highly specialized at the population level and lack variability at the individual level may not be able to adapt rapidly to novel conditions (Bolnick et al., 2003; Pistevos et al., 2011). However, generalist species with high levels of individual specialization that exhibit multiple foraging strategies may be less vulnerable to environmental changes, like extreme climate events and habitat degradation, or population crashes due to disease and over-exploitation (Abrahms et al., 2018; Gallagher et al., 2015). Individual variation in foraging strategies may be particularly important for long-lived top predators, because variability within the population may serve to buffer that population during periods in which preferred prey are scarce or unavailable (Polito et al., 2015; Pusineri et al., 2008).

Female northern elephant seals (*Mirounga angustirostris*) are deep-diving marine predators that forage across the eastern North Pacific (LeBoeuf et al., 2000; Robinson et al., 2012), and their vast foraging range encompasses three mesopelagic biogeographic provinces: the Subarctic Pacific, the North Central Pacific, and the California Current (Sutton et al., 2017). The foraging dives of female northern elephant seals follow a clear diel pattern that matches the daily vertical migrations of the deep acoustic scattering layers (Figure 3.1A), which contain the majority of deep ocean biomass, including fishes and squids (Irigoien et al., 2014; Kaartvedt et al., 2012; Klevjer et al., 2016). The vertical distribution of the prey in the deep scattering layers varies across the biogeographic provinces as a function of oceanographic conditions, including sunlight attenuation and dissolved oxygen concentration (Klevjer et al., 2016; Koslow et al., 2011; 2014; Netburn and Koslow, 2018).

Female elephant seals display evidence of intraspecific niche partitioning in foraging behavior related to spatiotemporal variation in their horizontal and vertical foraging habitat. Many female seals focus their foraging efforts in particular biogeographic provinces, demonstrating evidence of spatial foraging strategies within the population (Chapter 2). In addition, some female seals exhibit high interannual site fidelity to their foraging route, while others display more behavioral flexibility and vary their foraging routes year-to-year (Abrahms et al., 2018; Maxwell et al., 2012; Simmons, 2008). Individuals with high foraging site fidelity may be less specialized in diet if they consume prey that is abundant along their foraging route (Banks et al., 2014; Naito et al., 2013); whereas, seals with low site fidelity may have more specialized diets if they are tracking specific prey types. Vertical foraging behavior shows similar signs of distinct foraging strategies, with some seals displaying consistent bimodal and trimodal distributions of foraging dive depth during the day (Robinson et al., 2012). These diving patterns may be indicative of foraging strategies that target particular prey types (i.e. diet specialization) or track the spatial variation in prey distribution among provinces. Indeed, elephant seal foraging strategies may be due to a combination of horizontal and vertical foraging niche partitioning, as seals respond to changes in prey distribution across their foraging range (Chapter 2). Evidence for individual foraging strategies been found in a wide range of marine predators, including seabirds, marine mammals, sharks, and squids, but has not been evaluated for northern elephant seals (*Mirounga angustirostris*) (Baylis et al., 2015; Field et al., 2001; Hückstädt et al., 2012; Kim et al., 2012; Lorrain et al., 2011; Lowther and Goldsworthy, 2011; McHuron et al., 2016; Tinker et al., 2007; Villegas-Amtmann et al., 2008).

We used movement and dive data from biologging instruments to quantify multiple foraging strategies for female northern elephant seals, and, then, examined the links between foraging strategy and diet composition. Our specific objectives were to (1) identify and describe vertical foraging strategies for female seals, (2) examine the spatial patterns in the prevalence of these strategies, (3) determine whether spatial and seasonal variation in vertical foraging strategies was related to similar spatiotemporal patterns in foraging route and diet composition, (4) quantify the degree of individual diet specialization, and (5) determine if the degree of individual diet specialization was associated with either vertical or horizontal foraging strategies. Understanding elephant seal diet and foraging strategies in relation to spatiotemporal variation in the horizontal and vertical distribution of prey in the deep ocean may offer insights to the success and resilience of this deep-diving predator.

3.3 Materials and Methods

3.3.1 Elephant Seal Sampling

We examined the relationship between foraging dive behavior and diet composition by instrumenting adult female northern elephant seals (n = 122) with time-depth recorders and satellite transmitters during 2005-2006 and 2010-2012 at Año Nuevo State Reserve, CA. Diving and movement behavior was recorded for the winter-spring (n = 74) and summer-fall (n = 48) foraging trips (see Chapter 2 for details). Upon each seal's return to the colony, we recovered the bio-logging instruments and collected a 6 mm blubber biopsy for lipid analysis. Methods for seal immobilization, attachment and recovery of bio-logging devices, and tissue sampling followed established protocols (Robinson et al., 2012; Chapters 1 and 2).

3.3.2 Diet Determination

Elephant seal diet composition was estimated with quantitative fatty acid signature analysis (QFASA) (package qfasar in R v.3.4.1, R Core Team), using calibration coefficients specific to adult female northern elephant seals and a library of mesopelagic prey fatty acid (FA) profiles (Goetsch et al., 2018). Detailed methods on prey sample collection, lipid analysis, and QFASA diet estimation are described in Goetsch et al. (2018). Three key prey functional groups were found to contribute most to the differences in spatiotemporal differences in elephant seal diet: (1) surface migrating zooplanktivores, (2) non-migrating piscivores, and (3) non-migrating squid (Chapter 2). These functional groups represent fauna from three corresponding vertical midwater habitats: (1) migrating species associated with the upper boundary of the oxygen minimum zone (OMZ), (2) non-migrating species associated with the lower OMZ boundary, and (3) species that largely remain within the core of the OMZ, respectively.

To summarize broad-scale spatial patterns in diet and the degree of diet specialization at the level of a foraging trip, individual seals were classified to a primary foraging province (Subarctic Pacific, using a modification to the methodology from Chapter 2 which used total time spent in a province as a proxy for foraging. In this study, we classified individual seals to a foraging province if > 50%

of that seal’s total forage dives were in that province. Since we were primarily interested in examining trip-level differences among province, seals that did not have greater than 50% of their foraging dives in a single province (n = 7) were excluded from the these broad-scale summaries. The mean and standard deviation of the proportion of the key prey functional groups in the diet were recalculated for each province according to the updated classifications (Table 3.1).

3.3.3 Diving and Movement Data Processing

Diving and satellite location data were processed and standardized using established filtering and interpolation techniques and dives georeferenced using their respective satellite track (Robinson et al., 2012). Dives were first classified into four types with associated putative behavior using a forced-choice dive typing protocol: active-bottom dives (pelagic foraging), U- or V-bottom dives (transit), flat-bottom dives (benthic foraging/transit), drift dives (resting/food processing) (custom function in Matlab, Robinson et al., 2012). We then separated the non-foraging (U-shaped) dives from foraging (V-shaped) dives, using a threshold value of 1.3 of the benthic index, a parameter calculated as part of the dive typing algorithm. Previously published jaw accelerometer data (Naito et al., 2013) was used on a subset of females (n = 4) to verify that shallow, U-shaped dives were mostly non-foraging (0-1 jaw motion events), while deep, V-shaped dives had > 2 jaw motion events, indicating foraging activity. The benthic index accurately sorted these dive types > 80% of the time. Detailed methods on the collection and analysis of the jaw accelerometry data are described in Naito et al. (2013 and 2017).

3.3.4 Classification of Vertical Foraging Strategies

Midwater foraging dives (active bottom and V-shaped dives) were classified spatially (ArcGIS, v.10.5.1, ESRI Inc) to one of three mesopelagic biogeographic provinces: the Subarctic Pacific, the North Central Pacific, and the California Current (Sutton et al., 2017). As we were focused on the behavior and diet of seals foraging in the mesopelagic ocean, we excluded dives occurring over the continental shelf. Female elephant seals display a diel foraging pattern (LeBoeuf et al., 1986; 2000; Robinson et al., 2012), so we further classified all foraging dives as day, twilight, or night using the solar zenith angle at the time of each dive (Figure 1A). To examine vertical patterns in forage dive behavior, we used an optimal k-means univariate cluster analysis on the depth of day, twilight, and night dives (package Ckmeans.1d.dp in R v.3.4.1, R Core Team). Cluster analysis on day foraging dives resulted in three optimal depth clusters (hereafter, vertical foraging strategies): (1) surface to upper mesopelagic (hereafter, shallow), (2) middle to lower mesopelagic (hereafter, mid-depth), and 3) lower mesopelagic to bathypelagic (hereafter, deep). Twilight foraging dives did not display multiple vertical foraging strategies and night foraging dives resulted in 29 vertical strategies (see Results section); therefore, further analyses to assess the relationships between diet and vertical foraging behavior were limited to the clearly stratified day foraging dives.

3.3.5 Individual Diet Specialization and Site Fidelity

We determined degree of specialization in diet for each individual seal by calculating the proportional similarity index (PSI) which compares how similar the diet composition of an individual is to the population-level diet (Bolnick et al., 2002; Roughgarden, 1972; Tinker et al., 2012). PSI values close to one indicate a diet generalist or seals with diets that are highly similar to the average population diet, while PSI values close to zero indicate diet specialists with diets that overlap less with the population-level diet.

To assess whether seals with more specialized diets had higher interannual site fidelity, we used a site fidelity index previously calculated for a subset (n = 24) of our study animals (Abrahms et al., 2018). This index used Bhattacharya's affinity metric (BA index, 0-1) to quantify the degree of overlap in the 95% kernel density utilization distribution for individual seals that were tracked in two or more years during the summer-fall migration. We used this site fidelity index as a measure of horizontal niche specialization in interannual migration patterns. Seals with a BA index value close to 1 had high interannual foraging site fidelity, while seals with a BA index close to 0 had low interannual site fidelity.

3.3.6 Statistical Analyses

Spatial and temporal variation in elephant seal diet is dependent upon the season of the foraging migration (Chapter 2); therefore, we conducted all analyses separately for winter-spring (n = 74 seals) and summer-fall (n = 48 seals) foraging migrations. Dive data from seals that were previously excluded from the broad-scale diet summaries, were included for all analyses conducted at the scale of foraging dive location. To determine whether variation in the depth of day and night foraging dives was associated with the spatial location (province) of the dive, the individual seal, or other factors (residual), we conducted a variance components analysis, using random effects linear models (package lme4, R Core Team). Then, we tested whether certain daytime vertical foraging strategies were more associated with specific biogeographic provinces. To accomplish this, we calculated the proportion of dives of each foraging strategy (shallow, mid-depth, and deep) from the total of day foraging dives that took place in that province. ANOVA tests were conducted to determine whether certain vertical foraging strategies were more prevalent in certain provinces. Then, we tested whether diet composition (i.e. the proportion of key prey functions groups in the diet) was correlated with the prevalence of vertical foraging strategies. Since, both vertical foraging strategies and diet composition are dependent upon spatial and seasonal factors, we tested for vertical foraging strategy correlations separately within each biogeographic province by season using linear regression models. If the proportion of foraging dives in a strategy was < 0.05 for a particular province, we excluded that province from the model. Outliers were also excluded.

To examine the influence of the degree of diet specialization on vertical foraging strategies, we conducted a series of tests at two scales: (1) the level of the trip with individual seals classified to a primary foraging province based on where the majority of their foraging dives occurred, and (2) the level of dive location with all foraging dives spatially classified to a province. At the trip level, we tested whether seals that primarily foraged in certain provinces were more or less specialized in diet than seals foraging in a different province. At the level of dive location, we tested within each province to determine if vertical foraging strategies were associated with the degree of individual specialization (PSI), using linear regression. Finally, we used linear regression to test whether seals with high foraging site fidelity were also diet specialists. Unless otherwise specified, all analyses were conducted in the R statistical computing program (R Core Team) and results were considered significant if p-values were < 0.05.

3.4 Results

3.4.1 Spatial Variability in Diet: Key Prey Functional Groups

Whether seals were classified according to total time spent in a province or the number of foraging dives within a province, the spatiotemporal differences in the consumption of the key functional groups (surface migrating zooplanktivores, non-migrating piscivores, and non-migrating squids) remained the same, as did the differences in the consumption of those prey groups between the two foraging trips (Chapter 2, Table 3.1).

3.4.2 Variation in Foraging Dive Behavior

We identified 681,337 total foraging dives, 77% of all dives, which was slightly less than the 80-91% reported as foraging dives based on jaw movements (Naito et al., 2013). A diel pattern was apparent in forage dive depths (Figure 1A), which was consistent with previous studies (LeBoeuf et al., 1986; 2000; Naito et al., 2013; Robinson et al., 2007). More foraging dives occurred at night (46% of all forage dives) than day (40%) with the remainder occurring during twilight hours (14%) (Figure 1). Day foraging dives exhibited three distinct vertical foraging strategies (clusters explained 78.4% of the variation in dive depth): shallow day dives (n = 37,591 cluster center = 394.1 m), mid-depth day dives (n = 190,448, center = 639.5 m), and deep day dives (n = 44,189, center = 840.9 m, Figure 1B). Twilight foraging dives had no distinct clustering pattern (n = 190,448, center = 532.0 m, Figure 1C). However, night foraging dives displayed the most variation in dive depth with 29 optimal clusters (Figure 1D). During the night, 14 clusters occurred within the depth range of the day shallow clusters, with nearly 5 times the total number of shallow day forage dives (181,431 dives). There were also 9 night clusters that occurred within the depth range of the day mid-depth cluster, accounting for 112,155 dives. Though more infrequent, there were 6 night clusters (n = 7,178 dives) that covered the range of deep day foraging dives, indicating that some seals still foraged in the deep mesopelagic and bathypelagic even at night. Variation in day and night foraging dive depths was due to dive location (> 95% of variance explained), rather than individual seal (< 1% of variance explained), or other factors (unexplained error: < 5%, Table 3.2).

3.4.3 Spatiotemporal Variability in Vertical Foraging Strategies

Day vertical foraging strategies displayed distinct patterns among provinces and between seasons (Figures 3.2 and 3.3). During the winter-spring foraging trip, seals utilized the shallow foraging strategy more frequently when in the Subarctic Pacific (0.21 ± 0.18, $p < 0.001$) and the California Current (0.21 ± 0.13, $p < 0.001$) than when they foraged in the North Central Pacific (0.04 ± 0.11; Table 3.3 and Figure 3.3A). The same spatial pattern was evident during the summer-fall trip ($p < 0.001$ for both,

Table 3.3 and Figure 3.3B), but the proportion of shallow dives within the Subarctic Pacific for the summer-fall (0.11 ± 0.13) was half that seen in the winter-spring (Table 3.3 and Figure 3.3B). The mid-depth foraging strategy was the most common regardless of province or season (Table 3.3 and Figure 3.3).

During the winter-spring trip, when seals foraged in the California Current, they used the mid-depth foraging strategy more frequently (0.74 ± 0.11) than when they foraged in either the Subarctic Pacific (0.66 ± 0.20) and the North Central Pacific (0.62 ± 0.23. $p < 0.05$ and 0.01, respectively; Table 3.3 and Figure 3.3A). However, during the summer-fall trip, this pattern changed. The proportion of mid-depth foraging dives increased when seals foraged in the North Central Pacific, while the proportion of mid-depth dives in the other two provinces remained similar to that seen during the winter-spring trip (Table 3.3 and Figure 3.3B). Thus, when seals foraged in the North Central Pacific they utilized a mid-depth strategy more often (0.79 ± 0.14) than when they foraged in the Subarctic Pacific (0.68 ± 0.19) or the California Current (0.74 ± 0.14). However, this relationship was only significant between mid-depth dives in the North Central Pacific and the Subarctic Pacific, as neither of these differed significantly from the California Current in this season (Table 3.3 and Figure 3.3B).

During the winter-spring trip, seals used the deep foraging strategy most frequently when they foraged in the North Central Pacific (0.33 ± 0.23); however, the proportion of deep foraging dives differed among all provinces ($p < 0.05$). In contrast, during the summer-fall trip, the use of the deep foraging strategy in the North Central

Pacific was half as frequent (0.17 ± 0.14) as during the winter-spring trip. In addition, during the summer-fall trip, the frequency of deep dives increased when seals foraged in the Subarctic Pacific (0.21 ± 0.19 in the summer-fall versus 0.13 ± 0.16 in the winter-spring) making the prevalence of the deep foraging strategy comparable between these provinces (Table 3.3, Figure 3.3). However, in the winter-spring, when seals in the Subarctic Pacific did forage deeply, they dived deeper than those in the other two provinces ($p < 0.05$, Figure 3.2). The frequency of the deep diving strategy was low in the California Current during both foraging migrations (Table 3.3, Figures 3.2 and 3.3).

3.4.4 Vertical Foraging Strategies and Diet

Shallow foraging strategy and diet

When seals foraged in the North Central Pacific during the winter-spring foraging trips, they utilized the shallow foraging strategy for 5% or less of their foraging dives (Table 3.3), thus this strategy was not examined for correlations with diet. When seals foraged in the Subarctic Pacific and the California Current (CC), the prevalence of the shallow foraging strategy increased as the seals consumed more surface migrating zooplanktivores (Subarctic: df = 47; CC: df = 71; $p < 0.001$, $R^2 = 0.21$, for both; Figure 3.4A). Conversely, in the Subarctic Pacific as the prevalence of the shallow foraging strategy increased, seals consumed less non-migrating piscivores ($p < 0.01$, $R^2 = 0.15$, Figure 3.4B), but this pattern was not significant in the California Current. Finally, as seals utilized the shallow foraging strategy more frequently, they also consumed more non-migrating squid in both the Subarctic

Pacific and the California Current (Subarctic: $p < 0.01$, $R^2 = 0.15$; CC: $p < 0.001$, $R^2 = 0.15$, Figure 4C).

During the summer-fall, the relationship between the shallow foraging strategy and the consumption surface migrating zooplanktivores disappeared within both provinces (Figure 4D) as well as for the consumption non-migrating piscivores (Figure 4E). However, the positive relationship between the shallow foraging strategy and the consumption of non-migrating squid remained in the Subarctic Pacific (df = 44, $p < 0.001$, $R^2 = 0.46$, Figure 4F).

Mid-depth foraging strategy and diet

During the winter-spring foraging trip, when seals increased their use of the mid-depth foraging strategy in the Subarctic Pacific and the California Current provinces, their consumption of surface migrating zooplanktivores decreased (Subarctic: df = 47, $p < 0.01$, $R^2 = 0.15$; CC: df = 71, $p < 0.001$, $R^2 = 0.15$; Figure 3.5A). However, there was no relationship between the prevalence of the mid-depth strategy and the consumption of surface migrating zooplanktivores in the Subarctic Pacific province (Figure 3.5A). Similarly, no relationship was seen during the winter-spring trip between the mid-depth foraging strategy and the consumption of non-migrating piscivores for any province (Figure 3.5B). There was, however, a negative relationship between the mid-depth foraging strategy and the consumption of non-migrating squid in both the Subarctic Pacific and the California Current (Subarctic: $p < 0.05$, $R^2 = 0.08$; CC: $p < 0.01$, $R^2 = 0.11$; Figure 3.5C).

During the summer-fall foraging trip, there were no significant relationships between the mid-depth foraging strategy and the consumption of surface migrating zooplanktivores or non-migrating piscivores for any province (Figure 3.5D and E). However, the same negative relationship seen during the winter-spring trip between the mid-depth foraging strategy and the consumption of non-migrating squid was still evident in the Subarctic Pacific during the summer-fall (df = 43, $p < 0.01$, $R^2 = 0.17$), but was no longer evident in the California Current (Figure 3.5F).

Deep foraging strategy and diet

For both seasons, when seals foraged in the California Current, less than 5% of their foraging dives were deep (Table 3.3); therefore, we did not test for correlations between the deep foraging strategy and diet composition. During the winter-spring foraging trip, the only relationship seen between the deep diving strategy and diet composition occurred in the Subarctic Pacific (Figure 3.6). In that province, as seals dived deep more frequently, they consumed more non-migrating piscivores (df = 17, $p < 0.05$, $R^2 = 0.08$), but no relationships were seen between the other two prey functional groups tested (Figure 3.6B). During the summer-fall trip, there were no significant correlations between vertical foraging strategy and diet in any province (Figure 3.6).

3.4.5 Diet Specialization

The degree of similarity between an individual's diet and the average population-level diet varied widely for northern elephant seals (PSI: 0.15 – 0.08; Figure 3.7A). The majority of seals had a PSI value > 0.5, indicating that they were mostly diet generalists. However, 20 individuals (16% of 122 females) had PSI values < 0.5, indicating a higher degree of individual diet specialization (Figure 3.7A). Two had PSI values < 0.3, indicating highly specialized diets. There was no pattern to diet composition for seals with specialist diets (PSI < 0.5). The two most specialized individuals (Seal 1733 and Seal U203) consumed moderate proportions of non-migrating squid (0.33 and 0.39, respectively), within average levels (0.33 ± 0.9) seen for the population. Seal 1733 consumed the highest proportion of surface migrating and non-migrating zooplanktivores, while Seal U203, consumed the third highest amount of non-migrating zooplanktivores. Both of their diets were limited to three of the eleven functional groups. The other seals with a high degree of diet specialization generally consumed higher proportions of non-migrating squid (> 50%). One specialist individual consumed more vertically migrating squid (22%) than any other seal.

Spatial variability in diet specialization

There was no difference between seasons for the degree of individual specialization overall. Of the two extreme specialists, one foraged in the winter-spring and the other during the summer-fall. Within the winter-spring there were differences in the degree of specialization between seals foraging primarily in different provinces (Figure 3.7B and C). Seals that foraged in the Subarctic Pacific had lower PSI values, showing a greater degree of individual diet specialization than seals that primarily foraged in the North Central Pacific ($p < 0.05$). However, there were no differences in PSI values between provinces during the summer-fall migration.

Vertical foraging strategies and diet specialization

During the winter-spring trip, the only correlation seen between vertical foraging strategy and diet specialization occurred in the Subarctic Pacific. When seals foraged shallow more frequently, individual diet became more specialized (df = 47, $p < 0.05$ $R^2 = 0.13$, Figure 3.8A). During the summer-fall foraging trip, the relationship between the shallow foraging strategy and individual diet specialization was evident for both the Subarctic Pacific (df = 44, $p < 0.01$, $R^2 = 0.21$) and the California Current (df = 46, $p < 0.01$ $R^2 = 0.15$; Figure 3.8D). In addition, there was also a positive relationship between the mid-depth foraging strategy and diet specialization, so as seals increased mid-depth foraging, individuals had less specialized diets. However, this relationship only occurred for seals foraging in the California Current (Figure 3.8E). No relationships were evident between the deep foraging strategy and diet specialization in any province or season (Figure 3.8C and F).

Degree of diet specialization and site fidelity

The degree of dietary specialization was not correlated with site fidelity, indicating that seals that tend to return to the same oceanographic province to forage are not dietary specialists ($p > 0.05$, Figure 3.9).

3.5 Discussion

3.5.1 Vertical Foraging Behavior Varies on Multiple Scales

We found clear vertical stratification of both day and night foraging dives likely attributed to diel variation in prey depth within the deep scattering layers. We only found three daytime foraging dive clusters – shallow, mid-depth, and deep foraging strategies, but there were nearly 3 times as many foraging depth clusters at night. This suggests that there is less variation in the vertical stratification of prey in the deep scattering layers during the day despite spatial and seasonal differences among provinces. The increased variation in the depth of night foraging dives is likely associated with differences in diel migration patterns of prey. For example, some species of myctophids migrate to within 20 m of the surface, while others stay below 60 or 100 m in depth (Beamish et al., 1999; Brodeur et al., 2003). Timing of the start and rate of diel migration also differs among species within the deep scattering layers (Bianchi and Mislan, 2015; Bianchi et al., 2013). All of these factors can vary spatially and temporally. For example, vertically migrating fish in the North Central Pacific are distributed deeper in the water column during the day than migrating fish in the Subarctic Pacific (Gallo and Levin, 2016; Klevjer et al., 2016). Consequently, prey in the North Central Pacific must travel further to reach the surface, resulting in earlier onset of migration at night and faster rates of migration than in the Subarctic Pacific (Bianchi and Mislan, 2015). The high variation in the night migration behavior of prey within the deep scattering layers is a likely explanation for the increased variation in night foraging dive depths of elephant seals and may explain why there was no clear spatiotemporal pattern for night dives.

3.5.2 Diet, Vertical Foraging Strategies, and the Oxygen Minimum Zone (OMZ)

Elephant seal diet composition varies with these spatiotemporal patterns in the OMZ due to its influence on the vertical distribution and abundance of prey in the deep scattering layers (Bianchi and Mislan, 2015; Klevjer et al., 2016; Netburn and Koslow, 2015; Chapter 2). Particular prey functional groups are associated with vertical microhabitats created by these variations in the vertical location and relative intensity of the OMZ (Gallo and Levin, 2016; Gilly et al., 2013; Maas et al., 2014; Netburn and Koslow, 2015). Vertically migrating species, such as myctophids, tend to associate with the upper boundary of the OMZ and, if that boundary is sufficiently shallow, can become densely-packed in an effort to avoid visual predators while still having access to sufficiently oxygenated water (Gilly et al., 2013; Koslow et al., 2011; Whitney et al., 2007). In contrast, non-migrating species, such as piscivorous viperfishes, tend to associate with the lower boundary of the OMZ, which in some locations can extend deeper than the typical foraging depths (~600m) for female elephant seals. We found that on broad scales, diet differences for female northern were correlated with vertical foraging strategies, as predicted by previous work that related diet to spatial variation in the OMZ and deep scattering layers (Naito et al., 2017, Chapter 2). Nearly all significant relationships between vertical foraging strategies and diet occurred during the winter-spring foraging trip, so we restrict our discussion to that time period.

The Subarctic Pacific

During the winter-spring, an intense, seasonal shoaling and thickening of the OMZ occurs in the Subarctic Pacific province (~ 300 m upper boundary, lower boundary > 1,000 m) (Gallo and Levin, 2016; Moffitt et al., 2015; Paulmier and Ruiz-Pino, 2009). In the Subarctic Pacific, the migrating layer is compressed during the day between sunlight from above and the anoxic waters below (Gilly et al., 2013; Koslow et al., 2011; Whitney et al., 2007), making this functional group an easy target for foraging elephant seals (Chapter 2). Overall, we found that the proportion of dives in the shallow foraging strategies was higher in this province than the North Central Pacific, mirroring the expected distribution of the deep scattering layers. The amount of deep foraging dives in the Subarctic Pacific during the winter-spring was lower than in the North Central Pacific during this season. Female seals that forage in the Subarctic Pacific in the winter-spring consume large quantities of surface migrating zooplanktivores and lower quantities of non-migrating piscivores (Chapter 2). As consumption of surface migrating zooplanktivores increased, we found a corresponding increase in the frequency of the shallow foraging strategy, supporting our hypothesis that female seals exhibit shallower foraging behavior when foraging in the Subarctic Pacific. Correspondingly, we observed the opposite relationship for the mid-depth foraging strategy: as the frequency of mid-depth dives increased, the consumption of migrating prey decreased providing further support for our hypothesis. In addition, with the thickening of the OMZ in this province, the lower boundary where non-migrating fishes congregate becomes deeper, which may make it less energetically advantageous for seals to forage on non-migrating prey. Generally, the non-migrating piscivore functional group is not prevalent in the diet of seals foraging in the Subarctic Pacific during the winter-spring (Chapter 2, Table 3.1). However, when this functional group was consumed, it was correlated with a decrease in the frequency of shallow foraging dives and an increase in deep foraging dives, indicating that seals were foraging deeper to access non-migrating fishes in the Subarctic Pacific. For, non-migrating meso-bathypelagic squid, which tend to associate with the lower oxygen core of the OMZ, increased consumption was linked to an increase in the frequency of the shallow foraging strategy and decrease in the mid-depth foraging strategy. This may be due to an expanded vertical range for these squids concurrent with the expanded low oxygen core of the thick OMZ. Thus, non-migrating squids may be located at shallower depths in this province than would otherwise be expected. Little is known about spatial patterns in the vertical distributions of non-migrating squid species (Hoving and Robison, 2017), so this cannot be stated with certainty and bears further investigation.

The North Central Pacific

In contrast to the Subarctic Pacific in the winter-spring, the OMZ in the North Central Pacific is considerably deeper (~ 500 m upper boundary depth) and considerably narrower than in the Subarctic Pacific (Moffitt et al., 2015). The deeper location of the OMZ in this province would allow vertically migrating fish to be more dispersed, because they would have more oxygen-rich habitat from which to escape visual predators during the day (Bianchi et al., 2013). We found that seals utilized the deep foraging strategy more frequently here than either the Subarctic Pacific or the

California Current, with negligible use of the shallow foraging strategy. The scarcity of the shallow foraging strategy for seals foraging in the North Central Pacific is consistent with the lower consumption of migrating prey than seen in the other provinces (Chapter 2). However, we found no strong correlations between particular prey groups and the frequency of mid-depth or deep foraging strategies here, perhaps indicating that when the migrating prey disperse more deeply in the water column, the vertical stratification of prey functional groups in the deep scattering layers is decreased. As the vertical stratification of prey declines, we would not expect a vertical foraging strategy to be associated with particular prey.

The California Current

The pelagic California Current is characterized by a shallow OMZ (~300-400 m), created by intense upwelling processes within the eastern boundary current (Bograd et al., 2008; Chan et al., 2008; Klevjer et al., 2016; Urmy and Horne, 2016), making its vertical structure similar to that of the Subarctic Pacific. Further, during the winter-spring, the OMZ in the California Current shoals and the non-migrating scattering layer associated with the lower OMZ boundary disappears (Urmy and Horne, 2016). Correspondingly, diet composition is similar between the Subarctic and California Current provinces, especially in terms of migrating fishes and non-migrating squids (Chapter 2, Table 3.1). We found that most of the prevalent relationships between vertical foraging strategy and the consumption of key functional groups that we observed in the Subarctic were also evident in the California. Since the vertical structure of the water column and seal diet composition between these provinces is similar, our results are unsurprising, and further support our hypothesis that vertical diving strategy should reflect spatiotemporal patterns in foraging habitat.

3.5.3 Flexible Foraging Tactics in Female Northern Elephant Seals

We found that the foraging dive behavior of individual female northern elephant seals was decidedly plastic, as individuals altered their vertical foraging strategy when they traveled through different biogeographic provinces. We found clear associations between their vertical foraging strategies and the vertical distribution of prey in the water column that corresponded with the consumption of key prey functional groups. This within-individual variation in vertical foraging strategy spatially across their migration, has important implications for the functional role of seals within the deep ocean ecosystem. For example, when foraging in in the Subarctic Pacific, seals adopt a shallow vertical foraging strategy and consume more migrating prey. However, when foraging in the North Central Pacific, they adjust to the differences in prey distribution by diving deeper and will consume more non-migrating prey. Therefore, elephant seals are feeding on different trophic levels in each province, altering their role as predators and their associated impact on the trophic dynamics in the deep ocean.

3.5.4 Individual Diet Specialization and Associations with Foraging Behavior

Female northern elephant seals were primarily diet generalists, though a few seals had specialized diets. Unlike in sea otters, where individual diet specialization is clearly linked to specific prey functional groups (Newsome et al., 2009; Tinker et al., 2007; 2008; 2012) we found little evidence for seals that specialized on fishes or squids. Considering the broad array of prey species that inhabit the deep scattering layers and the individual flexibility we observed in vertical foraging behavior, simple specialized diets composed of broad prey functional groups may not be an adequate descriptor of diet specialization in this complex trophic system. We did find that the shallow foraging strategy was associated with the degree of diet specialization for seals foraging in the Subarctic Pacific during both seasons, and for seals foraging in the California Current during the summer-fall, suggesting that shallow diving seals have a more specialized diets, which is likely a consequence of spatiotemporal oceanographic processes causing high density aggregations of prey at shallow depths.

3.5.5 Possible Implications due to Climate Variability and Change

As the climate changes, the Subarctic Pacific is predicted to contract due to the extension of the subtropical North Central Pacific northward, resulting in an expansion of OMZ, both in depth and breadth (Doney et al., 2012; Pierce et al., 2002; Polovina et al., 2011). Previous estimates of habitat change for top predators predicted a slight increase in habitat for elephant seals, although this used only surface variables that do not capture sub-surface processes (Hazen et al., 2013). Since female elephant seals display flexibility in foraging behavior across their range, even within a single foraging trip, they may be able to adjust to changes in prey distribution. However, many individual seals exhibit high site fidelity with lower success during warm phases of the Pacific Decadal Oscillation (Abrahms et al., 2018). Furthermore, extreme El Niño events have been shown to increase trip length and decrease foraging success (Crocker et al., 2006), and diet composition also changes even in less extreme El Niño conditions (Chapter 2). This indicates that if conditions change too much from the average, even species with flexible foraging behaviors may not be able to compensate adequately to avoid a decrease in fitness or reproductive success.

Seals that are more specialized in behavior like the few individuals that do not leave the California Current may be at increased risk due to accelerating climate change as compared to seals that forage across multiple provinces. However, one diet specialist, Seal O55, did not leave the California Current and consumed a diet extremely high in squid. In the same year, there was a northward expansion in the distribution Humboldt squid (*Dosidicus gigas*), associated with abnormally warm waters that year in the California Current and an expansion of the oxygen minimum zone citations. It is possible that Seal O55 was able to exploit this new prey resource in the California Current despite abnormally warm conditions, potentially documenting rapid adaptation to variable climate conditions.

3.5.6 Conclusions

In contrast to many other species where individual specialization is common, we found northern elephant seals are extreme generalists in diet and vertical foraging strategy at both the individual and population levels. Flexible vertical foraging tactics displayed by female northern elephant seals are reflective of biogeographic region and are likely due to corresponding spatiotemporal patterns in the vertical distribution of prey deep scattering layers. For female elephant seals, within- and between-individual patterns in spatial habitat selection are more rigid: most females settle upon a particular spatial foraging strategy and display interannual fidelity to that strategy. However, their vertical foraging dive depths change as they move along their foraging route and encounter changes in the distribution and relative availability of prey. This suggests a high level of foraging plasticity that provides elephant seals with resilience to changing environmental conditions and may explain why they were able to recover from near extinction.

3.6 References

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Table 3.1 Sample sizes of adult female northern elephant seals by primary foraging province, the proportion of three important prey functional groups in their diets, and the degree of individual diet specialization (PSI), for adult female northern elephant seals with tracking, diving, and diet data (n = 122) for mesopelagic biogeographic province by season. Seals were classified to a primary foraging province if > 50% of their foraging dives were in that province; 7 seals could not be classified to a primary foraging province when classified by this method and are not included here.

Winter-Spring Trip	**n**	**Surface migrating zooplanktivores** *mean ± SD*	**Non-migrating piscivores** *mean ± SD*	**Non-migrating squid** *mean ± SD*	**PSI** *mean ± SD*
Subarctic Pacific	32	0.289 ± 0.12	0.099 ± 0.09	0.379 ± 0.1	0.56 ± 0.12[a]
North Central Pacific	31	0.183 ± 0.1	0.168 ± 0.07	0.292 ± 0.05	0.262 ± 0.17
California Current	6	0.219 ± 0.14	0.135 ± 0.07	0.358 ± 0.08	0.55 ± 0.08
Summer-Fall Trip					
Subarctic Pacific	28	0.267 ± 0.16	0.190 ± 0.18	0.368 ± 0.10	0.57 ± 0.11
North Central Pacific	15	0.255 ± 0.15	0.262 ± 0.14	0.289 ± 0.06	0.62 ± 0.09
California Current	3	0.276 ± 0.06	0.122 ± 0.06	0.435 ± 0.09	0.50 ± 0.17

Table 3.2 Percentage of variance in foraging dive depth (m) by season explained by random-effects only linear models: variation attributable to dive location (province), between-individuals, and other factors (residual).

Effect	**Variance explained (%)**	
	Day Forage Dives	**Night forage dives**
Winter-spring		
Dive location	95.94	95.86
Between-individuals	0.52	0.57
Residual	3.54	3.57
Summer-fall		
Dive location	95.78	95.49
Between-individuals	0.66	0.23
Residual	3.57	4.27

Table 3.3 Vertical foraging strategies quantified by total foraging dives in each strategy by province and the proportion of foraging dives per strategy of all dives within each province. Differences in the relative frequency of the three vertical foraging strategies were tested between provinces, using ANOVA. The number of seals represented in each province varies due to differences in the foraging routes of individual seals. For example, a seal that forages within the California Current for their entire trip will not be represented in the other provinces, while a seal that foraged mainly in the Subarctic Pacific may also have foraging dives in the other provinces depending on her migration route. All seals will have some proportion of their dives in the California Current, since they must travel through that province to reach the others.

	Subarctic Pacific			North Central Pacific			California Current		
Winter-Spring	Seals	Dives	Proportion *Mean* ± *SD*	Seals	Dives	Proportion *Mean* ± *SD*	Seals	Dives	Proportion *Mean* ± *SD*
Shallow		8,880	0.21 ± 0.18^{a}		920	0.04 ± 0.11^{b}		8,183	0.20 ± 0.13^{a}
Mid-depth	49	23,750	0.66 ± 0.20^{a}	42	23,944	0.62 ± 0.23^{a}	74	27,795	0.74 ± 0.11^{b}
Deep		3,975	0.13 ± 0.16^{a}		13,344	0.33 ± 0.23^{b}		2,310	0.06 ± 0.05^{c}
Summer-Fall									
Shallow		9,930	0.11 ± 0.13^{a}		2,058	0.05 ± 0.03^{b}		7,531	0.23 ± 0.15^{a}
Mid-depth	46	55,481	0.68 ± 0.19^{a}	35	37,324	0.79 ± 0.14^{b}	48	22,243	0.74 ± 0.14
Deep		15,805	0.21 ± 0.19^{a}		7,731	0.17 ± 0.14^{a}		1,024	0.03 ± 0.04^{b}

Provinces with the same letter are not significantly different from each other.

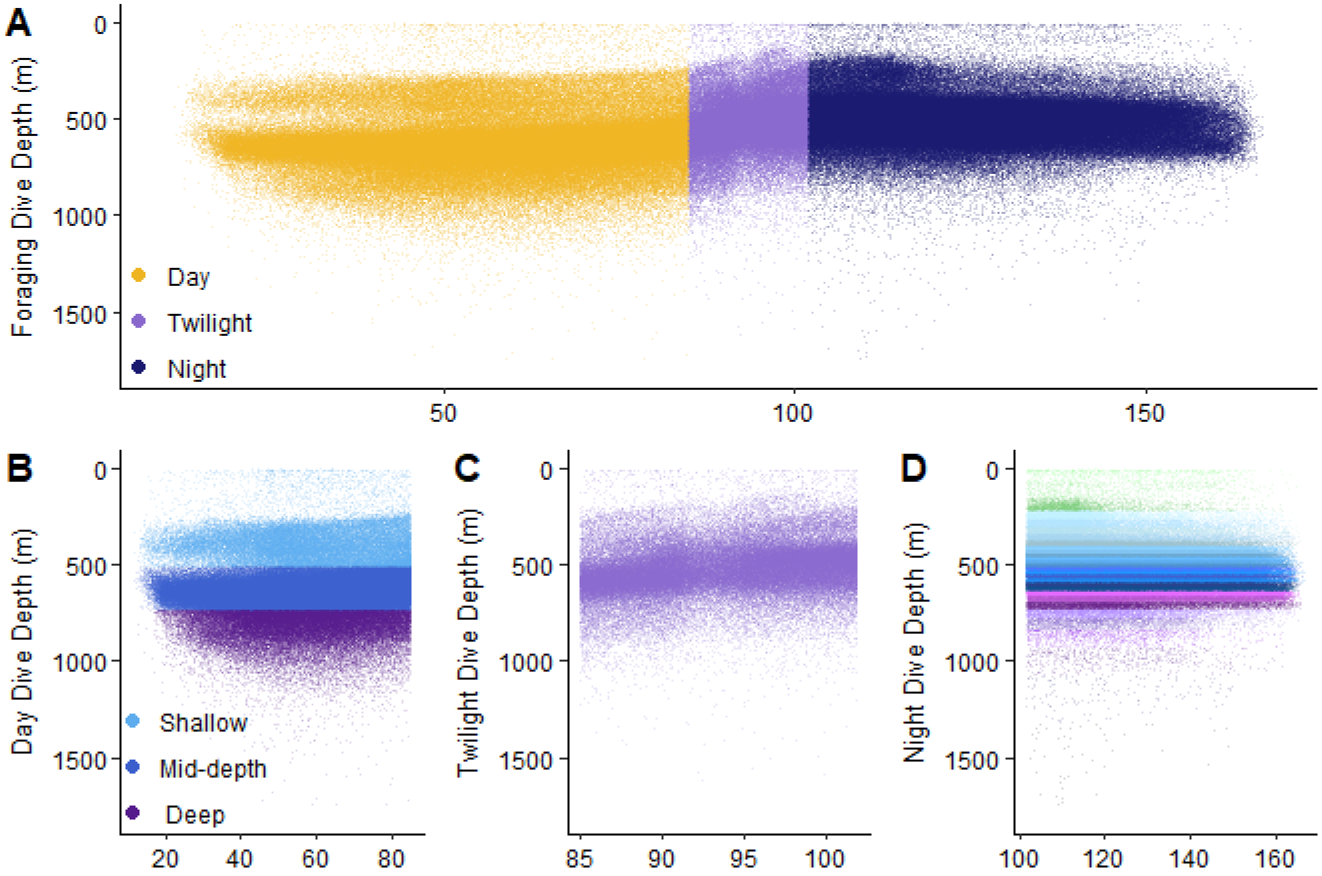

Figure 3.1 (A) Diel patterns of foraging dives depths (m) of female northern elephant seals (n = 122), with time of day determined from solar zenith angle. **(B)** Day foraging dives had three optimal dive clusters (shallow: n = 37,591 dives, center = 393.1 m, range = 15-516.5 m; mid-depth: n = 190,448 dives, center = 649.5 m, range = 517-740 m; and deep: n = 44,189 dives, center = 840.9 m, range = 740.5-1,747.5 m) as determined by k-means cluster analysis. **(C)** Twilight foraging dives only had one cluster (n = 94,172 dives, center = 532.0 m). **(D)** Night foraging dives had 29 clusters (n = 314,218 dives)

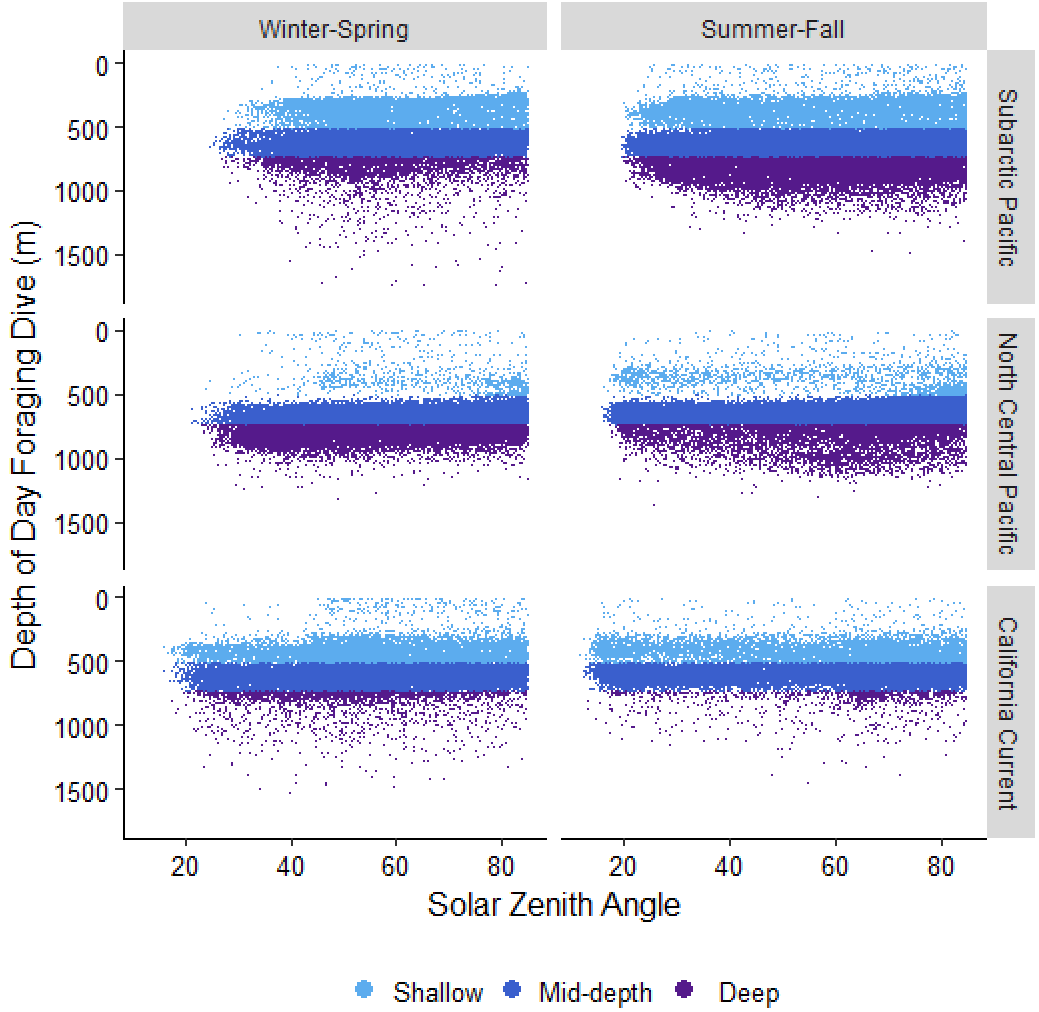

Figure 3.2 Optimal clusters of day forage dive depths (m) for female northern elephant seals (n = 122) by province and season as determined by k-means cluster analysis. The three clusters were used to define vertical foraging dive strategies: shallow (light blue), mid-depth (royal blue), and deep (purple). Spatial and seasonal patterns in the prevalence of vertical strategies are evident between provinces and seasons. For total number of dives within each strategy by province and season refer to Table 3.3.

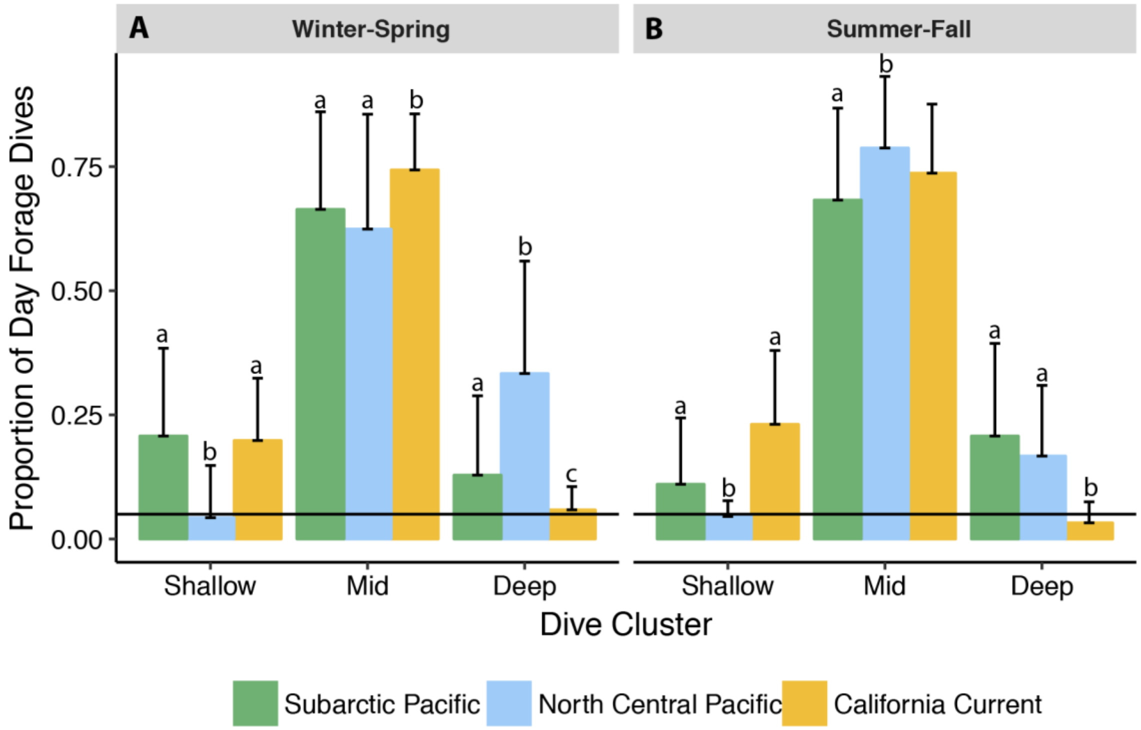

Figure 3.3 Spatial differences in the usage of vertical foraging strategies (shallow, mid-depth, and deep) by season: **(A)** winter-spring, **(B)** summer-fall. The shallow foraging strategy occurred most frequently in the Subarctic Pacific for both seasons. The mid-depth foraging strategy was common in all provinces. The deep foraging strategy was most frequent in the North Central Pacific during the winter-spring. ANOVA was used to test for differences between provinces in the proportion of foraging dives in each strategy. Within vertical foraging strategies, provinces with the same letter are not significantly different from each other.

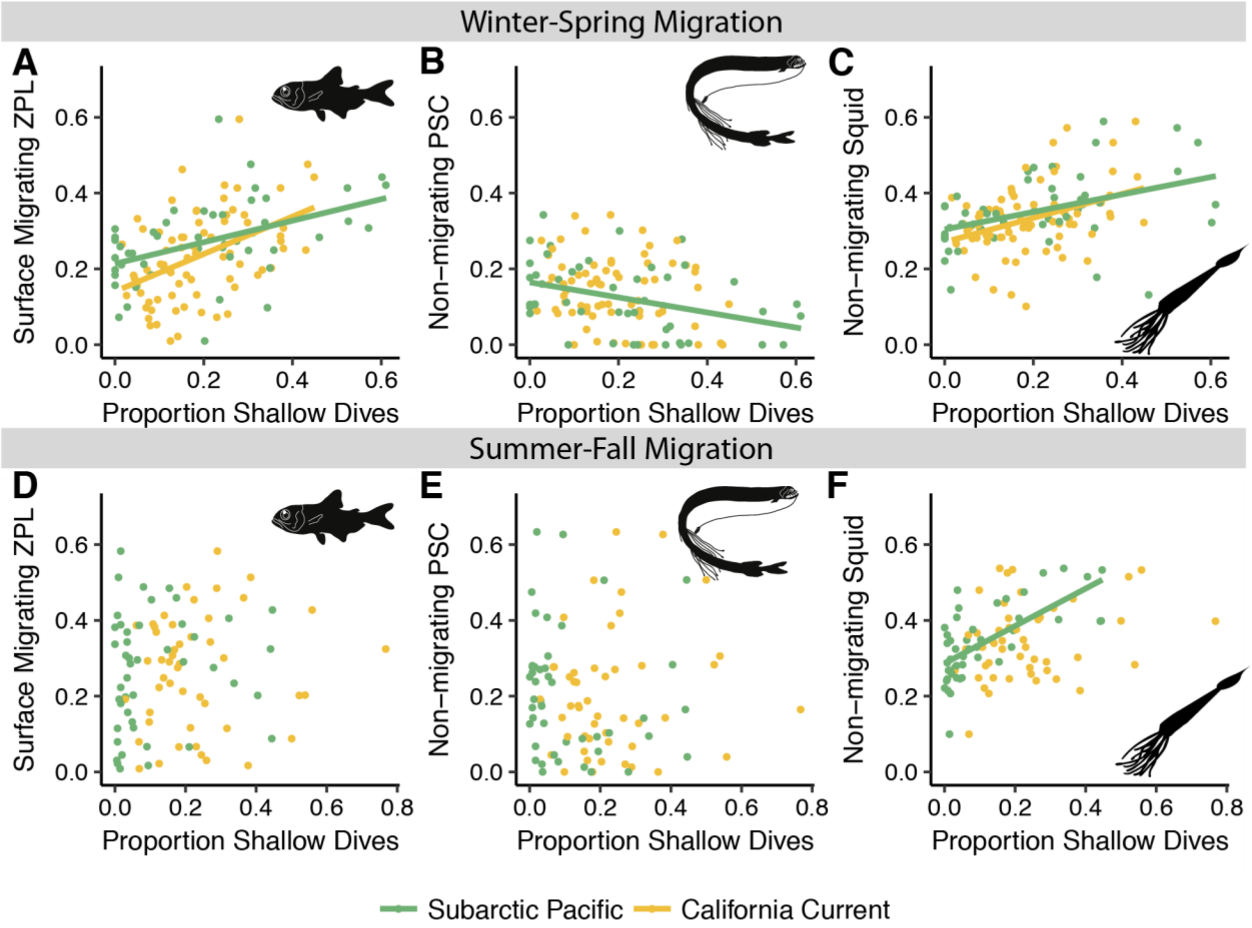

Figure 3.4 Relationships between the proportion of shallow day foraging dives occurring within a province and the proportion of surface migrating zooplanktivores (ZPL), non-migrating piscivores (PSC), or non-migrating squid in the diet. **(A-C)** Winter-spring foraging trip; **(D-F)** Summer-fall foraging trip. Only provinces with a proportion of shallow day foraging dives > 0.05 % were analyzed.

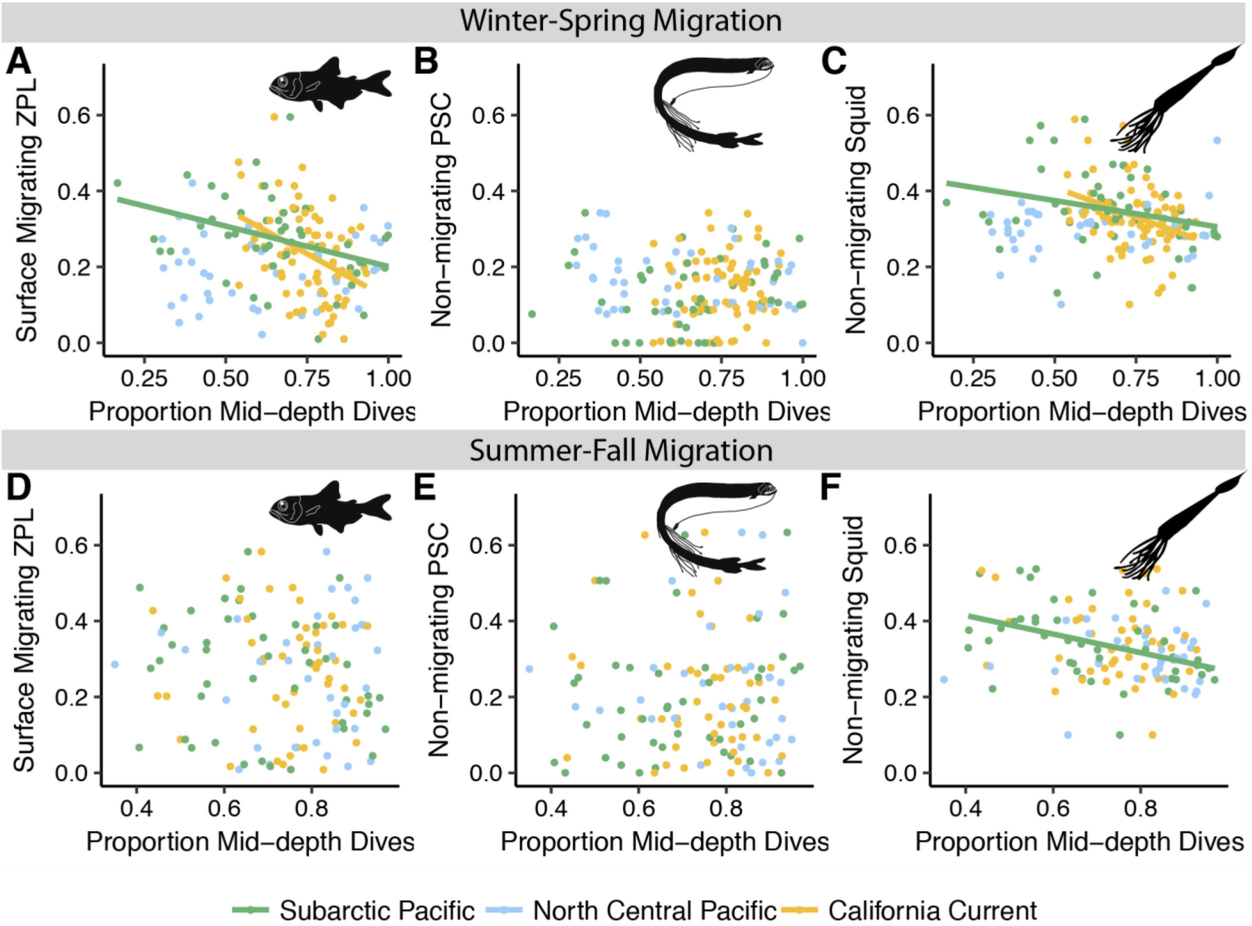

Figure 3.5 Relationships between the proportion of mid-depth day foraging dives occurring within a biogeographic province and the proportion of surface migrating zooplanktivores (ZPL), non-migrating piscivores (PSC), or non-migrating squid in the diet. **(A-C)** Winter-spring foraging trip; **(D-F)** Summer-fall foraging trip.

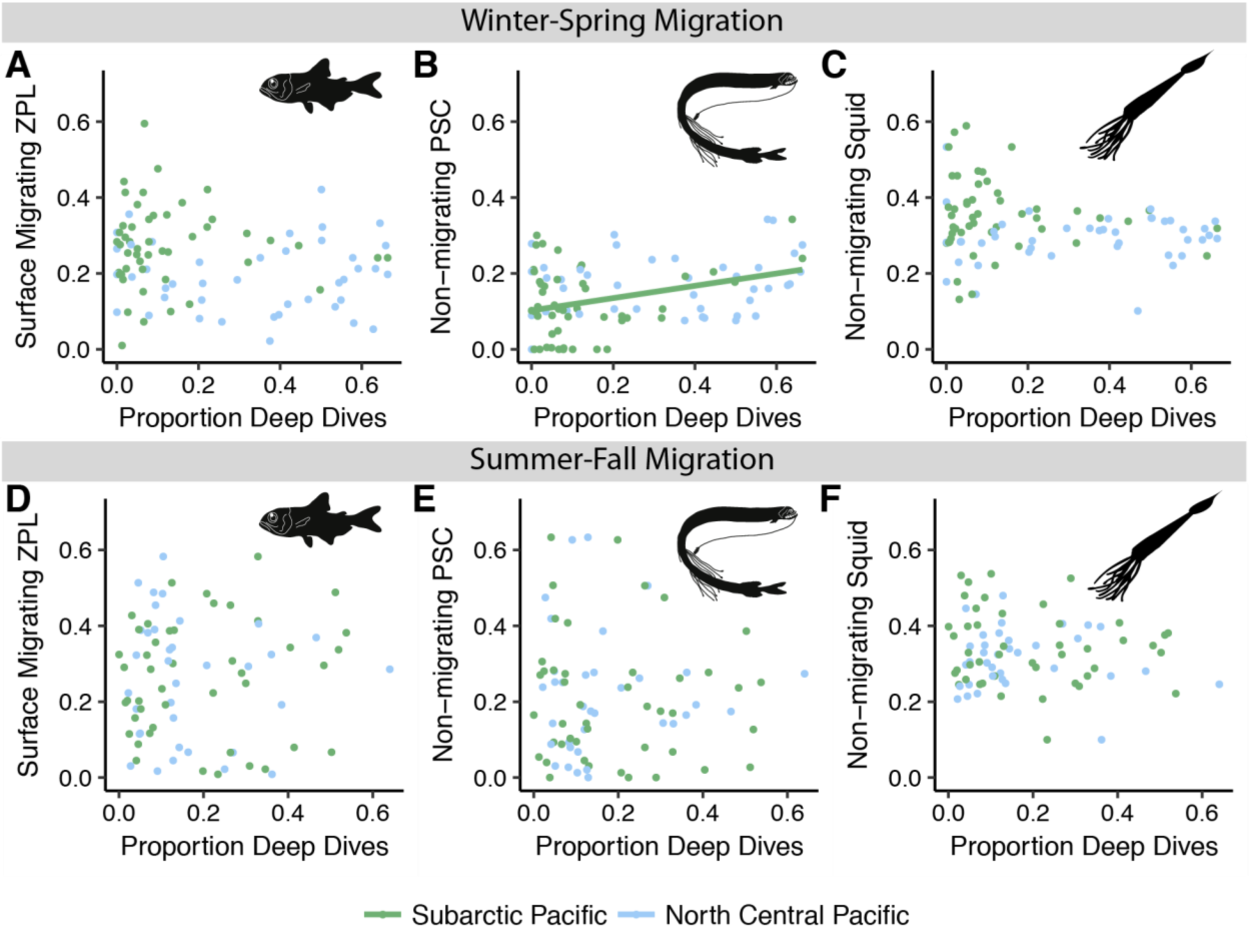

Figure 3.6 Relationships between the proportion of deep day foraging dives occurring within a biogeographic province and the proportion of surface migrating zooplanktivores (ZPL), non-migrating piscivores (PSC), or non-migrating squid in the diet. **(A-C)** Winter-spring foraging trip; **(D-F)** Summer-fall foraging trip. Only provinces with a proportion of deep day foraging dives > 0.05 % were analyzed.

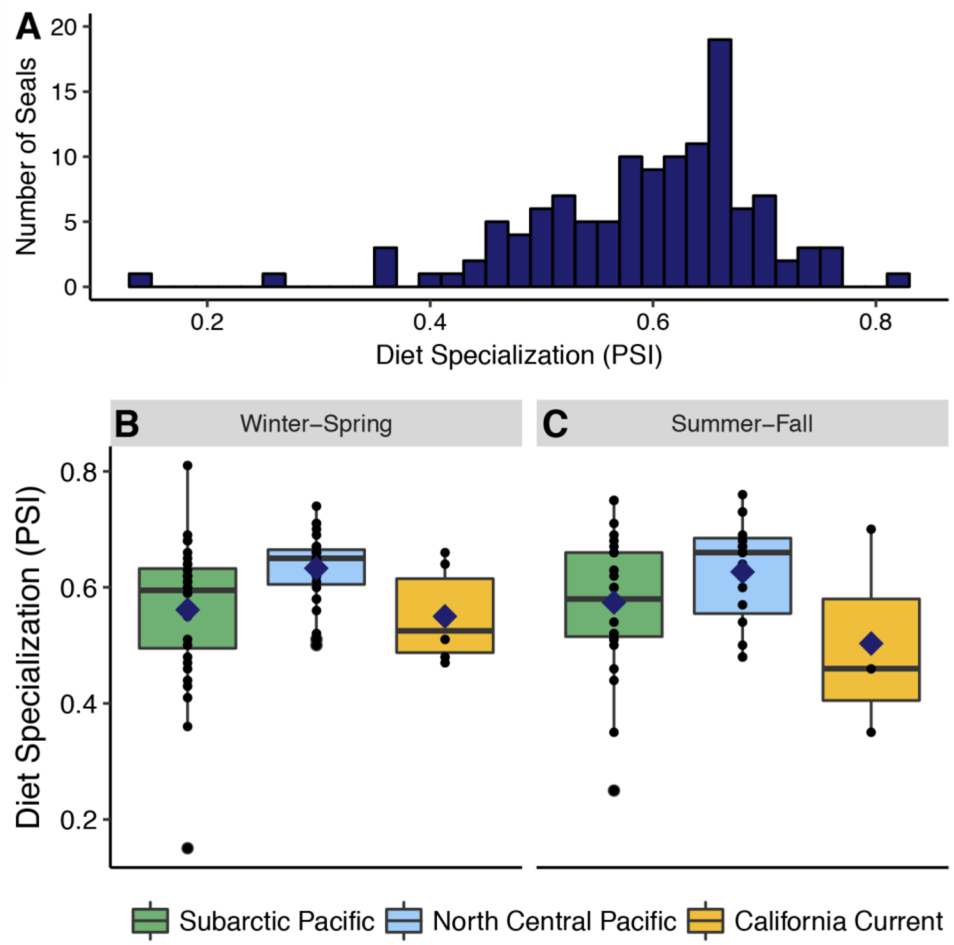

Figure 3.7 (A) Histogram showing the distribution of the degree of diet specialization (PSI) for female northern elephant seals (n = 122). PSI values close to 0 indicate a higher degree of diet specialization, while PSI values close to 1 indicate generalists. Only 16% of all seals had values < 0.5 and can be considered diet specialists, **(B)** The distribution of PSI by biogeographic province. Seals were classified if > 50% of their foraging dives occurred in one province (n = 115, 7 seals did not have > 50% of their dives in a single province). All seals except for a few that remain in the California Current, have dives in at least two regions since they must travel through the California Current to get to their primary foraging province.

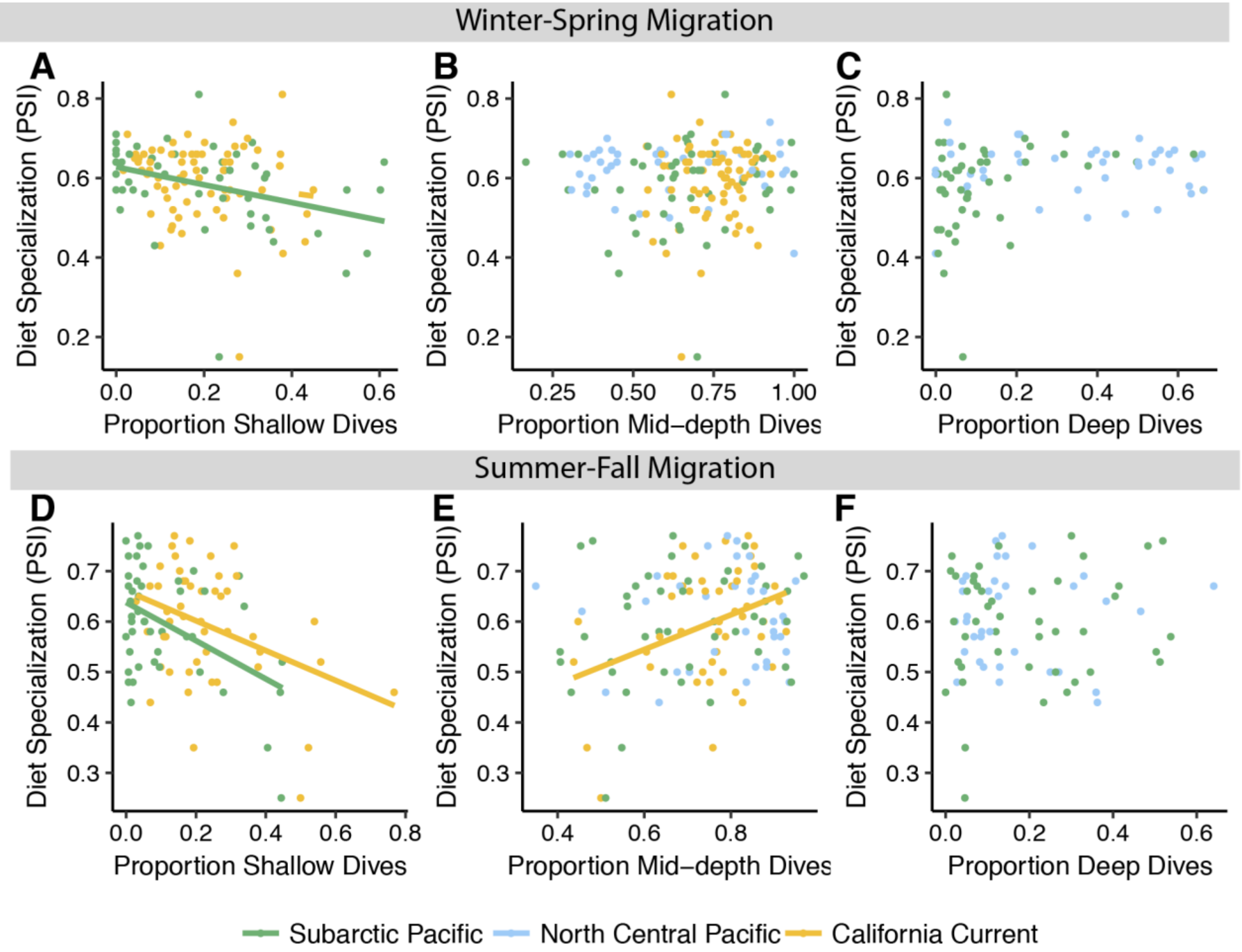

Figure 3.8 Relationships between the proportion of shallow (A and D), mid-depth (B and E), and deep (C and F) the degree of individual diet specialization by province**. (A-C)** Winter-spring foraging trip; **(D-F)** Summer-fall foraging trip. Only provinces with proportions of day foraging dives in a depth cluster > 0.05 % were analyzed.

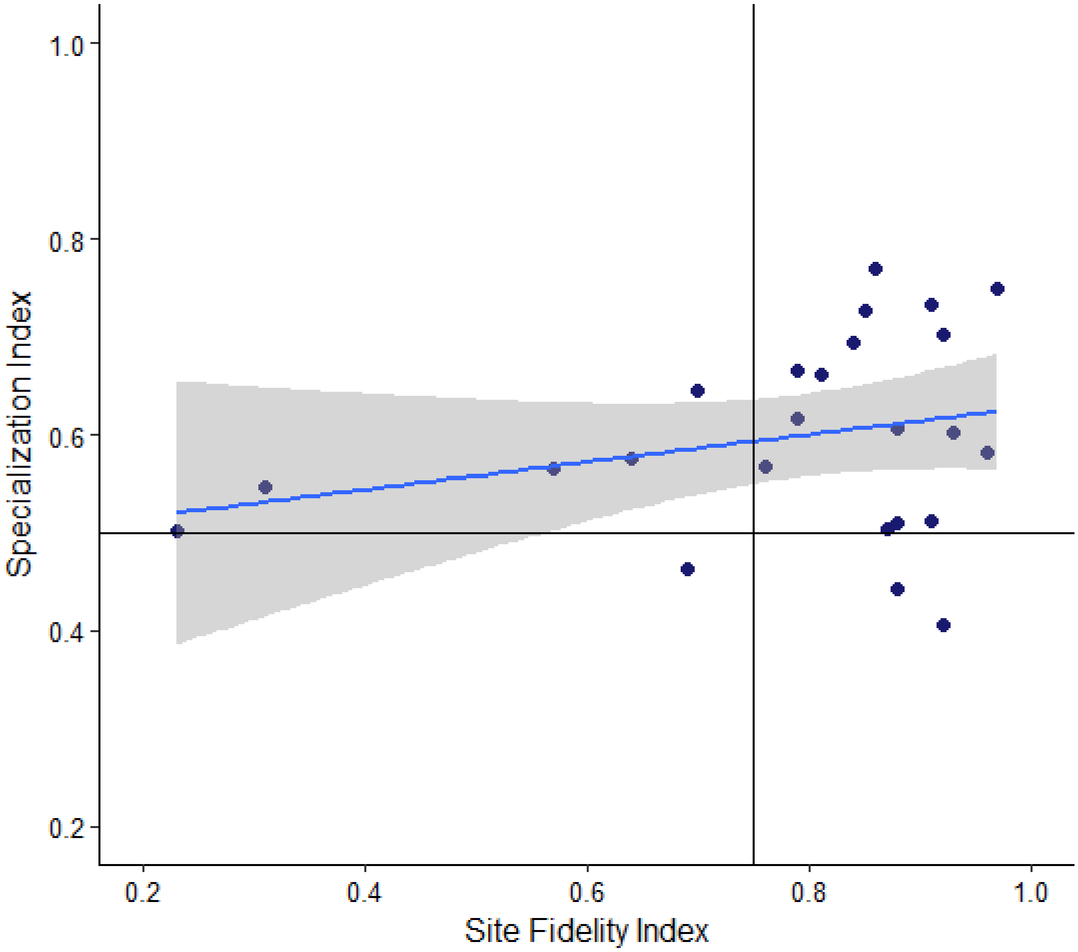

Figure 3.9 The degree of site fidelity (Bhattacharya's affinity metric) of female northern elephant seals (n = 24) to their foraging route is not correlated with the degree of individual diet specialization (PSI: proportional similarity index; $p > 0.05$). For the site fidelity index, values close to 1 indicate high site fidelity, while values close to 0 indicate low site fidelity. For the specialization index, values closer to 0 indicate more specialized diet, while values closer to 1 indicate more generalized diet. $p > 0.05$. The blue line was calculated from linear regression model and the shaded area indicates the 95% confidence interval.

SYNTHESIS

Quantitative fatty acid signature analysis (QFASA): A solution and a challenge

QFASA can circumvent many biases and limitations inherent in traditional methods of diet determination (Bowen and Iverson, 2013; Budge et al., 2006; Iverson et al., 2004). For example, only biochemical methods, such as QFASA, stable isotope analysis and DNA barcoding, can quantify the presence of soft-bodied, easily digestible prey types that are typically not detectable in stomach or scat contents (Boecklen et al., 2011; Bowen, 2011; Bowen and Iverson, 2013; Harvey and Antonelis, 1994; Ramos and González-Solís, 2012). Further, QFASA-derived diet estimates integrate dietary information for individuals over long timescales of 2-3 months, depending on the tissue examined, rather than just a snapshot of the most recent meal. For northern elephant seals that spend months foraging at sea, QFASA is a valuable approach for obtaining a more comprehensive understanding of their long-term diet. However, QFASA can be a challenging methodological approach for wide-ranging generalist predators that have little *a priori* data on diet composition and have a large variety of potential prey. Due to mathematical constraints, QFASA models can result in inaccurate diet estimates if derived from large prey libraries containing more prey species than dietary fatty acids (Goetsch et al., 2018). In addition, reliable calibration coefficients are critical for the accurate quantification of fatty acids due *in vivo* predator metabolic processes (Bromaghin et al., 2016; Rosen and Tollit, 2012), but can be difficult to obtain for elusive predators.

To avoid inaccurate or misleading QFASA-derived diet estimates for species that require a large prey library, I developed a novel method, the drop core prey (DCP) method, to exclude prey species from the library based on quantitative, non-arbitrary criteria. The DCP method extends the feasibility of QFASA to predators with access to many potential prey and where available data are insufficient to narrow those options. In addition to the development of the DCP method, I employed an innovative combination of two previously developed cross-validation techniques, leave-one-prey-out (LOPO) analysis and diet simulations to provide complementary information on the ability of the QFASA model to distinguish prey species from one another. These validation methods provide two independent quantifications of the model error and allow a robust assessment of model accuracy that can easily be employed in future QFASA studies.

Diet and foraging strategies of northern elephant seals

This body of work provides QFASA-derived diet estimates for female northern elephant seals that align more closely to predictions based on seal movement data and relative prey energy density than traditional diet estimates that considered northern elephant seals to be squid specialists (Antonelis et al., 1987; 1994; Condit and Le Boeuf, 1984; Huey, 1930; Naito et al., 2013; 2017). Furthermore, these diet estimates are now more consistent with evidence their Southern Ocean congener, the southern elephant seal, that also feeds predominately on deep-sea fishes (Banks et al., 2014; Bradshaw et al., 2003; Cherel et al., 2008). Foraging dives of female northern elephant seals follow a clear diel pattern that matches the daily vertical migration of the deep acoustic scattering layers, which contain the majority of deep ocean biomass, including fishes and squids (Irigoien et al., 2014; Kaartvedt et al., 2012; Klevjer et al., 2016). Observations of their deep diving behavior from biologging instruments led to the hypothesis that northern elephant seals must be consuming deep-sea fishes, although no evidence of these fishes were found in stomach contents (Antonelis et al., 1987; 1994; Condit and Le Boeuf, 1984). My research shows that the population-level diet of northern elephant seals is broadly general, dominated by energy-dense deep-sea fishes rather than pelagic squids, an observation consistent with diving behavior (LeBoeuf et al., 2000; Robinson et al., 2012; Naito et al., 2013) and animal-borne cameras (Naito et al., 2013; 2017).

Studies on the long-term spatial and temporal trophic dynamics of wide-ranging, deep ocean predators are rare, yet crucial, to provide insight on predator-prey interactions in the understudied deep-sea ecosystem (St John et al., 2016; Webb et al., 2010). By covering multiple years and sampling over 100 individual seals, I robustly tested for spatial, seasonal, and interannual differences in diet of female northern elephant seals. The midwater oxygen minimum zone (OMZ) may be advantageous foraging habitat for female seals, since it may concentrate prey during the day and decrease prey mobility by lowering prey metabolism (Naito et al., 2017). The depth, thickness, and dissolved oxygen levels of the OMZ vary spatially and seasonally in the North Pacific (Gilly et al., 2013; Moffitt et al., 2015; Paulmier and Ruiz-Pino, 2009), affecting the vertical location, density, and migratory behavior of prey in the deep scattering layers (Gallo and Levin, 2016; Gilly et al., 2013; Maas et al., 2014;

Netburn and Koslow, 2015). My research shows that female elephant seals foraging in specific biogeographic provinces consumed diets specific to that region, indicating that seals may preferentially consume prey that are aggregated by variation in the vertical structure of the OMZ.

Finally, in studies of deep-sea predators it is challenging to link specific foraging behaviors with diet composition for individuals, especially across the entire foraging range of the species. I explicitly tested for correlations between foraging dive strategies and diet composition for northern elephant seals. I was able to confirm that foraging dive depth closely mirrored what would be expected based on a seal's diet composition and that foraging dive behavior was consistent with spatial differences in the vertical distribution of the deep scattering layers. Female seals appear to adjust their foraging behavior as they travel through biogeographic provinces on their foraging trips, taking advantage of the spatiotemporal variation in abundance and location of prey. In addition, I quantified the prevalence of individual diet specialization in the population and tested whether individuals that were more specialized diet had different foraging dive strategies than those that were more generalist in their diets. I found that in contrast to many other species where individual specialization is common, northern elephant seals are extreme generalists in diet and foraging strategy at both the individual and population levels. This suggests a high level of foraging plasticity which may increase the resilience of seals to changes in environmental conditions and possibly explains why elephant seals were able to recover from near extinction.

Implications of anthropogenic climate change

My research suggests that interannual variability in climate phenomena, such as the El Niño Southern Oscillation (ENSO), influences the diet composition of northern elephant seals. I found a clear change in the composition of seal diets during the 2010 El Niño, which was short, but strong. While strong El Niño events have been shown to increase foraging trip duration and reduce foraging success for northern elephant seals (Crocker et al., 2006), these effects were not seen during the 2010 El Niño that occurred during my study period (Robinson et al., 2012). This suggests that while net foraging success may not change during years with small deviations from ENSO neutral conditions, foraging effort may increase, indicating that seals may have to work harder for the same amount of energy gain (Costa, 2008; Costa et al., 2012).

Considerable changes in the eastern North Pacific Ocean have been predicted from climate models incorporating global warming scenarios, particularly a reduction in the extent of the Subarctic Pacific province due to a northward movement of the Subtropical Gyre, and an expansion of the OMZ (Polovina et al., 2011; Doney et al., 2012). With these changes, the faunal composition, abundance, and distribution of prey in the deep scattering layers may be profoundly altered. Climate change may result in more extreme and continued change to the availability and distribution of prey in marine ecosystems than can be seen in studies using average climate variability. These profound changes in ecosystem trophic dynamics may result in drastically decreased foraging success for many marine predators. Climate-driven changes in oceanographic cues, such as sea surface temperature or thermocline depth, may also result in inappropriate foraging strategies, also impacting foraging success. Ultimately, decreased foraging success can result in population-level effects such as reduction in reproductive success and decreased population growth. My research has shown that intraspecific variation in the diet of northern elephant seals is linked to spatiotemporal variation in the deep ocean environment, especially the OMZ. While elephant seals may be negatively affected by the northward retreat of the Subarctic Pacific and OMZ expansion, their flexible foraging strategies and extreme generalist diets may allow them to adapt to these unprecedented changes.

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APPENDICES

A1 Supplemental Tables

Table A1.1 Winter-spring foraging trip: Mean percent (%) of elephant seal diet by biogeographic province.

Functional group	**Mean percent (%) of diet**			
	SAP	**NCP**	**CC**	**Mixed**
Total Fishes	**59.6**	**67.2**	**64.6**	**66.2**
Surface migrating ZPL	**30.0**	**18.2**	**22.4**	**20.2**
D. perspicillatus	3.6	5.4	1.9	8.5
D. theta	3.0	5.3	3.7	4.2
E. risso	12.4	2.1	8.8	3.4
S. californiensis	0.4	0.0	0.0	0.0
T. taylori	10.6	5.4	8.0	4.0
Surface Migrating PSC	**0.0**	**0.0**	**0.0**	**0.2**
T. macropus	0.0	0.0	0.0	0.2
Midwater Migrating ZPL	**0.2**	**0.0**	**0.0**	**0.0**
A. sladeni	0.0	0.0	0.0	0.0
L. urophaos	0.2	0.0	0.0	0.0
Midwater Migrating PSC	**3.0**	**3.4**	**4.5**	**3.1**
A. scintillens	3.0	3.4	4.5	3.1
Bathy-midwater Migrating GEL	**5.4**	**5.1**	**2.1**	**5.7**
B. pacificus	1.7	1.2	0.0	0.0
L. ochotensis	3.7	4.0	2.1	5.7
Non-migrating ZPL	**2.6**	**3.9**	**2.1**	**2.7**
M. lugubris	2.4	3.9	2.1	2.7
S. harryi	0.0	0.1	0.0	0.0
S. nannochir	0.2	0.0	0.0	0.0
Non-migrating GEL	**9.4**	**19.9**	**21.6**	**9.8**
M. bericoides	5.2	19.9	12.1	9.8
M. microstoma	0.0	0.0	0.0	0.0
W. telescopa	4.2	0.0	9.5	0.0
Non-migrating PSC	**9.1**	**16.6**	**12.0**	**24.6**
B. dentata	0.0	0.0	0.0	0.0
C. macouni	2.7	3.1	0.0	15.0
I. antrostomas	0.4	2.9	1.4	1.1
L. ringens	0.0	0.0	0.0	0.0

O. mitsuii	0.0	0.1	0.0	0.0
S. rothschildi	6.0	10.4	10.6	8.5
Non-migrating Generalist	**0.0**	**0.0**	**0.0**	**0.0**
A. cornuta	0.0	0.0	0.0	0.0
Squids	**40.4**	**32.8**	**35.4**	**33.8**
Vertically migrating	**2.2**	**3.8**	**0.4**	**3.2**
B. anonychus	0.4	1.9	0.4	0.7
G. borealis	0.0	0.0	0.0	0.0
O. bartramii	0.2	1.0	0.0	0.1
Adult *O. borealijaponica*	1.5	0.9	0.0	2.4
Subadult *O. borealijaponica*	0.0	0.0	0.0	0.0
Nonmigrating	**38.2**	**29.0**	**35.0**	**30.7**
C. c. f. *calyx*	27.4	28.7	27.6	25.9
G. phyllura	0.1	0.1	0.0	0.0
S. dofleini	10.7	0.2	7.4	4.7

Table A1.2 Summer-fall foraging trip: Mean percent (%) of northern elephant seal diet by biogeographic province.

Functional group	**Mean percent (%) of diet**			
	SAP	**NCP**	**CC**	**Mixed**
Total Fishes	**59.2**	**65.1**	**55.9**	**67.8**
Surface migrating ZPL	**26.3**	**26.2**	**27.6**	**23.5**
D. perspicillatus	3.4	7.6	0.0	2.7
D. theta	4.2	4.0	0.0	2.6
E. risso	5.2	3.1	23.4	1.4
S. californiensis	0.2	0.0	0.4	0.0
T. taylori	13.4	11.5	3.8	16.9
Surface Migrating PSC	**0.0**	**0.0**	**0.0**	**0.2**
T. macropus	0.0	0.0	0.0	0.2
Midwater Migrating ZPL	**0.0**	**0.0**	**0.0**	**0.0**
A. sladeni	0.0	0.0	0.0	0.0
L. urophaos	0.0	0.0	0.0	0.0
Midwater Migrating PSC	**2.9**	**2.0**	**0.0**	**5.7**
A. scintillens	2.9	2.0	0.0	5.7
athy-midwater Migrating GEL	**2.3**	**3.0**	**4.5**	**1.4**
B. pacificus	0.7	1.4	0.0	0.0
L. ochotensis	1.6	1.6	4.5	1.4
Non-migrating ZPL	**1.7**	**1.9**	**0.8**	**1.9**
M. lugubris	1.6	1.9	0.8	1.9

S. harryi	0.0	0.0	0.0	0.0
S. nannochir	0.0	0.0	0.0	0.0
Non-migrating GEL	**6.8**	**6.1**	**9.1**	**7.8**
M. bericoides	6.2	5.2	3.8	7.2
M. microstoma	0.0	0.5	0.0	0.0
W. telescopa	0.6	0.4	5.3	0.6
Non-migrating PSC	**19.1**	**25.9**	**12.2**	**27.5**
B. dentata	0.1	0.0	0.0	0.0
C. macouni	11.0	10.6	0.0	15.2
I. antrostomas	0.6	1.4	0.0	2.4
L. ringens	0.3	0.9	0.0	0.0
O. mitsuii	0.0	0.0	0.0	0.0
S. rothschildi	7.2	13.0	12.2	9.9
Non-migrating Generalist	**0.0**	**0.0**	**1.7**	**0.0**
A. cornuta	0.0	0.0	1.7	0.0
Squids	**40.8**	**34.9**	**44.1**	**32.2**
Vertically migrating	**3.8**	**3.7**	**0.5**	**2.7**
B. anonychus	0.6	0.9	0.0	1.6
G. borealis	0.0	0.2	0.0	0.0
O. bartramii	0.7	0.4	0.0	0.0
Adult *O. borealijaponica*	2.4	1.3	0.5	1.1
Subadult *O. borealijaponica*	0.0	0.8	0.0	0.0
Nonmigrating	**37.1**	**31.1**	**43.5**	**29.5**
C. c. f. *calyx*	26.2	25.8	17.4	24.5
G. phyllura	0.6	1.4	0.0	0.0
S. dofleini	10.2	3.9	26.2	5.0

Table A1.3 Winter-spring foraging trip: Mean percent (%) of northern elephant seal diet by year.

Functional Group	Mean percent (%) in the diet				
	2005	**2006**	**2010**	**2011**	**2012**
Total Fisesh	**60.2**	**62.6**	**67.0**	**65.0**	**63.7**
Surface migrating ZPL	**23.0**	**25.8**	**20.8**	**19.5**	**27.9**
D. perspicillatus	5.4	10.3	0.0	3.9	5.9
D. theta	0.0	0.5	3.7	5.1	9.4
E. risso	11.2	11.2	5.6	4.7	3.5
S. californiensis	0.1	0.0	0.6	0.0	0.0
T. taylori	6.3	3.8	11.0	5.8	9.1
Surface Migrating PSC	**0.1**	**0.0**	**0.0**	**0.0**	**0.0**
T. macropus	0.1	0.0	0.0	0.0	0.0
Midwater Migrating ZPL	**0.0**	**0.0**	**0.0**	**0.0**	**0.4**
A. sladeni	0.0	0.0	0.0	0.0	0.0
L. urophaos	0.0	0.0	0.0	0.0	0.4
Midwater Migrating PSC	**0.0**	**0.0**	**0.4**	**6.5**	**8.0**
A. scintillens	0.0	0.0	0.4	6.5	8.0
Bathy-midwater Migrating GEL	**6.2**	**9.2**	**4.5**	**3.8**	**3.0**
B. pacificus	1.9	4.7	0.2	0.0	0.0
L. ochotensis	4.3	4.5	4.3	3.8	3.0
Non-migrating ZPL	**3.4**	**4.1**	**3.5**	**2.5**	**2.3**
M. lugubris	3.4	3.6	3.5	2.5	2.2
S. harryi	0.0	0.0	0.0	0.0	0.1
S. nannochir	0.0	0.5	0.0	0.0	0.0
Non-migrating GEL	**14.2**	**9.2**	**22.7**	**16.4**	**9.8**
M. bericoides	13.5	9.2	17.0	11.5	9.6
M. microstoma	0.0	0.0	0.0	0.0	0.0
W. telescopa	0.7	0.0	5.7	4.9	0.2
Non-migrating PSC	**13.3**	**14.3**	**15.1**	**16.4**	**12.3**
B. dentata	0.0	0.0	0.1	0.0	0.0
C. macouni	4.9	5.7	3.2	4.2	3.1
I. antrostomas	2.5	2.3	1.2	1.6	0.7
L. ringens	0.0	0.0	0.0	0.0	0.0
O. mitsuii	0.0	0.0	0.2	0.0	0.0
S. rothschildi	5.9	6.3	10.3	10.5	8.5
Non-migrating Generalist	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
A. cornuta	0.0	0.0	0.0	0.0	0.0
Squids	**39.8**	**37.4**	**33.0**	**35.0**	**36.3**

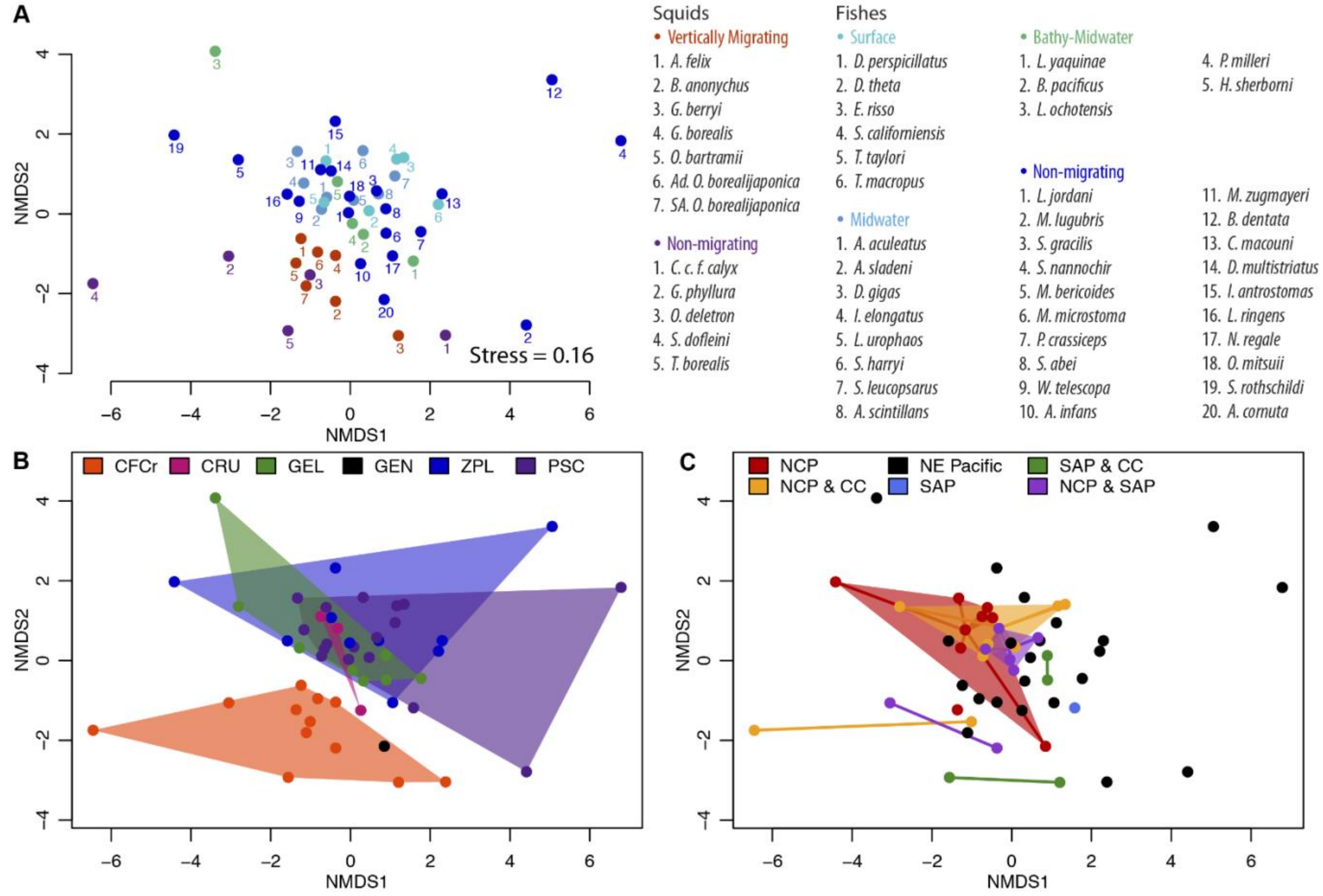
Vertically migrating	**2.0**	**2.6**	**4.1**	**3.9**	**1.4**
B. anonychus	0.5	0.1	1.5	2.6	0.4
G. borealis	0.0	0.0	0.0	0.0	0.0
O. bartramii	1.0	1.2	0.6	0.0	0.0
Adult *O. borealijaponica*	0.5	1.3	2.1	1.3	1.0
Subadult *O. borealijaponica*	0.0	0.0	0.0	0.0	0.0
Nonmigrating	**37.8**	**34.8**	**28.9**	**31.0**	**34.9**
C. c. f. *calyx*	25.5	25.8	27.1	28.8	30.6
G. phyllura	0.1	0.2	0.0	0.2	0.0
S. dofleini	12.3	8.8	1.8	2.0	4.3

Table A1.4 Summer-fall foraging trip: Mean percent (%) of northern elephant seal diet by year.

Functional Group	**Mean percent (%) in diet**			
	2005	**2010**	**2011**	**2012**
Total Fishes	**61.8**	**63.0**	**61.1**	**61.0**
Surface migrating ZPL	**34.2**	**25.2**	**33.8**	**12.2**
D. perspicillatus	11.4	0.4	5.0	0.4
D. theta	2.7	5.6	8.0	0.0
E. risso	5.5	3.7	3.0	7.9
S. californiensis	0.1	0.4	0.0	0.1
T. taylori	14.6	15.2	17.8	3.8
Surface Migrating PSC	**0.1**	**0.0**	**0.0**	**0.0**
T. macropus	0.1	0.0	0.0	0.0
Midwater Migrating ZPL[#]	**0.00**	**0.00**	**0.00**	**0.04**
A. sladeni	0.00	0.00	0.00	0.04
L. urophaos	0.0	0.0	0.0	0.0
Midwater Migrating PSC	**1.3**	**1.7**	**8.2**	**0.3**
A. scintillens	1.3	1.7	8.2	0.3
Bathy-midwater Migrating GEL	**3.2**	**3.3**	**1.3**	**2.6**
B. pacificus	1.0	0.0	0.4	1.8
L. ochotensis	2.2	3.3	0.9	0.8
Non-migrating ZPL	**2.1**	**2.5**	**1.2**	**1.1**
M. lugubris	2.1	2.5	1.1	1.1
S. harryi	0.0	0.0	0.1	0.0
S. nannochir	0.0	0.0	0.0	0.0
Non-migrating GEL	**5.4**	**14.1**	**5.2**	**3.6**
M. bericoides	4.2	12.7	5.0	2.6
M. microstoma	0.0	0.0	0.0	0.7
W. telescopa	1.2	1.4	0.2	0.3
Non-migrating PSC	**15.2**	**16.2**	**11.3**	**41.3**
B. dentata	0.1	0.0	0.0	0.0
C. macouni	4.5	3.6	4.7	27.3
I. antrostomas	1.5	1.4	0.1	0.7
L. ringens	0.5	1.4	0.0	0.0
O. mitsuii	0.0	0.0	0.0	0.0
S. rothschildi	8.5	9.8	6.5	13.3
Non-migrating Generalist	**0.3**	**0.0**	**0.0**	**0.0**
A. cornuta	0.3	0.0	0.0	0.0
Squids	**38.2**	**37.0**	**38.9**	**39.0**

Vertically migrating	**1.7**	**6.0**	**1.9**	**4.6**
B. anonychus	0.0	1.5	0.2	1.5
G. borealis	0.0	0.0	0.0	0.3
O. bartramii	0.2	1.5	0.3	0.3
Adult *O. borealijaponica*	1.5	3.0	1.4	1.6
Subadult *O. borealijaponica*	0.0	0.0	0.0	1.0
Nonmigrating	**36.5**	**31.0**	**37.0**	**34.3**
C. c. f. *calyx*	24.9	27.7	28.5	22.0
G. phyllura	2.6	0.0	0.3	0.0
S. dofleini	9.1	3.3	8.2	12.3

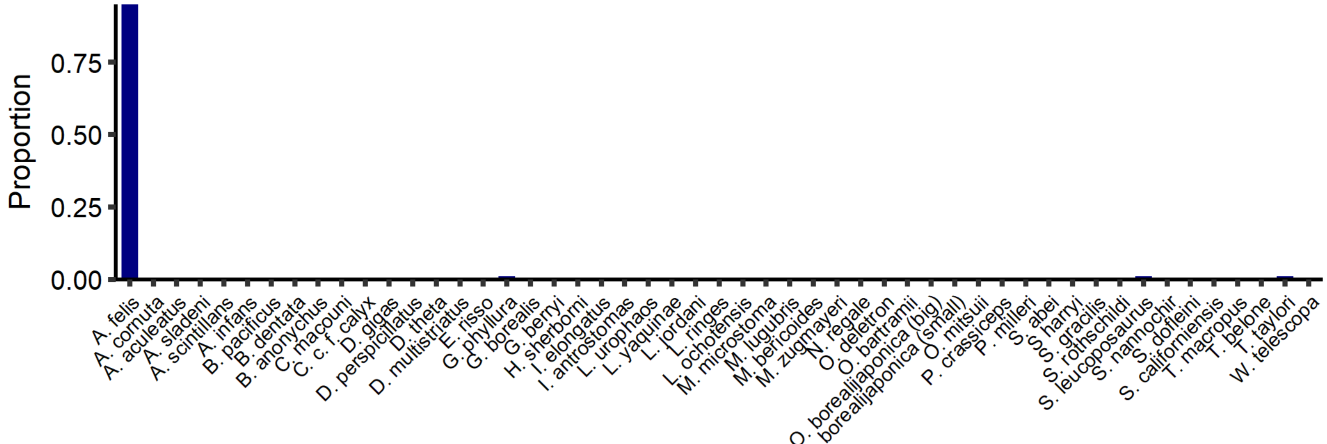
A2 Supplemental Figures



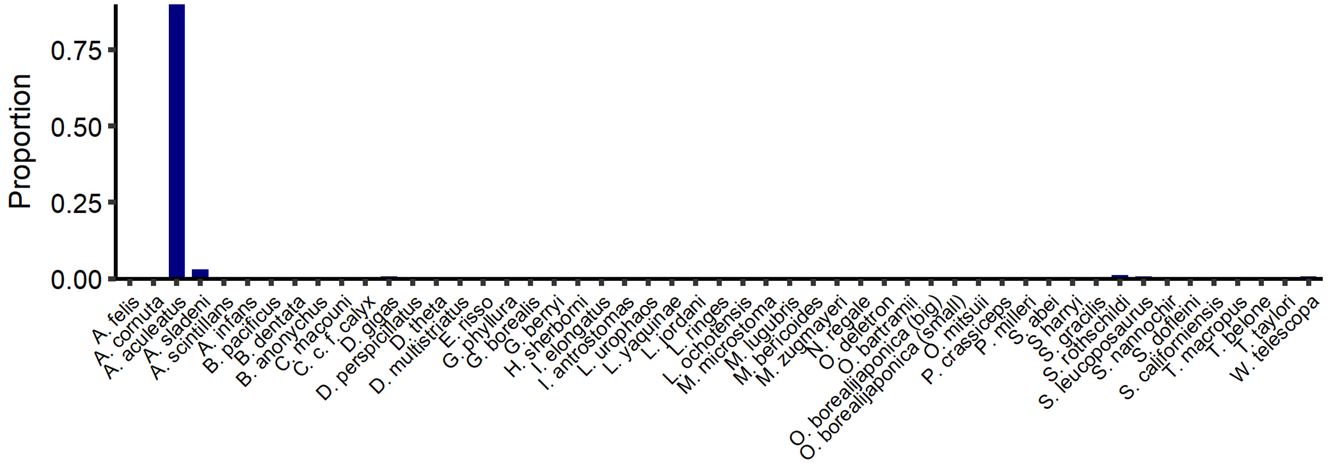
A2.1 NMDS analyses of prey dietary fatty acid profiles. (A) migrator types, **(B)** diet guilds (PSC: Piscivore , CRU: Macrocrustacivore; GEL: Gelativore; ZPL: Zooplanktivore, GEN: Generalist, CFCr: Cephalopods, fishes, crustaceans), and **(C)** mesopelagic biogeographic region (NCP: North Central Pacific, SAP: Subarctic Pacific, CC: California Current).

A2.2 Leave-One-Prey-Out (LOPO) Analysis. Panels (**A2.2.1 – A2.2.48**) depict the prey "diet" when a fatty acid (FA) profile is removed from the prey library and used as the predator profile. Low prey confounding is indicated when most of the removed prey's "diet" is composed of that same prey item (i.e. good model discrimination among prey species). The prey library is presented alphabetically, excluding prey species with single FA profile.

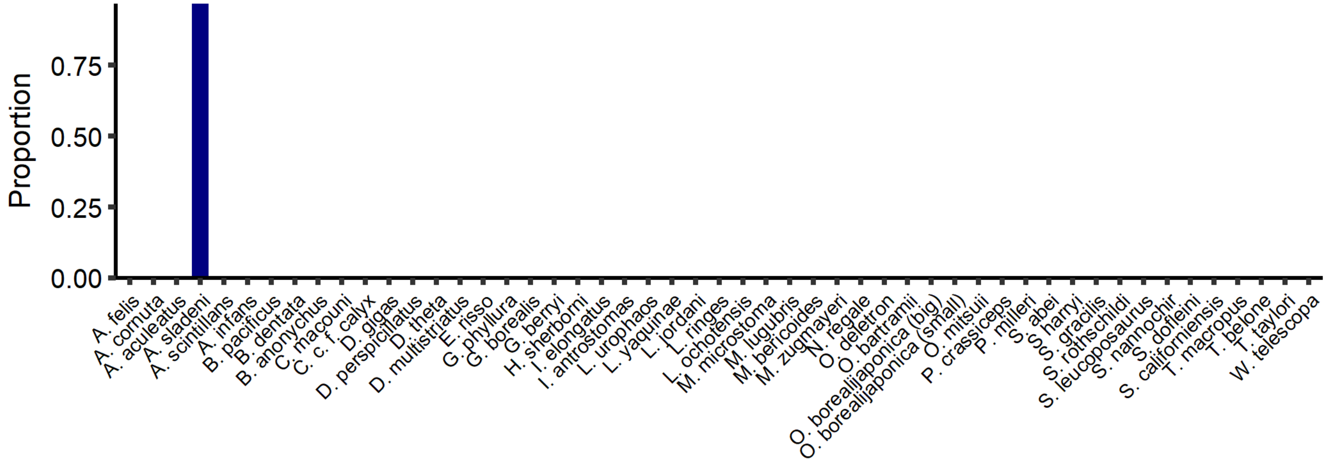
A2.2.1 *Abraliopsis felis*



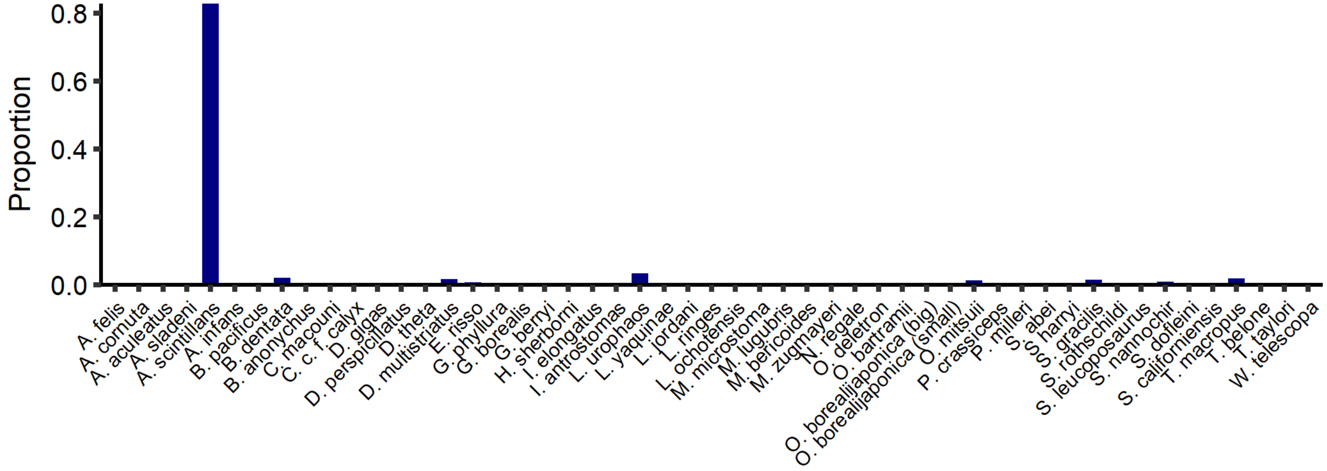
A2.2.2 *Argyropelecus aculeatus*



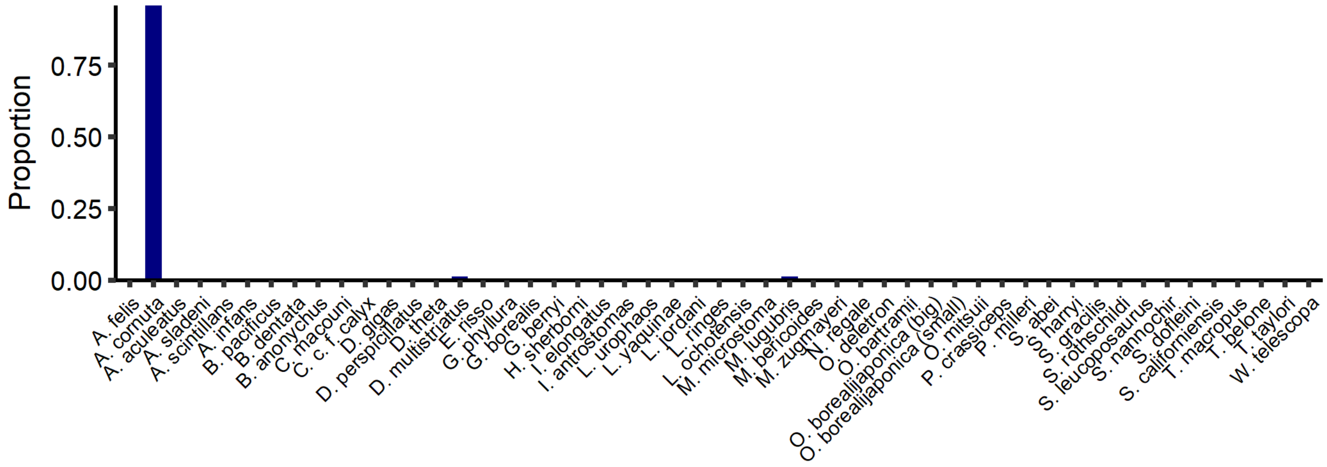
A2.2.3 *Argyropelecus sladeni*



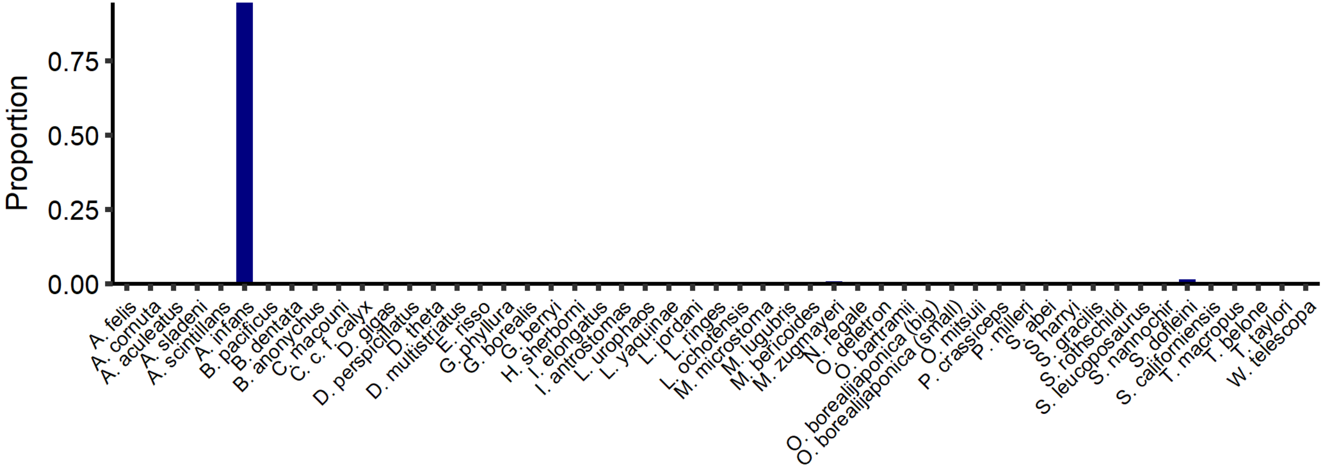
A2.2.4 *Aristostomias scintillans*



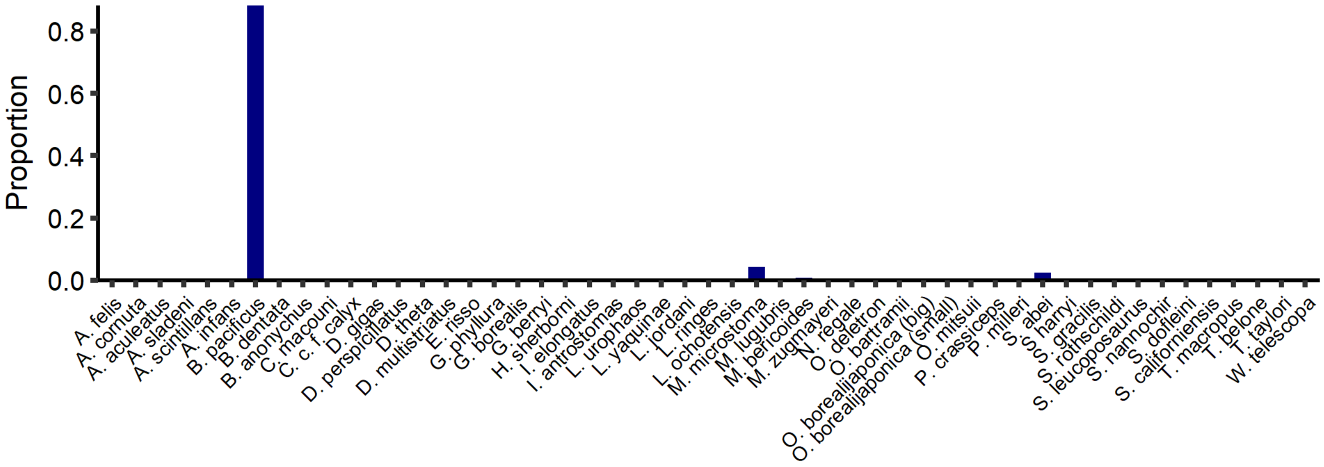
A2.2.5 *Anoplogaster cornuta*



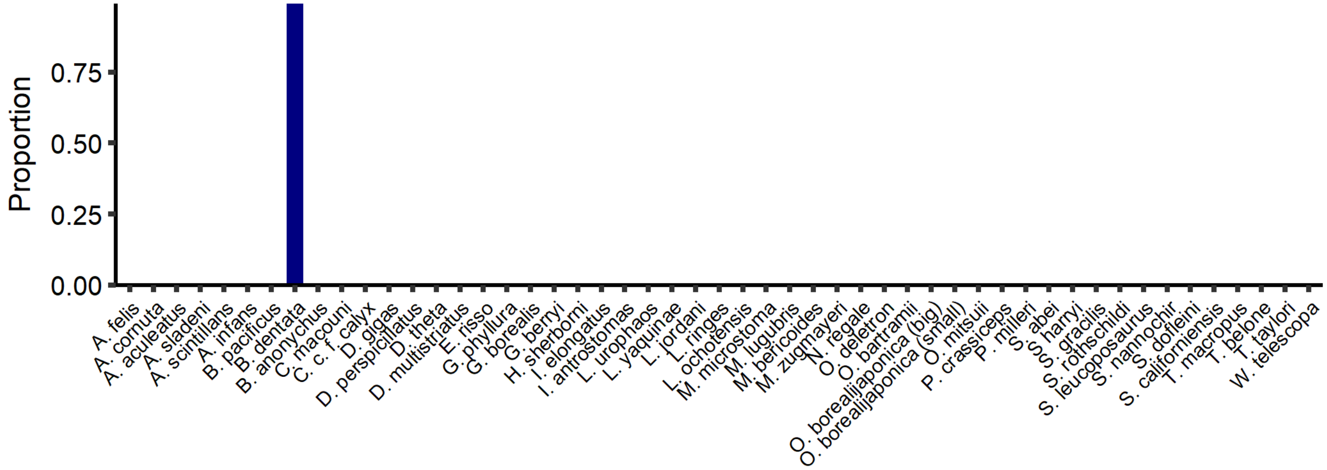
A2.2.6 *Avocettina infans*



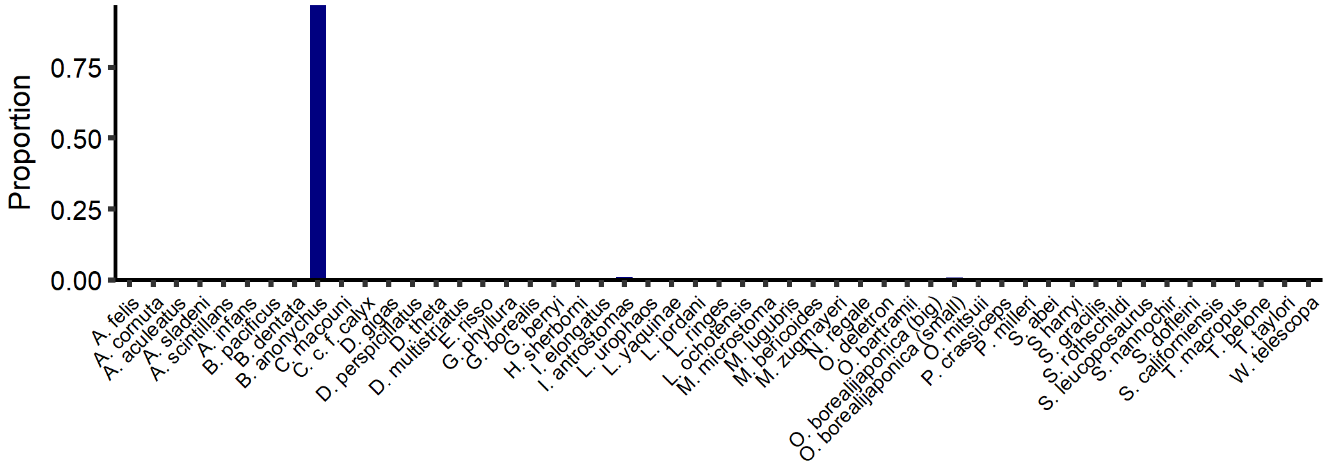
A2.2.7 *Bathylagus pacificus*



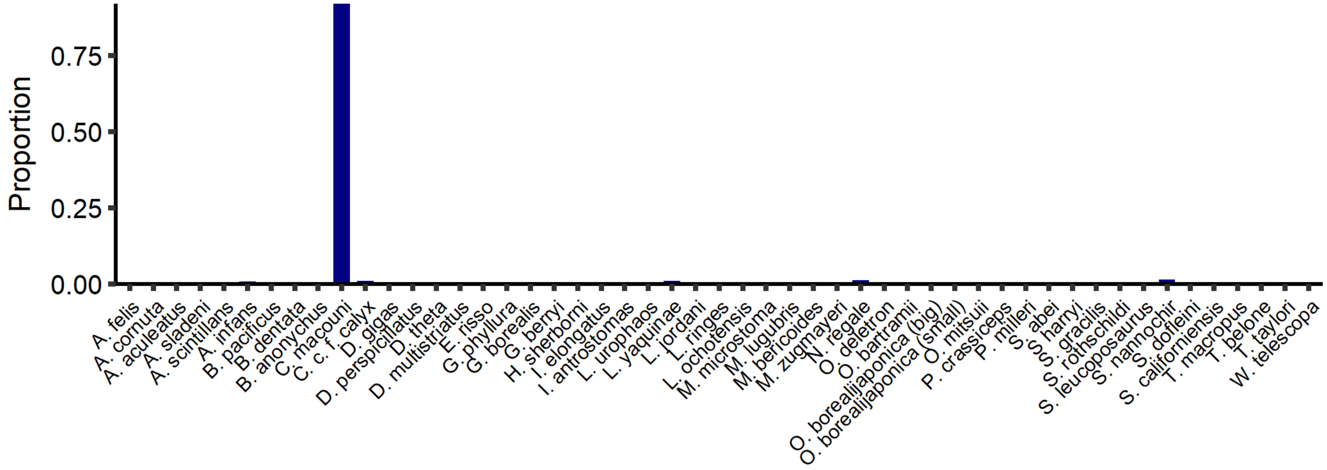
A2.2.8 *Benthalbella dentata*



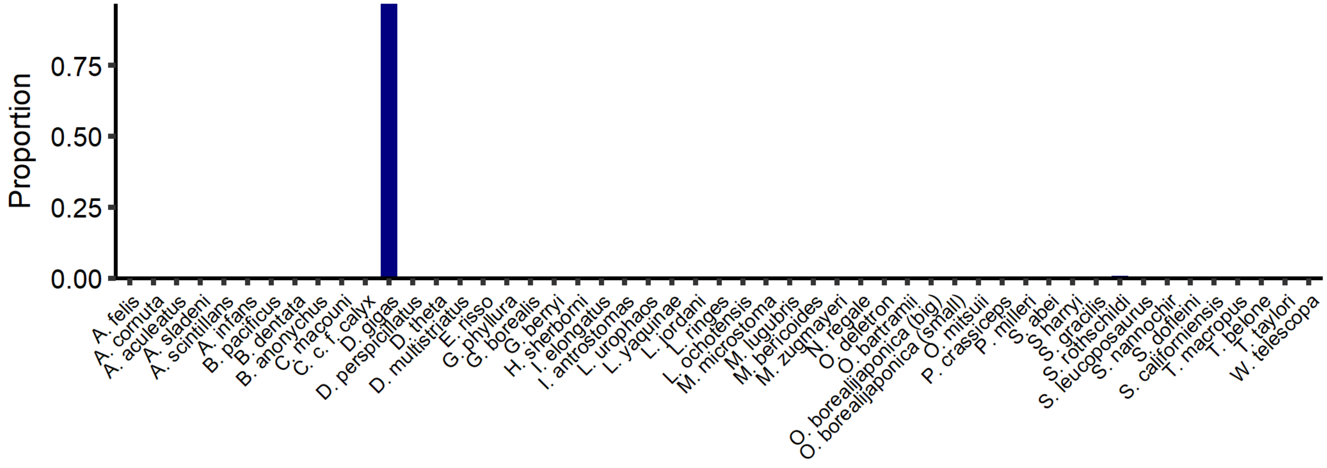
A2.2.9 *Berryteuthis anonychus*



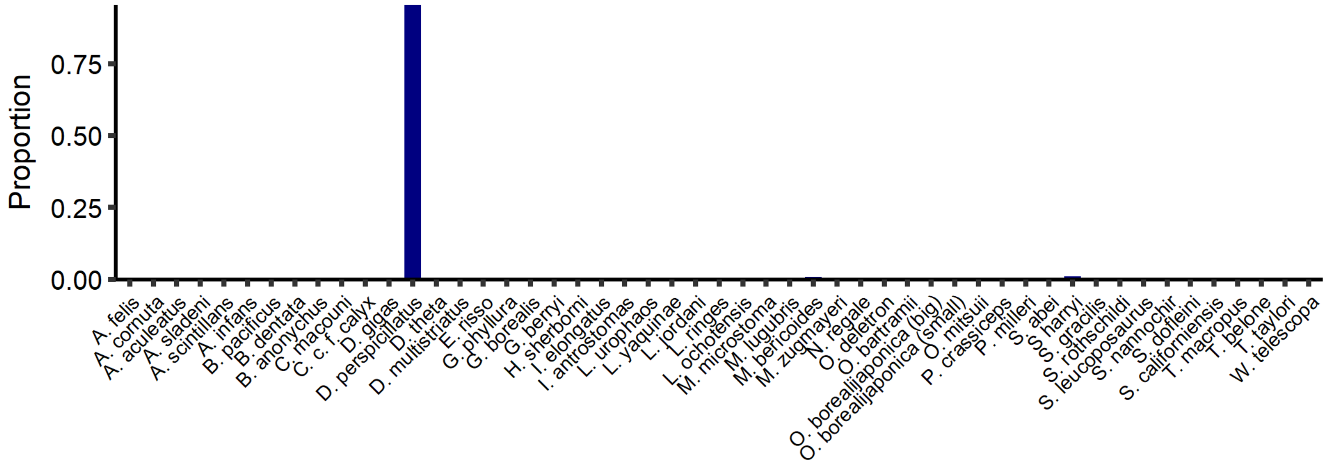
A2.2.10 *Chauliodus macouni*



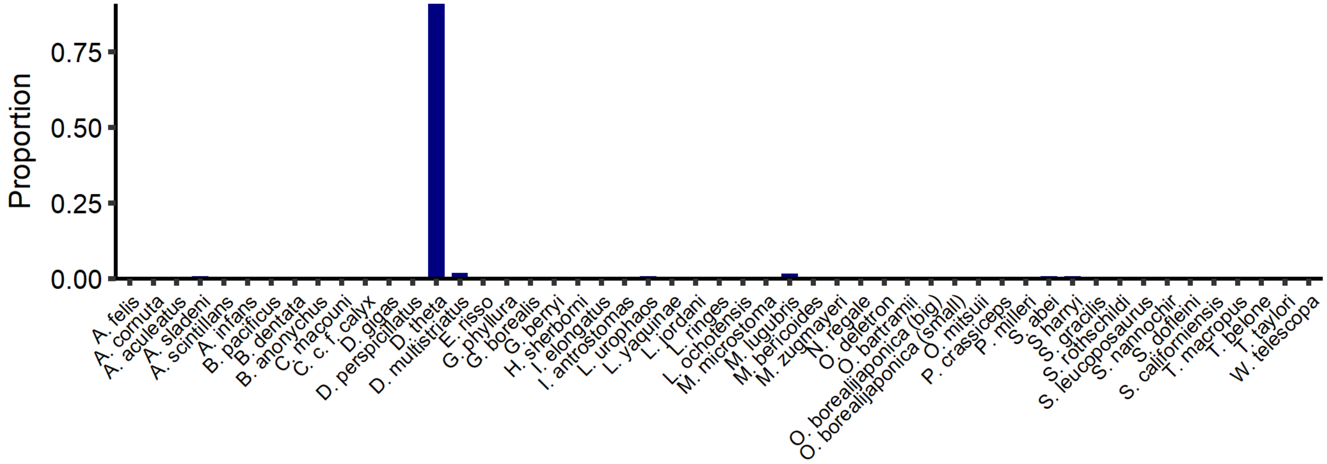
A2.2.11 *Diaphus gigas*



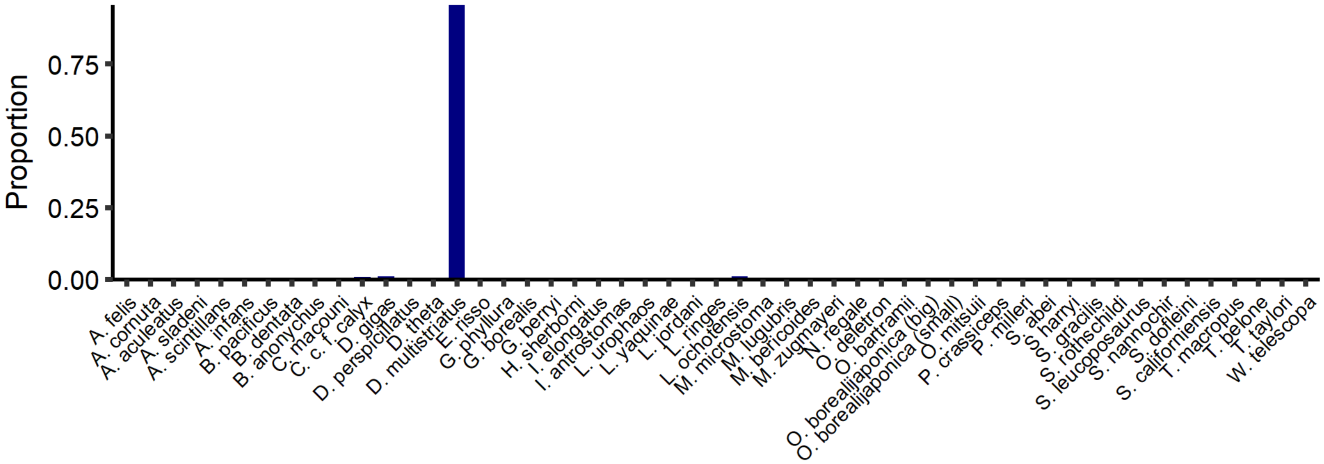
A2.2.12 *Diaphus perspicillatus*



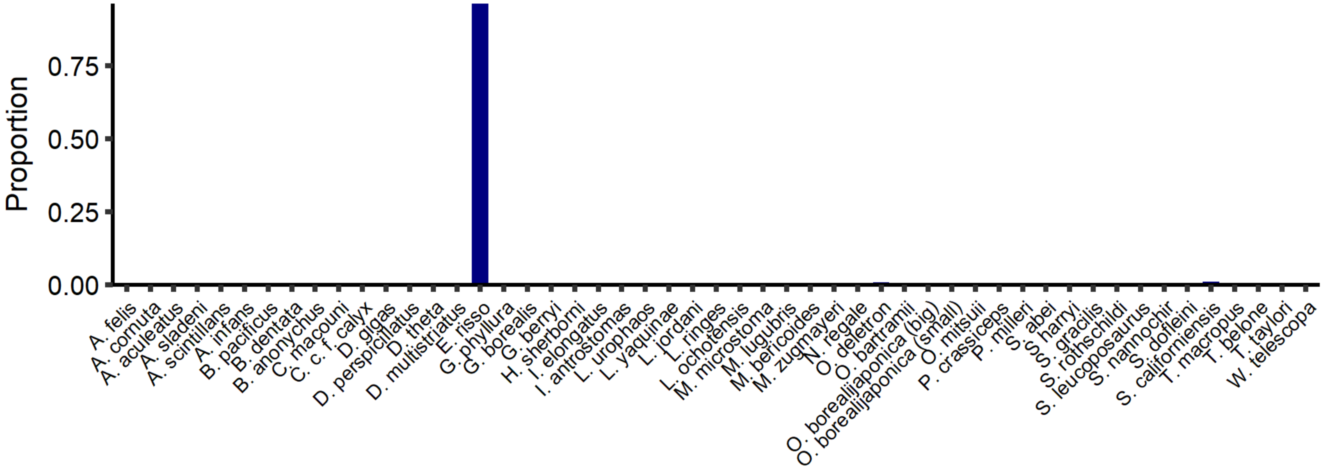
A2.2.13 *Diaphus theta*



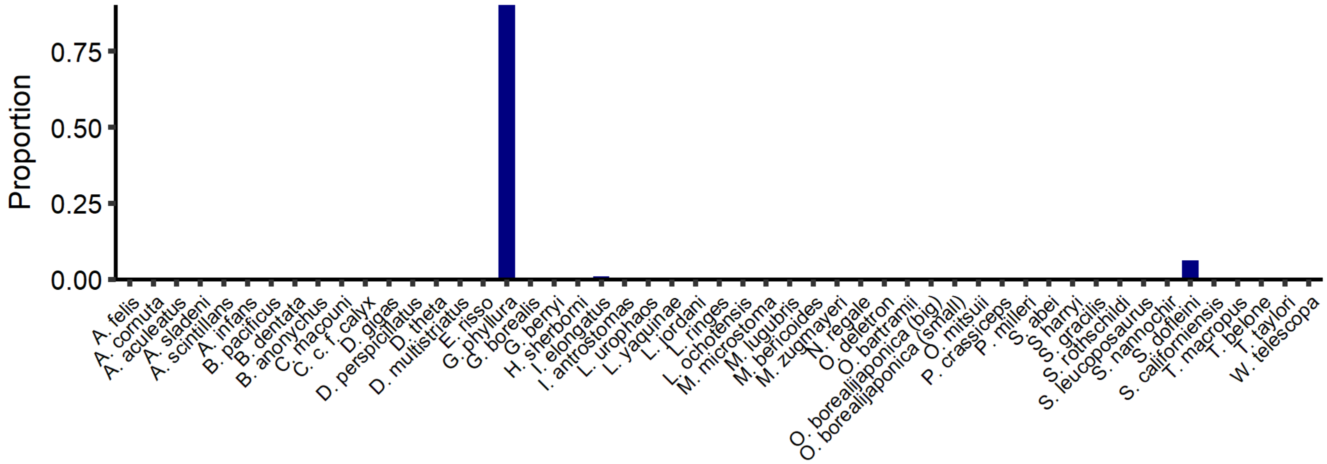
A2.2.14 *Diplospinus multistriatus*



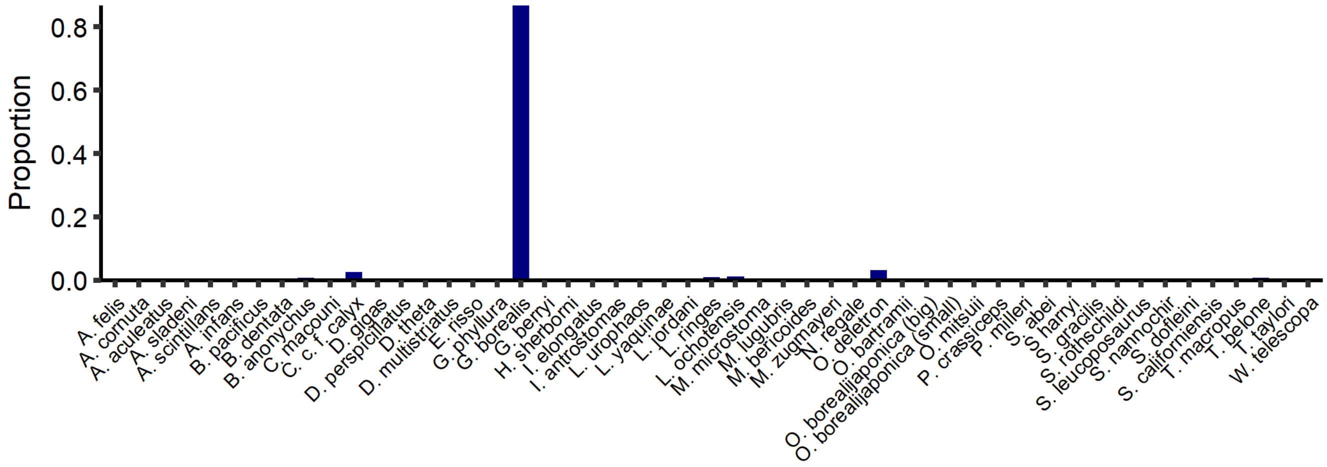
A2.2.15 *Electrona risso*



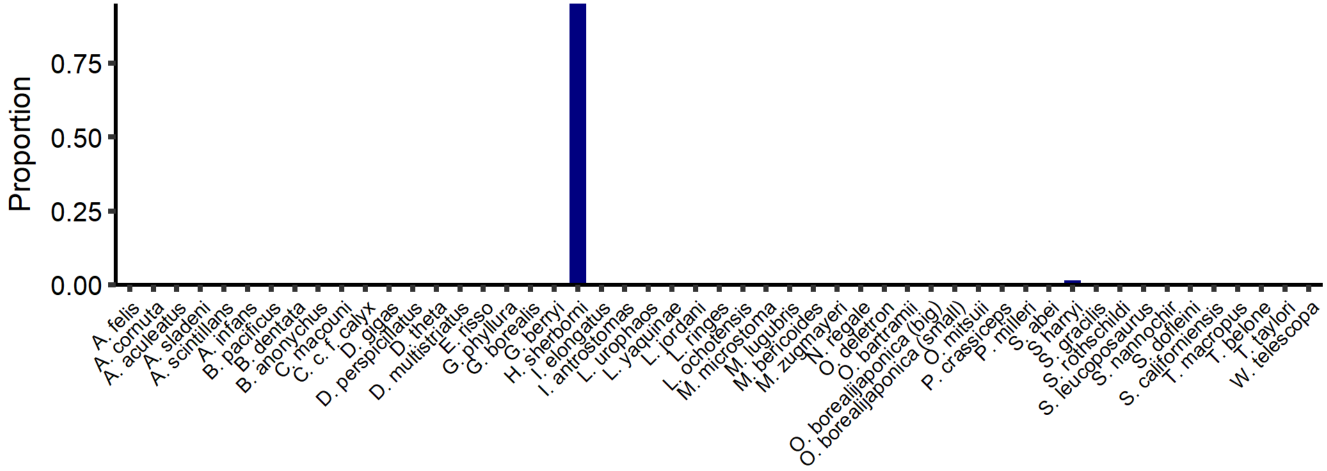
A2.2.16 *Galiteuthis phyllura*



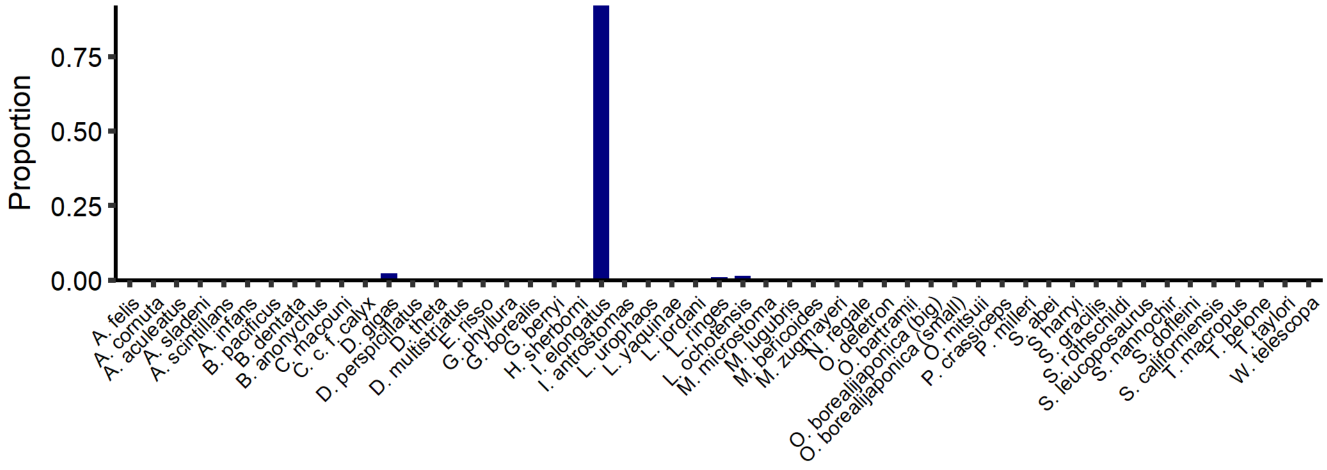
A2.2.17 *Gonatopsis borealis*



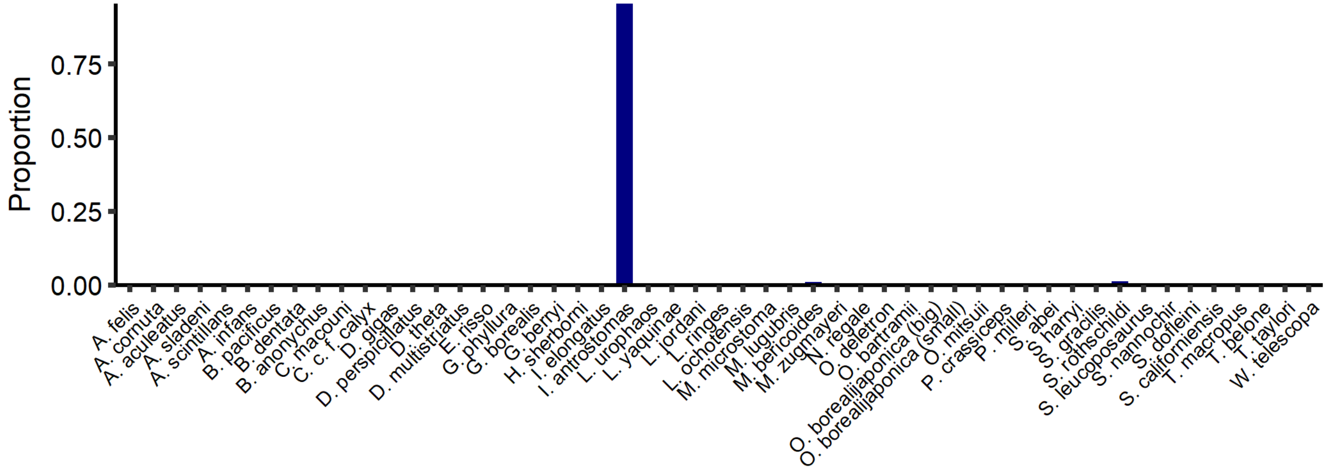
A2.2.18 *Howella sherborni*



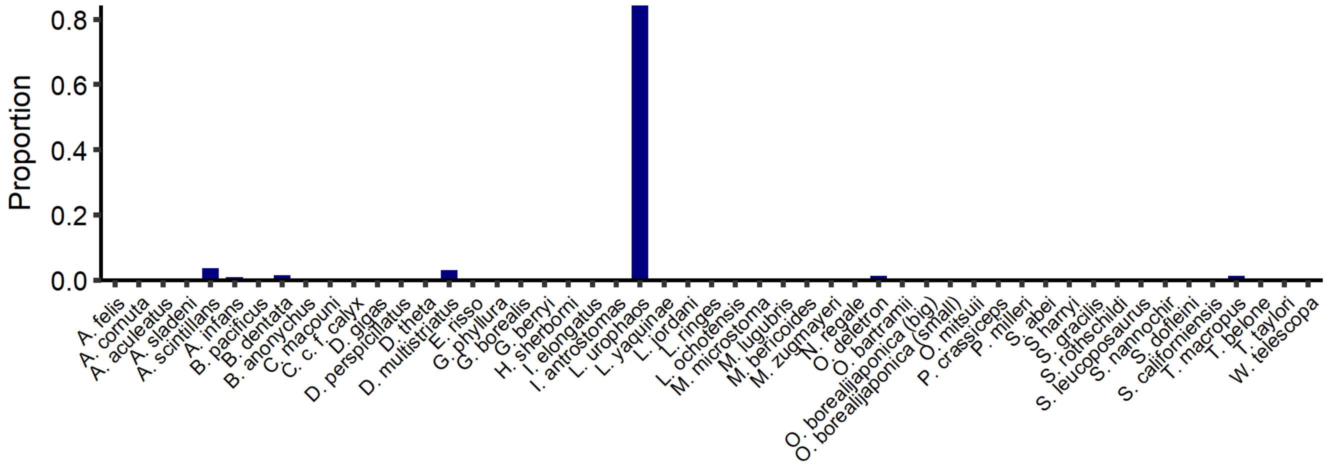
A2.2.19 *Ichthyococcus elongatus*



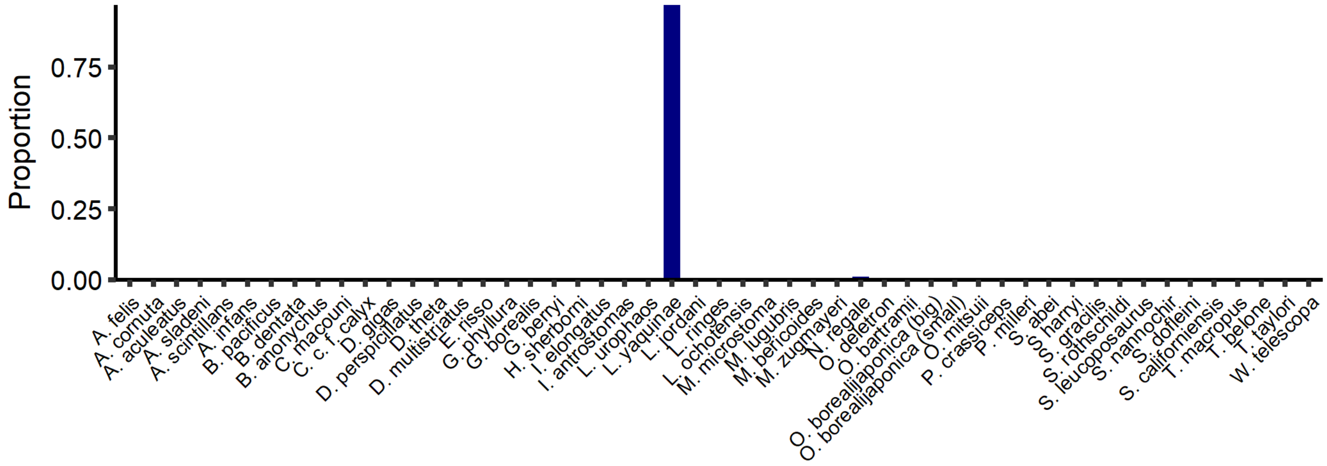
A2.2.20 *Idiacanthes antrostomas*



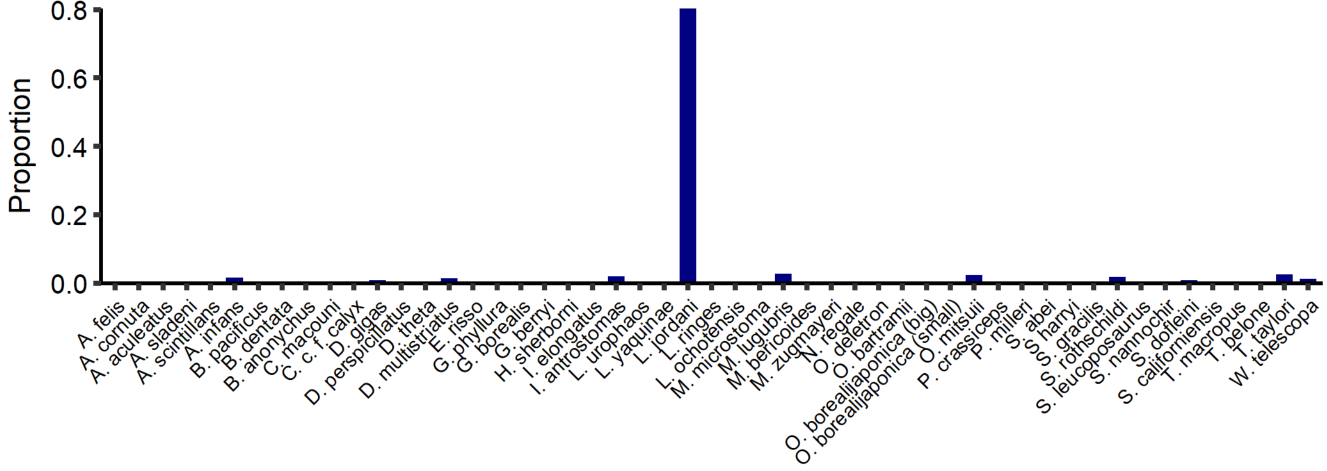
A2.2.21 *Lampadena urophaos*



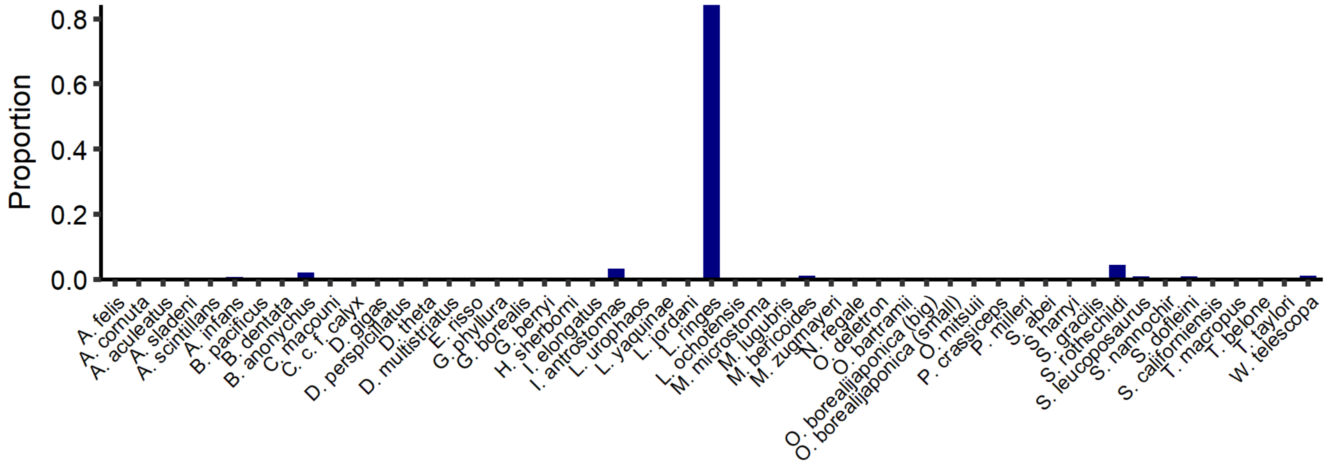
A2.2.22 *Lampadena yaquinae*



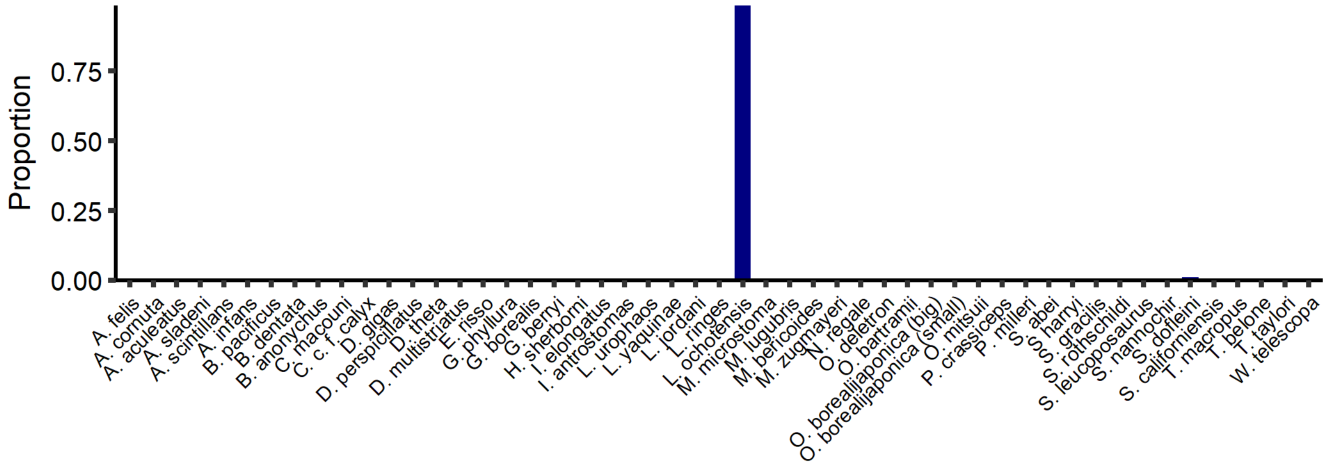
A2.2.23 *Lampanyctus jordani*



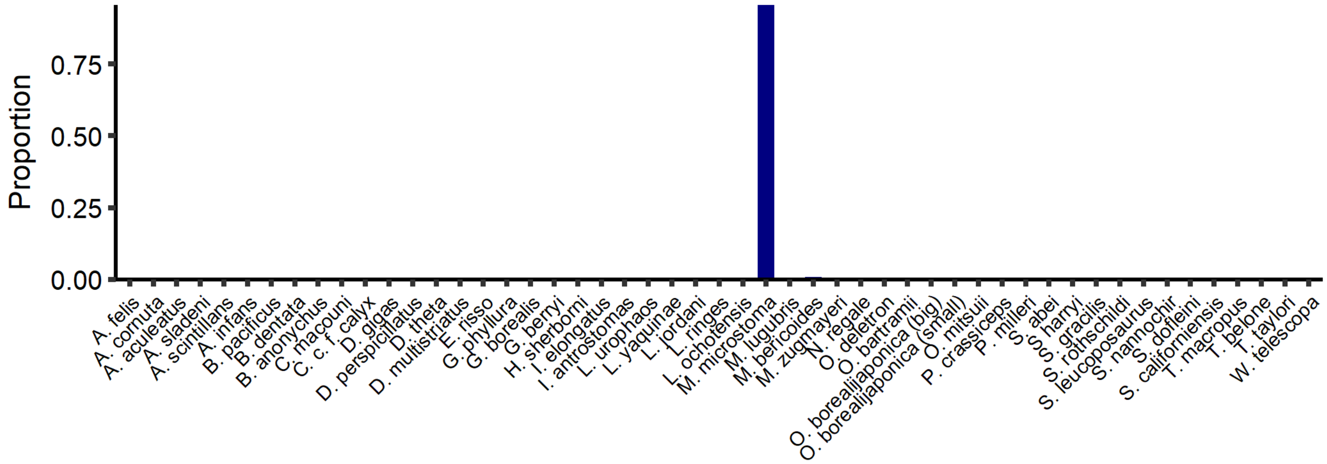
A2.2.24 *Lestidiops ringes*



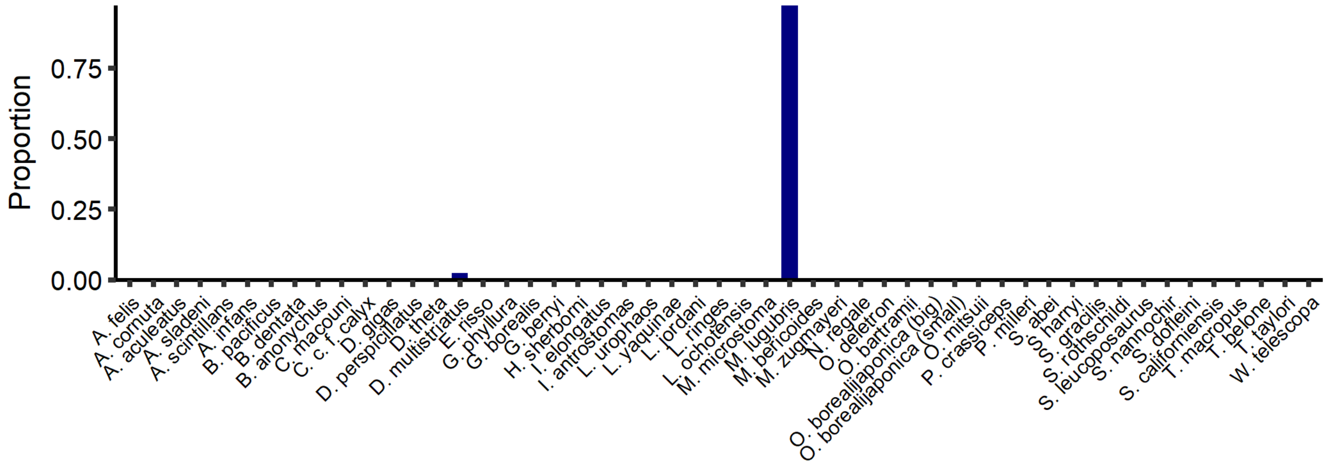
A2.2.25 *Lipolagus ochotensis*



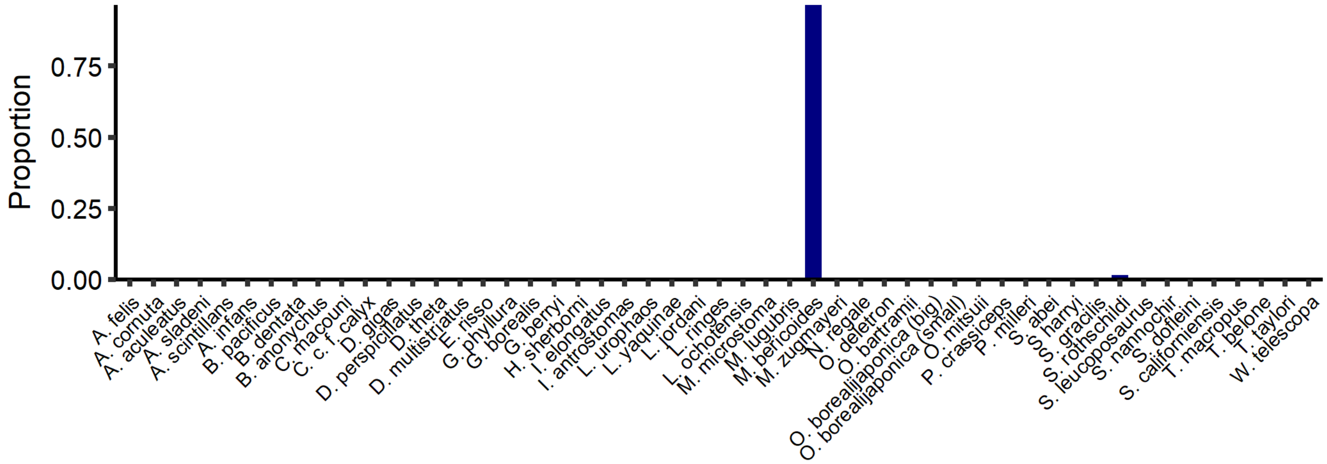
A2.2.26 *Macropinna microstoma*



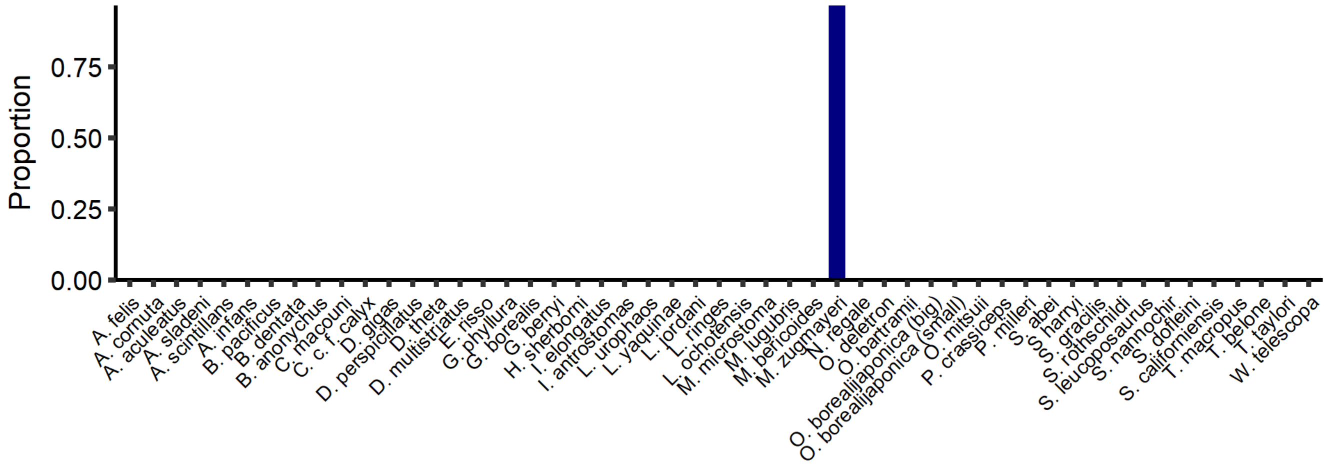
A2.2.27 *Melamphaes lugubris*



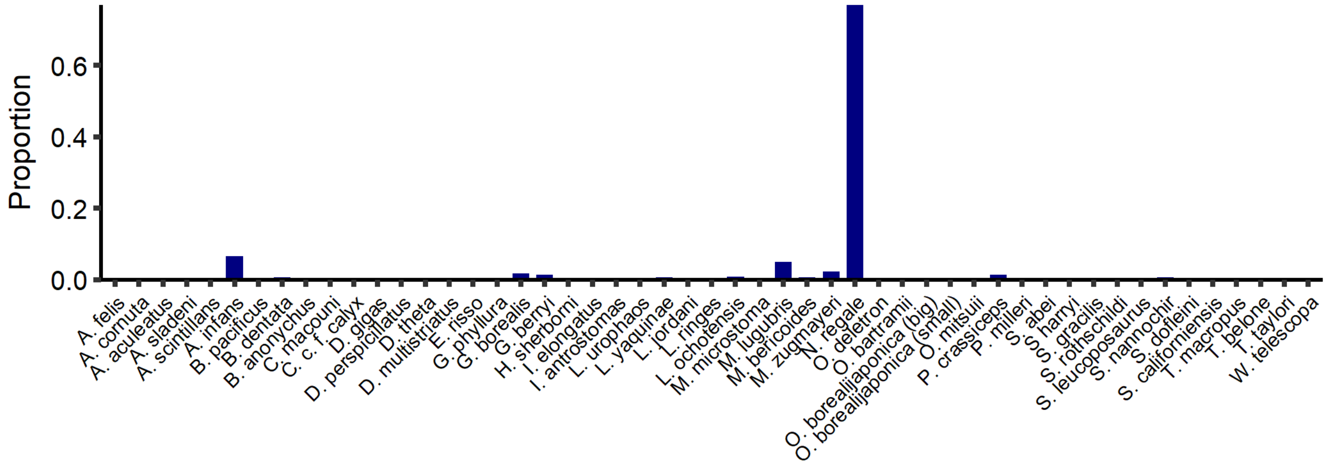
A2.2.28 *Melanolagus bericoides*



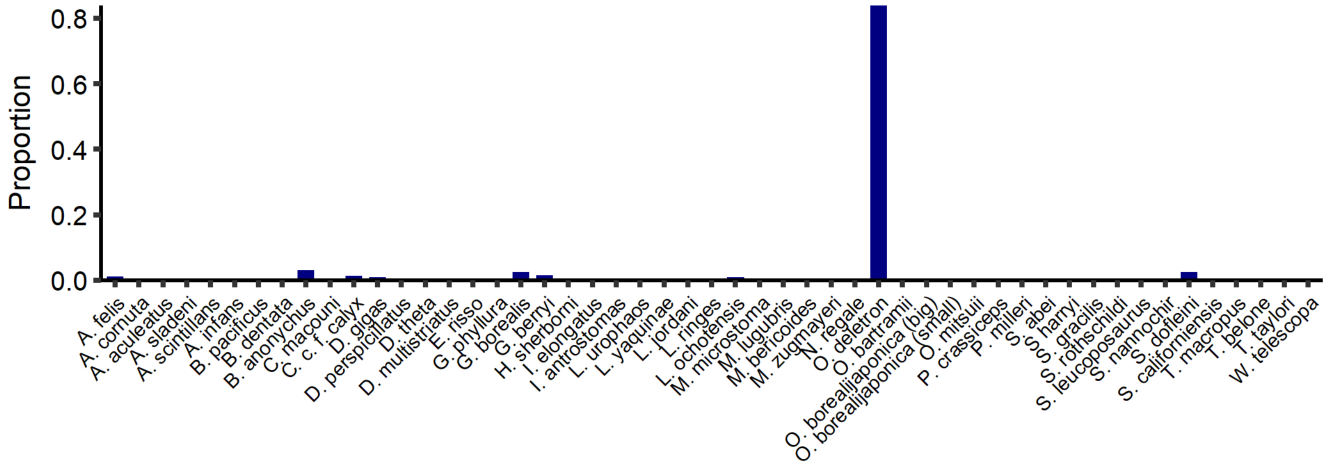
A2.2.29 *Melanonus zugmayeri*



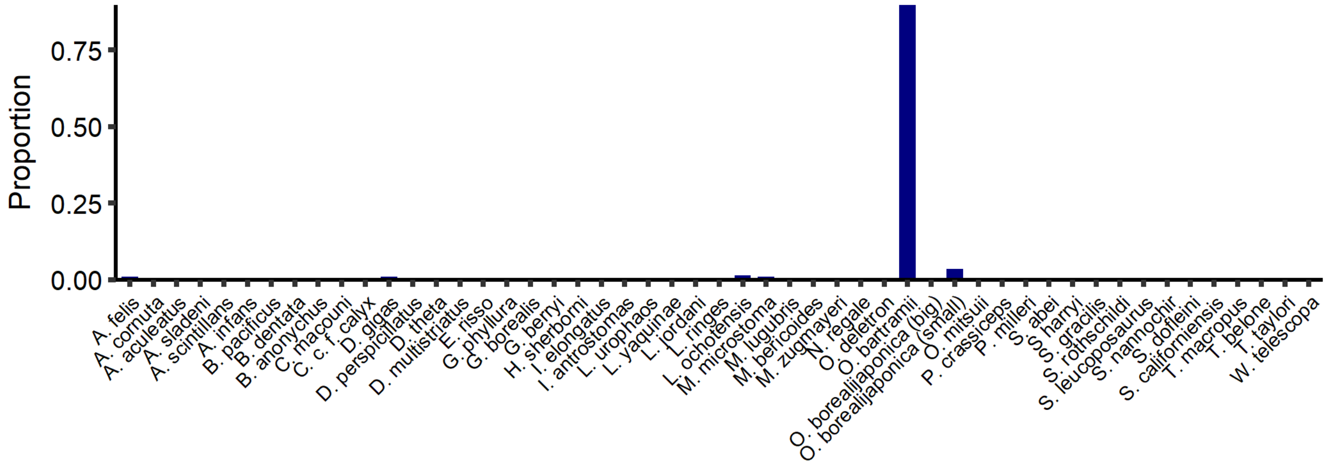
A2.2.30 *Nannobrachium regale*



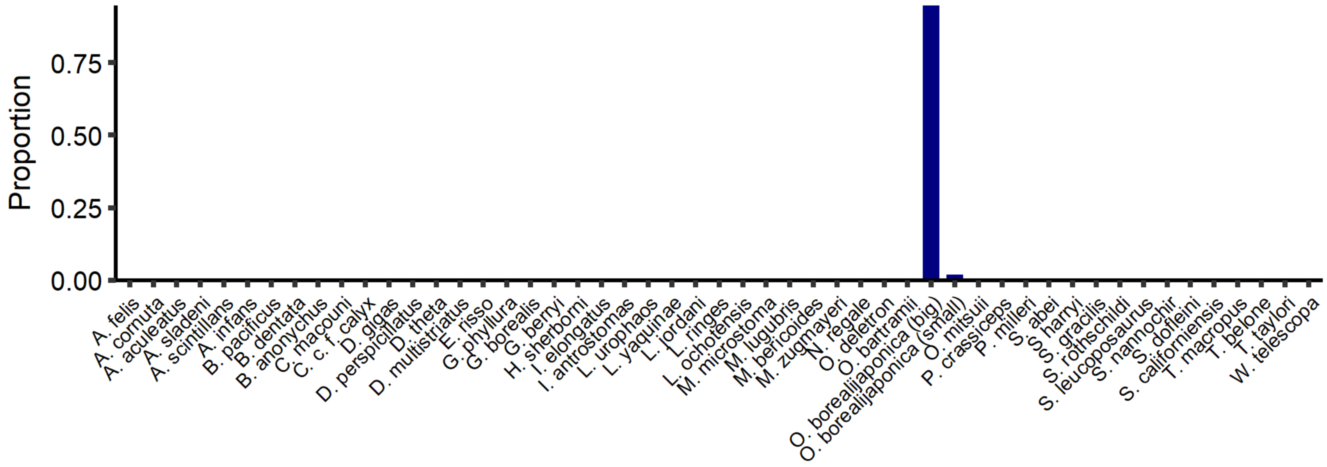
A2.2.31 *Octopoteuthis deletron*



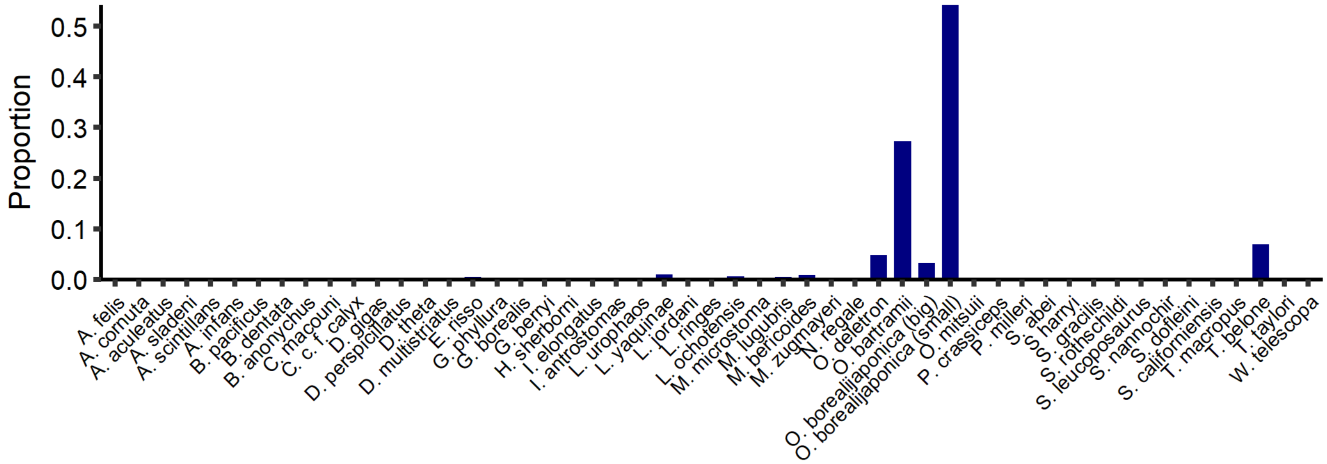
A2.2.32 *Ommastrephes bartramii*



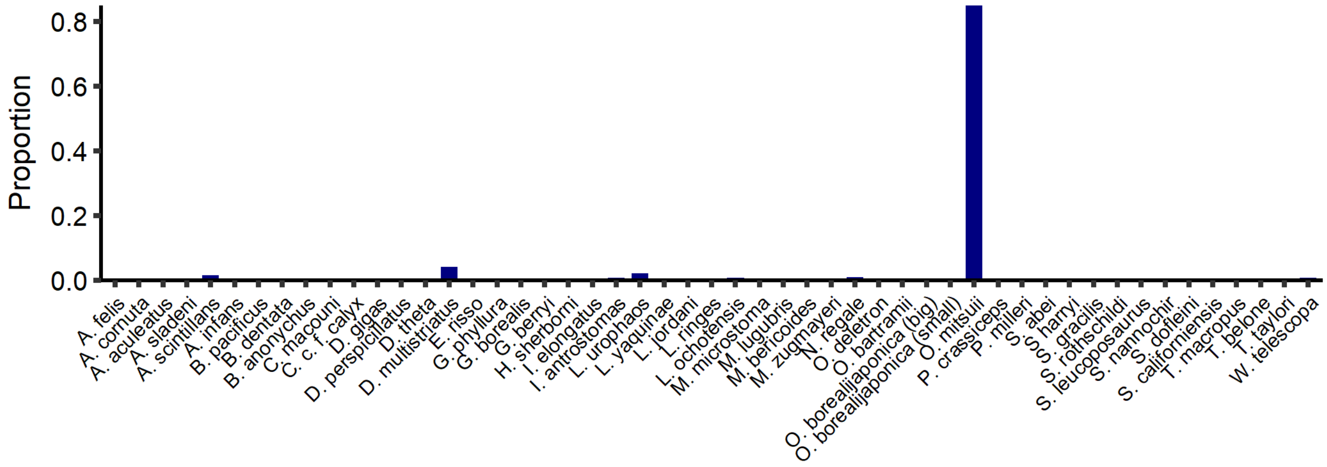
A2.2.33 *Onychoteuthis borealijaponica* (Adult)



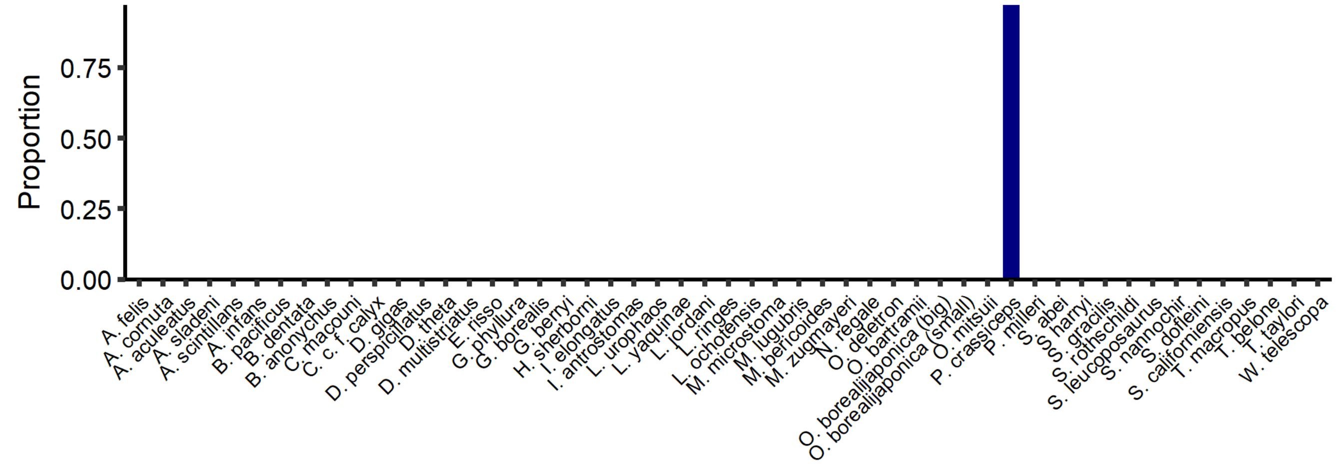
A2.2.34 *Onychoteuthis borealijaponica* (Subadult)



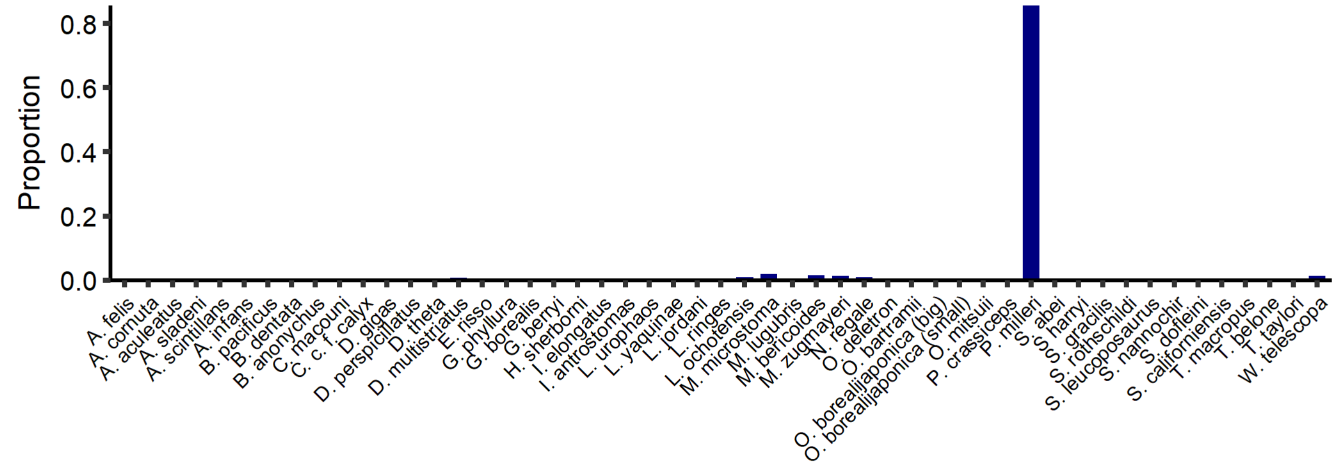
A2.2.35 *Opostomias mitsuii*



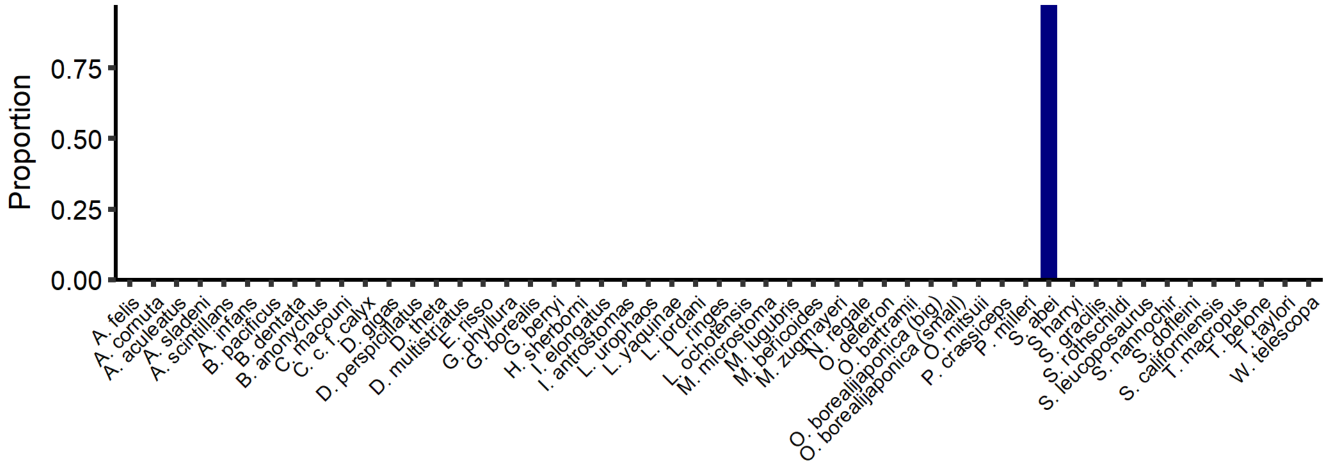
A2.2.36 *Poromitra crassiceps*



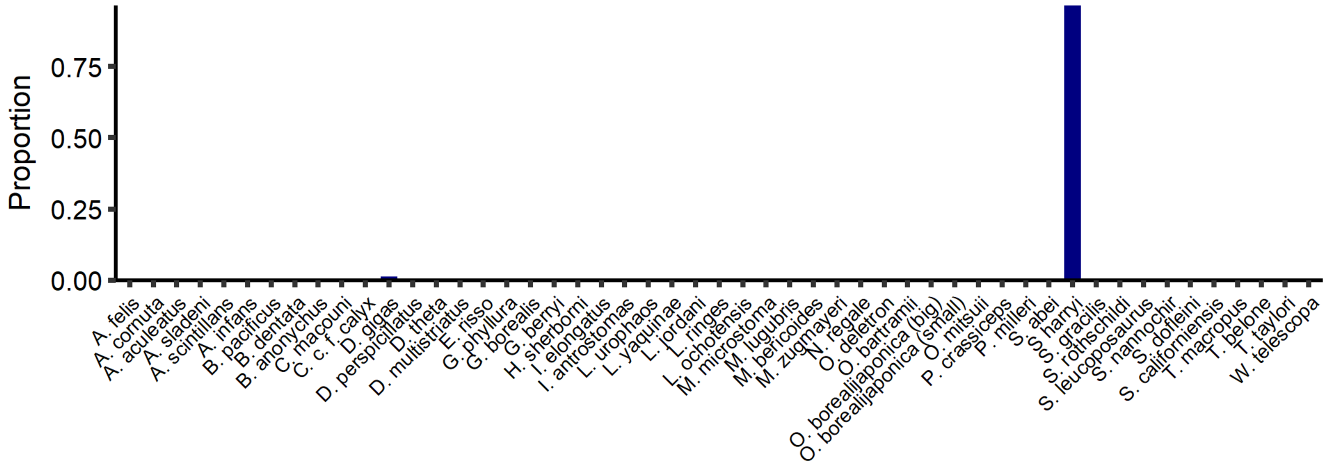
A2.2.37 *Pseudobathylagus milleri*



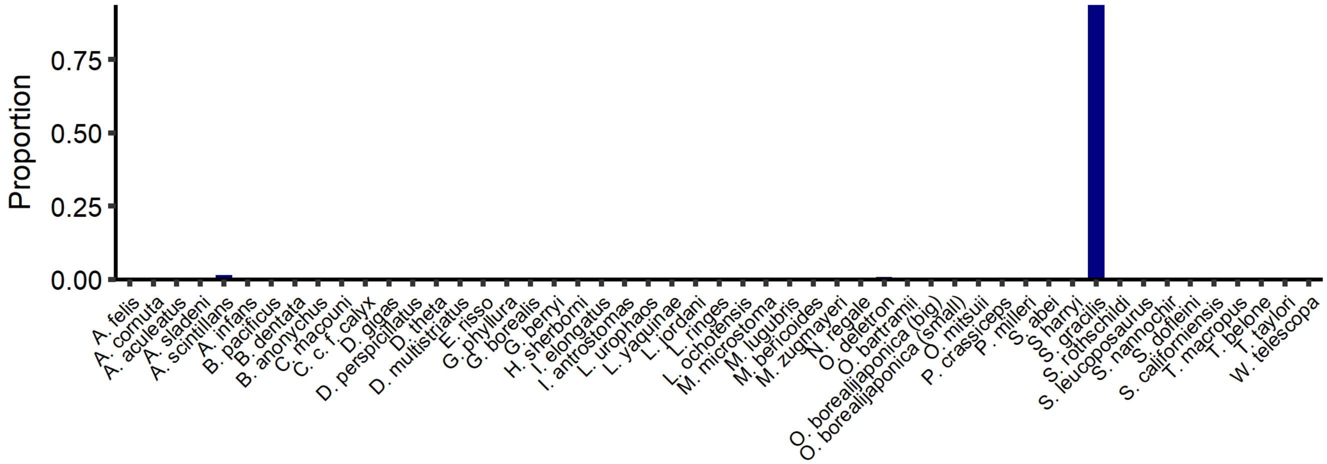
A2.2.38 *Sagamichthys abei*



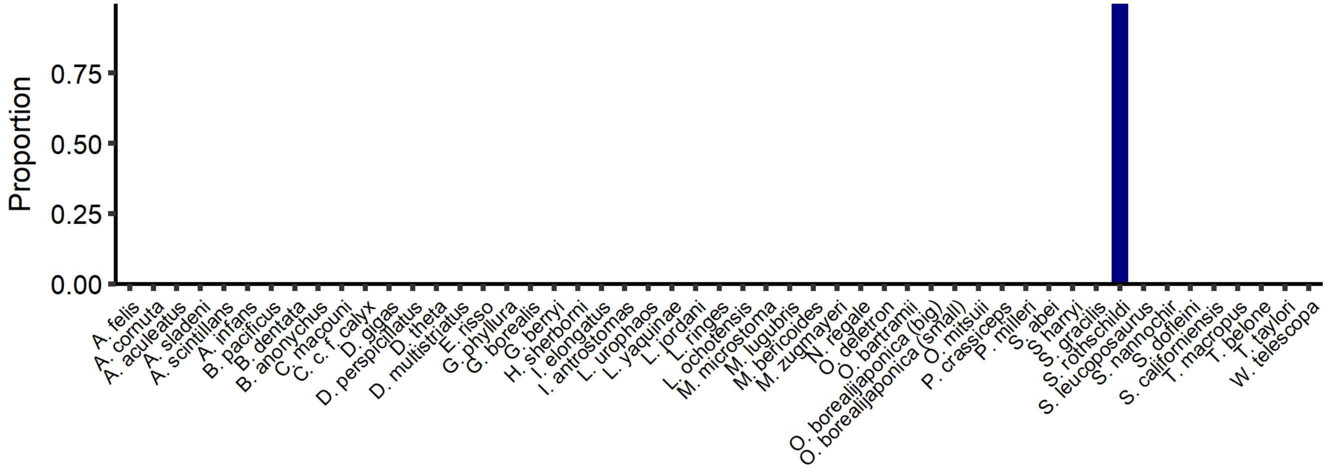
A2.2.39 *Scopelosaurus harryi*



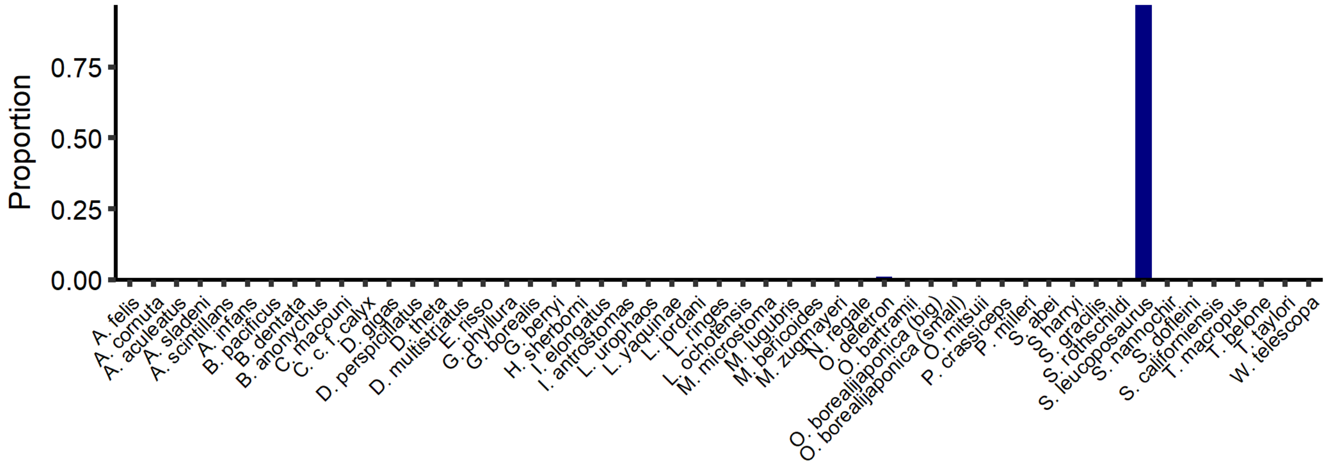
A2.2.40 *Sigmops gracilis*



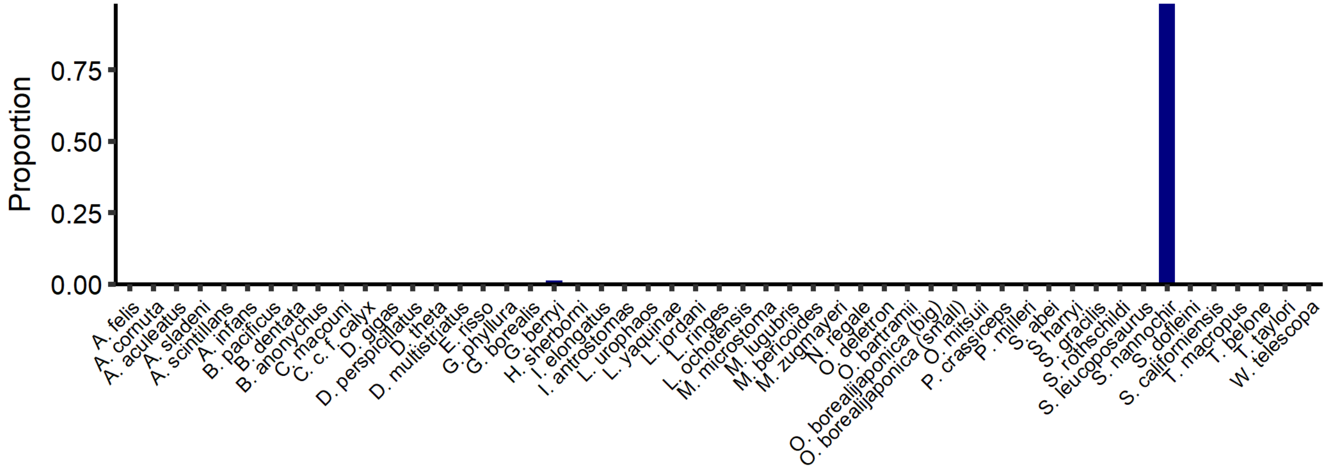
A2.2.41 *Stemonosudis rothschildi*



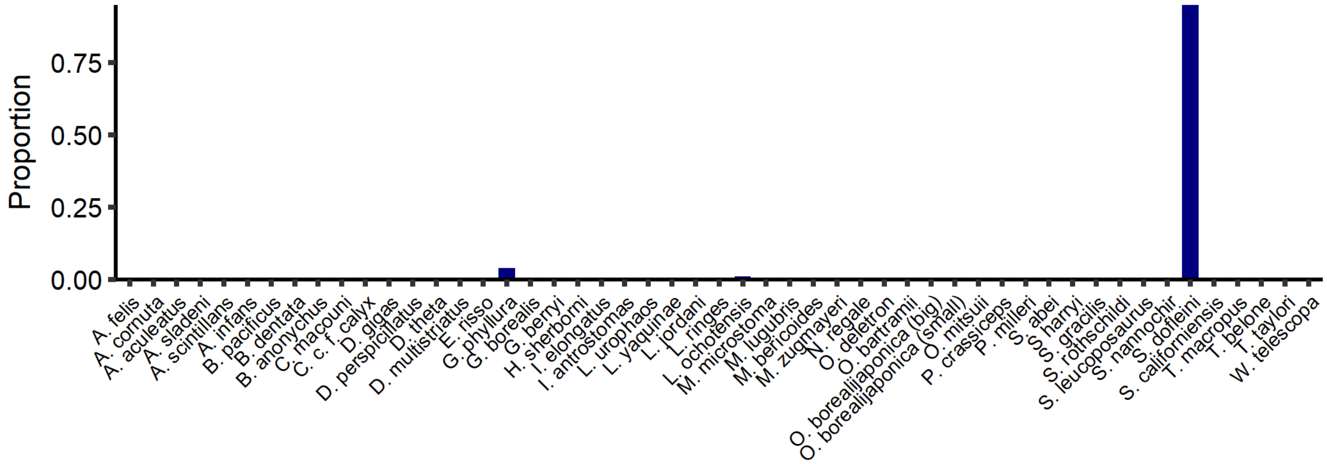
A2.2.42 *Stenobrachius leucopsarus*



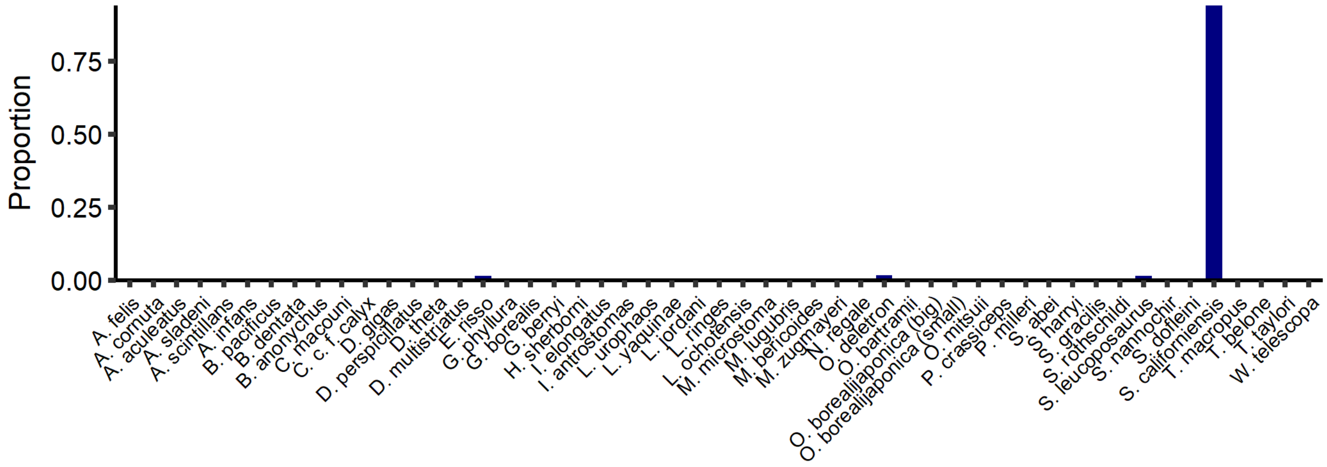
A2.2.43 *Stenobrachius nannochir*



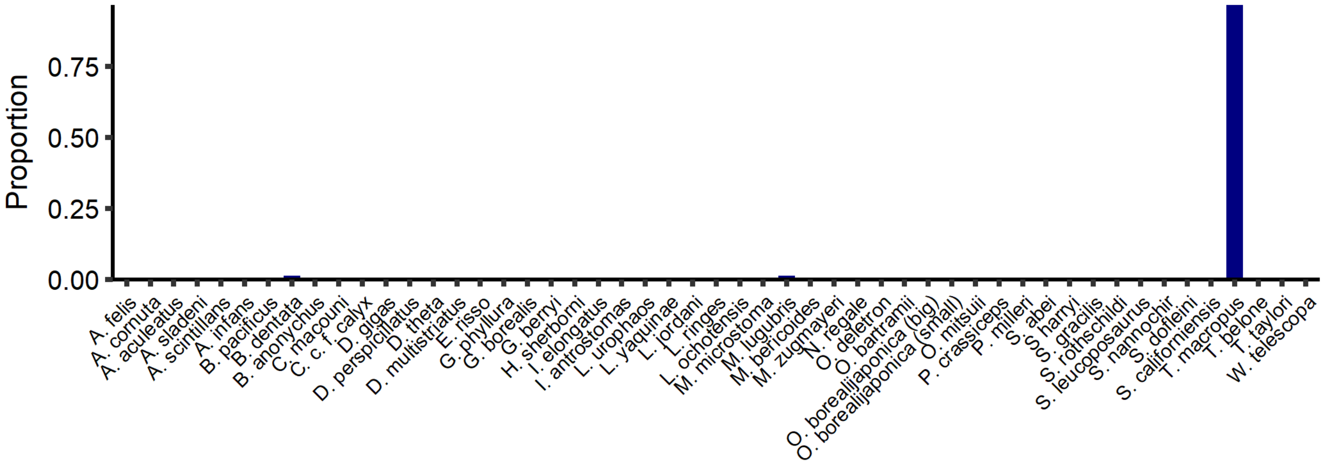
A2.2.44 *Stigmatoteuthis dofleini*



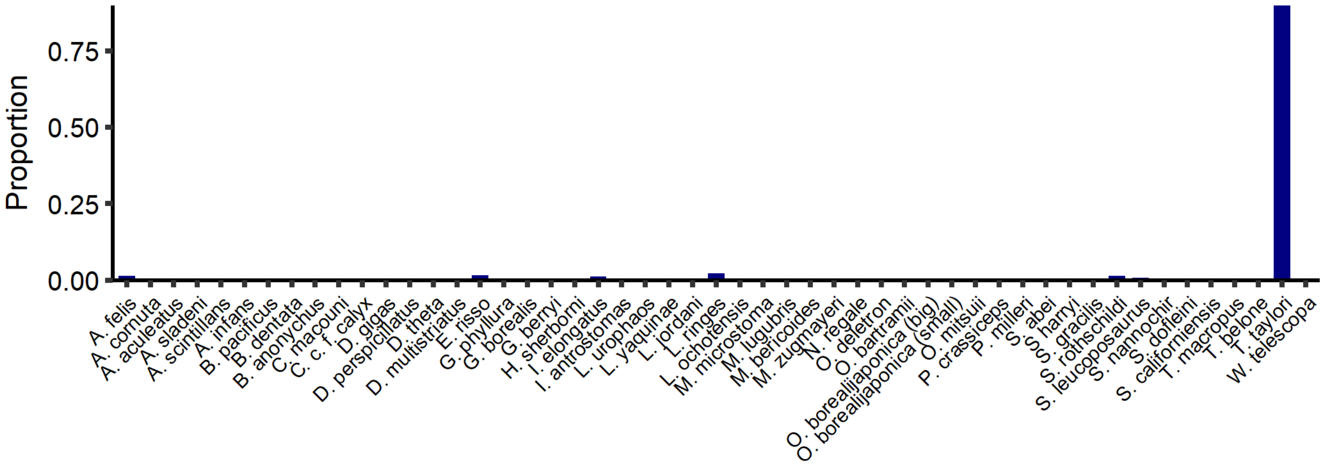
A2.2.45 *Symbolophorus californiensis*



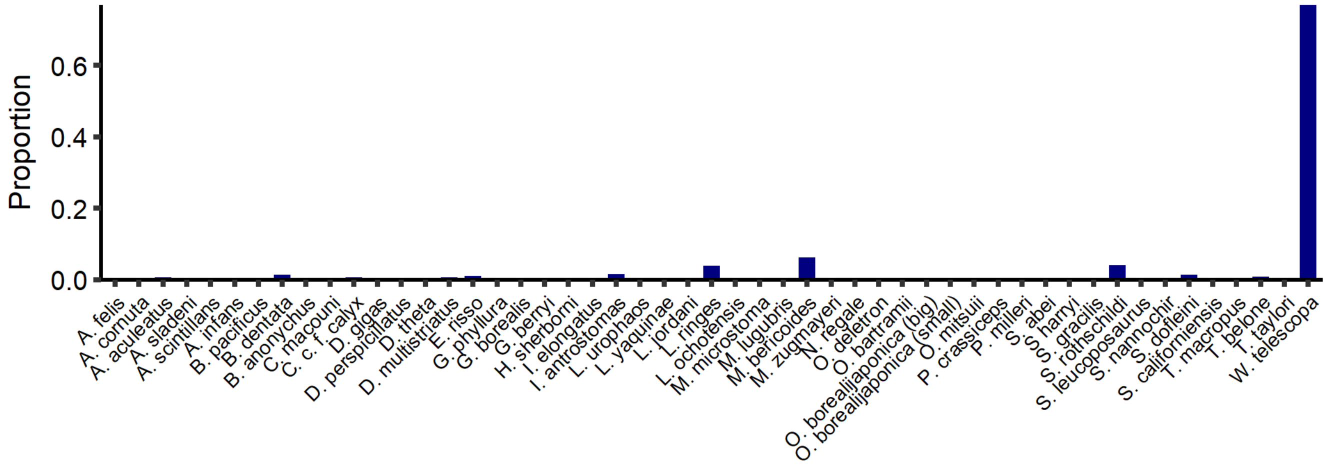
A2.2.46 *Tactostoma macropus*



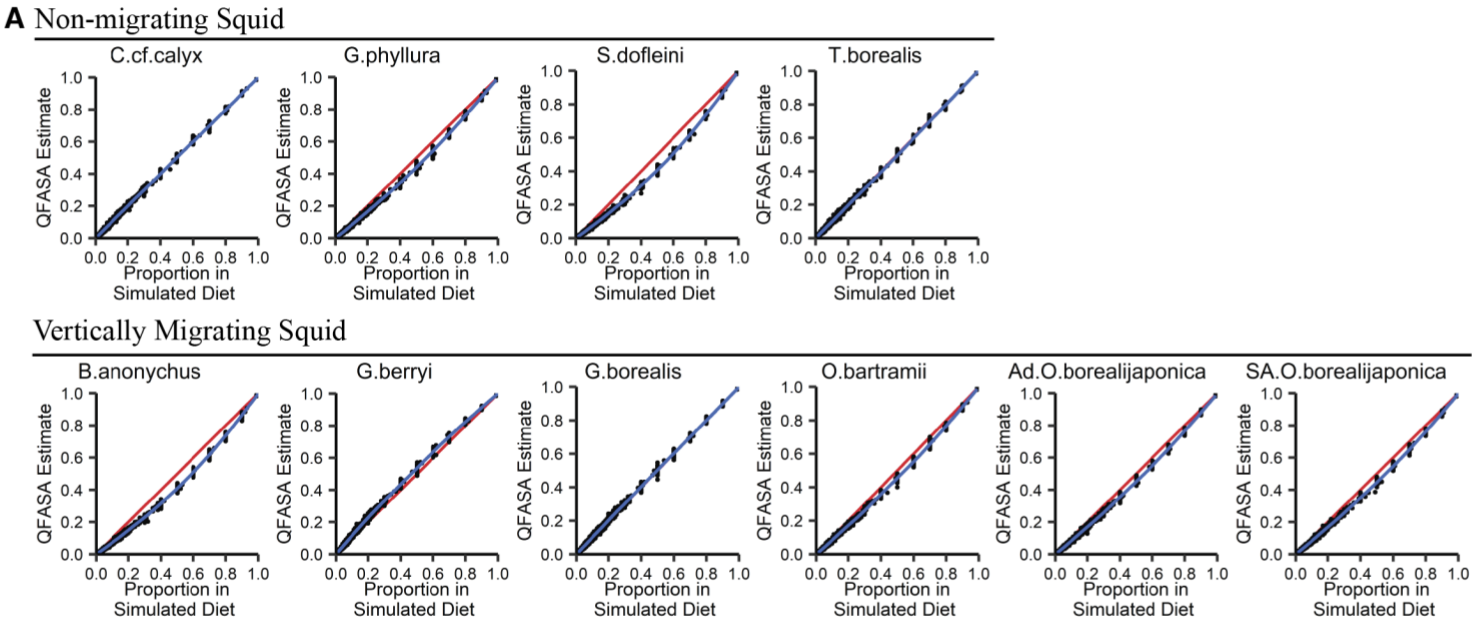
A2.2.47 *Tarletonbeania taylori*

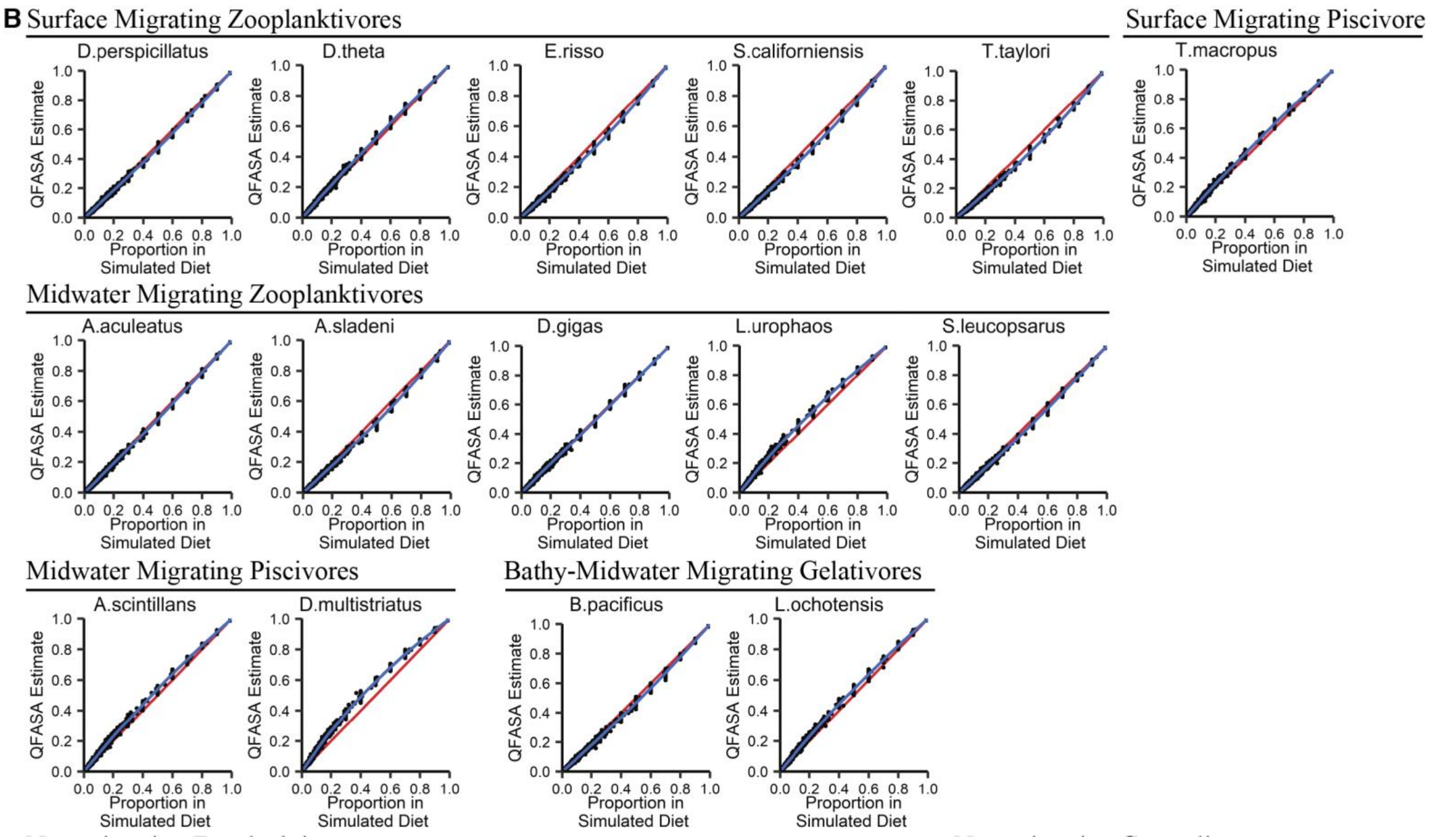


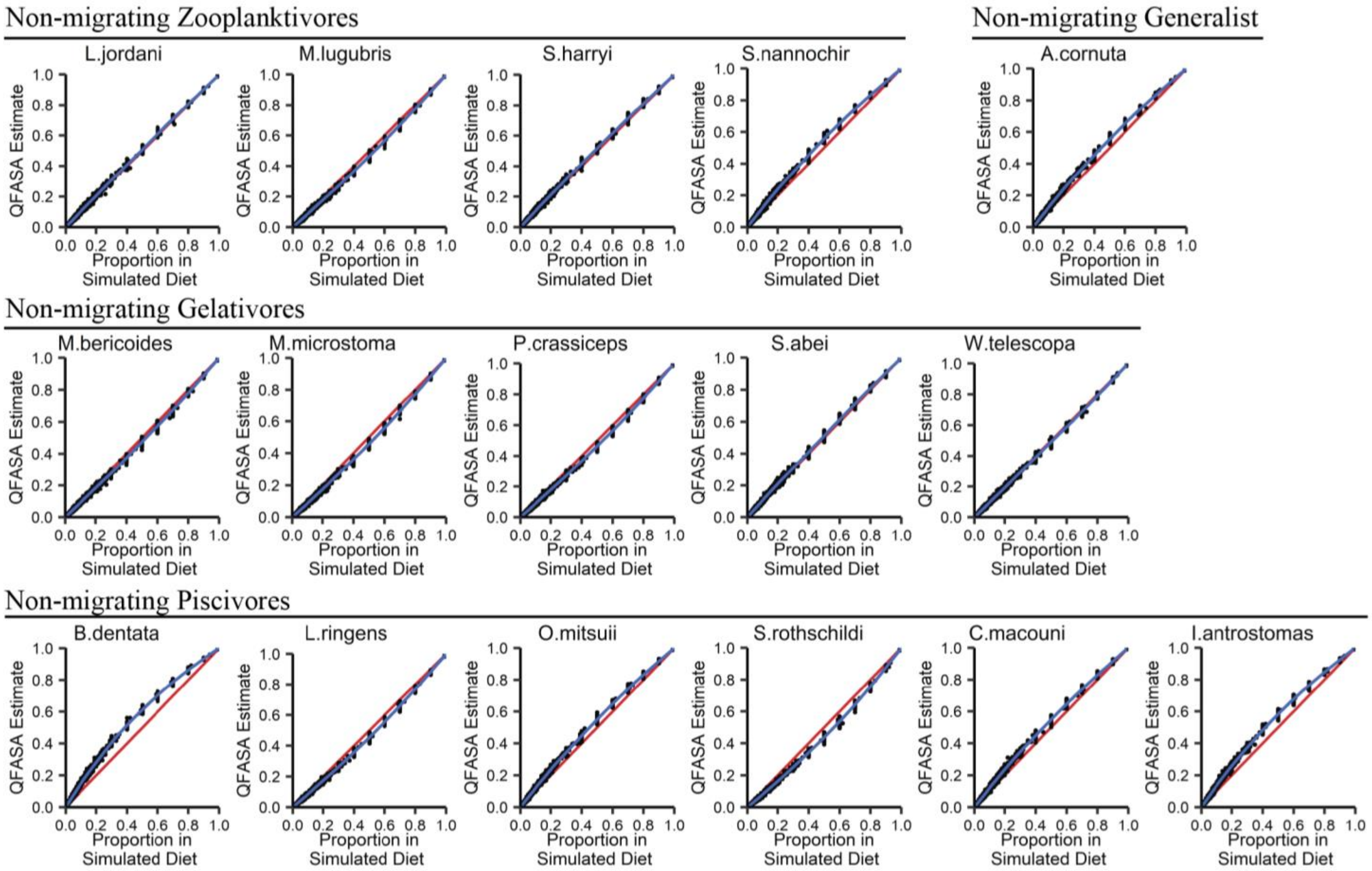
A2.2.48 *Winteria telescopa*



A2.3 Diet simulations quantify error in the QFASA model. The known proportion from the simulated diet is plotted against the proportion from the estimated diet, which was generated from the pseudopredator fatty acid profiles. The 1:1 line (red) indicates a perfect match between simulated and estimated diets. The blue line is a generalized additive model (GAM) fit to the data. **(A)** Squid and **(B)** fish species are presented by functional group.




B
Surface Migrating Zooplanktivores
D.perspicillatus
D.theta
E.risso
S.californiensis
T.taylori
Surface Migrating Piscivore
T.macropus
Midwater Migrating Zooplanktivores
A.aculeatus
A.sladeni
D.gigas
L.urophaos
S.leucopsarus
Midwater Migrating Piscivores
A.scintillans
D.multistriatus
Bathy-Midwater Migrating Gelativores
B.pacificus
L.ochotensis
QFASA Estimate
Proportion in Simulated Diet
0.0
0.2
0.4
0.6
0.8
1.0


Non-migrating Zooplanktivores
L.jordani
M.lugubris
S.harryi
S.nannochir
Non-migrating Generalist
A.cornuta
Non-migrating Gelativores
M.bericoides
M.microstoma
P.crassiceps
S.abei
W.telescopa
Non-migrating Piscivores
B.dentata
L.ringens
O.mitsuii
S.rothschildi
C.macouni
I.antrostomas
QFASA Estimate
0.0
0.2
0.4
0.6
0.8
1.0
Proportion in Simulated Diet

SUPPLEMENTAL FILES

Supplemental Table 1 Distributional, behavioral, and physiological characteristics of deep-ocean fish and squid species comprising the complete prey library
Supplemental Table 2 Mean fatty acid profiles and lipid content of the complete prey library