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Intraspecific variation and behavioral flexibility in the foraging strategies of seals

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INTRASPECIFIC VARIATION AND BEHAVIORAL FLEXIBILITY IN THE FORAGING STRATEGIES OF SEALS

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by

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INTRASPECIFIC VARIATION AND BEHAVIORAL FLEXIBILITY IN THE FORAGING STRATEGIES OF SEALS

Sarah S. Kienle

ABSTRACT

Feeding is a complex process that is essential to an organism's fitness. Individuals often show intraspecific variation when feeding, from utilizing different foraging habitats to targeting different prey. These individual differences in foraging strategies are important as they can directly affect fitness, population dynamics, behavioral flexibility, and ecosystem functioning. For several decades, intraspecific variation was largely ignored in biological studies, but, more recently, there has been a growing effort to understand the role of intraspecific variation in ecological and evolutionary processes. Phocids (true seals) are a widespread group of marine carnivores that exhibit a diversity of underwater foraging strategies. In this dissertation, I integrate field methods, bio-logging technologies, morphological and physiological sampling, and controlled feeding experiments to examine intraspecific variation and behavioral flexibility in the foraging strategies of seals. Specifically, I compare the at-sea foraging strategies of northern elephant seals (*Mirounga angustirostris*) across the species range and find that the species exhibits intraspecific variation across their range based on the interplay of life history, season, and geography. I also conduct a detailed analysis of the sex-specific foraging strategies of northern elephant seals, one of the most sexually dimorphic mammal species on the planet. My results reveal that male and female northern elephant seals have distinct foraging strategies and that intraspecific niche divergence helps maintain sexual dimorphism in this species. I then examine specific feeding (or prey capture) strategies used by seals and find that bearded (*Erignathus barbatus*), harbor (*Phoca vitulina*), Hawaiian monk (*Neomonachus schauinslandi*), ringed (*Pusa hispida*), and spotted seals (*Phoca largha*) have converged on two underwater strategies—biting and suction feeding, and these strategies are associated with different behaviors and kinematics. I also demonstrate that seals show intraspecific variation and behavioral flexibility in their use of these different strategies, with individuals switching behaviors and kinematics when targeting different prey. Cumulatively, the results of this dissertation reveal that intraspecific variation and behavioral flexibility are widespread in this group of marine carnivores, and this plasticity has likely contributed to the ability of seals to successfully occupy the role of top predators in marine ecosystems worldwide.

DEDICATION

To my best friend and husband Sean

and to our darling son Calvin

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

Chapter 3

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For this chapter, I was responsible for the study design, data collection, the majority of data analysis, statistical analyses, manuscript preparation, and manuscript submission. The second co-author in this publication, H. Hermann-Sorensen, assisted with data collection, kinematic data analysis, and manuscript revisions. The fourth co-author, C. Reichmuth, assisted with the experimental design and provided manuscript revisions. The third and fifth authors, D. Costa and R. Mehta, directed and supervised the research that forms the basis for the dissertation. Signed statements of permission from H. Hermann-Sorensen and C. Reichmuth are available in the supplementary material.

Chapter 4

Kienle, S.S., Cacanindin, A., Kendall, T., Richter, B., Ribeiro-French, C., Castle, L., Lentes, G., Costa, D.P., and Mehta, R.S. 2019. Hawaiian monk seals exhibit behavioral flexibility when targeting prey of different size and shape. *Journal of Experimental Biology* **222**: jeb194985.

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INTRODUCTION

Feeding directly affects an organism's survival and reproductive success. Across the Tree of Life, organisms have evolved diverse strategies for capturing and consuming prey (Schoener, 1971; Taylor, 1987; Schwenk, 2000; Werth, 2000a). These strategies integrate behavioral, ecological, morphological, and physiological processes and are adapted to maximize foraging success in a given environment (Schoener, 1971). Within a species, individuals often use different foraging strategies, and this can be the result of both intrinsic and extrinsic factors. For example, in some species, individuals exhibit seasonal variation in foraging strategies (Festa-Bianchet, 1988; Hill, 1997; Costa and Gales, 2003), while in others, individuals undergo ontogenetic shifts in foraging behavior (Werner and Hall, 1988; Lowe, 1996; Orr et al., 2011). Historically, these intraspecific differences were largely ignored or treated as noise in biological studies; more recently, however, there has been a growing effort to document and understand the role of intraspecific variation in evolutionary and ecological processes (Bolnick et al., 2003, 2011; Araújo et al., 2011). From an evolutionary perspective, these intraspecific differences are a source of variation on which natural selection can act, potentially resulting in novel adaptations, diversification, and speciation (Darwin, 1859; Foster, 1999). From an ecological perspective, intraspecific variation can affect population dynamics and ecosystem functioning, through changes in predator-prey dynamics, competition, and/or resource use (Darwin, 1859; Roughgarden, 1972; Bolnick et al., 2003, 2011; Araújo et al., 2011).

Intraspecific variation in foraging strategies can arise among geographically separated populations (Foster, 1999; Tremblay and Cherel, 2003; Wells et al., 2016), between conspecifics with different life histories (e.g., age, sex; Houston and Shine, 1993; Breed et al., 2006; Vales et al., 2015), and even within populations of individuals with similar life histories (Bolnick et al., 2003; Estes et al., 2003; Abrahms et al., 2018). Additionally, individuals can exhibit behavioral flexibility, changing their feeding behavior depending on the specific context (Arnold, 1981; Dill, 1983; Harding et al., 2007; Wainwright et al., 2008). Together, intraspecific variation and behavioral flexibility are often beneficial, allowing individuals and populations to respond to spatially and temporally dynamic resources (Harding et al., 2007; Woo et al., 2008, Villegas-Amtmann et al., 2011; Abrahms et al., 2018).

During the transition from terrestrial to aquatic habitats, the ability to exploit underwater prey resources was critical to the success of marine mammals (Taylor, 1987; Werth, 2000a). Several mammalian lineages (cetaceans—whales and dolphins; mustelids—sea otters; pinnipeds—seals, sea lions, and walruses; sirenians—manatees and dugongs; and ursids—polar bears) have independently adapted to feeding underwater (Taylor, 1987; Werth, 2000a; Hocking et al. 2017; Kienle et al., 2017). Historically it has been challenging to study marine mammal foraging behavior, as individuals are often dispersed throughout the open ocean, travel extensive distances, or are found in remote, inaccessible locations (Williams et al. 2004, Davidson et al. 2012). More recently, rapid advances in bio-logging technologies and analytical techniques have shed new light on the underwater foraging strategies used by marine mammals (Iverson et al., 2004; Newsome et al., 2010; Block et al., 2011; Costa et al., 2012; Sequeira et al., 2018). In conjunction with studies of wild animals, there has been a growing effort to document and describe the feeding strategies of marine mammals through the use of feeding experiments conducted with captive animals (Werth, 2000b; Kane and Marshall, 2009; Marshall et al., 2008, 2014; 2015; Hocking et al., 2012, 2014, 2015, 2016, 2017b). Together, these approaches have provided data on the diverse foraging strategies used by marine mammals, but there still remains a paucity of data on the role of intraspecific variation and behavioral flexibility (Werth, 2000a; Hocking et al., 2017a; Kienle et al., 2017).

Among marine mammals, pinnipeds are one of the few groups that have retained an amphibious lifestyle, spending portions of their life cycle on land (e.g., breeding, molting) and at sea (e.g., feeding). Pinnipeds exhibit diverse suites of foraging behaviors—from traveling thousands of kilometers from their breeding colony to distant foraging grounds (e.g., northern elephant seals, *Mirounga angustirostris*; Le Boeuf et al., 2000; Robinson et al., 2012) to feeding in aquatic, inland lakes (e.g., Baikal seal, *Pusa sibirica*; Watanabe et al. 2004). These diverse foraging strategies have allowed pinnipeds to occupy the role of top predator in marine ecosystems worldwide (King, 1983; Riedman, 1990; Werth, 2000a). Over the last few decades, the general foraging strategies and diet have been described for most pinniped species (King, 1983; Riedman, 1990; Pauly et al., 1998). However, many of these studies are limited by small sample sizes, are from a single population, and/or focus only on specific cohorts of individuals.

This dissertation addresses key knowledge gaps in our understanding of intraspecific variation and behavioral flexibility in the foraging strategies of pinnipeds, specifically for phocids (true seals). In Chapters 1 and 2, a series of studies are designed to examine intraspecific variation in the at-sea foraging strategies of seals and investigate the factors that drive differences in foraging across the species range and between individuals with different life histories. In Chapters 3 and 4, controlled feeding trials are conducted with multiple seal species to characterize intraspecific variation and behavioral flexibility in the use of different feeding strategies. Together, the four chapters of this dissertation examine intraspecific variation in phocid foraging strategies and mechanisms at multiple scales, from individuals to species, to better understand the factors that have allowed this group to become such a diverse and successful group of marine carnivores.

Chapter 1 of this dissertation examines species-level patterns in foraging strategies. In this chapter, I compare the foraging strategies of northern elephant seals, a wide-ranging, sexually dimorphic species, across its range and examine the factors that drive intraspecific variation in this species. I use data collected from biologging instruments deployed on adult male and female northern elephant seals, as well as morphometric and physiological sampling to describe the geospatial patterns, dive behavior, and foraging success of individuals from four breeding colonies spanning the species range. In this chapter, I use principal components analyses, geospatial analyses, and mixed effects models to examine and compare different foraging strategies based on sex, season, and breeding colony.

Chapter 2 examines intraspecific niche divergence in the foraging strategies of northern elephant seals. Northern elephant seals are an extreme example of sexual dimorphism in mammals, fulfilling many of the hypotheses associated with sexual selection theory. Based on the results of Chapter 1 where I identify that sex is the primary driver of foraging strategy differences in northern elephant seals, in Chapter 2, I conduct an examination of sex-specific foraging strategies and examine risk-reward trade-offs between different strategies. In this chapter I compare data collected from biologging instruments deployed over a ten-year period, as well as morphometric measurements, physiological data, and mortality rates to examine the movement patterns, dive behavior, foraging success, and survival of male and female northern elephant seals. I use principal components analysis, hierarchical clustering analysis, geospatial analyses, and mixed effects models to identify sources of intraspecific variation and examine the relationship between foraging success and survival associated with these different strategies.

Chapter 3 examines intraspecific variation in seal feeding strategies. In this chapter, I compare the foraging behavior and kinematics of four seal species (bearded, harbor, ringed, and spotted seals) and examine intraspecific variation b and between species and individuals. I use controlled feeding trials to describe and quantify different feeding behaviors and associated kinematics. I use principal components analysis, mixed effects models, and tests of variability to compare inter- and intraspecific variation in these four species.

Chapter 4 examines behavioral flexibility and intraspecific variation in feeding strategies in response to changes in prey. In this chapter, I conduct controlled feeding trials with Hawaiian monk seals to document and describe different feeding strategies used by this species. I use principal components analysis, mixed effects models, and statistical tests (e.g., analyses of variance, coefficient of variation) to examine flexibility and variability in feeding behavior and kinematics when seals target prey of different shapes and sizes.

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CHAPTER 1

INTRASPECIFIC VARIATION IN THE FORAGING STRATEGIES OF A MARINE PREDATOR ACROSS ITS SPECIES RANGE

ABSTRACT

Intraspecific variation in foraging strategies is widespread throughout the animal kingdom, resulting in conspecifics differing in habitat use, foraging behavior, and resource selection. Understanding these intraspecific differences is important for interpreting ecological and evolutionary processes but often difficult to study in wide-ranging marine animals. Here, we examine intraspecific variation in the foraging strategies of northern elephant seals (*Mirounga angustirostris*), a wide-ranging and abundant predator in North Pacific Ocean ecosystems. We compare satellite telemetry, dive behavior, and foraging success data from 145 adult female and 18 adult male seals from four breeding colonies across the species range. Using quantitative comparative methods, we find that northern elephant seals show intraspecific variation in foraging strategies. Sex is the most important driver of intraspecific variation in northern elephant seal foraging strategies. Male seals utilize benthic foraging habitats along the continental shelf, while female seals forage in mesopelagic habitats throughout the North Pacific Ocean. Males and females from all colonies undertake biannual foraging trips, but only females exhibit different foraging strategies between the two trips. For females, the short post-breeding trip is associated with traveling shorter distances, taking focused foraging trips, having smaller foraging areas, all of which result in lower foraging success compared to the long post-molt trip. Following sex and season, male and female seals exhibit colony-specific foraging strategies. Seals from northern colonies travel farther north and west on the at-sea trips than seals from southern colonies; additionally, some seals from

southern colonies forego the long foraging trip, feeding within 1,000 km of the colony. During the post-breeding trip, female seals from northern colonies have greater foraging success, but these differences disappear during the post-molt trip. Our results highlight the high degree of intraspecific variation in northern elephant seal foraging strategies across the species range and reveal that these strategies are the result of the interplay of sex, season, and geography. Northern elephant seals have dramatically rebounded from their near-extinction 150 years ago, and this high degree of intraspecific variation when feeding has likely contributed to their current success and growth across their range.

INTRODUCTION

Individuals within populations show variation in behavioral, ecological, morphological, and physiological traits (Bolnick et al., 2003, 2011). Intraspecific variation can arise in multiple ways—among geographically separated populations (Arnold, 1981; Foster, 1999; Tremblay and Cherel, 2003; Wells et al., 2016; Corman et al., 2016), between individuals with different life histories (e.g., sex, age class; Holtby and Healey, 1990; Houston and Shine, 1993; Breed et al., 2006; Vales et al., 2015), and even within populations of individuals sharing similar life histories (Estes et al., 2003; Villegas-Amtmann et al., 2008; Abrahms et al., 2018; Botha and Pistorius, 2018). From an evolutionary perspective, these differences between conspecifics are a source of variation on which natural selection can act and, over time, result in adaptation, diversification, and speciation (Darwin, 1859; Bolnick et al., 2003, 2011; Araújo et al., 2011). Similarly, these individual trait differences are often ecologically important. Intraspecific variation can affect predator-prey dynamics, inter- and intraspecific competition, and resource use (Bolnick et al., 2003, 2011; Araújo et al., 2011) and, in turn, these differences can affect community dynamics and ecosystem functioning (Araújo et al., 2011; Bolnick et al, 2011).

In recent years, there has been a growing appreciation of the importance of intraspecific variation in resource use, resulting in a concerted effort to understand and quantify differences in the foraging strategies of individuals (Bolnick et al., 2003; Wakefield et al., 2015; Paez-Rosas et al., 2017; Des Roches et al., 2018; McHuron et al., 2018). However, for many large marine predators, there remains a paucity of data on their basic foraging ecology, making it difficult to examine intraspecific variation in resource use. Northern elephant seals (*Mirounga angustirostris*) are a model species for investigating intraspecific variation in foraging behavior. While on land biannually to breed and molt, adult northern elephant seals show high site fidelity to specific breeding colonies that extend from Baja California, Mexico to northern California, USA (Robinson et al., 2012; Lowry et al., 2014). Most of the year (<9 months), northern elephant seals travel thousands of kilometers to mesopelagic and benthic foraging habitats throughout the North Pacific Ocean. Most of what is known about northern elephant seal foraging behavior comes from research conducted at one of the northern-most breeding colonies, Año Nuevo State Park, CA, USA (Le Boeuf et al., 1993; Le Boeuf et al., 2000; Simmons et al., 2007, 2010; Robinson et al., 2012; Naito et al., 2013; Chapter 2); these studies have shown that northern elephant seals exhibit individual differences in foraging behavior based on intrinsic and extrinsic factors, including sex (Le Boeuf et al., 1993, 2000), foraging location (Simmons et al., 2007; Peterson et al., 2015), season (Robinson et al., 2012; Chapter 2), and resource use (Abrahms et al., 2018; Goetsch et al., 2018).

These general foraging strategies used by northern elephant seals at the Año Nuevo colony are often assumed to be species typical, but little is known about the foraging behavior of seals from other colonies. Studies of other species have highlighted the importance of comparing foraging strategies between colonies, as behavior can substantially differ among geographically separated populations (Foster, 1999; Tremblay and Cherel, 2003; Grémillet et al., 2004; Robson et al., 2004;

Corman et al., 2016). Similar sex-specific differences in northern elephant seal foraging strategies have been documented in two breeding colonies in the middle of the species range (San Miguel Island, San Nicolas Island; Stewart and DeLong, 1995; Stewart, 1997). However, in one of the only studies to compare the at-sea behavior of northern elephant seals from different colonies, Robinson et al. (2012) found that a subset of female seals from a southern Mexican colony (Isla San Benito) did not undertake the long foraging migration to northern feeding grounds like female seals from the Año Nuevo colony, but rather fed close to the breeding colony. Additionally, female seals from San Benito had smaller body masses at the start of the foraging trip compared to female seals from San Benito; however, San Benito females put on proportionally more body mass while at-sea feeding compared to female seals from Año Nuevo (Robinson et al., 2012). The results of that study suggest that geography may be another source of intraspecific variation in the foraging strategies of northern elephant seals (Robinson et al., 2012).

The goal of this work is to conduct a comparative analysis of intraspecific variation in the foraging strategies of northern elephant seals. Here, we examine the foraging strategies of adult male and female northern elephant seals from four breeding colonies: Año Nuevo State Park (CA, USA), San Nicolas Island (CA, USA), Isla San Benito (Baja California, Mexico), and Isla Guadalupe (Baja California, Mexico). Together these four colonies span nearly the entire range of the northern elephant seal and encompass over 1,150 km (straight line distance) and 10° of latitude (Fig. 1). The objectives of this study are to examine species-wide patterns in foraging behavior and to determine the factors that lead to intraspecific variation in northern elephant seals foraging strategies. To do this, we conduct quantitative analyses coupling data on the spatial patterns, dive behavior, and foraging success of adult male and female northern elephant seals from across the species range. Building on previous studies, we predict that northern elephant seal foraging strategies are influenced by sex, breeding colony, season (i.e., foraging trip), and foraging habitat. We test the hypothesis that northern elephant seal foraging strategies are primarily determined by sex and breeding colony, and that seals will exhibit sex-specific and colony-specific movement patterns and dive behavior that result in differences in foraging success. This study provides insight into the species and population-level foraging strategies of northern elephant seals and will highlights the role of both extrinsic and intrinsic factors in shaping the foraging strategies of a highly migratory marine predator.

METHODS

Animal Handling and Instrumentation

We deployed satellite transmitters and time-depth recorders (TDRs) on adult male and female northern elephant seals from 2004 to 2018 at four breeding colonies—Año Nuevo State Park, San Mateo County, California, USA (108 females, 4 males); San Nicolas Island, Channel Islands, California, USA (8 females); Isla San Benito, Baja California, Mexico (20 females, 14 males); and Isla Guadalupe, Baja

California, Mexico (9 females); this resulted in tracking 145 females and 18 males in total across the four colonies.

Instruments were deployed on northern elephant seals at the beginning of both biannual foraging trips: the post-breeding trip (females: February-May; males: March-August) and the post-molt trip (females: May-January, males: August-January). Seals were instrumented with a combination of satellite transmitters (SPOT or SPLASH tags, Wildlife Computers or Conductivity-Temperature-Depth tags, Sea Mammal Research Unit), TDRs (MK9 or MK10, Wildlife Computers), and VHF radio transmitters (Advanced Telemetry Systems). We chemically immobilized seals to deploy instruments, took morphometric data, and collected tissue samples following established protocols previously reported for northern elephant seals (Le Boeuf et al., 1988; Le Boeuf et al., 2000; Simmons et al., 2010; Robinson et al., 2012). Instruments were recovered and additional morphometric data and sampling occurred when seals returned to the breeding colony after the foraging trip. Behavioral research was approved by the Animal Care and Use Committee at the University of California, Santa Cruz and conducted under federal authorizations for marine mammal research under National Marine Fisheries Service permits 87-1743, 14636, and 19108. Research at the Mexican colonies was approved by Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) permits SGPA/DGVS/06286/16 and SGPA/DGVS/011039/17 for Isla Guadalupe and SGPA/DGVS/05734 and SGPA/DGVS/05321for Isla San Benito. Research at Isla Guadalupe was also approved by Comisión Nacional de Áreas Naturales Protegidas

(CONANP) y Dirección Regional Península de Baja California y Pacífico Norte F00.1.DRPBCPN-000190.

Body Composition

We measured the body composition of seals during instrument deployment and recovery following methods previously established for northern elephant seals (Le Boeuf et al., 2000; Simmons et al., 2010; Robinson et al., 2012). Girth and length measurements were taken at eight locations along the length of the seal's body. Blubber thickness was measured using a handheld ultrasound and/or a backfat meter at 12 to 18 locations along the body (2-3 per girth measurement, excluding the head and tail). For female seals, mass was measured with a Dyna-Link digital scale (1,000 +/- 1 kg) attached to a tripod. For male seals, mass was estimated from the combination of lengths, girths, and ultrasound measurements following a method validated for male northern elephant seals by Crocker et al. (2012). For all seals, mass was corrected for the amount of time each seal spent on shore before and after the foraging trip. For female seals, mass change on shore was estimated using an equation derived from serial mass measurements of fasting seals: mass change (kg d^{-1}) = 0.51 + 0.0076*mass, n=27, r^2= 0.79, p<0.01 (Simmons et al. 2010). For female seals arriving after the post-molt trip, the recovery procedure always occurred after parturition, and the pup's mass, which was measured during the recovery procedure, was added to the female's mass. For male seals, mass change on shore was estimated using a metabolic rate of 2*Kleiber during the molt (Kleiber, 1975; Worthy et al.,

1992) and 3.1*Kleiber during the breeding season (Kleiber, 1975; Crocker et al., 2012). Fat and protein contributions to metabolism were derived from established methods (Crocker et al., 2012).

Data Processing

We processed the satellite transmitter and TDR data following standard protocols (Robinson et al. 2010, 2012). We truncated the raw ARGOS and GPS tracks to the exact departure and arrival times from the breeding colony according to the TDR record. A speed, distance, and angle filter removed unlikely position estimates in R v. 3.3.3 (argosfilter package: Freitas, 2013; R Core Team, 2017). Tracks were smoothed using a state-space model and provided hourly estimates of position (crawl package: Johnson, 2016). If a seal was tracked during both the post-breeding and post-molt trip in the same year, both tracks were kept to compare seasonal differences in behavior. For seals that were tracked over multiple years, we randomly removed repeat tracks so each seal was only included once in the analysis. From the TDR data, each dive was assigned to day or night using the solar zenith angle associated with each dive.

Foraging Metrics

We compared northern elephant seal foraging strategies using quantitative and qualitative metrics of spatial patterns, dive behavior, and foraging success. For each complete track (n=124), we examined eight geospatial variables. We determined the total numbers of days at sea from the arrival and departure dates to and from the colony. We calculated the mean distance to the continental shelf (km; straight-line distance from each foraging location to the continental shelf) and the farthest distance that each seal traveled from the colony (km; straight-line distance from the colony to the farthest foraging location in the track). We also calculated the total horizontal distance (km) covered by each seal on the foraging trip and the proportion of time each seal spent feeding while at-sea. Utilization distributions were generated from kernel density analyses on the two-dimensional foraging locations (latitude and longitude) for each track using a 2 km cell size and the default bandwidth in ArcGIS 10.3.1. The foraging area (km^2) was calculated for each seal and defined as the area of the 95% contour determined from the utilization distribution. Each track was assigned to a mesopelagic ecoregion ('feeding ecoregion'; Sutton et al., 2017) based on where the majority (≥50%) of foraging locations occurred. Each track was also assigned to a habitat type; tracks were categorized as continental shelf (on or near the continental shelf) habitat, continental shelf-oceanic habitat, or oceanic habitat following criteria used by Hakoyama et al. (1994) and Simmons et al. (2007). Additionally, tracks were categorized as 'focused' or 'throughout' based on the number of foraging locations in relation to the furthest point of the track from the breeding colony. 'Focused' trips occurred where feeding locations were clustered at the furthest part of the track from the breeding colony and <5 foraging locations were identified in other portions of the track, while trips were classified as 'throughout' when >5 foraging locations occurred outside the farthest point from the colony (Visscher and Seeley, 1982; Gilmour et al., 2018).

We analyzed six dive metrics to compare differences in seal dive behavior, and each metric was calculated separately for day and night to account for diel patterns; this resulted in a total of 12 dive metrics from each complete dive record (n=102). We calculated the mean maximum depth (m) and the mean dive duration (s). We also calculated the mean bottom time (s; amount of time spent at the bottom of a dive) and the mean post-dive surface interval (s; amount of time the seal spent at the water's surface after a dive). We also measured the mean number of vertical excursions ('wiggles'; Le Boeuf et al., 1988, 1993) at the bottom of each dive, which is indicative of prey capture attempts (Naito et al., 2013). Additionally, we calculated the mean dive efficiency (bottom time/ dive duration), where values closer to 0 indicate lower dive efficiency and values closer to 1 indicate higher dive efficiency.

We compared four foraging success metrics that were generated from the body composition data collected during instrument deployment and recovery (n=117). We measured body mass at departure (kg) and calculated total mass gain over the foraging trip (kg; the difference between the departure and arrival masses). We calculated the proportion of mass gain on the foraging trip (total mass gain on trip/ body mass at departure) and the seal's rate of mass gain over the trip (kg d^{-1}; mass gain/ days at sea).

Statistical Analyses

Principal components analysis (PCA) was used to examine the primary axes of variation in northern elephant seal foraging strategies and to reduce the dimensionality of the dataset. We conducted PCA on 21 quantitative foraging variables (FactoMineR package: Le et al., 2008; missMDA package: Josse and Husson, 2016). Seals with missing values were excluded from the analysis, and this resulted in a dataset of 119 females and 11 males. Based on the PCA results from the full dataset where sex and season explained more than half (54.9%), we ran PCA separately for males (post-molt trip only; 13 males), post-breeding females (n=39), and post-molt females (n=64). Because the foraging variables differed in magnitude, all variables were standardized (i.e., centered and scaled) prior to PCA. A scree plot was used to examine natural breaking points in the variance, and principal components (PCs) with eigenvalues ≥1.0 and that explained ≥10.0% of the variation were retained for further analysis. A coefficient correlation analysis was used to assess the positive or negative contribution of each variable to each PC axis. The most significant PCs were then used in a hierarchical clustering analysis (HCA) to examine naturally occurring distinct clusters of foraging strategies. For the HCA, we created a dissimilarity matrix based on Euclidean distances and performed an agglomerative HCA using ‘hclust’ and the Ward’s linking method on the retained PC scores (cluster package: Maechler et al., 2017; factoextra package: Kassambara and Mundt, 2017). We used the elbow and average silhouette methods to determine the optimal number of clusters, and each seal was then assigned to a specific cluster.

Based on the results of the multivariate analyses (i.e., PCA and HCA), we used Welch Two Sample tests to compare quantitative foraging metrics between sexes and seasons (i.e., post-breeding and post-molt trips). For each cluster of seals (i.e., post-breeding females, post-molt females, and male seals), we ran linear models for each feeding variable with breeding colony as the predictor variable. An analysis of variance (ANOVA) was used to determine significant differences among colonies (‘car’ package, Fox et al, 2012), and we used least-square means to perform Tukey post-hoc pairwise contrasts between each colony (lsmeans package: Lenth, 2016). We examined residual plots of all feeding variables for deviations from normality or homoscedasticity using histograms and Q-Q plots and used log transformations when needed.

To examine variability in northern elephant seal foraging behavior, we calculated the coefficient of variation (CV=standard deviation/mean) for each feeding variable for each sex, season, and breeding colony. A low CV (values closer to 0) indicates stereotypy, or consistency in a trait, while a high CV (values closer to 1) indicates variability (Gerhardt, 1991, Wainwright et al., 2008). All statistical analyses were conducted in R v. 3.3.3 (R Core Team, 2017).

RESULTS

We found that sex, season, and breeding colony were the primary drivers of northern elephant seal foraging strategies from multivariate analyses of movement patterns, dive behavior, and foraging success.

Sex

Sex was the most important driver of northern elephant seal foraging strategies (Table 1). In the full PCA dataset, PC1 (31.2% of the variation) resulted in the separation of male and female seals (Table S1, Fig. 2). Seven foraging metrics significantly differed between the sexes based on the linear mixed effects models. Males spent less time at sea (p<0.001), fed closer to the continental shelf (p<0.001), did not travel as far on the foraging trip (p=0.03), and had smaller foraging areas (p<0.001) compared to females. Unlike males, female showed a strong diurnal pattern when diving. Males had higher foraging success than females on the at-sea trips. Specifically, males had larger body masses at departure (p<0.001), gained more mass (p=0.001), and had higher rates of mass gain (p=0.001) compared to females.

Season

For female seals, season was the second-most important factor in determining northern elephant seal foraging strategies (Table 2). In the full PCA dataset, principal component 2 (23.7% of the variation) resulted in the clustering of female seals by season (i.e., post-breeding vs. post-molt trip; Table S1, Fig. 2). Fifteen foraging metrics differed between the two foraging trips. During the post-breeding trip, females spent less time at sea (p<0.001), fed closer to the continental shelf (p=0.001), stayed closer to the breeding colony (p<0.001), and had smaller foraging areas (p<0.001) compared to females on the post-molt trip. When diving, post-breeding females had shorter dives (p=0.01), shorter bottom times (p=0.02), more vertical excursions (p<0.001), and higher daytime dive efficiency (p=0.02) compared to post-molt females. While post-breeding females were larger at departure (p<0.001), post-molt females had higher foraging success; post-molt females gained more mass (p<0.001) and had higher rates of mass gain (p<0.001) than post-molt females.

Breeding Colony

Breeding colony played an important role in determining northern elephant foraging strategies, after accounting for sex and season.

Male seals: In the male PCA, PC1 (40.5% of the total variation) and PC2 (19.2 %) resulted in the general separation of male seals from different colonies (Table S2), with males from Año Nuevo and San Benito significant differing in 4 variables (Table 3; Fig. 3). Año Nuevo males traveled to the Subarctic Pacific and primarily undertook focused foraging trips; in comparison, San Benito males primarily traveled to the California Current and took both focused (56%) trips, as well as foraged throughout the trip (44%). Año Nuevo males traveled farther from the breeding colony, fed farther from the continental shelf, and had larger core foraging areas than San Benito males (p<0.05). Unlike Año Nuevo males, San Benito males stayed closer to the breeding colony (p<0.05), with 60% of the San Benito males feeding within 1,000 km of the colony (Table 3S; Fig. 4). Año Nuevo males also had larger body masses at departure than San Benito males (p<0.02).

Post-breeding female seals: In the post-breeding PCA, PC1 (37.5% of the total variation) and PC2 (19.8%) resulted in the general clustering of females by breeding colony (Table S4), and post-breeding females from Año Nuevo, San Benito, and Guadalupe significantly differed in 12 foraging variables (Table 4; Fig. 5). Año Nuevo females primarily fed in the Subarctic Pacific (46%) and North Central Pacific (32%); San Benito females primarily fed in the California Current (67%); and all Guadalupe females fed in the California Current. Año Nuevo and San Benito females mostly fed in oceanic habitats on focused foraging trips, while Guadalupe females mostly fed throughout the trip in continental shelf-oceanic habitats. Año Nuevo females traveled the farthest from the colony, with most Año Nuevo females (97%) feeding more than 2,000 km from the colony ($p<0.02$). In contrast, San Benito females traveled the shortest distances ($p<0.02$), with one-third of San Benito females (33%) staying local, traveling <1,000 km from the breeding colony (Table 3S; Fig. 4). Guadalupe females had the longest tracks and largest foraging areas compared to the other colonies ($p<0.03$). When diving, Año Nuevo females had shorter bottom times and post-dive surface intervals, fewer vertical excursions, and lower dive efficiency compared to San Benito females ($p<0.05$). Año Nuevo females had the highest foraging success compared to the other colonies, indicated by higher relative and absolute mass gain ($p<0.001$).

Post-molt female seals: In the PCA for post-molt females, PC1 (32.3% of the total variation) and PC2 (17.8%) resulted in the general clustering of seals by breeding colony (Table S5). Post-molt female seals from Año Nuevo, San Nicolas, San Benito, and Guadalupe showed significant differences in 11 foraging variables (Table 4, Fig. 6). All female seals on the post-molt trip fed throughout the trip in multiple ecoregions in oceanic habitats. San Nicolas females had the largest foraging areas ($p<0.001$), with most females traveling >3,000 km from the breeding colony; in contrast, San Benito females had the smallest foraging areas ($p<0.01$) with a subset (20%) of San Benito females stayed within 1,000 km of the breeding colony (Table 3S; Fig. 4). Año Nuevo females had the deepest daytime dives, the longest daytime bottom times, and highest daytime dive efficiency ($p<0.03$) compared to females from other colonies. San Nicolas females had the most vertical excursions and, along with San Benito females, had the highest nighttime dive efficiency compared to the other colonies ($p<0.03$). San Benito females had the shortest dive durations and longest post-dive surface intervals compared to other colonies ($p<0.001$). Guadalupe females had the shortest bottom times and post-dive surface intervals, the fewest number of vertical excursions, and the lowest dive efficiency during daytime dives compared to other colonies ($p<0.002$). During nighttime dives, Guadalupe females had the longest dive durations, shortest post-dive surface intervals, fewest vertical excursions, and lowest dive efficiency ($p<0.006$). San Nicolas females had the largest body masses at departure ($p<0.02$), while San Benito females had the smallest body masses at departure ($p<0.001$).

Variability in Foraging Behavior

We compared variability (CV) in feeding metrics between post-breeding, post-molt, and male seals and between breeding colonies (Table 5). Between the sexes, males had higher average variability, while females were more stereotyped. Between seasons, post-breeding females had higher average variability, while post-molt females were more stereotyped. When comparing breeding colonies, San Benito seals had the highest average variability, and Año Nuevo seals were the most stereotyped. Overall, the movement metrics were the most variable, especially foraging area and distance to the continental shelf. The dive metrics were the most stereotyped, especially dive duration and dive efficiency at night.

DISCUSSION

Northern elephant seals occupy a wide ecological niche that extends from the continental shelf along the western coast of North America to offshore mesopelagic ecosystems across the North Pacific Ocean. Across their range, northern elephant seals show a high degree of intraspecific variation in foraging strategies. These different strategies represent combinations of movement patterns and dive behavior that result in foraging success differences among individuals. In this species intraspecific variation is driven by the interplay of sex, season, and geography, and this variation likely plays an important role in the expansion and success of northern elephant seals.

Sex-Specific Foraging Strategies

Sex is the most important driver of northern elephant seal foraging strategies, with males and females showing intraspecific niche divergence in their at-sea behavior. Males are benthic foragers that feed on or near the bottom of the continental shelf, with foraging habitats ranging from Baja California, Mexico to the Aleutian Islands, Alaska. The male strategy results in high foraging success, with males gaining more than 80% of their initial body mass on average. In contrast, female seals are mesopelagic foragers that undertake deep foraging dives in foraging habitats that extend throughout the western North Pacific Ocean. The female foraging strategy results in lower foraging success when compared to the male strategy, but females are still gaining an average of 66% of their initial body mass. The sex-specific foraging patterns we document here are concordant with the only other studies to compare male and female northern elephant seal foraging behavior, suggesting that these strategies are stable over time (Stewart and De Long, 1995; Le Boeuf et al., 2000; Chapter 2).

Northern elephant seals are an extreme example of sexual dimorphism in mammals (Bartholomew, 1970; Ralls, 1977), and intraspecific niche divergence helps maintain sexual dimorphism in the species (Chapter 2). Similar to northern elephant seals, many sexually dimorphic species exhibit sex-specific foraging strategies (Selander, 1966; Gonzalez-Solis et al., 2000; Breed et al., 2006), and these differing strategies can arise as a way to reduce competition, to meet different physiological demands, or as the result of different feeding morphologies (Selander, 1966; Shine, 1989; Houston and Shine, 1993). In northern elephant seals, the sex-specific foraging strategies represent a trade-off between foraging success and survival. Males have higher foraging success but also have a significantly higher mortality rate on the at-sea foraging trips than females (Le Boeuf et al., 2000; Chapter 2), with only 56% of males surviving these trips compared to 87% of females (Chapter 2). These trade-offs are likely related to the different life history strategies of male and female northern elephant seals. Males need to gain mass quickly to attain and support the large body size necessary to compete for mating opportunities, as only a subset of males are reproductively successful (Le Boeuf, 1974; Reiter et al., 1981; Condit et al., 2014). Continental shelf ecosystems provide the prey resources necessary for male seals, even though these areas are associated with higher mortality (Chapter 2). In comparison, females need to gain enough mass each year to support themselves and their offspring and maximize reproductive success by weaning a pup annually throughout their lifetime (Reiter et al., 1981; Condit et al., 2014). As the smaller sex, females do not have the same energetic requirements as males, and pelagic ecosystems provide the prey resources necessary for them; this results in lower mortality compared to continental shelf ecosystems (Chapter 2). The relationship between foraging and life history strategies in northern elephant seals is reflected in sex being the most important determinant of foraging strategies in this species, irrespective of all other intrinsic and extrinsic variables.

Seasonal Differences in Foraging Strategies

Following sex, season is the next most important driver of female northern elephant seal foraging strategies. Both males and females undertake biannual foraging trips (i.e., post-breeding and post-molt), but only females exhibit season-specific foraging strategies. Females have a shorter post-breeding trip (~2.7 months) and a longer post-molt trip (~7.2 months).

While all female seals use the general female foraging strategy, females on the post-breeding trip do not travel as far from the breeding colony and have smaller foraging areas than females on the post-molt trip. In addition, most post-breeding females feed at the farthest point of their track from the colony. On the post-breeding trip, females are limited in how far and how long they can travel searching for prey. Therefore, once these females find a productive foraging area that meets their energetic requirements, post-breeding females stop searching for other places to feed and remain in a single foraging location until they need to return to land for the annual molt. In addition, females on the post-breeding trip show increased dive efficiency, with more prey capture attempts per dive compared to females on the post-molt trip; this likely allows post-breeding females to maximize their prey consumption during the limited time they have to feed. Despite this increased dive efficiency and staying closer to the breeding colony, females on the post-breeding trip have lower foraging success, gaining only 20% of their starting body mass compared to a 95% increase for females on the post-molt trip. Females on the post-molt trip have three times as long to spend feeding, and, as a result, females can be more selective in their foraging habitats and move between prey patches in order to maximize their energy intake.

Most of these differences in foraging strategy between females on the post-breeding and post-molt trip are likely related to the differences in duration between the two trips. However, there are additional factors that likely contribute to the maintenance of these different strategies in female seals. Specifically, the seasonal variation in foraging strategies for females may be associated with changes in prey resources, as the diet of female northern elephant seals changes seasonally (Goetsch et al., 2018). Furthermore, during the post-molt trip, females are pregnant, and gestation is associated with increased energetic demands and physiological constraints on diving (Huckstadt et al., 2018). Similar to northern elephant seals, seasonal variation in foraging strategies is common (Costa et al., 2003; Phillips et al., 2004; Miller et al., 2009; Botha and Pistorius, 2018), and it is often most pronounced in the sex that gives birth and/or provides parental care (González-Solis et al., 2003; Dahle and Swenson, 2003; Breed et al., 2006; Villegas-Amtmann et al., 2012).

Geographic Variation in Foraging Strategies

Following sex and season, breeding colony also plays a role in shaping northern elephant seal foraging strategies. Northern elephant seals from different colonies show spatial segregation of foraging habitats. Año Nuevo males and females travel farther north and west on their foraging trips compared to seals from other colonies and are the only northern elephant seals that utilize foraging habitats in the

Gulf of Alaska and Aleutian Islands. Conversely, seals from the southern breeding colonies (San Benito and Guadalupe) feed farther south than seals from Año Nuevo and San Nicolas. Regardless of colony, all northern elephant seals spend the same amount of time at sea annually, and it appears that seals from southern colonies are unable to travel as far north and west as those from northern colonies. Seals from more northern colonies have the advantage of accessing novel foraging habitats that are inaccessible to northern elephant seals from more southern colonies. However, in the southernmost breeding colony, San Benito, some male and female seals do not undertake the long foraging migrations thought to characterize the species. Instead, between 20-30% of females and 60% of males from San Benito stay local when feeding, traveling less than 1,000 km from the colony; these seals spend the same amount of time at sea but travel shorter distances and feed closer to the continental shelf than their migrating counterparts. These findings are concordant with previous studies of San Benito females that found a subset of females stayed local and had isotopic signatures that suggested they foraged ~8° south of females from Año Nuevo (Aurioles et al., 2006; Robinson et al., 2012). Considering the two strategies exhibited by San Benito females (i.e., local vs. migrating), these two strategies may be a way that northern elephant seals partition foraging habitats to reduce intraspecific competition, while also mitigating the transit costs associated with traveling to northern feeding grounds.

Colony-specific movement patterns and dive behavior result in differences in foraging success. During the short post-breeding trip, there are no differences in the initial body mass of females from different colonies at the start of the foraging trip. However, Año Nuevo females have higher foraging success on the post-breeding trip, gaining 3.5 times as much mass as San Benito females over the same time period. This leads to Año Nuevo females increasing their starting body mass by 22% compared to only a 6% increase in San Benito females. On the short post-breeding trip, females have a limited window in which to travel to foraging areas, feed, and gain mass before having to return to the breeding colony for the annual molt. On this short post-breeding trip, San Benito seals appear to be at a disadvantage, potentially as a result of being unable to reach the more productive pelagic foraging areas utilized by Año Nuevo females. Knowing that San Benito seals had lower foraging success than seals from northern colonies, we hypothesized that locally foraging San Benito females may have greater foraging success by removing transit costs associated with distant feeding grounds. However, we found no significant differences in foraging success between the local and migrating strategies of San Benito females on the post-breeding trip.

Foraging success differences between females from different colonies disappear during the longer post-molt trip, in which the only difference in foraging success is in their starting body masses. Año Nuevo and San Nicolas females are larger at the start of the post-molt trip compared to San Benito and Guadalupe females. A similar pattern was found for male seals, where Año Nuevo males are ~300 kilograms heavier than San Benito males at the start of the trip. We suggest that these differences in body masses for females are related to foraging success on the post-breeding trip. Specifically, females from the southern breeding colonies gain less mass during the post-breeding trip compared to females from Año Nuevo; consequently, they returned to land for the annual molt smaller and in poorer body condition. Therefore, assuming the energetic demands of the molt are consistent across colonies, females in the southern colonies start their post-molt trip with a smaller mass because they were smaller upon their arrival at the colony. Additionally, it is also possible that seals in southern colonies lose more mass during the annual molt as a result of increased energetic demands, such as coping with increased air temperatures in these warmer terrestrial habitats. Females in southern breeding colonies have been observed to move more frequently to and from the water's edge during the breeding and molting seasons (pers. obs.), likely to deal with the warmer temperatures they experience during these periods on land. Despite the differences in starting body masses, seals from all breeding colonies have high foraging success during the post-molt trip, with all females showing similarly high mass gain. The longer duration of the post-molt trip provides added time for seals to travel to productive foraging areas, as well as the ability to move between prey patches as needed, giving seals from all colonies ample opportunities to maximize their foraging efforts.

In addition to exhibiting colony-specific foraging strategies, we also document differences in variability between seals from different colonies. Año Nuevo male and female seals exhibit the most stereotyped foraging strategies of all colonies, showing little variation among individuals in regards to their spatial patterns, dive behavior, and foraging success. San Benito males and females have the highest variability in foraging strategies. This is partly attributed to the two foraging strategies found in the San Benito colony—some seals travel long distances to foraging areas, while others stay close to the breeding colony. Interestingly, the wide range of variability found between colonies, irrespective of sample size, shows that we have captured natural colony-level differences in behavioral plasticity.

These colony-specific foraging strategies suggest that male and female northern elephant seals partition their at-sea foraging habitats by exhibiting different suites of feeding behaviors during the post-breeding and post-molt foraging trips. These foraging strategies maximize foraging success while minimizing energetic costs and likely represent trade-offs associated with traveling different distances to and from southern versus northern breeding colonies. These strategies are probably the result of balancing the location of the breeding colony with the location of productive foraging areas. Other species have shown colony-specific foraging strategies and, in conjunction with northern elephant seals, demonstrate that individual colonies cannot be used to describe the behavior of an entire species (Tremblay and Cherel, 2003; Grémillet et al., 2004; Robson et al., 2004; Corman et al., 2016).

Intraspecific Variation in Foraging Strategies

This is the first comparative study of northern elephant seal foraging strategies across the species range, and our results highlight the importance of comparative studies in understanding and interpreting species-level patterns in behavior and ecology. Until now, most of our knowledge on northern elephant seals' foraging behavior come from a single breeding colony at the northern end of the species range—Año Nuevo. Over the past forty years, countless publications have described the biology of northern elephant seals at Año Nuevo, from early studies of dive behavior (Le Boeuf et al., 1988) and development (Reiter et al., 1978) to more recent studies linking foraging behavior with oceanography (Simmons et al., 2007) and examining site fidelity to at-sea foraging habitats (Abrahms et al., 2018). While these studies provide an incredible wealth of knowledge about northern elephant seals from Año Nuevo, the lack of studies at other breeding colonies hinders our ability to understand range-wide patterns and processes. Additionally, these studies are often interpreted as representative of the entire species. By studying multiple colonies, we have increased our understanding of northern elephant foraging patterns across the species range. Our study finds that northern elephant seals occupy a broad ecological niche that includes continental shelf ecosystems from Baja California to the Aleutian Islands and mesopelagic ecosystems from the California Current ecoregion to the Subarctic Pacific ecoregion. Our results confirm previously described patterns that highlighted the importance of sex-specific differences in foraging behavior (Le Boeuf et al., 2000; Chapter 2) and seasonal differences in female foraging behavior (Robinson et al., 2012; Peterson et al., 2015; Chapter 2). This study adds breeding colony as an additional, important driver of intraspecific variation. We also extend the foraging areas utilized by northern elephant seals, showing that seals from southern colonies exploit areas of the California Current ecoregion that have not been previously associated with seals from Año Nuevo.

Assessing the degree of intraspecific variation allows for a more accurate and detailed understanding of resource use and the ecological niche of a species (Bolnick et al., 2003). Populations of species with high levels of intraspecific variation are often more resilient and have higher evolutionary potential (Des Roches et al., 2018). Northern elephant seals have already proven to be such a species; the species has had a remarkable recovery after their near extinction in the late 1800's and now occupy most of their original distribution in Baja California and California (Bonnell and Selander, 1974; Lowry et al., 2014). The high degree of intraspecific variation in foraging behavior across their range is likely one of reasons northern elephant seals are so resilient. The type of information for a species is especially timely in an era of widespread and rapid environmental change.

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TABLES

TABLE 1. Movement, dive behavior, and foraging success metrics reported (mean ± s.d.) for adult male (n=11) and female (n=119) northern elephant seals.

Variable	**Males**	**Females**
Days at sea	**131.42 ± 19.22**	**164.35 ± 70.75**
Distance to the continental shelf (km)	**14.22 ± 24.22**	**562.47 ± 385.41**
Distance from breeding colony (km)	2,117 ± 1,405	2,834 ± 1,173
Total track distance (km)	**4,539 ± 3,553**	**7667 ± 3467**
Foraging area (km^2)	**54,223 ± 99,861**	**354,145 ± 508,295**
Maximum dive depth, day (m)	411.77 ± 97.53	550.31 ± 79.24
Dive duration, day (s)	1,517 ± 216	1,506 ± 188
Bottom time, day (s)	761.05 ± 122.91	637.77 ± 140.29
Post-dive interval, day (s)	157.49 ± 12.90	144.51 ± 143.90
No. vertical excursions at bottom, day	16.51 ± 2.92	14.03 ± 3.70
Efficiency, day	0.45 ± 0.02	0.38 ± 0.06
Maximum dive depth, night (m)	367.55 ± 79.45	456.33 ± 52.82
Dive duration, night (s)	1,383 ± 182	1,301 ± 148
Bottom time, night (s)	554.38 ± 25.36	564.82 ± 112.42
Post-dive interval, night (s)	164.85 ± 13.86	140.06 ± 34.49
No. vertical excursions at bottom, night	10.14 ± 0.96	12.74 ± 2.86
Efficiency, night	0.36 ± 0.03	0.39 ± 0.05
Body mass at departure (kg)	**813.27 ± 229.42**	**292.63 ± 48.02**
Mass gain on trip (kg)	**688.89 ± 199.26**	**183.52 ± 108.95**
Mass gain rate on trip (kg/day)	**5.35 ± 1.59**	**1.04 ± 0.43**
Proportion of mass gain on trip	0.80 ± 0.32	0.66 ± 0.42

Bolded values indicate significant differences between clusters ($p \leq 0.05$).

TABLE 2. Movement, dive behavior, and foraging success metrics reported (mean ± s.d.) for adult female northern elephant seals on the post-breeding (n=39) and post-molt (n=64) foraging trips.

Variable	**Post-Breeding**	**Post-Molt**
Days at sea	**78.60 ± 15.32**	**216.88 ± 24.75**
Distance to the continental shelf (km)	**406.12 ± 357.81**	**639.68 ± 377.02**
Distance from breeding colony (km)	**1,995 ± 665**	**3,308 ± 1,133**
Total track distance (km)	**4,567 ± 1,631**	**9,408 ± 2,974**
Foraging area (km^2)	**175,239 ± 493,525**	**440,235 ± 495,662**
Maximum dive depth, day (m)	537.25 ± 84.76	559.02 ± 74.79
Dive duration, day (s)	**1,450 ± 172**	**1,544 ± 190**
Bottom time, day (s)	630.48 ± 129.39	642.63 ± 147.99
Post-dive interval, day (s)	133.52 ± 20.26	151.84 ± 185.31
No. vertical excursions at bottom, day	**15.92 ± 2.81**	**12.77 ± 3.71**
Efficiency, day	**0.40 ± 0.06**	**0.37 ± 0.06**
Maximum dive depth, night (m)	464.31 ± 67.10	451.01 ± 40.41
Dive duration, night (s)	**1,233 ± 144**	**1,347 ± 133**
Bottom time, night (s)	**530.91 ± 122.95**	**587.44 ± 99.57**
Post-dive interval, night (s)	139.88 ± 25.11	140.18 ± 39.73
No. vertical excursions at bottom, night	**13.68 ± 2.46**	**12.11 ± 2.94**
Efficiency, night	0.39 ± 0.06	0.39 ± 0.04
Body mass at departure (kg)	**333.32 ± 37.36**	**269.98 ± 37.18**
Mass gain on trip (kg)	**65.07 ± 30.85**	**256.69 ± 67.09**
Mass gain rate on trip (kg/day)	**0.84 ± 0.40**	**1.17 ± 0.40**
Proportion of mass gain on trip	**0.20 ± 0.10**	**0.95 ± 0.25**

Bolded values indicate significant differences between clusters ($p \leq 0.05$).

TABLE 3. Movement, dive behavior, and foraging success metrics reported (mean ± s.d.) for adult male northern elephant seal from the Año Nuevo and San Benito breeding colonies (n=13).

Variable	**Año Nuevo**	**San Benito**
Days at sea	139.26 ± 15.49	131.86 ± 22.01
Distance to the continental shelf (km)	**41.44 ± 46.50**	**6.76 ± 12.73**
Distance from breeding colony (km)	**2,976 ± 1,654**	**1,421 ± 1,275**
Total track distance (km)	7,619 ± 2,238	3,369 ± 3,303
Foraging area (km^2)	**227,962 ± 104,994**	**2,904 ± 2,650**
Maximum dive depth, day (m)	411.77 ± 97.53	-
Dive duration, day (s)	1517 ± 216	-
Bottom time, day (s)	761.05 ± 122.91	-
Post-dive interval, day (s)	157.49 ± 12.90	-
No. vertical excursions at bottom, day	16.51 ± 2.91	-
Efficiency, day	0.46 ± 0.02	-
Maximum dive depth, night (m)	367.55 ± 79.45	-
Dive duration, night (s)	1383 ± 182	-
Bottom time, night (s)	554.39 ± 25.36	-
Post-dive interval, night (s)	164.85 ± 13.86	-
No. vertical excursions at bottom, night	10.14 ± 0.95	-
Efficiency, night	0.36 ± 0.03	-
Body mass at departure (kg)	**1,021 ± 135**	**708.03 ± 210.06**
Mass gain on trip (kg)	712.33 ± 280.02	559.22 ± 240.70
Mass gain rate on trip (kg/day)	5.05 ± 1.57	4.61 ± 2.58
Proportion of mass gain on trip	0.72 ± 0.37	0.78 ± 0.33

Bolded values indicate significant differences between clusters ($p \leq 0.05$).

TABLE 4. Movement, dive behavior, and foraging success variables for adult female northern elephant seal from Año Nuevo, San Nicolas, San Benito, and Guadalupe on the post-breeding and post-molt foraging trips.

	Post-Breeding Foraging Trip		
Variable	**Año Nuevo**	**San Benito**	**Guadalupe**
Days at sea	76.04 ± 9.49	87.75 ± 27.10	80.21 ± 18.12
Distance to the continental shelf (km)	436.17 ± 367.54	357.83 ± 392.22	244.42 ± 72.51
Distance from breeding colony (km)	**2,102 ± 579**	**1,475 ± 893**	1,772 ± 647
Total track distance (km)	**4,753 ± 1,153**	**3,189 ± 1,707**	**6,412 ± 5,147**
Foraging area (km^2)	134,327 ± 382,156	**24,087 ± 53,710**	**896,142 ± 1,262,881**
Maximum dive depth, day (m)	540.01 ± 84.80	524.25 ± 90.02	-
Dive duration, day (s)	1440 ± 107	1494 ± 359	-
Bottom time, day (s)	**607.98 ± 90.67**	**736.55 ± 221.50**	-
Post-dive interval, day (s)	**129.65 ± 16.83**	**151.77 ± 26.20**	-
No. vertical excursions at bottom, day	15.62 ± 2.58	17.34 ± 3.62	-
Efficiency, day	0.39 ± 0.06	0.44 ± 0.06	-
Maximum dive depth, night (m)	470.10 ± 62.32	437.01 ± 86.59	-
Dive duration, night (s)	1222 ± 99	1282 ± 279	-
Bottom time, night (s)	**506.24 ± 77.02**	**647.18 ± 217.96**	-
Post-dive interval, night (s)	**136.33 ± 23.24**	**156.63 ± 28.68**	-
No. vertical excursions at bottom, night	**13.29 ± 1.96**	**15.56 ± 3.73**	-
Efficiency, night	**0.38 ± 0.05**	**0.44 ± 0.07**	-
Body mass at departure (kg)	329.62 ± 38.15	353.31 ± 30.04	349.20 ± 27.97
Mass gain on trip (kg)	**71.15 ± 23.71**	**20.03 ± 42.64**	-
Mass gain rate on trip (kg/day)	**0.92 ± 0.30**	**0.28 ± 0.58**	-
Proportion of mass gain on trip	**0.22 ± 0.08**	**0.06 ± 0.12**	-

Bolded values indicate significant differences between clusters ($p \leq 0.05$).

TABLE 4 (Continued)

	Post-Molt Foraging Trip			
Variable	**Año Nuevo**	**San Nicolas**	**San Benito**	**Guadalupe**
Days at sea	219.05 ± 22.91	205.08 ± 36.43	210.31 ± 26.87	230.79 ± 2.82
Distance to the continental shelf (km)	653.78 ± 384.23	755.15 ± 337.98	467.26 ± 378.03	636.18 ± 337.36
Distance from breeding colony (km)	3,311 ± 1,072	3,852 ± 1,137	2,907 ± 1,494	3,419 ± 1,210
Total track distance (km)	9,772 ± 2,866	10,027 ± 1,930	7,198 ± 2,996	9,045 ± 4,465
Foraging area (km^2)	**427,292 ± 527,863**	**752,099 ± 325,383**	**195,117 ± 305,841**	571,273 ± 460,187
Maximum dive depth, day (s)	553.72 ± 78.51	560.56 ± 46.44	561.35 ± 78.30	620.89 ± 66.08
Dive duration, day (s)	**1,574 ± 187**	**1,560 ± 179**	**1,404 ± 147**	**1,510 ± 259**
Bottom time, day (s)	**673.86 ± 140.66**	**637.67 ± 94.80**	595.91 ± 125.83	**367.56 ± 129.01**
Post-dive interval, day (s)	**134.09 ± 34.41**	**97.04 ± 12.20**	**304.13 ± 462.63**	**65.56 ± 16.78**
No. vertical excursions at bottom, day	**13.10 ± 2.98**	**14.81 ± 1.10**	**13.08 ± 3.48**	**2.52 ± 0.75**
Efficiency, day	**0.38 ± 0.05**	**0.37 ± 0.02**	**0.37 ± 0.07**	**0.21 ± 0.04**
Maximum dive depth, night (m)	450.74 ± 32.33	427.31 ± 32.63	445.61 ± 55.45	526.17 ± 34.52
Dive duration, night (s)	1,355 ± 117	1,381 ± 154	**1,239 ± 140**	**1,475 ± 120**
Bottom time, night (s)	597.54 ± 82.77	604.21 ± 115.19	572.23 ± 144.92	455.85 ± 39.71
Post-dive interval, night (s)	**140.79 ± 31.00**	**106.32 ± 20.41**	**177.73 ± 56.84**	**98.16 ± 12.85**
No. vertical excursions at bottom, night	**12.25 ± 2.34**	**13.74 ± 1.71**	**12.99 ± 2.15**	**3.71 ± 0.50**
Efficiency, night	**0.39 ± 0.03**	**0.40 ± 0.04**	**0.40 ± 0.06**	**0.28 ± 0.02**
Body mass at departure (kg)	**276.43 ± 34.96**	**280.19 ± 34.77**	**233.12 ± 27.10**	249.02 ± 41.26
Mass gain on trip (kg)	263.18 ± 51.97	248.14 ± 153.46	243.60 ± 32.81	190.31 ± 10.01
Mass gain rate on trip (kg/day)	1.18 ± 0.20	1.29 ± 1.17	1.10 ± 0.17	0.83 ± 0.06
Proportion of mass gain on trip	0.96 ± 0.20	0.89 ± 0.58	1.03 ± 0.17	0.83 ± 0.14

Bolded values indicate significant differences between clusters ($p \leq 0.05$).

TABLE 5. Coefficient of variation for each feeding metric for each northern elephant seal breeding colony and foraging trip. Abbreviations for each colony as follows: Año Nuevo (AN), San Nicolas (SN), San Benito (SB), and Guadalupe (IG).

	Post-Breeding Females			**Post-Molt Females**				**Males**	
Variable	**AN**	**SB**	**IG**	**AN**	**SN**	**SB**	**IG**	**AN**	**SB**
Days at sea	0.12	0.31	0.23	0.11	0.18	0.13	0.01	0.11	0.17
Distance to the continental shelf (km)	0.84	1.1	0.3	0.59	0.45	0.81	0.53	1.12	1.88
Distance from breeding colony (km)	0.25	0.61	0.37	0.32	0.3	0.51	0.36	0.35	0.86
Total track distance (km)	0.24	0.54	0.8	0.29	0.19	0.42	0.49	0.29	0.98
Foraging area (km2)	2.84	2.23	1.41	1.24	0.43	1.57	0.81	0.46	0.91
Maximum dive depth, day (m)	0.16	0.17	-	0.14	0.08	0.14	0.11	0.24	-
Dive duration, day (s)	0.07	0.24	-	0.12	0.12	0.1	0.17	0.14	-
Bottom time, day (s)	0.15	0.3	-	0.21	0.15	0.21	0.35	0.16	-
Post-dive interval, day (s)	0.13	0.17	-	0.26	0.13	1.52	0.26	0.08	-
No. vertical excursions at bottom, day	0.16	0.21	-	0.23	0.07	0.27	0.3	0.18	-
Efficiency, day	0.16	0.13	-	0.14	0.06	0.19	0.16	0.05	-
Maximum dive depth, night (m)	0.13	0.2	-	0.07	0.08	0.12	0.07	0.22	-
Dive duration, night (s)	0.08	0.22	-	0.09	0.11	0.11	0.08	0.13	-
Bottom time, night (s)	0.15	0.34	-	0.14	0.19	0.25	0.09	0.05	-
Post-dive interval, night (s)	0.17	0.18	-	0.22	0.19	0.32	0.13	0.08	-
No. vertical excursions at bottom, night	0.15	0.24	-	0.19	0.12	0.17	0.13	0.09	-
Efficiency, night	0.12	0.16	-	0.08	0.1	0.15	0.06	0.08	-
Body mass at departure (kg)	0.12	0.09	0.08	0.13	0.12	0.12	0.17	0.13	0.3
Mass gain on trip (kg)	0.33	2.13	-	0.2	0.62	0.13	0.05	0.39	0.43
Mass gain rate on trip (kg/day)	0.33	2.11	-	0.17	0.91	0.16	0.07	0.31	0.56
Proportion of mass gain on trip	0.37	2.18	-	0.2	0.65	0.16	0.17	0.52	0.43
MEAN	**0.34**	**0.66**	**0.53**	**0.24**	**0.25**	**0.36**	**0.22**	**0.25**	**0.72**

FIGURES

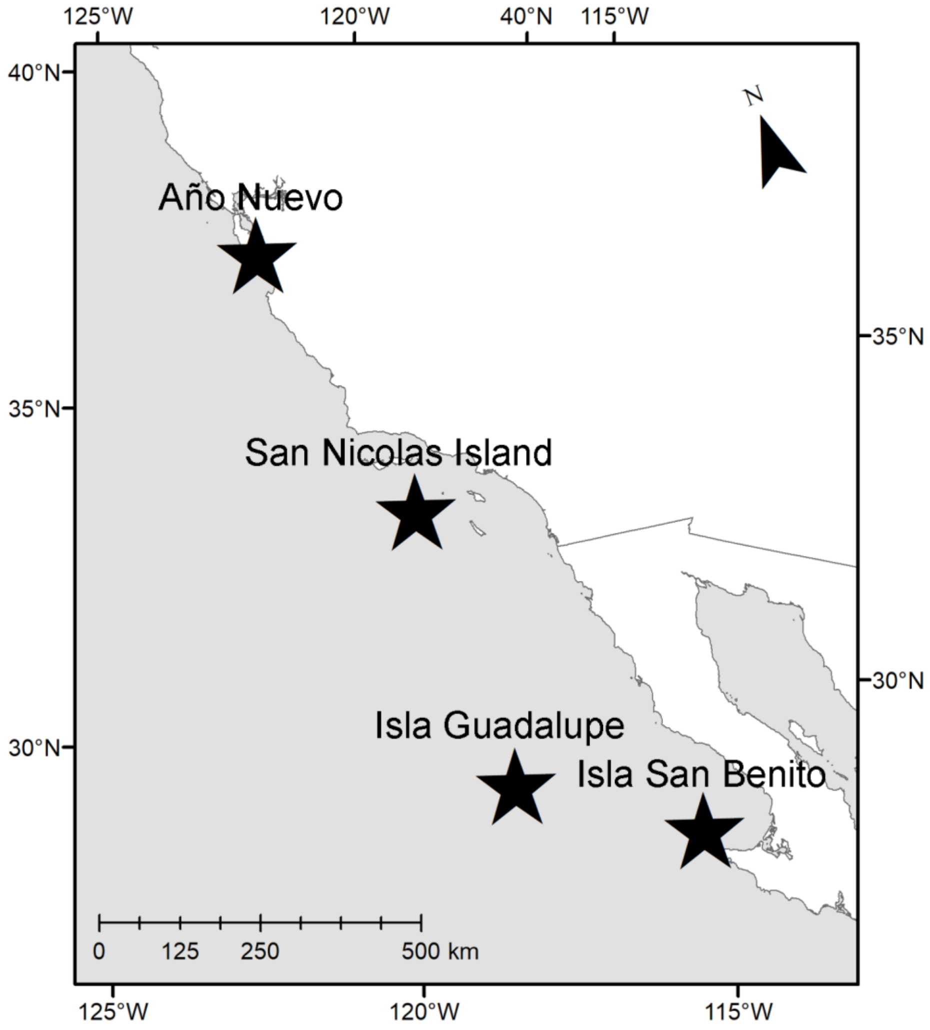

FIGURE 1. Location of the four breeding colonies where adult male and female northern elephant seals were instrumented with satellite transmitters and time-depth recovers between 2004 and 2018.

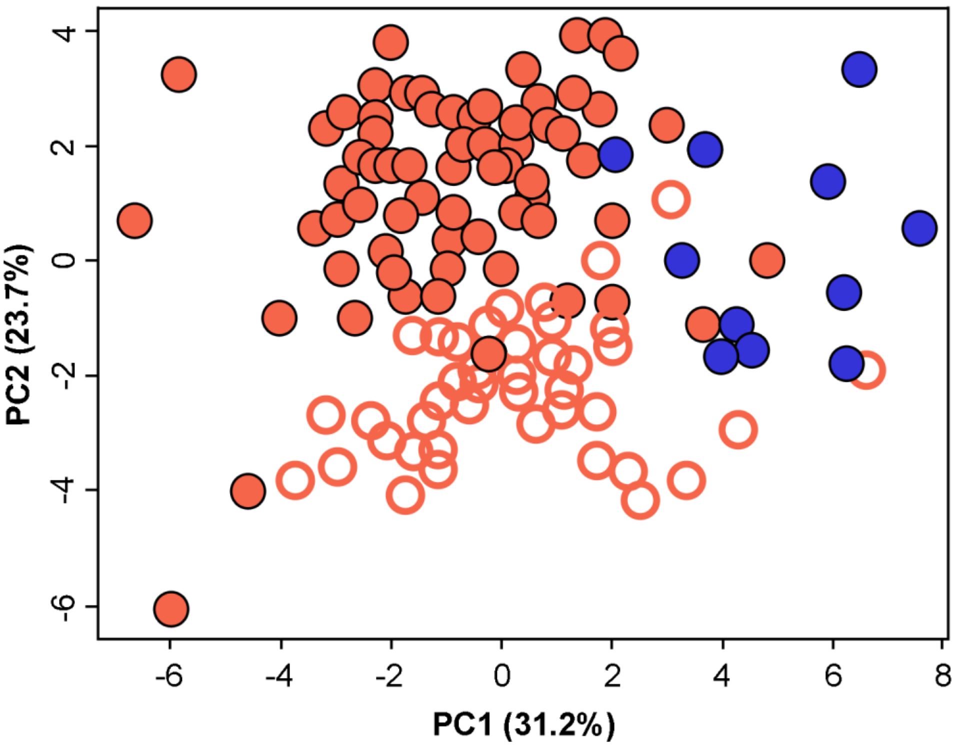

FIGURE 2. Scatterplot of principal components (PCs) 1 and 2 showing the separation of northern elephant seal foraging strategies based on the movement patterns, dive behavior, and foraging success of adult male and female seals from four breeding colonies. The sexes cluster along PC1 (males: blue circles; females: orange circles), and females cluster by season along PC2 (post-breeding females: filled orange circles; post-molt females: open orange circles).

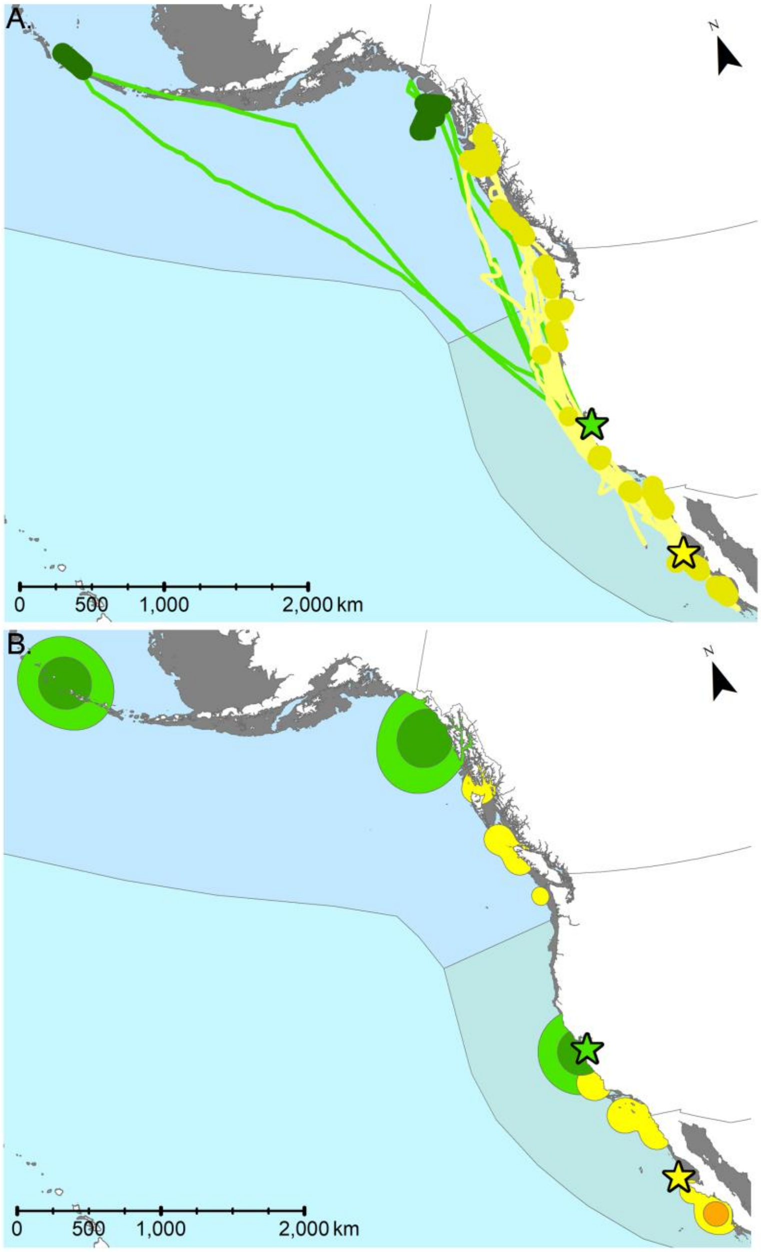

FIGURE 3. Satellite tracks and utilization distributions (UDs) showing the foraging areas utilized by adult male northern elephant seals from the Año Nuevo (green) and San Benito (yellow) colonies. Stars represent breeding colonies. The continental shelf is dark grey, the California Current is light green, the Subarctic Pacific is light blue, and the North Central Pacific is blue-grey. (A) Satellite tracks of male seals, where lines represent the track of each seal and circles along the track represent foraging locations. (B) 95% and 50% UDs of male seal foraging locations as determined from kernel density analysis. Lighter polygons represent the 95% UD and darker polygons represent the 50% UD.

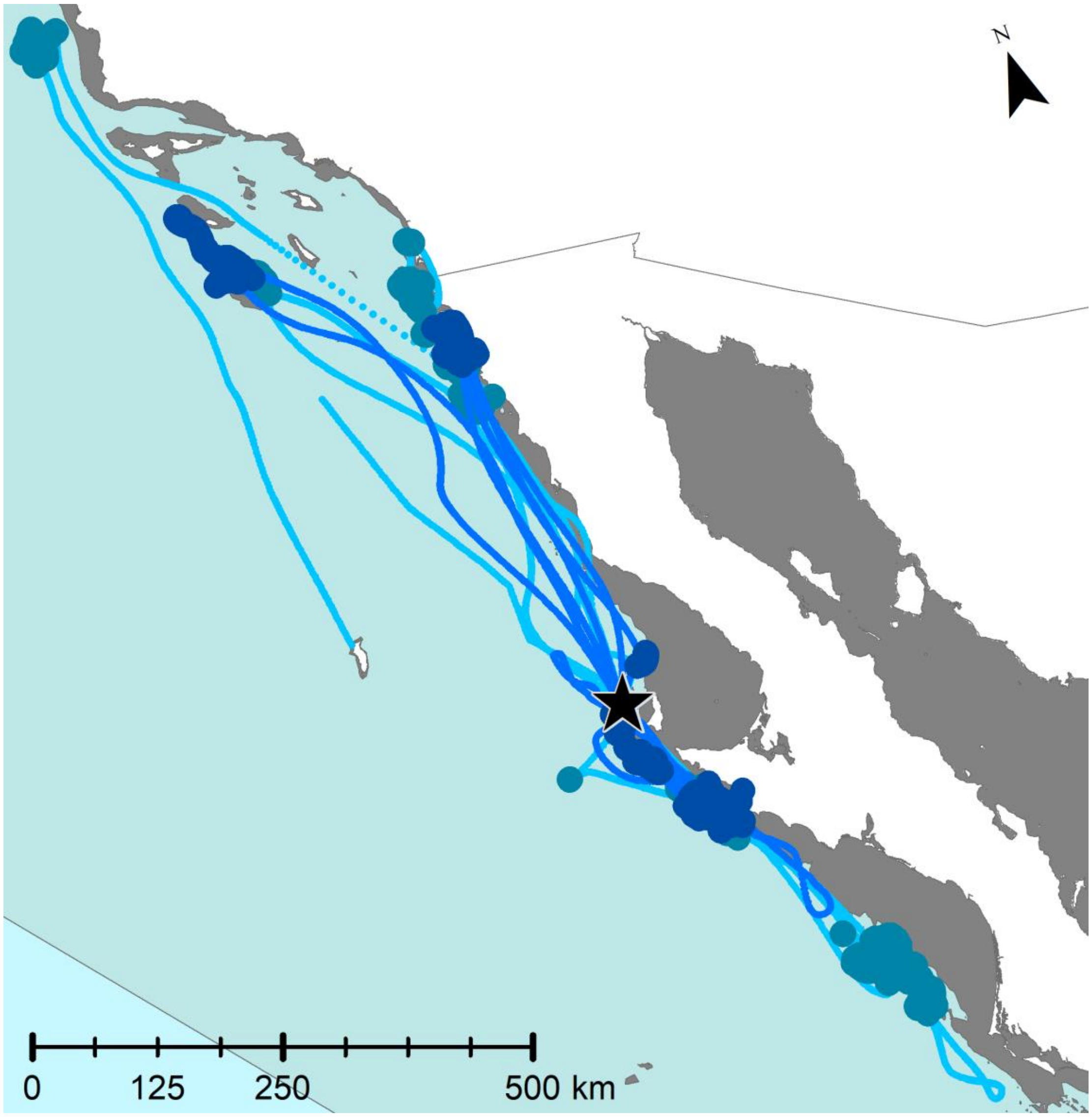

FIGURE 4. Satellite tracks of adult male and female northern elephant seals from San Benito (black star) that stayed local, traveling <1,000 km from the colony on their at-sea foraging trips. Adult males are shown in light blue, and adult females are shown in dark blue. Lines represent the track, and circles along the track represent foraging locations. The continental shelf is dark grey, the California Current is light green, and the North Central Pacific is blue-grey.

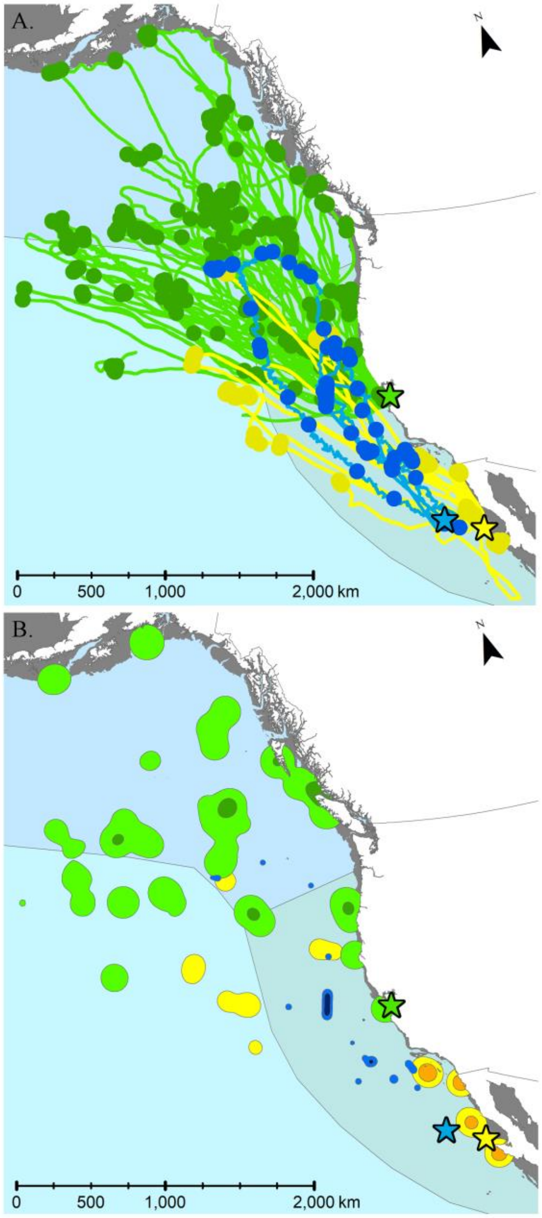

FIGURE 5. Satellite tracks and utilization distributions (UDs) showing the foraging areas utilized by adult female northern elephant seals during the post-breeding trip from Año Nuevo (green), Guadalupe (blue), and San Benito (yellow). Stars represent breeding colonies. The continental shelf is dark grey, the California Current is light green, the Subarctic Pacific is light blue, and the North Central Pacific is blue-grey. (A) Satellite tracks of females on their post-breeding trip, where lines represent the track, and circles along the track represent foraging locations. (B) 95% and 50% UDs of foraging locations of females on the post-breeding trip as determined from kernel density analysis, where the lighter polygons represent the 95% UD and the darker polygons represent the 50% UD.

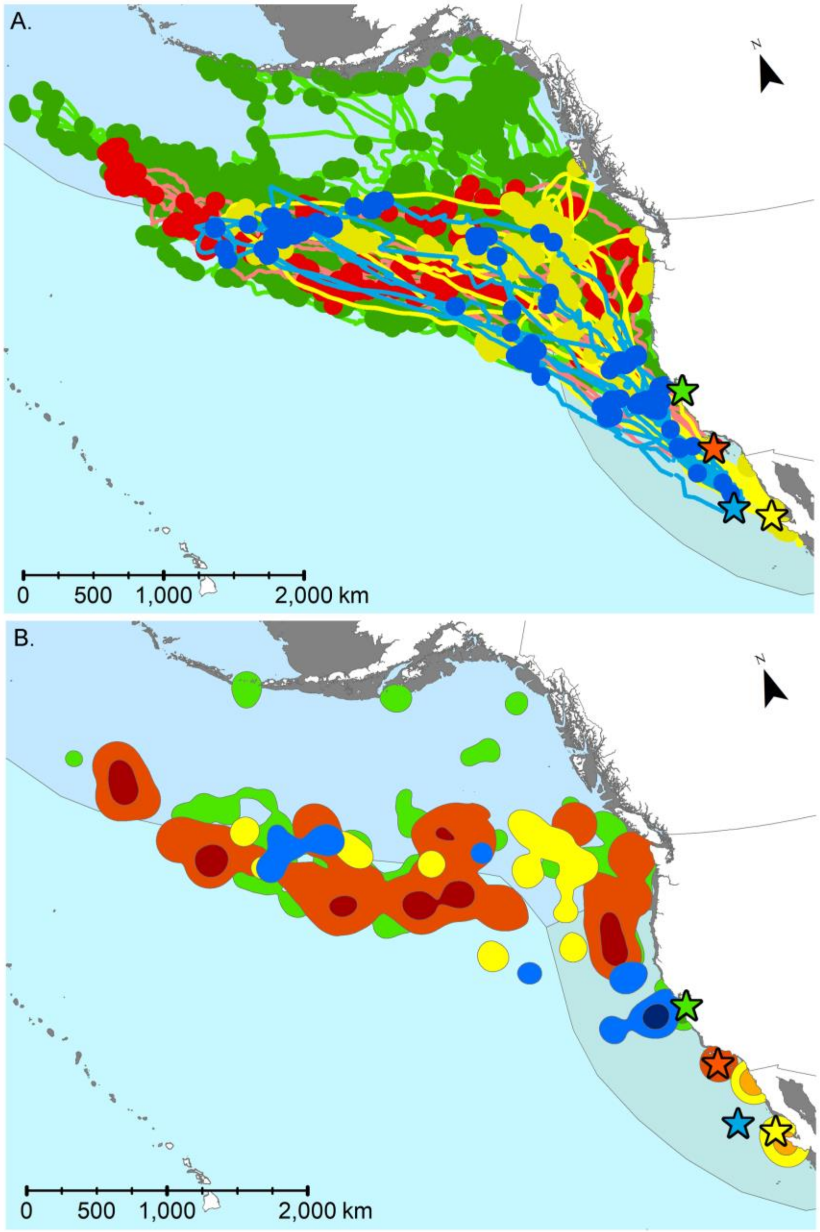

FIGURE 6. Satellite tracks and utilization distributions (UDs) of adult female northern elephant seals during the post-molt trip from Año Nuevo (green), San Nicolas (red), Guadalupe (blue), and San Benito (yellow). Stars represent the breeding colonies. The continental shelf is dark grey, the California Current is light green, the Subarctic Pacific is shown in light blue, and the North Central Pacific is blue-grey. (A) Satellite tracks of females on their post-molt trip, where lines represent the track and circles along the track represent foraging locations. (B) 95% and 50% UDs of foraging locations of females as determined from kernel density analysis, where the lighter polygons represent the 95% UD and the darker polygons represent the 50% UD.

CHAPTER 1

SUPPLEMENTARY INFORMATION

TABLE S1. Principal component (PC) loadings for PCs 1-3 for all foraging variables analyzed from adult female (n=119) and adult male (n=11) northern elephant seals.

Variable	**PC1 (31.2%)**	**PC2 (23.7%)**	**PC3 (13.6%)**
Days at sea	**-0.27**	**0.77**	0.00
Distance to the continental shelf (km)	**-0.55**	**0.43**	**0.34**
Distance from breeding colony (km)	**-0.53**	**0.63**	-0.07
Total track distance (km)	**-0.48**	**0.74**	-0.04
Foraging area (km^2)	**-0.26**	**0.44**	0.16
Maximum dive depth, day (m)	**-0.78**	**0.23**	**0.29**
Dive duration, day (s)	0.11	**0.81**	**0.26**
Bottom time, day (s)	**0.78**	**0.48**	**0.22**
Post-dive interval, day (s)	**-0.39**	**-0.29**	**0.41**
No. vertical excursions at bottom, day	**0.82**	-0.12	**0.34**
Efficiency, day	**0.95**	0.01	0.09
Maximum dive depth, night (m)	**-0.68**	-0.02	**0.28**
Dive duration, night (s)	**0.32**	**0.79**	**0.18**
Bottom time, night (s)	**0.63**	**0.57**	**0.42**
Post-dive interval, night (s)	**0.32**	-0.17	-0.11
No. vertical excursions at bottom, night	**0.59**	-0.06	**0.67**
Efficiency, night	**0.70**	**0.20**	**0.49**
Body mass at departure (kg)	**0.61**	-0.02	**-0.49**
Mass gain on trip (kg)	**0.33**	**0.64**	**-0.63**
Mass gain rate on trip (kg/day)	**0.53**	**0.31**	**-0.71**
Proportion of mass gain on trip	-0.14	**0.70**	**-0.28**

*Bolded numbers indicate variables that are significantly correlated with each PC axis.

TABLE S2. Principal component (PC) loadings for PCs 1-4 for quantitative foraging variables analyzed from adult male northern elephant seals (n=13) on the post-molt foraging trip.

Variable	**PC1 (40.5%)**	**PC2 (19.2%)**	**PC3 (17.8%)**	**PC4 (11.6%)**
Days at sea	-0.22	**-0.76**	0.07	0.52
Distance to the continental shelf (km)	0.27	0.43	0.10	**0.71**
Distance from breeding colony (km)	0.76	-0.13	**0.59**	-0.21
Total track distance (km)	**0.61**	-0.37	**0.65**	-0.18
Foraging area (km^2)	**0.85**	-0.05	0.08	0.35
Body mass at departure (kg)	**0.68**	**0.60**	0.16	0.03
Mass gain on trip (kg)	**-0.71**	0.26	0.54	0.25
Mass gain rate on trip (kg/day)	**-0.62**	0.54	0.46	-0.10
Proportion of mass gain on trip	**-0.71**	-0.29	0.53	0.02

*Bolded numbers indicate variables that were significantly correlated with each PC axis.

TABLE S3. Movement, dive behavior, and foraging success variables reported (mean ± s.d.) for adult northern elephant seal from San Benito.

	Female Post-Breeding Trip		Female Post-Molt Trip	
Variable	**Local**	**Migrating**	**Local**	**Migrating**
Days at sea	75.15 ± 12.51	93.14 ± 30.59	218.69 ± 0.59	208.22 ± 30.05
Distance to the continental shelf (km)	**2.89 ± 0.75**	**570.80 ± 343.56**	**2.54 ± 1.53**	**583.44 ± 326.51**
Distance from breeding colony (km)	**434 ± 263**	**1,995 ± 524**	**371 ± 97**	**3,542 ± 755**
Total track distance (km)	**1,409 ± 345**	**4,523 ± 453**	**2,063 ± 778**	**8,481 ± 1,429**
Foraging area (km^2)	1002 ± 786	41,400 ± 69,546	1,950 ± 1,703	243,409 ± 327,014
Maximum dive depth, day (m)	**454.17 ± 42.07**	**576.79 ± 80.22**	**431.69 ± 25.83**	**598.40 ± 29.30**
Dive duration, day (s)	1,258 ± 66	1671 ± 397	1328 ± 33	1,426 ± 162
Bottom time, day (s)	644.99 ± 16.05	805.21 ± 288.59	**715.47 ± 46.26**	**561.75 ± 120.94**
Post-dive interval, day (s)	159.69 ± 40.57	145.84 ± 12.88	155.33 ± 36.34	346.64 ± 525.03
No. vertical excursions at bottom, day	15.84 ± 2.66	18.46 ± 4.19	**18.37 ± 0.09**	**11.57 ± 2.05**
Efficiency, day	0.45 ± 0.43	0.43 ± 0.08	**0.48 ± 0.03**	**0.35 ± 0.05**
Maximum dive depth, night (m)	**364.3 ± 48.16**	**491.54 ± 64.79**	**359.64 ± 27.32**	**470.18 ± 28.43**
Dive duration, night (s)	1159 ± 76	1,374 ± 354	**1,369 ± 55**	**1,202 ± 135**
Bottom time, night (s)	607.89 ± 54.61	676.65 ± 300.54	**746.49 ± 60.52**	**522.44 ± 119.91**
Post-dive interval, night (s)	173.60 ± 36.73	143.90 ± 15.53	263.05 ± 72.78	153.36 ± 17.47
No. vertical excursions at bottom, night	14.43 ± 2.56	16.41 ± 4.61	**15.08 ± 0.33**	**12.39 ± 2.07**
Efficiency, night	0.46 ± 0.03	0.43 ± 0.09	**0.48 ± 0.02**	**0.38 ± 0.05**
Body mass at departure (kg)	342.53 ± 17.88	364.09 ± 39.84	219.14 ± 9.84	236.61 ± 29.34
Mass gain on trip (kg)	18.19 ± 40.18	22.80 ± 63.39	243.22 ± 29.72	243.79 ± 38.72
Mass gain rate on trip (kg/day)	0.19 ± 0.40	0.40 ± 0.89	1.11 ± 0.13	1.10 ± 0.21
Proportion of mass gain on trip	0.06 ± 0.12	0.06 ± 0.18	1.11 ± 0.19	0.99 ± 0.17

Bolded values indicate significant differences between clusters ($p \leq 0.05$).

TABLE S3 (Continued)

	Males	
Variable	**Local**	**Migrating**
Days at sea	138.06 ± 22.77	121.53 ± 20.06
Distance to the continental shelf (km)	9.39 ± 15.30	1.49 ± 0.97
Distance from breeding colony (km)	**540 ± 251**	**2,987 ± 422**
Total track distance (km)	1685 ± 769	8,420 ± 2,320
Foraging area (km2)	2,220 ± 2,332	4,044 ± 3,254
Maximum dive depth, day	-	-
Dive duration, day	-	-
Bottom time, day	-	-
Post-dive interval, day	-	-
No. vertical excursions at bottom, day	-	-
Efficiency, day	-	-
Maximum dive depth, night	-	-
Dive duration, night	-	-
Bottom time, night	-	-
Post-dive interval, night	-	-
No. vertical excursions at bottom, night	-	-
Efficiency, night	-	-
Body mass at departure (kg)	670.45 ± 22.43	753.14 ± 210.61
Mass gain on trip (kg)	240.55	665.44 ± 138.57
Mass gain rate on trip (kg/day)	1.52	5.64 ± 1.90
Proportion of mass gain on trip	0.49	0.88 ± 0.33

TABLE S4. Principal component (PC) loadings for PCs 1-4 for all quantitative foraging variables analyzed from adult female northern elephant seals (n=43) during the post-breeding trip.

Variable	**PC1 (37.5%)**	**PC2 (19.8%)**	**PC3 (14.4%)**	**PC4 (10.9%)**
Days at sea	**-0.63**	0.15	-0.18	0.01
Distance to the continental shelf (km)	-0.23	**0.62**	**0.49**	0.30
Distance from breeding colony (km)	**-0.34**	**0.51**	0.29	**-0.55**
Total track distance (km)	**-0.62**	0.14	0.25	**-0.55**
Foraging area (km^2)	**-0.64**	**-0.60**	**0.34**	-0.14
Maximum dive depth, day (m)	**-0.33**	**0.49**	**0.65**	**0.32**
Dive duration, day (s)	**0.66**	**0.46**	**0.48**	0.04
Bottom time, day (s)	**0.95**	0.01	0.20	-0.05
Post-dive interval, day (s)	0.14	0.01	-0.24	**0.80**
No. vertical excursions at bottom, day	**0.82**	-0.11	0.23	-0.24
Efficiency, day	**0.82**	**-0.40**	-0.14	-0.23
Maximum dive depth, night (m)	-0.29	**0.48**	**0.65**	0.30
Dive duration, night (s)	**0.80**	**0.32**	**0.35**	0.12
Bottom time, night (s)	**0.96**	0.02	0.11	0.10
Post-dive interval, night (s)	0.04	-0.04	**-0.37**	**0.71**
No. vertical excursions at bottom, night	**0.90**	-0.13	0.22	-0.12
Efficiency, night	**0.90**	-0.23	-0.12	-0.02
Body mass at departure (kg)	**0.40**	**-0.34**	**0.58**	0.02
Mass gain on trip (kg)	0.30	**0.81**	**-0.43**	-0.18
Mass gain rate on trip (kg/day)	**0.40**	**0.80**	**-0.37**	-0.15
Proportion of mass gain on trip	0.18	**0.81**	**-0.52**	-0.16

*Bolded numbers indicate variables that were significantly correlated with each PC axis.

TABLE S5. Principal component (PC) loadings for PCs 1-3 for all quantitative foraging variables analyzed from adult female northern elephant seals (n=64) during the post-molt trip.

Variable	**PC1 (32.3%)**	**PC2 (17.8%)**	**PC3 (15.0%)**
Days at sea	**0.31**	**0.56**	0.15
Distance to the continental shelf (km)	0.02	**0.60**	**0.34**
Distance from breeding colony (km)	**-0.33**	**0.63**	**0.39**
Total track distance (km)	**-0.34**	**0.64**	0.22
Foraging area (km^2)	**-0.32**	**0.44**	0.06
Maximum dive depth, day (m)	**-0.30**	**0.44**	**0.36**
Dive duration, day (s)	**0.57**	**0.57**	**0.44**
Bottom time, day (s)	**0.89**	0.14	**0.28**
Post-dive interval, day (s)	**-0.32**	**-0.63**	**0.50**
No. vertical excursions at bottom, day	**0.85**	-0.23	0.16
Efficiency, day	**0.90**	-0.18	0.06
Maximum dive depth, night (m)	**-0.55**	0.17	**0.26**
Dive duration, night (s)	**0.49**	**0.39**	**0.25**
Bottom time, night (s)	**0.87**	0.03	**0.27**
Post-dive interval, night (s)	**0.34**	**-0.47**	-0.20
No. vertical excursions at bottom, night	**0.74**	**-0.26**	0.23
Efficiency, night	**0.88**	-0.16	0.23
Body mass at departure (kg)	**0.51**	0.09	**0.28**
Mass gain on trip (kg)	**0.50**	**0.47**	**-0.69**
Mass gain rate on trip (kg/day)	**0.41**	**0.38**	**-0.77**
Proportion of mass gain on trip	**0.34**	**0.44**	**-0.79**

*Bolded numbers indicate variables that were significantly correlated with each PC axis.

CHAPTER 2

SEX-SPECIFIC FORAGING STRATEGIES OF A SEXUALLY DIMORPHIC MARINE PREDATOR, THE NORTHERN ELEPHANT SEAL

ABSTRACT

Many sexually dimorphic species exhibit intraspecific niche divergence, which results in the sexes behaving differently. However, little is known about the foraging behavior of wide-ranging, deep-diving marine predators. We documented sex-specific foraging strategies in a sexually dimorphic marine mammal, the northern elephant seal (*Mirounga angustirostris*). We coupled satellite telemetry, diving behavior, and foraging success metrics from 39 adult male and 152 adult female seals and showed that most foraging metrics differed between the sexes. Males are benthic continental shelf predators with small foraging areas and high foraging success, as measured by mass and energy gain. Males are extremely consistent in their feeding behavior, showing little to no flexibility. Females are mesopelagic predators with large foraging areas and moderate to low foraging success. Females show more behavioral flexibility than males. Within females, feeding strategies differ seasonally. On the short post-breeding trip (February-May), females have small foraging areas, short pelagic foraging dives with low dive efficiency, and low foraging success compared to females on the long post-molt trip (May-January). There is little to no overlap between male and female strategies, indicating that the sexes act as different ecological species in benthic and mesopelagic habitats in the North Pacific Ocean. Male seals have higher foraging success but also higher mortality compared to female seals. Male seals may adopt a riskier foraging strategy to attain and maintain the large body sizes required to compete for mating opportunities, while female seals may adopt a risk-adverse strategy to maximize fitness over their lifetime.

INTRODUCTION

Sexual dimorphism is widespread throughout the animal kingdom, with males and females showing dramatic differences in size and shape (Darwin, 1871). This dichotomy between conspecifics arises as a result of sexual selection or intraspecific niche divergence, driving behavioral, ecological, and physiological differences between the sexes (Shine, 1989; Perry, 1996; Gonzalez-Solis et al., 2000; Phillips et al., 2004; Hierlihy et al., 2013). In turn, these sex-specific differences can lead to diverse strategies for maximizing fitness.

Sexual selection is the prevailing explanation for the evolution and maintenance of sexual dimorphism (Clutton-Brock, 2007), Sexual selection occurs when trait differences evolve as a result of intrasexual competition for mating opportunities or attracting the opposite sex; these traits result in increased fitness (Darwin, 1871; Trivers, 1972; Ralls, 1977; Clutton-Brock, 2007). Alternatively, intraspecific niche divergence occurs when trait disparity between the sexes arise from the occupation of different ecological niches, resulting sex-specific ecological adaptations (Darwin, 1871; Slatkin, 1984; Shine, 1989).

Sexual selection and intraspecific niche divergence are not mutually exclusive hypotheses (Hedrick and Temeles, 1989; Shine, 1989; Blanckenhorn, 2005), and the end result is often the same: many sexually dimorphic species exhibit sex-specific foraging strategies (Shine, 1989; Perry, 1996; Gonzalez-Solis et al., 2000; Phillips et al., 2004; Hierlihy et al., 2013). Individuals of the larger sex may require additional or different prey resources to attain and maintain their body size (Moors, 1980; Shine, 1989; Rose, 1994). Alternatively, some species exhibit sex-specific morphologies that affect feeding behavior (e.g., changes in mouthparts, gape size; Herrel et al., 1999; Vincent et al., 2004; Issac, 2005; Law et al., 2018). These sex-specific foraging strategies are ecologically important, providing the raw material for natural selection, expanding the ecological niche of a species, affecting predator-prey dynamics, and changing ecosystem functioning (Bolnick et al. 2003, 2011; Araújo et al., 2011).

Northern elephant seals (*Mirounga angustirostris*) provide an example of extreme sexual dimorphism in mammals (Le Boeuf et al., 1974; Haley et al., 1994; Lindenfors et al., 2002). Adult male seals are three to four times as large and one and a half times as long as adult female seals (Deutsch et al., 1990; Le Boeuf et al., 1993). Male seals also have secondary sexual characteristics, including the long proboscis that inspired the name ‘elephant seals’ (Deutsch et al. 1994).

Northern elephant seals fulfill many of the predictions of sexual selection theory. The species is highly polygynous (Bartholomew, 1970; Cullen et al., 2014). Adult males defend harems of females during the breeding season, undergo fierce combats with other males for access to mating opportunities, and less than 1% of adult males are reproductively successful (Le Boeuf et al., 1974; Deutsch et al., 1990; Le Boeuf, 1994; Haley et al., 1994; Crocker et al., 2012; Casey et al., 2015). Female seals, on the other hand, have high reproductive success, often breed annually from the time they reach sexual maturity to death, and are the only sex to provide parental care for offspring (Reiter et al., 1981; Condit et al. 2014).

Few studies have examined intraspecific niche divergence in northern elephant seals. Satellite tags and time-depth recorders (TDRs) deployed on adult northern elephant seals in the 1990’s showed that males and females appear to exhibit different at-sea movement patterns and dive behavior. Specifically, adult males were shown to be benthic foragers along the western North Pacific coast, while female seals were mesopelagic foragers in the central North Pacific Ocean (Le Boeuf et al., 1993; Stewart et al., 1995; Le Boeuf et al., 2000). Additionally, males gained more mass than females (Le Boeuf et al., 2000). More recent analyses of female seals, however, suggest that there is not a clear dichotomy between male and female foraging strategies. Some female seals have been documented using benthic foraging dives on or near the continental shelf similar to males with high foraging success, similar to males (Simmons et al., 2007; Robinson et al. 2012). The apparent overlap between male and female foraging strategies suggests that, rather than sex-specific, these strategies are spatially specific, where particular foraging behaviors are best suited for different habitats. Recent studies of more than 50 marine megafauna species have documented distinct movement patterns, irrespective of taxonomic group, associated with coastal versus open ocean habitats, (Humphries et al., 2010; Sequeira et al., 2018).

Based on the results from these previous studies, a quantitative comparative analysis is needed to further characterize northern elephant seal foraging strategies, test hypotheses about the use of different strategies, and investigate trade-offs between strategies. Therefore, our first objective is to examine northern elephant seal foraging strategies by integrating data on spatial patterns, dive behavior, and body composition. Building on previous descriptive studies (Le Boeuf et al., 1993, 2000; Stewart et al., 1995; Simmons et al., 2007), we test the hypothesis that northern elephant seals exhibit sex-specific foraging strategies but that these strategies are also associated with particular foraging habitats. We predict that male and female seals will exhibit distinct foraging strategies that are associated with different movement patterns, dive behavior, and foraging success. We also predict that seals feeding in the same habitat (e.g., continental shelf, open ocean) will adopt similar feeding strategies, regardless of sex. The second objective of this study is to examine the relationship between foraging success and survival. We test the hypothesis that seals foraging on the continental shelf have higher foraging success but decreased survival compared to seals foraging in the open ocean.

METHODS

Instrumentation and Animal Handling

We deployed satellite transmitters and time depth recorders (TDRs) on 32 adult male and 152 adult female seals at Año Nuevo State Park (San Mateo County, California, USA) between 2006 and 2015. Instruments were deployed at the start of both biannual at-sea foraging trips: the post-breeding trip (females: February-May; males: March-August) and the post-molt trip (females: May-January, males: August-January). Seals were instrumented with a combination of satellite transmitters (SPOT or SPLASH tags, Wildlife Computers or Conductivity-Temperature-Depth tags, Sea

Mammal Research Unit), TDRs (MK9 or MK10, Wildlife Computers), and VHF radio transmitters (Advanced Telemetry Systems). We followed established protocols to chemically immobilize seals to deploy instruments, collect morphometric data, and collect tissue samples (Le Boeuf et al., 1988; Le Boeuf et al., 2000; Simmons et al., 2010; Robinson et al., 2012). Instruments were recovered and additional morphometric data and tissue sampling occurred on the seal's return to the breeding colony at the end of the foraging trip. Behavioral research was approved by the Animal Care and Use Committee at the University of California, Santa Cruz and conducted under federal authorizations for marine mammal research under National Marine Fisheries Service permits 87-1743, 14636, and 19108.

Body Composition

We measured the body composition of each seal during instrument deployment and recovery following established methods (Le Boeuf et al., 2000; Simmons et al., 2010; Robinson et al., 2012). Girth and length measurements were taken at eight locations along the length of the seal's body. Blubber thickness was measured using a handheld ultrasound and/or a backfat meter at 12 to 18 locations along the body (2-3 per girth measurement, excluding the head and tail). For female seals, we measured mass with a Dyna-Link digital scale (1,000 +/- 1 kg) attached to a tripod. For male seals, mass was estimated from the combination of lengths, girths, and ultrasound measurements; this method has been validated by Crocker et al. (2012). Mass was corrected for the amount of time each seal spent on shore prior to departure and arrival to and from the breeding colony. For female seals, mass change on shore was estimated using an equation derived from serial mass measurements of fasting seals: mass change (kg d^{-1}) = 0.51 + 0.0076*mass, n=27, r^2= 0.79, $p<0.01$ (Simmons et al. 2010). For female seals arriving after the post-molt trip, the recovery procedure always occurred after parturition, and the pup's mass, which was measured at instrument recovery, was added to the female's mass. For male seals, mass change on shore was estimated using an assumed metabolic rate of 2*Kleiber during the molt (Kleiber, 1975; Worthy et al., 1992) and 3.1*Kleiber during the breeding season (Kleiber, 1975; Crocker et al., 2012) and fat and protein contributions to metabolism from Crocker et al. (2012). Energy gain was estimated assuming the adipose tissue was 90% lipid, lean tissue was 27% protein, with a gross energy content of 37.33 kJ g^{-1} for lipids and 23.5 kJ g^{-1} for protein (Crocker et al., 2001). These estimates of body composition have been validated against those from the dilution of isotopically-labeled water (Webb et al., 1998). In this dataset, 145 seals had body composition data (18 males, 127 females).

Data Processing

We followed standard protocols for processing the satellite transmitter and TDR data (Robinson et al. 2010, 2012). We truncated the raw ARGOS and GPS tracks to the exact departure and arrival times from the breeding colony according to the TDR record. A speed, distance, and angle filter was used to remove unlikely position estimates in R v. 3.3.3 (argosfilter package; R Core Team, 2017). Tracks were then smoothed using a state-space model, yielding hourly estimates of position (crawl package). For female seals that were tracked in multiple years, we randomly removed repeat tracks so that each individual was only included in the analysis once. Dives were classified into one of four dive types using a hierarchical classification analysis based on dive characteristics (e.g., depth, shape, duration; Le Boeuf et al., 1988; Robinson et al., 2010, 2012): pelagic foraging dives (active bottom), benthic foraging dives (flat bottom), drift dives (food processing/ rest), or transit (v-shaped) dives. Because female seals exhibit diel diving patterns, we assigned each dive to day or night using the solar zenith angle associated with each dive. In this dataset, 151 seals had complete tracking data (30 males, 121 females), and 130 seals had complete dive records (14 males, 116 females).

Foraging Variables

We compared northern elephant seal foraging strategies using quantitative and qualitative metrics describing foraging success, spatial patterns, and dive behavior. For each complete track, we analyzed 6 movement variables. For each foraging location, we calculated the distance to the continental shelf (km), measured as the straight-line distance from each foraging location to the continental shelf. We determined the proportion of time spent feeding on the at-sea trip relative to total trip duration. The foraging region (km^2) was calculated for each seal and defined as the area of the 95% contour determined from the utilization distribution. Utilization distributions were generated from kernel density analyses on the two-dimensional foraging locations (latitude and longitude) for each track using a 2km cell size and default bandwidth in ArcGIS 10.3.1. Each track was assigned to a mesopelagic ecoregion (‘feeding ecoregion’; Sutton et al., 2017) based on where the majority (≥50%) of foraging locations occurred. Each track was also assigned to a habitat type following criteria modified from Hakoyama et al. (1994) and Simmons et al. (2007); tracks were categorized as continental shelf (on or near the continental shelf; formerly referred to as ‘coastal’) habitat, continental shelf-oceanic (formerly referred to as ‘coastal-oceanic’) habitat, or oceanic habitat. Lastly, each track was categorized as ‘focused’ or ‘throughout’ based on the foraging points in relation to the furthest point from the breeding colony. ‘Focused’ trips occurred where feeding occurred at the furthest part of the track from the breeding colony and <5 foraging locations were identified in other portions of the track. Trips were classified as ‘throughout’ when >5 foraging locations occurring outside the farthest point from the colony (Visscher and Seeley, 1982; Gilmour et al., 2018).

For each dive record, we analyzed 26 dive metrics to examine sex-specific differences in dive behavior. First, we determined the proportion of the dive record in which seals used each of the following dive types: transit, pelagic foraging, drift, and benthic foraging. For the two dive types indicative of foraging (i.e., benthic foraging and pelagic foraging dives), we calculated several additional dive metrics, and each of these metrics was calculated separately for day and night to account for diel patterns in dive behavior. We determined the mean maximum depth (m). We also calculated the mean bottom time (s), measured as the amount of time spent at the bottom of a dive (i.e., not in ascent or descent), and the post-dive surface interval (s), which was the amount of time the seal spent at the water's surface after a dive. In addition to these standard dive metrics that have been used in previous studies comparing male and female dive behavior (Stewart et al., 1995; Le Boeuf et al., 1993; Le Boeuf et al., 2000), we included some additional dive metrics. The additional metrics were the mean number of vertical excursions ('wiggles'; Le Boeuf et al., 1988, 1993) at the bottom of each type of foraging dive and the mean dive efficiency (bottom time/dive duration), where values closer to 0 indicate lower dive efficiency and values closer to 1 indicate higher dive efficiency.

Eight foraging success metrics were determined from the body composition data collected during instrument deployment and recovery. We measured the seal's body mass at departure (kg) and determined the seal's total mass gain over the foraging trip (kg). We calculated the proportion of mass gain on the foraging trip by dividing the total mass gain by the seal's body mass at departure. We also determined the seal's rate of mass gain over the entire trip (kg d^{-1}). These foraging success variables provided direct comparisons to previous work (Le Boeuf et al., 2000). We also included additional metrics for comparing sex-specific differences in foraging success. We measured the rate of mass gain relative to time spent feeding (kg d^{-1}), where time spent feeding was determined from transit speed and dive behavior (Robinson et al., 2010). Based on the rates of mass gain and body composition, we calculated the seal's total energy gain on trip (MJ), the rate of energy gain over trip (MJ d^{-1}), and the rate of energy gain relative to time spent feeding (MJ d^{-1}).

Survival Analyses

We compared the movement patterns of satellite tagged male and female seals that were presumed to die at sea. For each seal that stopped transmitting and was not subsequently recovered at the breeding colony, we determined whether the seal was seen alive in subsequent years using historical records from 2006 to present from Año Nuevo. We also examined the quality of the satellite positions sent by the satellite tag across the duration of the trip to determine whether the tag may have malfunctioned at the time of last transmission, which would be evident by a degraded location quality signal over time, or whether the tag was functioning properly, represented by a random distribution of location qualities throughout the trip. If a tag stopped transmitting, the tag was functioning at the time of last transmission, and the tagged seal was never seen alive again, the seal was presumed dead and included in subsequent analyses. For each seal that died, we determined the following metrics for the last known location: latitude and longitude, transit rate (m s^{-1}), distance to the continental shelf (km), ecoregion (Sutton et al., 2017), and portion of the trip (outward, farthest point, or return).

Statistical Analyses

Principal components analysis (PCA) was used to examine the primary axes of variation in feeding behavior between male and female northern elephant seals and to reduce the dimensionality of the dataset. We conducted PCA on all 37 quantitative foraging variables (FactoMineR package: Le et al., 2008; missMDA package: Josse and Husson, 2016). Seals with missing values were excluded from the analysis, resulting in a final dataset comprised of 32 male and 130 female seals. Because the foraging variables varied in magnitude, variables were centered and scaled prior to PCA. A scree plot was used to examine natural breaking points in the variance, and principal components (PCs) with eigenvalues ≥1.0 and that explained ≥10.0% of the variation were retained for further analysis. A coefficient correlation analysis was used to assess the positive or negative contribution of each variable to each PC axis. Four PCs explained 72.4% of the total variation, and all of the feeding variables were significantly correlated with one or more PC axes based on the correlation coefficient matrix (Table S1).

To examine feeding strategies in northern elephant seals, PCs 1-4 were used in a hierarchical clustering analysis (HCA), which is a method for determining naturally occurring clusters in a dataset. We created a dissimilarity matrix based on Euclidean distances and performed an agglomerative HCA using 'hclust' and the Ward's linking method on the retained PC scores (cluster and factoextra packages). We used the elbow and average silhouette methods to determine the optimal number of clusters, and each seal was assigned to a specific cluster.

To determine the feeding variables that best discriminated among the clusters from the HCA, we ran linear models for each variable with cluster as the predictor variable. An analysis of variance (ANOVA) was used to determine significant differences among clusters ('car' package). We then used least-square means to perform Tukey post-hoc pairwise contrasts between each cluster (lsmeans package: Lenth, 2016). We examined residual plots of all feeding variables for obvious deviations from normality or homoscedasticity using histograms and Q-Q plots. When deviations from normality were observed, we used log and square root transformations so that all variables approached a normal distribution. To examine variability in feeding behavior between the clusters we calculated the coefficient of variation (CV=standard deviation/mean) for each feeding variable and a mean for each cluster. A low CV (values close to 0) indicates stereotypy, or consistency in a given trait, while a high CV (values close to 1) indicates variability in a given trait (Gerhardt, 1991, Wainwright et al., 2008).

We examined overlap between male and female two-dimensional (2D) and three-dimensional (3D) foraging ranges and core foraging areas by comparing utilization distributions (UDs) between males and females. We used kernel density estimation to determine the 95% and 50% utilization distributions for male and female seals, which represented foraging range (km^2) and core foraging areas (km^2), respectively. Maximum dive depth was determined for each 2D foraging location (latitude and longitude) to create the 3D dataset. We only included locations and dives associated with foraging to examine overlap in foraging space. A data-based 'plug-in' bandwidth selector (Hpi) was calculated for each dataset, and 2D and 3D kernel density utilization distributions (2D-UDs and 3D-UDs) were calculated for male and female seals (ks package; see Simpfendorfer et al., 2012 and Cooper et al., 2014 for details). We calculated the proportion of overlap in area (km^2, 2D-UD) and volume (km^3, 3D-UD) between male and female seals and calculated the Utilization Distribution Overlap Index (UDOI), which provided a measure of space-sharing use where values close to 0 represented no overlap and 1 indicated complete overlap (Fieberg and Kochanny, 2005; Cooper et al., 2014).

To examine differences in the movement patterns between male and female northern elephant seals that presumably died at sea, we used Welch Two Sample t-tests to compare all metrics. All statistical analyses were conducted in R v. 3.3.3 (R Core Team, 2017).

RESULTS

Male seals had similar trip durations for both the post-breeding and post-molt trips (post breeding: 124.25 ± 21.12 days, post-molt: 127.73 ± 15.21 days), while female seals had a short post-breeding foraging trip (76.05 ± 12.51 days) and a long post-molt foraging trip (220.00 ± 19.96 days). The percentage of time spent feeding across both trips was broadly similar between males (58%) and females (53%).

Foraging Strategies

We found support for three distinct foraging strategy clusters (e.g., post-breeding females, post-molt females, and males) as determined from multivariate analyses of their movement patterns, dive behavior, and foraging success (Table 1, Fig. 1-2). The two female foraging strategies were more similar to each other than to the male strategy.

The first foraging cluster was the largest (n=94) and comprised of female seals, most (87%) of which were tracked on the post-breeding trip (hereafter, 'post-breeding females'; Table 1, Fig. 1A, 2). In terms of feeding ecoregions (Sutton et al., 2017), post-breeding females primarily fed in the Subarctic Pacific ecoregion (46%) and North Central Pacific (29%). Most post-breeding females foraged far from the continental shelf in oceanic habitats (76%). Seals in this cluster had intermediate-sized foraging areas that were larger than those of males but smaller than those of post-molt females. Post-breeding females undertook both focused foraging trips (57%), as well as foraging throughout the trip (43%). When diving, post-breeding female seals showed diurnal dive behavior. The only dive metrics that did not differ with time of day were the number of vertical excursions at the bottom of benthic foraging dives, dive efficiency, and pelagic foraging post-dive surface interval. Post-breeding females primarily undertook deep pelagic foraging dives (54% of all dives). Eight pelagic foraging dive variables significantly differed from the other clusters. Pelagic foraging dives of post-breeding female seals had the shortest timing variables, including nighttime dive duration (t-ratio=-7.53, $p<0.01$), daytime and nighttime bottom time (day: t-ratio=-5.37, $p<0.01$; night: t-ratio: -9.23, $p<0.01$), and post-dive surface interval (t-ratio=-4.25, $p<0.01$), compared to post-molt females and male seals. Additionally, pelagic foraging dives of post-breeding females had the fewest number of vertical excursions at the bottom of dives during the day (t-ratio=-2.34, $p<0.05$) and at night (t-ratio=-6.92, $p<0.01$) and the lowest dive efficiencies during the day (t-ratio=-2.35, $p<0.05$) and at night (t-ratio=-6.03, $p<0.01$) compared to the other clusters. In contrast to pelagic foraging dives, benthic foraging dives were used infrequently (4% of all dives). Two benthic foraging dives variables significantly differed from the other clusters. Benthic foraging dives of post-breeding females had the shallowest nighttime depths (t-ratio=-6.67, p<0.01) and the shortest post-dive intervals during the day (t-ratio=-5.37, p<0.01) compared to post-molt females and male seals. Post-breeding female seals had low foraging success. Post-breeding females had intermediate body masses at departure (t-ratio=2.31, p<0.05) but had the smallest mass gain (t-ratio=-8.36, p<0.01) and energy gain (t-ratio=-8.51, p<0.01) compared to post-molt females and males.

The second foraging cluster was also comprised of female seals (n=34), and most (88%) were tracked during the post-molt trip (hereafter, 'post-molt females'; Table 1, Fig. 1B, 2). Most post-molt females fed in multiple ecoregions (58%) and the Subarctic Pacific ecoregion (23%). Post-molt females typically fed far from the continental shelf in oceanic habitats (65%), although some fed in continental shelf-oceanic (29%) and continental shelf (6%) ecosystems. Post-molt females had large foraging areas, the largest of all clusters (t-ratio=-4.77, p<0.01). Post-molt female seals primarily foraged throughout the trip (87%). Post-molt female seals exhibited diurnal dive behavior, similar to post-breeding females. The only dive variables that did not significantly differ with time of day were benthic dive efficiency and the post-dive surface interval for pelagic and benthic foraging dives. Post-molt females undertook deep pelagic foraging dives (53% of all dives). Four pelagic foraging dive variables significantly differed from the other clusters. Post-molt females had the longest daytime dive durations (t-ratio=-4.96, p<0.01) compared to post-breeding females and male seals. Additionally, the pelagic foraging dives had intermediate post-dive surface intervals (t-ratio=-4.25, p<0.01), numbers of vertical excursions at the bottom of dives at night (t-ratio=-6.92, p<0.01), and daytime dive efficiency (t-ratio=-2.35, p<0.05). In comparison to pelagic foraging dives, benthic foraging dives were infrequent (7% of all dives). Six benthic foraging dive variables differed between post-molt females and the other clusters. Benthic foraging dives of post-molt females had the deepest depths during the day (t-ratio=-8.95, p<0.01) and at night (t-ratio=-6.67, p<0.01), the longest dive durations during the day (t-ratio=-10.76, p<0.01) and at night (t-ratio=-11.00, p<0.01), and the longest bottom times during the day (t-ratio=-6.61, p<0.01) and at night (t-ratio=-5.37, p<0.01). Post-molt females had intermediate foraging success compared to the other clusters. Post-molt females had smaller body masses at departure (t-ratio=-34.04, p<0.01) compared to post-breeding females and male seals. However, post-molt females had significantly higher mass gain (t-ratio=-8.36, p<0.01) and energy gain (t-ratio=-8.51, p<0.01) compared to post-breeding female seals. Post-molt females had the highest proportion of mass gain on the foraging trip (t-ratio=-9.15, p<0.01) compared to post-breeding females and males.

The third cluster was made up of male seals (n=32; hereafter, ‘males’; Table 1, Fig. 1C, 2). Most males fed in the Subarctic Pacific ecoregion (84%). Males fed significantly closer to the continental shelf than female seals (t-ratio=10.74, p<0.01). Most males traveled to continental shelf ecosystems (93% of males) and took focused foraging trips (73%). Male seals did not have diurnal dive behavior, which differed from female seals. The only dive variable that differed by time of day was the amount of time spent at the bottom of benthic dives. Males primarily used benthic foraging dives (40% of all dives). Benthic dive behavior of males was largely concordant with the other clusters, although males foraged at an intermediate depth at night (t-ratio=2.78, p<0.02). Pelagic foraging dives were used less frequently (15%). Five pelagic foraging dive variables differed between males and the other clusters. Males traveled to shallower depths during the day (t-ratio=12.03, p<0.01) and at night (t-ratio=11.41, p<0.01) compared to post-breeding and post-molt females. Additionally, the pelagic foraging dives of males had the longest post-dive intervals (t-ratio=-3.50, p<0.01), the highest number of vertical excursions at the bottom of nighttime dives (t-ratio=-2.81, p<0.02), and the highest daytime dive efficiency (t-ratio=-3.56, p<0.01) compared to the other clusters. Male seals had high foraging success, especially compared to the other clusters. Males had the largest body masses at departure (t-ratio=-38.46, p<0.01) compared to post-breeding and post-molt females. Males had the highest mass gain (t-ratio=-3.48, p<0.01) and energy gain (t-ratio=-4.16, p<0.01) compared to the other clusters. Additionally, males had higher rates of mass gain (t-ratio=-12.05, p<0.01) and rates of energy gain (t-ratio=-8.09, p<0.01) across the trip and relative to time spent feeding compared to post-breeding and post-molt females.

Variability in Feeding Behavior

We compared variability in feeding metrics among the three clusters and found that male seals had the highest average variability compared to the two female clusters (Table 2). Among females, the post-molt females were the most stereotyped, while the post-breeding females were the most variable. On average, the movement metrics were the most variable for all clusters, specifically foraging area and distance to the continental shelf. The most stereotyped movement metrics were feeding transit rate for the post-breeding and post-molt females and proportion of time spent feeding for the males. On average, the dive behavior variables were the most stereotyped for all clusters. The most stereotyped dive metrics were foraging dive efficiency for post-breeding females and male seals, and foraging dive maximum depth for post-breeding and post-molt females. The most variable dive metric was benthic foraging dive post-dive surface intervals at night for male seals and proportion of benthic diving for post-breeding and post-molt female seals. The foraging success metrics showed intermediate variability compared to the movement and dive metrics. The most stereotyped foraging success metric was body mass at departure for all three clusters, and the most variable metrics were the proportion of mass gain on the trip for post-breeding females, energy gain relative to feeding time for post-molt females, and mass gain relative to feeding time for post-molt females and males.

2D and 3D Foraging Overlap

Male seals had smaller 2D foraging ranges and core foraging areas compared to female seals (Table 3). Males and females had a small amount of overlap in their

2D foraging ranges (95% UDOI=0.002) but had no overlap in core foraging areas (50% UDOI=0.00). Males had smaller 3D foraging ranges but larger core foraging areas compared to females (Fig. 3). Male and female seals overlapped more in their 3D foraging ranges and core foraging areas (95% UDOI=0.04, 50% UDOI=0.05).

Survival Comparison

Of the 191 seals in this study (59 males, 132 females), 38 seals (16 males, 22 females) stopped transmitting while on their at-sea foraging trips. Males had a lower survival rate (mean: 56.41% survival, range: 0-75%) than females (mean: 87.29% survival, range: 68.42-100%), and this pattern was consistent across all years and seasons of the study. Males stopped transmitting most frequently at the farthest point of their trip from the breeding colony (43.75% of males) and on the outward portion of the trip (37.50%; Fig. 4A). Female seals stopped transmitting most frequently at the farthest point of the trip from the breeding colony (40.91% of females) and on the return portion of the trip (36.36%). Male seals most often went offline in the Subarctic Pacific ecoregion (68.75% of males), followed by the California Current (31.25%). Female seals most often went offline in the Subarctic Pacific (45.45% of females), followed by the California Current (31.82%) and the North Central Pacific (22.73%).

More than half of the male seals that died (66.67% of males) stopped transmitting while on (<5 km) or near (<30 km) the continental shelf, and the rest of the males (26.67%) stopped transmitting in the open ocean (>45 km from the continental shelf; Fig. 4A). Additionally, male seals were significantly closer to the continental shelf (67.19 ± 120.13 km) than female seals (469.98 ± 328.88 km, $p<0.01$; Fig. 4B) at their last known location. In contrast, none of the female seals that died were on (<5 km) the continental shelf and only a few (9.09% of females) were near (<30 km) the continental shelf. The majority of females that died were in the open ocean (90.91%). Male and female seals did not differ in their transit speed at their last known location (males: 1.73 ± 1.77 m s^{-1}, females: 2.53 ± 1.64 m s^{-1}).

DISCUSSION

Northern elephant seals exhibit sex-specific foraging strategies on their foraging trips. We identified a male foraging strategy and two female foraging strategies, all of which are characterized by distinct spatial patterns and dive behavior. Contrary to expectations, northern elephant seal foraging strategies are not associated with particular habitats; rather, male and post-breeding and post-molt female seals use different strategies even when feeding in similar areas. Foraging success differs between the male and female strategies, and this appears to result in a trade-off between foraging success and survival. The male foraging strategy has higher foraging success but lower survivorship (56% survival) compared to the female foraging strategies. These sex-specific foraging strategies and associated trade-offs are likely related to the different life history strategies employed by male and female northern elephant seals.

Sex-Specific Foraging Strategies

Male and female northern elephant seals traveled throughout the North Pacific Ocean on their biannual foraging trips, feeding in different marine ecosystems. Male seals fed on the continental shelf along the western coast of North America, from Oregon to the Aleutian Islands. Most male seals traveled to the Subarctic Pacific ecoregion. Upon leaving the breeding colony, male seals rarely, if ever, slowed down to feed until they reach the continental shelf at the farthest point of their trip from the breeding colony. Upon reaching the continental shelf, male seals spent their time in small core foraging areas. In these areas, male seals undertook repeated relatively shallow benthic foraging dives to target prey on or near the seafloor, and, unlike female seals, their dive behavior did not follow a diel pattern. Male seals showed little variation among individuals in their foraging behavior, and, to our knowledge, all adult male northern elephant seals that have ever been tracked exhibited these same patterns (Stewart et al., 1995; Le Boeuf et al., 2000; Simmons et al., 2007). Our quantitative analyses show that male seals exhibit strong fidelity to continental shelf ecosystems. Additionally, male seals are consistent and stereotyped in their foraging behavior between seasons and years.

In comparison to male seals, most female northern elephant seals fed in deep mesopelagic ecosystems far from the continental shelf. There was also a subset of female seals (6%) that fed on or near the continental shelf, similar to male seals. Female seals fed in multiple ecoregions in the North Pacific, including the Subarctic Pacific, North Central Pacific, and California Current. Some female seals had large core foraging areas with multiple core foraging areas spread along their track; other female seals undertook focused foraging trips, feeding in one area for the duration of the trip. Regardless of location, female seals primarily used deep pelagic foraging dives to target mesopelagic prey, and their dive behavior showed a strong diel pattern, with changes in behavior, depth, and duration depending on the time of day. Our results confirm and expand upon previous descriptions of female northern elephant seal foraging behavior (Stewart et al., 1995; Le Boeuf et al., 2000; Simmons et al., 2007; Robinson et al., 2012). Additionally, our results show that female seals exhibit behavioral flexibility in their foraging behavior, which differs from the more stereotyped foraging behavior of male seals.

Within this general female foraging strategy, we identified two strategies that are associated with different at-sea foraging trips. Female seals use different foraging strategies on the post-breeding trip and the post-molt trip. The post-breeding female foraging strategy was characterized by small foraging areas. Additionally, female seals on the post-breeding trip took short foraging dives that had low numbers of vertical excursions and low dive efficiency. In comparison, the post-molt female foraging strategy was characterized by large foraging areas. Female seals on the post-molt trip also had long foraging dives with high numbers of vertical excursions and high dive efficiency. These different patterns are likely associated with targeting different prey resources, as the diet of female northern elephant seals varies seasonally (Goetsch et al., 2018).

Foraging success differs between the three northern elephant seal foraging strategies. The male strategy resulted in higher foraging success than both female strategies. Male seals put on more mass and gained more energy and had higher rates of mass and energy gain than female seals. In fact, male seals putting on nearly four and half times as much mass as post-breeding female seals and twice as much mass as post-molt female seals. It is unclear what makes the male foraging strategy more successful than the female foraging strategies, although it is likely related to diet. The diet of male seals is not well known, but previous studies of stomach content have indicated that male seals consume a variety of benthic prey found along the continental shelf, including sharks, rays, hagfish, and benthic cephalopods, and fishes (Antonelis et al., 1987, 1994). In contrast, female seals primarily consume mesopelagic fish and squid (Naito et al., 2013; Goetsch et al., 2018). We hypothesize that in addition to consuming different prey species, the prey targeted by male and female seals differ in other characteristics, including energy composition, abundance, and/or ease of capture, although this needs to be investigated. Regardless, benthic foraging in continental shelf ecosystems appears to provide better foraging opportunities for northern elephant seals than mesopelagic ecosystems. Benthic continental shelf habitats may be more stable and homogenous environments with easily accessible prey compared to mesopelagic ecosystems, which are often dynamic and contain patchily distributed prey (McConnell et al., 1992; Le Boeuf et al., 2000; Sims et al., 2006; Simmons et al., 2007; Humphries et al., 2010).

While female northern elephant seals had lower foraging success compared to male seals, female seals are still successful foragers. Most female seals significantly increased their body mass over the foraging trip relative to their departure mass, which is indicative of a successful foraging trip. Foraging success also differed between the post-breeding and post-molt female strategies. The post-molt foraging strategy resulted in higher foraging success compared to the post-breeding strategy. Post-molt female seals increased their body mass by an average of 80% compared to their departure mass, while post-breeding female seals only showed a 32% increase in body mass over the trip. The differential foraging success between the two female strategies may be explained by several potentially interacting factors. First, female seals on the post-molt trip spent more time feeding because the post-molt trip (May-January) is nearly three times as long as the post-breeding trip (February-May), so the increased foraging success may be the result of the increased trip duration. Second, female seal diets change seasonally, so the two female foraging strategies may be related to differences in prey resources and/or oceanographic conditions during the different times of year (Goetsch et al., 2018). Additionally, female seals are in gestation during the post-molt trip and may have additional energetic demands and diving physiological constraints due to the developing fetus that affect feeding behavior (Huckstadt et al., 2018). The rate of energy gain on the post-molt foraging trip is correlated with natality in female seals, such that foraging success directly affects reproductive success (Robinson et al., 2012).

Overlap in Foraging Strategies

Contrary to expectations, male and female northern elephant seals showed no overlap in foraging strategies. We hypothesized that northern elephant seal foraging strategies were associated with particular habitats based on previous studies that showed some female seals traveling to continental shelf habitats and using more benthic foraging diving in those habitats (Simmons et al., 2007; Robinson et al., 2012). Similar to previous studies, a subset of female seals (6% of satellite tracked female seals) in this study traveled on or near the continental shelf when feeding. However, these female seals rarely, if ever, foraged on the continental shelf and did not show greater proportions of benthic diving. Instead, these female seals primarily fed in pelagic waters immediately adjacent to the continental shelf using deep pelagic foraging dives. Additionally, the female seals that traveled on or near the continental shelf did not have higher foraging success compared to other female seals. Northern elephant seal foraging strategies are therefore sex-specific and not associated with particular habitats. This differs from recent studies that have found strong convergence in the movement patterns of marine animals foraging in similar habitats. Across more than 50 vertebrate taxa, individuals within a species typically foraged in the same habitat (e.g., coastal or open ocean), and each habitat was associated with distinct animal movement patterns (Humphries et al., 2010; Sequeira et al., 2018). In contrast, northern elephant seals show sexual segregation in foraging habitats, with males foraging in coastal areas and females foraging in the open ocean. Additionally, even when female seals traveled to similar areas as male seals, there was no overlap in foraging strategies. These results suggest that the sex-specific differences in morphology, behavior, and life history appear to play a stronger role than habitat in shaping northern elephant seal foraging behavior.

Trade-Offs Between Foraging Strategies

Male and female northern elephant seal foraging strategies result in a trade-off between foraging success and survival. Although the male strategy resulted in higher foraging success compared to the female strategies, it was also riskier. Nearly half of the male seals in the study (44%) presumably died on the foraging trip compared to only 13% of female seals. Demographic studies of northern elephant seals have shown that males have higher mortality across all age classes and a shorter lifespan than female seals (Le Boeuf et al., 1974, Condit et al., 2014). We documented a higher mortality rate among adult male seals than previously estimated (32% mortality, Condit et al., 2014). However, female mortality was nearly identical between studies (14% mortality, Condit et al., 2014).

It has been hypothesized that one of the causes of higher mortality in male northern elephant seals is predation by their two known predators, white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*; Le Boeuf et al., 1982, 2000). The amount of predation of northern elephant seals is currently unknown. However, fresh wounds and scars from white shark attacks are frequently observed on northern elephant seals hauled out at the breeding colonies (Le Boeuf et al., 1982; Le Boeuf and Crocker, 1996). There have also been an increase in the numbers of white sharks in continental shelf habitats, especially those surrounding breeding colonies, coinciding with times when northern elephant seals are present in large numbers at the colonies (Ainley et al., 1981; Klimley et al., 1992). Although we cannot provide evidence for a specific cause of mortality in this study, we documented that, in addition to dying more frequently, male seals were disproportionately closer to the continental shelf when they died compared to female seals. Two-thirds of male seals that died were on or near the continental shelf at their last known location, compared to less than 10% of the female seals. Interestingly, the female seals that exhibited ‘male-like’ movement patterns (i.e., traveled to on or near the continental shelf) also went offline near the continental shelf. The majority of all seals (male seals: 100%, female seals: 77%) went offline in the two ecoregions that bordered the continental shelf (e.g., Subarctic Pacific, California Current). Both killer whales and white sharks are known to hunt in coastal habitats (Le Boeuf et al. 1982; Klimley, 1994; Klimley and Ainley, 1996; Ford et al., 1998; Le Boeuf et al., 2000; Dahlheim and White, 2010). Although observational data are rare, northern elephant seal remains have occasionally been found in the stomach of marine mammal eating transient killer whales, and these remains are most often from adult male seals (Jefferson et al., 1991; Baird and Dill, 1995, 1996; Ford et al., 1998). Similarly, white sharks have been documented preying upon northern elephant seals, including male seals (Le Boeuf et al., 1982; Klimley, 1994; Klimley and Ainley, 1996), and male seals often have more white shark bites than female seals (Le Boeuf and Crocker, 1996). Our results suggest that predation may be a substantial cause of mortality in male northern elephant seals, although this requires further investigation. We also cannot rule out the possibility that animals die in areas where they spent the most time, so male seals are most likely to die in continental shelf habitats because this is where they spend their time feeding. However, we would predict that if a male seal were going to die from age, exhaustion, or poor body condition, this would occur during the long transit and fasting phase of the trip, especially when seals depart from the breeding colony after fasting for one to three months. This pattern was not observed in the majority (75%) of male seals that presumably died.

The sex-specific foraging strategies used by northern elephant seals are likely related to their different life history strategies, which evolved to maximize fitness. Female seals typically have high annual survivorship, reach sexual maturity quickly, and reproduce annually until their death (Reiter et al., 1981; Condit et al., 2014). Female seals maximize their lifetime fitness by starting to reproduce early and having a long lifespan in which to reproduce and rear offspring (Reiter et al., 1981). Pelagic habitats appear to provide adequate prey resources for female seals to meet their energetic needs, while also providing relatively safety from predators. In contrast, male seals typically have low survivorship, reach sexual and physical maturity later in life, and only a fraction of male seals that reach physical and sexual maturity successfully reproduce; additionally, male seals that are successful at breeding only survive one to two years after their peak (Le Boeuf, 1974; Reiter et al., 1981; Condit et al., 2014). Male seals maximize fitness by surviving to maturity, attaining large body sizes quickly to be competitive in physical combats, and successfully mating in the 1-2 years any given adult male has access to breeding opportunities (Le Boeuf, 1974). Even as pups, male seals are typically larger than female seals, and male seals have fast growth rates, suggesting that attaining body size quickly is more important for male seals (Reiter, 1978; Clinton, 1994). Continental shelf ecosystems provide the resources that male seals need to maintain and sustain their large body sizes, even though feeding in these areas result in higher mortality.

These sex-specific trade-offs between foraging success and survival in northern elephant seals align with broad-scale patterns seen in other sexually dimorphic and/or polygynous vertebrates. From coho salmon to lynx, many sexually dimorphic species show trade-offs between foraging behavior and mortality, where the larger sex often exhibits more risk-taking behavior that results in greater foraging success but increased mortality compared to the smaller sex (Spidle et al., 1998; Mooring et al., 2003; Bunnefeld et al., 2005; Issac, 2005). Similarly, among polygynous vertebrates, adult males often have higher mortality rates than adult females (Clutton-Brock and Isvaran, 2007). The higher mortality of adult males is often attributed to decreased selection for longevity, poorer body conditions related to intraspecific competition, and/or cumulative phenotypic damage (Clutton-Brock and Isvaran, 2007).

Sexual Dimorphism and Intraspecific Niche Divergence

Northern elephant seals are one of the most sexually dimorphic species on the planet (Bartholomew, 1970; Ralls, 1977), and the differences in morphology and life history strategies are reflected in their sex-specific foraging strategies. Male seals are benthic continental shelf foragers, while females are primarily pelagic foragers. Because male and female northern elephant seal foraging strategies are so distinct, the sexes essentially function as different ecological species, occupying different ecological niches in the North Pacific Ocean. These sex-specific foraging strategies also mean that there is little to no intraspecific competition for resources between adult male and female northern elephant seals.

Many sexually dimorphic species also exhibit intraspecific niche divergence (Selander, 1966; Hierlihy et al., 2013; Lewis et al., 2006; Breed et al., 2009), with male and females of the same species showing differences in diet (Houston and Shine, 1993; Bearhop et al., 2006; Hierlihy et al., 2013), foraging habitats (Phillips et al., 2004), behavior (Selander, 1966), feeding morphology (Hierlihy et al., 2013), and/or foraging strategies (Gonzalez-Solis et al., 2000). In fact, southern elephant seals (*Mirounga leonina*), the sister taxa to northern elephant seals, have remarkably similar sex-specific foraging strategies to their northern counterparts. When foraging in the Southern Ocean, male southern elephant seals forage on or near the bottom of the continental shelf, while female seals forage in deep, pelagic waters (Hindell et al., 1991a, b; McConnell and Fedak, 1996; Campagna et al., 1999; Lewis et al., 2006). Based on the remarkably similar patterns of intraspecific niche divergence in extant elephant seals, it appears that intraspecific niche divergence evolved early in this pinniped lineage. The origin of sexual dimorphism in elephant seals is likely due to sexual selection, as a function of their capital breeding system that includes terrestrial mating and parturition, polygynous mating, and offshore feeding (Bartholomew, 1970). However, even though sexual selection was presumably responsible for the initial morphological differences between the sexes in elephant seals, the pronounced differences in foraging behavior between males and females likely played an important role in the evolution and continued maintenance of sexual dimorphism in these species.

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TABLES

TABLE 1. Northern elephant seal foraging success, movement, and dive behavior variables (mean ± s.d.) associated with the three foraging strategy clusters determined from hierarchical clustering analysis.

Variable	**Males**	**Females**	
	(n=32)	**Post-breeding (n=94)**	**Post-molt (n=34)**
Distance to continental shelf (km)	**22.17 ± 55.73**	509.72 ± 353.15	569.53 ± 371.59
Proportion of time spent feeding	0.53 ± 0.16	0.58 ± 0.13	0.58 ± 0.08
Foraging area (km^2)	74,911 ± 203,029	171,159 ± 413,562	**334,526 ± 464,054**
Proportion of transit dives	0.35 ± 0.13	0.31 ± 0.10	0.28 ± 0.07
Proportion of foraging dives	**0.15 ± 0.08**	0.54 ± 0.14	0.53 ± 0.13
Proportion of drift dives	0.11 ± 0.04	0.11 ± 0.12	0.13 ± 0.06
Proportion of benthic dives	**0.40 ± 0.20**	0.04 ± 0.03	0.07 ± 0.11
Maximum depth, day foraging dives (m)	**406.51 ± 83.43**	597.17 ± 53.96*	605.11 ± 37.76*
Maximum depth, night foraging dives (m)	**364.60 ± 84.19**	503.45 ± 35.51*	494.18 ± 29.65*
Dive duration, day foraging dives (min)	23.90 ± 3.63	25.18 ± 2.13*	**27.98 ± 2.15***
Dive duration, night foraging dives (min)	22.75 ± 3.52	**20.42 ± 1.62***	23.82 ± 1.80*
Bottom time, day foraging dives (min)	12.50 ± 1.65	**11.22 ± 1.44***	13.13 ± 1.92*
Bottom time, night foraging dives (s)	11.99 ± 1.41	**560.73 ± 70.82***	719.57 ± 81.18*
Post-dive interval, foraging dives (s)	**153.41 ± 17.99**	**120.85 ± 15.22**	**135.51 ± 14.86**
No. vertical excursions at bottom, day foraging dives	19.54 ± 2.33	**17.50 ± 1.95***	18.60 ± 2.26*
No. vertical excursions at bottom, night foraging dives	**19.12 ± 2.22**	**15.00 ± 1.41***	**17.44 ± 1.91***
Efficiency, day foraging dives	**0.47 ± 0.04**	**0.41 ± 0.03**	**0.43 ± 0.04***
Efficiency, night foraging dives	0.47 ± 0.04	**0.42 ± 0.03**	0.46 ± 0.03*

Maximum depth, day benthic dives (m)	241.37 ± 104.52	255.29 ± 113.79*	**477.83 ± 106.40***
Maximum depth, night benthic dives (m)	**219.59 ± 87.35**	**165.08 ± 50.43***	**307.89 ± 182.10***
Dive duration, day benthic dives (min)	20.73 ± 2.95	19.93 ± 4.27*	**30.08 ± 4.62***
Dive duration, night benthic dives (min)	19.92 ± 2.28	18.20 ± 2.77*	**24.75 ± 2.53***
Bottom time, day benthic dives (min)	13.49 ± 1.46*	12.12 ± 2.90*	**16.03 ± 2.20***
Bottom time, night benthic dives (min)	12.06 ± 1.69*	11.14 ± 2.20*	**13.77 ± 2.39***
Post-dive interval, day benthic dives (min)	2.42 ± 0.47	**1.65 ± 0.47***	2.26 ± 0.64
Post-dive interval, night benthic dives (min)	3.43 ± 3.20	4.10 ± 9.70*	2.80 ± 1.07
No. vertical excurisons at bottom, day benthic dives	18.20 ± 2.65	20.99 ± 7.73	19.64 ± 5.50*
No. vertical excursions at bottom, night benthic dives	16.18 ± 3.22	19.07 ± 8.03	15.77 ± 4.04*
Efficiency, benthic dives	17.08 ± 2.98	20.18 ± 7.42	18.05 ± 4.62
Body mass at departure (kg)	**1,060.70 ± 182.47**	**318.27 ± 43.61**	**297.79 ± 48.21**
Mass gain on trip (kg)	**458.38 ± 218.26**	**96.43 ± 59.93**	**227.49 ± 67.30**
Mass gain rate on trip (kg day^{-1})	**3.63 ± 1.61**	0.96 ± 0.27	1.13 ± 0.22
Mass gain rate relative to feeding time (kg day^{-1})	**5.66 ± 4.40**	1.89 ± 0.89	2.03 ± 0.78
Proportion of mass gain on trip	0.44 ± 0.23	0.32 ± 0.25	**0.80 ± 0.26**
Energy gain (MJ)	**8,020 ± 2,085**	**1,638 ± 918**	**3,7949 ± 1,052**
Energy gain rate on trip (MJ day^{-1})	**67.31 ± 23.10**	17.28 ± 6.67	18.93 ± 4.77
Energy gain rate relative to feeding time (MJ day^{-1})	**98.46 ± 66.71**	30.97 ± 13.36	31.37 ± 12.32

Bolded values show significant differences between clusters ($p \leq 0.05$).

Starred values show significant differences between day and night dive variables within a cluster ($p \leq 0.05$).

TABLE 2. Coefficient of variation for each feeding variable associated with each northern elephant seal foraging strategy.

Variable	Males	Post-breeding females	Post-molt females
Distance to continental shelf (km)	2.51	0.69	0.65
Proportion of time spent feeding	0.29	0.22	0.14
Foraging area (km^2)	2.71	2.42	1.39
Proportion of transit dives	0.36	0.33	0.26
Proportion of foraging dives	0.50	0.26	0.24
Proportion of drift dives	0.42	1.12	0.44
Proportion of benthic dives	0.51	0.79	1.54
Maximum depth, day foraging dives (m)	0.21	0.09	0.06
Maximum depth, night foraging dives (m)	0.23	0.07	0.06
Dive duration, day foraging dives (s)	0.15	0.08	0.08
Dive duration, night foraging dives (s)	0.15	0.08	0.08
Bottom time, day foraging dives (s)	0.13	0.13	0.15
Bottom time, night foraging dives (s)	0.12	0.13	0.11
Post-dive interval, foraging dives (s)	0.12	0.13	0.11
No. vertical excursions at bottom, day foraging dives	0.12	0.11	0.12
No. vertical excursions at bottom, night foraging dives	0.12	0.09	0.11
Efficiency, day foraging dives	0.09	0.07	0.09
Efficiency, night foraging dives	0.09	0.07	0.07
Maximum depth, day benthic dives (m)	0.43	0.45	0.22
Maximum depth, night benthic dives (m)	0.40	0.31	0.59
Dive duration, day benthic dives (s)	0.14	0.21	0.15
Dive duration, night benthic dives (s)	0.11	0.15	0.10
Bottom time, day benthic dives (s)	0.11	0.24	0.14
Bottom time, night benthic dives (s)	0.14	0.20	0.17
Post-dive interval, day benthic dives (s)	0.20	0.28	0.28
Post-dive interval, night benthic dives (s)	0.93	0.51	0.38
No. vertical excursions at bottom, day benthic dives	0.15	0.37	0.28
No. vertical excursions at bottom, night benthic dives	0.20	0.42	0.26
Efficiency, benthic dives	0.13	0.14	0.10
Body mass at departure (kg)	0.17	0.14	0.16
Mass gain on trip (kg)	0.48	0.62	0.30

Mass gain rate on trip (kg day^{-1})	0.44	0.28	0.20
Mass gain rate relative to feeding time (kg day^{-1})	0.78	0.47	0.39
Proportion of mass gain on trip	0.52	0.78	0.32
Energy gain (MJ)	0.26	0.56	0.28
Energy gain rate on trip (MJ day^{-1})	0.34	0.39	0.25
Energy gain rate relative to feeding time (MJ day^{-1})	0.68	0.43	0.39
MEAN	**0.42**	**0.37**	**0.29**

TABLE 3. Comparison of the two-dimensional (2D) and three-dimensional (3D) foraging ranges (95% utilization distribution) and core foraging areas (50% utilization distributions) and percentage of overlap of the foraging ranges and core foraging areas between male and female northern elephant seals.

		2D		**3D**	
Sex	**Kernel Density**	**Area (km^2)**	**% Overlap**	**Area (km^3)**	**% Overlap**
Male	95%	188	9.92	51,509	21.6
	50%	42	0	447	3.88
Female	95%	463	4.03	221,876	5.01
	50%	93.3	0	278	6.25

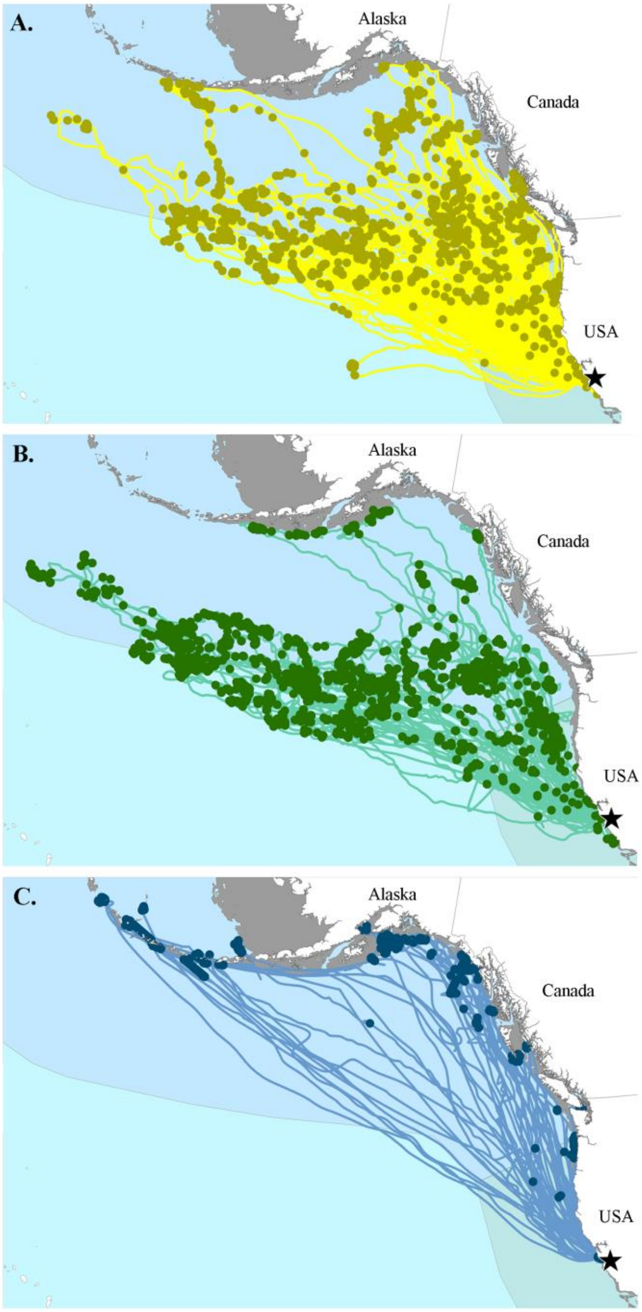

FIGURE 1. Comparison of satellite-tracks from male and two female northern elephant seal foraging strategies as determined from hierarchical clustering analysis of movement, dive, and foraging success variables. A) Post-breeding female seal foraging strategy (n=94), B) Post-molt female seal foraging strategy (n=34), and C) Male seal foraging strategy (n=32). The continental shelf is grey, the California Current is light green, the Subarctic Pacific is light blue, and the North Central Pacific is blue-grey. The Año Nuevo colony is represented by a black star.

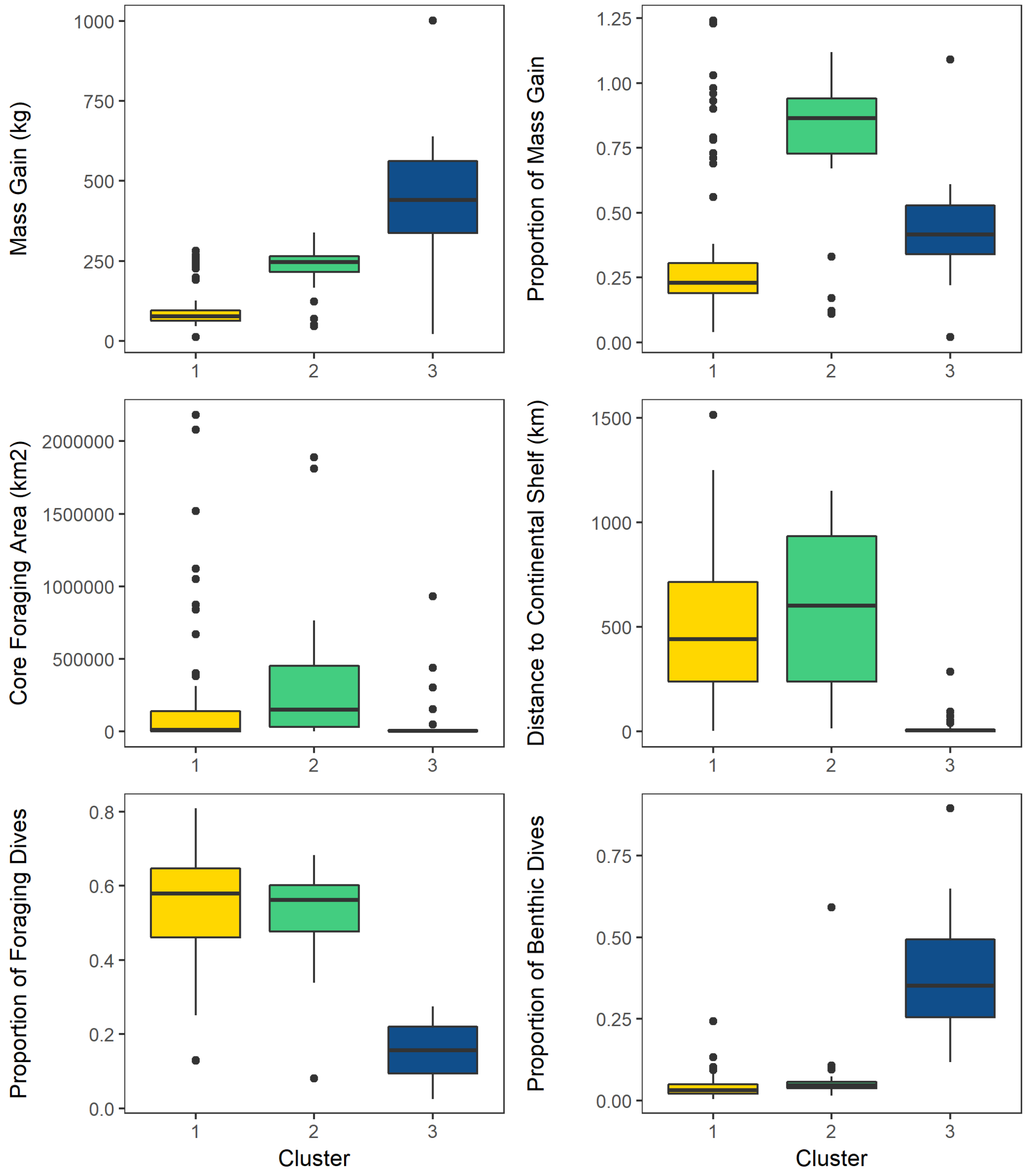

FIGURE 2. Representative boxplots of six feeding variables for the three northern elephant seal foraging strategy clusters. The post-breeding female seal strategy (cluster 1) is shown in yellow, the post-molt female foraging strategy (cluster 2) is shown in green, and the male seal foraging strategy (cluster 3) is shown in blue. Horizontal bars represent the median and vertical bars represent ± SE.

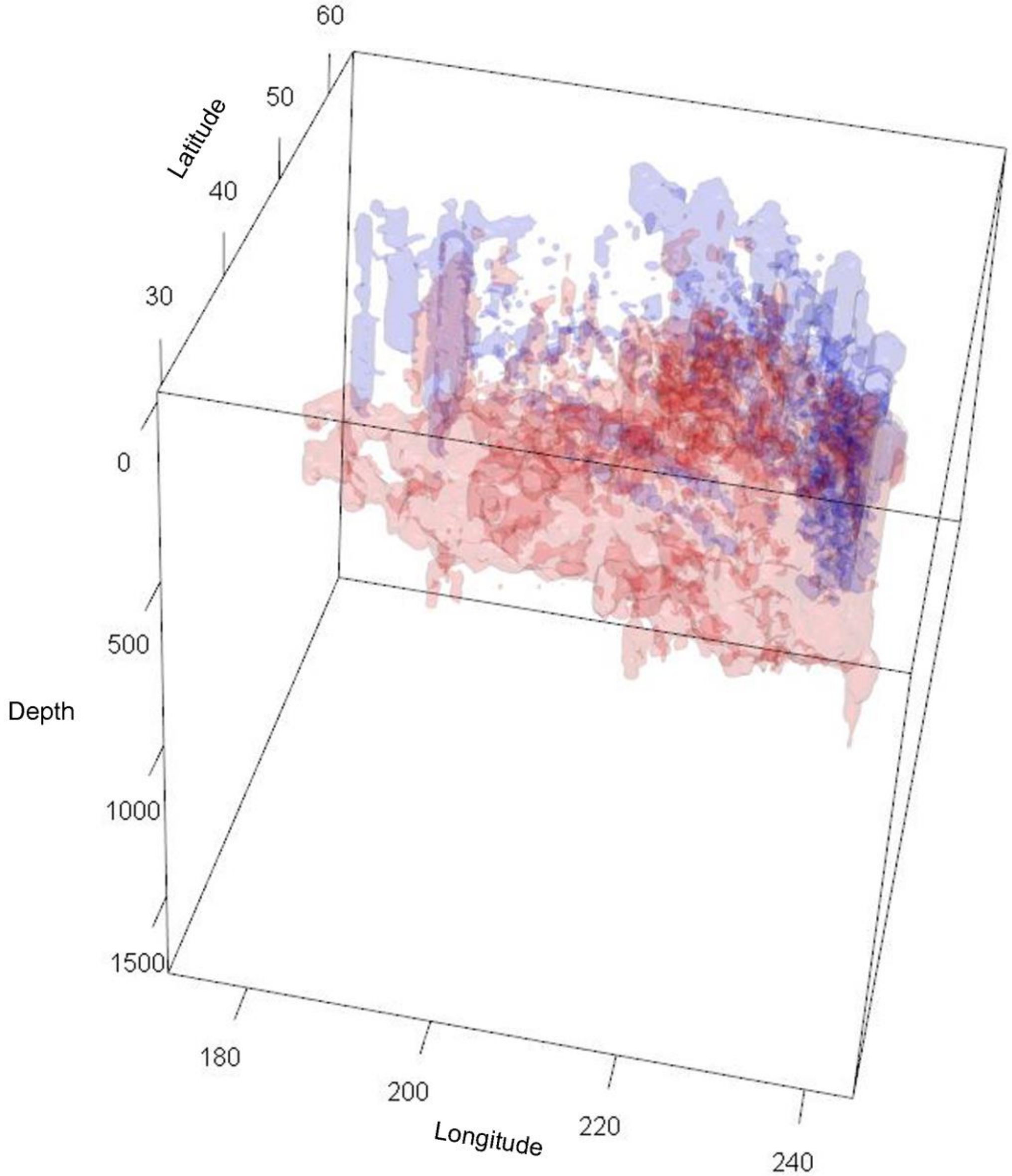

FIGURE 3. Three-dimensional kernel density utilization distribution of male and female northern elephant seal core foraging areas (95% 3D-UDs). Male seals are shown in blue, and female seals are shown in red.

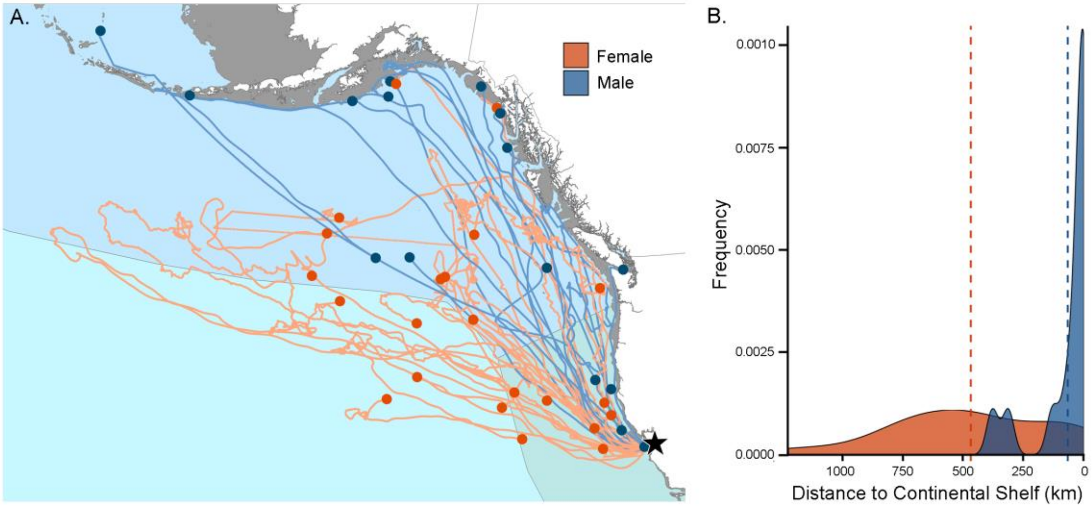

FIGURE 4. Male (n=16) and female (n=22) northern elephant seals that presumably died at sea. (A) Satellite tracks of male and female northern elephant seals that presumably died on the foraging trip. Male seal tracks are shown in navy blue with circles that represent the point of last satellite transmission. Female seal tracks are shown in orange with circles that represent the point of last satellite transmission. (B) Density plot of male and female northern elephant seals that presumably died at sea showing the distance to the continental shelf at their last satellite transmission.

CHAPTER 2

SUPPLEMENTARY INFORMATION

TABLE S1. Principal component loadings for each foraging variable for principal components (PCs) 1-4.

Variable	**PC1 (36%)**	**PC2 (14%)**	**PC3 (11%)**	**PC4 (10%)**
Body mass at departure (kg)	**0.86**	**-0.32**	0.13	-0.10
Mass gain on trip (kg)	**0.91**	**0.17**	**-0.20**	-0.04
Mass gain rate on trip (kg day^{-1})	**0.91**	**-0.16**	-0.03	-0.09
Mass gain rate relative to feeding time (kg day^{-1})	**0.77**	**-0.19**	**-0.17**	**0.32**
Proportion of mass gain on trip	**0.32**	**0.69**	**-0.41**	0.06
Energy gain (MJ)	**0.92**	0.12	**-0.18**	**-0.18**
Energy gain rate on trip (MJ day^{-1})	**0.91**	**-0.23**	0.02	**-0.17**
Energy gain rate relative to feeding time (MJ day^{-1})	**0.79**	**-0.27**	-0.13	**0.33**
Distance to continental shelf (km)	**-0.53**	**0.33**	**-0.35**	-0.10
Proportion of time spent feeding	**-0.29**	0.06	**0.45**	**-0.77**
Foraging area (km^2)	0.08	**0.29**	**-0.48**	**0.38**
Proportion of transit dives	**0.22**	**-0.22**	**-0.69**	0.06
Proportion of pelagic foraging dives	**-0.78**	**0.28**	**0.16**	**-0.39**
Proportion of drift dives	0.06	0.07	0.10	**0.88**
Proportion of benthic foraging dives	**0.81**	**-0.28**	**0.18**	-0.12
Bottom time, benthic foraging dives (s)	**0.25**	**0.61**	**0.40**	**0.26**
Bottom time, pelagic foraging dives (s)	**0.60**	**0.47**	**0.46**	-0.02
Dive duration, benthic foraging dives (s)	**0.27**	**0.87**	-0.01	0.12
Dive duration, pelagic foraging dives (s)	**0.28**	**0.62**	**0.33**	0.13
No. dive wiggles at bottom, benthic foraging dives	**-0.23**	-0.11	**0.57**	**0.62**
No. dive wiggles at bottom, pelagic foraging dives	**0.68**	**0.18**	**0.54**	0.02
Efficiency, benthic foraging dives	**-0.19**	**-0.43**	**0.62**	**0.22**
Efficiency, pelagic foraging dives	**0.70**	0.14	**0.47**	-0.12
Maximum depth, benthic foraging dives (m)	**0.27**	**0.78**	**-0.19**	-0.01
Maximum depth, pelagic foraging dives (m)	**-0.81**	**0.27**	0.02	0.04

Post-dive interval, benthic foraging dives (s)	0.04	**0.26**	0.10	**-0.21**
Post-dive interval, pelagic foraging dives (s)	**0.62**	**0.20**	-0.10	**-0.50**

*Bolded numbers indicate variables that were significant correlated with each PC axis.

CHAPTER 3

COMPARATIVE FEEDING STRATEGIES AND KINEMATICS IN PHOCID SEALS: SUCTION WITHOUT SPECIALIZED SKULL MORPHOLOGY

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RESEARCH ARTICLE

Comparative feeding strategies and kinematics in phocid seals: suction without specialized skull morphology

Sarah S. Kienle[1,*], Holly Hermann-Sorensen[2], Daniel P. Costa[1], Colleen Reichmuth[3,4] and Rita S. Mehta[1]

ABSTRACT

Feeding kinematic studies inform our understanding of behavioral diversity and provide a framework for studying the flexibility and constraints of different prey acquisition strategies. However, little is known about the feeding behaviors used by many marine mammals. We characterized the feeding behaviors and associated kinematics of captive bearded (*Erignathus barbatus*), harbor (*Phoca vitulina*), ringed (*Pusa hispida*) and spotted (*Phoca largha*) seals through controlled feeding trials. All species primarily used a suction feeding strategy but were also observed using a biting strategy, specifically pierce feeding. Suction feeding was distinct from pierce feeding and was characterized by significantly faster feeding times, smaller gapes and gape angles, smaller gular depressions and fewer jaw motions. Most species showed higher variability in suction feeding performance than in pierce feeding, indicating that suction feeding is a behaviorally flexible strategy. Bearded seals were the only species for which there was strong correspondence between skull and dental morphology and feeding strategy, providing further support for their classification as suction feeding specialists. Harbor, ringed and spotted seals have been classified as pierce feeders based on skull and dental morphologies. Our behavioral and kinematic analyses show that suction feeding is also an important feeding strategy for these species, indicating that skull morphology alone does not capture the true diversity of feeding behaviors used by pinnipeds. The ability of all four species to use more than one feeding strategy is likely advantageous for foraging in spatially and temporally dynamic marine ecosystems that favor opportunistic predators.

KEY WORDS: Prey capture, Foraging, Pierce feeding, Biting, Pinniped, Marine mammal

INTRODUCTION

Animals employ diverse feeding strategies to capture and consume prey, and these strategies often represent the combinations of behavior and morphology that are best suited for exploiting prey resources in a given environment (Schoener, 1971). The evolution of novel feeding behaviors in vertebrates provides functional biologists with opportunities to study the correspondence between behavior, kinematics and morphology. One such evolutionary event was the transition from terrestrial to aquatic habitats by marine mammals, which required behavioral, morphological and physiological adaptations for feeding to overcome the higher density and viscosity of water.

Carnivorous mammals have converged on a handful of aquatic feeding strategies: biting, filter feeding and suction feeding (Taylor, 1987; Werth, 2000a; Hocking et al., 2017; Kienle et al., 2017). A biting feeding strategy is characterized by prey being seized by the jaws and/or teeth and is divided into three subcategories: crushing, grip and tear feeding, and pierce feeding. Crushers break and reduce hard-shelled prey into pieces using powerful jaws and teeth (Riedman and Estes, 1990; Timm-Davis et al., 2017). Grip and tear feeders capture prey with powerful teeth, limbs and/or jaws, shake or rip prey apart and then consume the prey in pieces (King, 1983; Stirling, 1990; Hocking et al., 2016). Pierce feeders use the teeth to capture and pull prey into the mouth, often using a combination of biting and suction, and then swallow prey whole (Marshall et al., 2008, 2014, 2015; Kane and Marshall, 2009; Hocking et al., 2014). Filter feeding is a strategy where animals ingest prey from the water and use a specialized structure (e.g. baleen, multi-cusped postcanine teeth) as a sieve to trap prey as water is expelled from the mouth (Ross et al., 1976; Goldbogen et al., 2017). Suction feeding is a strategy where animals generate a pressure gradient within the oral cavity that draws water and prey into the mouth (Gordon, 1984; Werth, 2000b; Marshall et al., 2008; Kane and Marshall, 2009). In addition to being a feeding strategy, suction is also used to aid in prey capture and transport, such as in pierce feeding. The term ‘suction feeding’ is used throughout to refer to the feeding strategy, while ‘suction’ refers to the generation of a subambient pressure differential inside the mouth.

Pinnipeds (seals, sea lions and walruses) are one of the only marine mammal lineages to use all three aforementioned feeding strategies (King, 1983; Taylor, 1987; Werth, 2000a; Hocking et al., 2017; Kienle et al., 2017). The evolution of pinnipeds from terrestrial carnivores suggests that the ancestral feeding strategy is biting (Werth, 2000a), which is supported by the skull and dental morphologies of early pinnipedimorphs (extant pinnipeds and their fossil relatives; Adam and Berta, 2002; Churchill and Clementz, 2015). Most extant pinnipeds are classified as biters based on skull morphology (Adam and Berta, 2002; Jones and Goswami, 2010; Jones et al., 2013; Kienle and Berta, 2016), dentition (Churchill and Clementz, 2015) and some behavioral data (Penney and Lowry, 1967; Hückstädt and Antezana, 2003; Hocking et al., 2016). A few pinnipeds (e.g. bearded seals, *Erignathus barbatus*, and walruses, *Odobenus rosmarus*) exhibit modified skull, orofacial and dental morphologies associated with suction feeding and are referred to as suction feeding specialists (Adam and Berta, 2002; Marshall et al., 2008; Churchill and Clementz, 2015; Kienle and Berta, 2016; Marshall, 2016). Although once thought to be uncommon in pinnipeds (Werth, 2000a; Adam and Berta, 2002), recent feeding studies suggest that suction may be more widespread than previously considered (Hocking et al., 2012, 2014, 2015; Marshall et al., 2008, 2014, 2015). Lastly, a few pinnipeds use a filter feeding strategy (e.g. crabeater seals, *Lobodon carcinophaga*, and leopard seals, *Hydrurga*

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leptonyx; Ross et al., 1976; Adam and Berta, 2002; Hocking et al., 2012; Kienle and Berta, 2016).

Observations of pinnipeds feeding in the wild are scarce. Much of what is known about feeding behavior stems from studies on comparative skull and dental morphology (Adam and Berta, 2002; Jones and Goswami, 2010; Jones et al., 2013; Churchill and Clementz, 2015; Kienle and Berta, 2016) and diet (for review, see King, 1983; Riedman, 1990; Pauly et al., 1998). Therefore, an organized effort is underway to understand and document pinniped feeding behaviors through controlled feeding trials with captive animals (Marshall et al., 2008, 2014, 2015; Hocking et al., 2012, 2014, 2015, 2016). The results of these efforts show that some species vary feeding strategies contextually, while others are more constrained in their feeding behaviors. These studies have been fundamental to our understanding of the diversity of pinniped feeding behaviors and have provided insights on the trade-offs between different strategies and energy expenditure (Werth, 2000a), morphological constraints (Taylor, 1987; Bloodworth and Marshall, 2005), prey choice (Hocking et al., 2014, 2015) and behavioral flexibility (Kane and Marshall, 2009; Marshall et al., 2015).

Here, we conducted a comparative examination of feeding strategies and kinematics in four species of phocids (seals): bearded (*E. barbatus* Erxleben 1777), harbor (*Phoca vitulina* Linnaeus 1758), ringed [*Pusa hispida* (Schreber 1775)] and spotted seals (*Phoca largha* Pallas 1811). These species are in the Phocinae clade (northern seals) and have overlapping distributions in the Arctic and subarctic. Harbor and spotted seals (genus *Phoca*) are sister taxa and most closely related to the genus *Pusa* that includes ringed seals (Committee on Taxonomy, 2017). Bearded seals are the most ancestral phocine lineage, diverging from other phocines over 11 million years ago (Berta et al., 2018). Previous skull and dental morphological studies described harbor, ringed and spotted seals as pierce feeders (Adam and Berta, 2002; Churchill and Clementz, 2015; Kienle and Berta, 2016). A recent captive feeding study showed that harbor seals use pierce feeding, which corresponds with their skull and dental morphology, but also suction feeding (Marshall et al., 2014). In contrast, bearded seals exhibit skull, dental and orofacial morphological specializations for suction feeding and consistently use suction feeding during controlled feeding trials (Adam and Berta, 2002; Marshall et al., 2008; Churchill and Clementz, 2015; Kienle and Berta, 2016; Marshall, 2016). Several studies (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014, 2015, 2016) have shown that many pinnipeds alter their feeding behavior depending on context (e.g. prey size, type, presentation) but how stereotyped or variable species are in their feeding strategies and kinematics is currently unknown.

Our first objective was to document and comparatively describe the feeding strategies of bearded, harbor, ringed and spotted seals through controlled feeding trials with whole prey, a novel experimental treatment for all four species. The inclusion of the bearded seal provided the opportunity to directly compare feeding behavior of a suction feeding specialist with that of three species categorized as biters, specifically pierce feeders. We tested the hypothesis that suction feeding was the primary feeding strategy for bearded seals, and pierce feeding was the primary feeding strategy for harbor, ringed and spotted seals based on skull and dental morphology (Adam and Berta, 2002; Churchill and Clementz, 2015; Kienle and Berta, 2016). Our second objective was to compare the feeding kinematics and variation in the kinematics for each feeding strategy, among and within species. We predicted that in terms of feeding strategy, the harbor, ringed and spotted seals would be more kinematically similar to one another than to bearded seals, because of their close evolutionary history and similar skull and dental morphologies (Adam and Berta, 2002; Churchill and Clementz, 2015; Kienle and Berta, 2016).

MATERIALS AND METHODS

Study animals

This study was conducted at the Long Marine Laboratory (University of California Santa Cruz, Santa Cruz, CA, USA), SeaWorld San Diego (San Diego, CA, USA) and the Alaska SeaLife Center (Seward, AK, USA) using bearded (n=2), harbor (n=3), ringed (n=3) and spotted seals (n=2). Subject data (species, animal identification, sex, age, body length, head length and mass) are provided in Table 1. Data collection occurred from January 2015 to March 2017. All seals were conditioned using positive reinforcement and voluntarily participated in feeding trials. Behavioral research was approved by the Animal Care and Use Committee at the University of California, Santa Cruz, and conducted under federal authorizations for marine mammal research under National Marine Fisheries Service permits 15142, 14535 and 18902.

Feeding trials and kinematic variables

We designed and built a simple feeding apparatus to present seals with individual food items in a controlled and repeatable context. Prey were held by a metal clamp that was attached to the PVC frame of the apparatus. A rope tied to the clamp and tethered up the PVC pipe allowed prey to be released from the clamp when the apparatus was fully submerged. Prey were placed into the clamp tail-first and suspended from the feeding apparatus approximately 90 cm under the water's surface (Fig. 1). During each trial, the seal stationed with a trainer across the pool. Once the apparatus was submerged, the seal was cued to swim to the apparatus, and the clamp was released so that prey were free-floating in the water immediately before the animal reached the apparatus. After the prey was consumed, the seal returned to the trainer. The feeding trials took advantage of natural feeding behavior. Minimal training was used to maintain the seal's position at the surface before release to the apparatus. Seals were not exposed to the feeding apparatus prior to the start of the experiment at any of the locations where experiments were conducted. Two GoPro video cameras in underwater housing recording at 59.94 frames s^{-1} were mounted to the feeding apparatus to record anterior and lateral views of the feeding events.

Seals were fed individual freshly thawed whole capelin (standard length 15.15±5.85 cm, mass 0.04±0.01 g; means±s.d.) or, in the case of the ringed seal, half capelin (standard length 7.41±0.35 cm, mass <0.04 g). Ringed seals were the smallest species in this study, and the average whole capelin was longer than their heads (Table 1). To account for the smaller head size relative to prey size in the ringed seal, the ringed seals' capelin were halved. Capelin were within the size range of prey consumed by each species in the wild (Tollit et al., 1997; Brown and Pierce, 1998; Hauser et al., 2008; Boveng et al., 2009; Cameron et al., 2010; Kelly et al., 2010).

The sequence of feeding behaviors, feeding strategy, movements of the vibrissae and eyes, and prey manipulation were determined by viewing each feeding trial frame by frame in GoPro Studio v. 2.5.7 or QuickTime Player. A trial was classified as suction feeding if the animal formed a small, circular opening with the mouth and the prey moved in a fluid motion into the mouth; alternatively, a trial was classified as biting if the animal had a wide gape, curled back the lips, and used its teeth to contact prey during the feeding event (Marshall et al., 2008, 2014, 2015). Suction feeding and biting were mutually exclusive feeding strategies; an animal either used suction feeding or biting in a single feeding trial.

Table 1. Life history information for the 10 seals that participated in the feeding trials

Species	Individual	Sex	Estimated age (years)	Standard body length (cm)	Head length (cm)	Mass (kg)
Bearded seal (*Erignathus barbatus*)	Siku	M	2	158.0	21.8	100.4
	Noatak	M	1	150.1	17.9	89.7
Harbor seal (*Phoca vitulina*)	Sprouts	M	28	154.4	23.8	103.2
	HS1	F	13	139.2	20.3	74.0
	HS2	F	21	135.0	20.5	70.0
Ringed seal (*Pusa hispida*)	Nayak	F	5	116.2	14.4	23.8
	RS1	M	21	108.7	15.8	41.0
	Pimniq	M	3	89.2	13.2	28.5
Spotted seal (*Phoca largha*)	Amak	M	6	138.3	27.6	55.4
	Tunu	M	5	138.9	27.1	68.4

We used five homologous anatomical landmarks to quantify kinematic variables: (1) rostral tip of the upper jaw, (2) rostral tip of the lower jaw, (3) caudal-most point at the corner of the mouth, (4) rostral-most point of the eye and (5) rostral border of the hyoid apparatus (Fig. 1). Landmarks were digitized frame by frame for kinematic analysis in Tracker v. 4.92 (www.opensourcephysics.org). The kinematic variables measured in our study follow those defined by Marshall et al. (2008, 2014, 2015) and Hocking et al. (2012, 2014, 2015) and are as follows: (1) feeding event time (s): the duration of the entire feeding event, from when the seal began to open its jaws (the start of the feeding event) to when the entire prey item was inside the mouth; (2) maximum gape (cm): the maximum distance observed between the rostral tips of the upper and lower jaws during the feeding event; (3) time to maximum gape (s): the time from the start of the feeding event to maximum gape; (4) maximum gape angle (deg): the maximum angle between the rostral tips of the upper and lower jaws and the corner of the mouth; (5) time to maximum gape angle (s): the time from the start of the feeding event to maximum gape angle; (6) time to initial jaw closure (s): the time from the start of the feeding event to when the jaws and/or teeth first closed over the prey; (7) maximum gape angle opening velocity (deg s^{-1}): the angular rate of lower jaw opening; (8) time to maximum gape angle opening velocity (s): the time from the start of the feeding event to maximum gape angle opening velocity; (9) maximum gape angle closing velocity (deg s^{-1}): the angular rate of lower jaw closing; (10) time to maximum gape angle closing velocity (s): the time from the start of the feeding event to maximum gape angle closing velocity; (11) maximum gular depression (cm): the greatest distance between the rostral corner of the eye and the rostral edge of the hyoid apparatus; (12) time to maximum gular depression (s): the time from the start of the feeding event to maximum gular depression; (13) number of jaw motions: the number of dorso-ventral jaw movements throughout the feeding event. Kinematic analyses required the seal's head to be in lateral view throughout the feeding event, and the entire prey had to be consumed in frame. For this reason, more feeding trials were conducted than were included in the kinematic dataset.

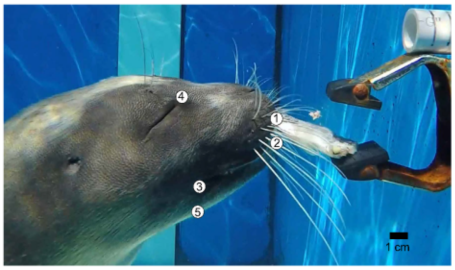

Fig. 1. Anatomical landmarks digitized during frame-by-frame video analyses, shown on the lateral profile of a ringed seal (RS1). Landmarks are as follows: (1) rostral tip of the upper jaw, (2) rostral tip of the lower jaw, (3) caudal-most point at the corner of the mouth, (4) rostral-most point of the eye and (5) rostral border of the hyoid apparatus.

Statistical analyses

We used linear mixed effects models to investigate the relationship between each kinematic variable and feeding strategy (lme4 package: Bates et al., 2015). Feeding strategy, species and head length were the fixed effects. There was an interaction term between feeding strategy and species. Individual was the random effect. We examined residual plots for obvious deviations from normality or homoscedasticity. When heteroscedasticity was observed, data were transformed using a power function (pbkrtest, lme4 and nmle packages: Halekoh and Højsgaard, 2014; Bates et al., 2015; https://CRAN.R-project.org/package=nlme). There were no significant intraspecific differences in feeding strategy related to age or sex. Chi-squared tests were run for each fixed effect to test for the significance of each predictor variable (car and lme4 packages: Fox and Weisberg, 2011; Bates et al., 2015). To test whether feeding strategy had a significant effect on each kinematic variable for each species, we performed *post hoc* contrasts for each kinematic variable across feeding strategies within species using the least-squares means (lsmeans package: Lenth, 2016).

We examined variability within the different feeding strategies for each species by quantifying the coefficient of variation (CV=standard deviation/mean) for each kinematic variable. Therefore, means and standard deviations were calculated for each kinematic variable. CV is a measure of variation in a behavior under a particular set of experimental conditions. A low CV (values close to 0) indicates stereotypy and a high CV (values close to 1) indicates high variability (Gerhardt, 1991; Wainwright et al., 2008).

We conducted a principal components analysis (PCA) (FactoMineR: Le et al., 2008; missMDA: Josse and Husson, 2016) to determine the major axes of variation between feeding strategies. We first size corrected the mean of each kinematic variable by extracting the residuals from linear regressions between each kinematic variable and individual head size. Twelve of the 13 size-corrected kinematic variables were included in the PCA; time to maximum gape angle was removed from the analysis as it was significantly correlated with time to maximum gape and a redundant variable. We used a coefficient correlation analysis to assess the positive or negative contribution of each kinematic variable to each principal component axis. Principal components (PCs) that explained more than 10% of the variation were retained, which was determined from scree plots of the variance explained by each eigenvalue. All statistical analyses were conducted in R v. 3.3.3 (https://www.R-project.org/).

RESULTS

We conducted 994 feeding trials across all individuals (bearded seals, *n*=223; harbor seals, *n*=279; ringed seals, *n*=260; spotted seals, *n*=232). Suction feeding was the primary feeding strategy for all species (58–94% of all feeding trials; Table 2, Fig. 2). Pierce feeding was also used by all species but less frequently (6–42% of all feeding trials). For most species, this pattern was consistent at the individual level, with the exception of one ringed seal that primarily used pierce feeding (75% of all feeding trials) and one harbor seal that exclusively used suction feeding.

Suction feeding

Suction feeding was characterized by a similar sequence of behavioral events for all species (Fig. 3A–C; Movie 1). When approaching prey, the seal pursed its lips to form a small, circular opening. The lateral facial muscles visibly tightened, and the rostral-most portions of the lips separated as the seal quickly depressed its lower jaw during initial prey capture (Fig. 3A). Shortly after, the prey was drawn partially or entirely into the mouth in a rapid, fluid motion (Fig. 3B), followed by lower jaw elevation that resulted in jaw closure (Fig. 3C). Jaw closure was followed by water expulsion from the sides of the mouth (58% of suction feeding trials). During suction feeding, the postcanine teeth were not visible. Suction feeding took one of two forms (Fig. 4): (1) the seal pulled the prey entirely inside the mouth during the first bout of suction (referred to as pure suction; 41% of suction feeding trials) or (2) the seal pulled the prey partially into the mouth by suction, held the prey in the mouth, then used another bout of suction to pull the prey the rest of the way into the mouth (referred to as multiple bouts of suction; 59% of suction feeding trials). During the multiple bouts of suction, the seal repeatedly used its lips to create a small, circular opening and followed the sequence described above (Fig. 3). This process continued until the prey was entirely inside the mouth.

Some individual harbor, ringed and spotted seals made repeated ventral depression of the lower jaw and small dorso-ventral movements in the gular region after the prey was inside the mouth prior to swallowing. Similar behaviors have been described as chewing in subantarctic fur seals (*Arctocephalus tropicalis*), Australian fur seals (*Arctocephalus pusillus doriferus*) and Australian sea lions (*Neophoca cinerea*; Hocking et al., 2014, 2015, 2016), where chewing is defined as modifying prey using repetitive motions of the jaw/teeth to pierce, cut or crush items that are inside the mouth (Hiiemae and Crompton, 1985; Reilly et al., 2001; Schwenk, 2000; Hocking et al., 2017; Kienle et al., 2017). In pinnipeds, chewing is separate from mastication because the teeth are not in occlusion (Adam and Berta, 2002; Berta et al., 2006; Hocking et al., 2015). It should be noted that chewing in general is the subject of a much larger debate (e.g. Reilly et al., 2001; Kolmann et al., 2016). In this study, it is unclear whether or how these repeated jaw motions were used to manipulate or reduce the size of the ingested prey, as in chewing; regardless, these repeated jaw motions were observed and seemed to aid in transporting prey to the back of the throat prior to swallowing. Only the harbor seal Sprouts was observed using this behavior in the majority of suction feeding trials.

All species actively flexed the supraorbital and mystacial vibrissae forward when approaching prey, and the vibrissae

Table 2. Summary of kinematic data for each species

	Bearded seals (*n*=2)		Harbor seals (*n*=3)		Ringed seals (*n*=3)		Spotted seals (*n*=2)	
Kinematic variable	Suction	Pierce	Suction	Pierce	Suction	Pierce	Suction	Pierce
Proportion	0.92±0.01	0.09±0.01	0.94±0.05	0.06±0.05	0.58±0.30	0.42±0.30	0.87±0.04	0.14±0.04
Feeding event time (s)	0.39±0.20	0.46±0.14	0.34±0.21	0.69±0.22	0.22±0.10	0.62±0.45	0.27±0.16	0.38±0.11
Max. gape (cm)	3.31±0.82	4.45±1.43	3.07±0.82	3.47±0.52	2.00±0.45	3.37±0.79	2.78±0.96	3.76±1.44
Time to max. gape (s)	0.11±0.08	0.09±0.04	0.09±0.05	0.07±0.03	0.10±0.04	0.13±0.07	0.10±0.03	0.08±0.06
Max. gape angle (deg)	20.80±7.73	26.91±9.08	22.90±10.20	25.27±4.70	22.16±6.08	37.53±8.23	16.86±4.70	22.22±5.47
Time to max. gape angle (s)	0.11±0.07	0.08±0.03	0.09±0.05	0.08±0.03	0.09±0.04	0.13±0.07	0.10±0.04	0.08±0.06
Time to initial jaw closure (s)	0.17±0.05	0.20±0.07	0.18±0.09	0.19±0.11	0.15±0.05	0.20±0.07	0.14±0.04	0.18±0.07
Max. gape angle opening velocity (deg s^{-1})	242.85±132.33	277.13±47.99	303.34±185.54	231.64±45.00	213.85±98.18	424.28±85.27	214.45±112.88	260.60±124.73
Time to max. gape angle opening velocity (s)	0.06±0.07	0.02±0.02	0.06±0.08	0.04±0.04	0.06±0.04	0.08±0.08	0.05±0.03	0.04±0.02
Max. gape angle closing velocity (deg s^{-1})	175.19±116.07	205.23±136.95	222.54±152.71	141.69±56.15	269.07±113.68	314.24±123.24	173.69±127.09	212.82±112.79
Time to max. gape angle closing velocity (s)	0.16±0.08	0.14±0.07	0.14±0.08	0.12±0.04	0.14±0.06	0.17±0.07	0.14±0.03	0.13±0.06
Max. gular depression (cm)	9.50±1.20	9.31±2.28	9.64±1.24	11.75±0.76	6.16±0.83	7.41±0.80	9.50±1.46	10.68±1.87
Time to max. gular depression (s)	0.16±0.09	0.13±0.01	0.11±0.08	0.02±0.00	0.12±0.05	0.14±0.08	0.13±0.05	0.10±0.02
Number of jaw movements	2.38±0.95	2.43±0.79	3.71±2.46	7.38±2.45	2.42±1.90	3.65±1.57	2.88±1.17	3.56±1.24

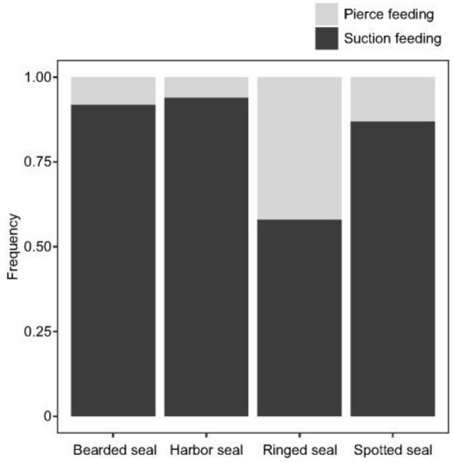

Fig. 2. Frequency of each mutually exclusive feeding strategy (suction feeding or pierce feeding) used by bearded (*n*=2), harbor (*n*=3), ringed (*n*=3) and spotted (*n*=2) seals.

remained protracted during the entire feeding event (Fig. 3). The mystacial vibrissae made initial contact with the prey. In some trials, seals contacted prey with the lateral mystacial vibrissae, centered their mouth over the prey after initial contact, and maintained vibrissal contact with the prey until it was pulled into the mouth. Bearded seals rotated their vibrissae rostrally and medially, and the rostral-most vibrissae were in direct contact with the prey, often surrounding the prey throughout the feeding event. When suction feeding, seals varied in whether their eyes were open, open and focused on the prey, or closed. Only spotted seals approached prey with their eyes open and maintained visual contact until the prey was obscured by the rostrum and/or the mystacial vibrissae contacted the prey (Fig. 3).

Although prey were always presented head-first relative to the seal's approach during the feeding trials, we observed variation in the direction in which seals consumed prey. Spotted seals always consumed prey head-first. Bearded, ringed and harbor seals occasionally manipulated the prey prior to it entering the mouth. These seals sometimes reoriented the prey to pull it in sideways so the lateral surface or tail of the fish entered the mouth first. Alternatively, seals sometimes approached the prey from the side, repositioned it by pushing with the rostrum, or used suction to turn the prey to the side or tail-first before it entered the mouth.

Pierce feeding

Pierce feeding followed a more variable sequence of behavioral events compared with suction feeding (Fig. 4; Movie 1). When biting was used initially, forward motion of the head and/or body positioned the seal's mouth close to the prey (Fig. 5A). The lateral sides of the lips were drawn back so that the incisors, canines and postcanine teeth were exposed in lateral view, and the lower jaw was quickly depressed. The seal bit down on the prey with the teeth and jaws, leaving a portion of the prey visible from between the lips (Fig. 5B,C). When suction was used initially, it followed the same pattern as described in the suction feeding trials (Fig. 3A,B). Prey were never pulled entirely into the mouth during initial jaw closure in pierce feeding trials. After the mouth closed over the prey, the seal alternated using biting and suction to pull it inside the oral cavity (Figs 4 and 5). Biting was characterized by the curling back of the upper and lower lips so that teeth were exposed, quick dorso-ventral movements of the jaws, and the use of the incisors and canines to hold prey in place. When suction was used, teeth were never visible. As in the suction feeding trials, after jaw closure, the seal frequently expelled water from the sides of the mouth prior to swallowing (48% of pierce feeding trials).

Two individuals (harbor seal Sprouts; ringed seal RS1) made chewing-like motions after the prey was inside the mouth (see description in 'Suction feeding', above). Only the harbor seal used this behavior in the majority of pierce feeding trials. The use of the supraorbital and mystacial vibrissae was similar to that observed during suction feeding trials, as was the use of vision (see descriptions in 'Suction feeding', above). As in suction feeding trials, prey presentation upon the seal's initial approach did not affect the feeding behavior of spotted seals. The bearded, ringed and harbor seals occasionally manipulated the prey prior to it entering the mouth. Biting was typically used to reposition the prey; the seal shifted the prey from the incisors and canines to the postcanines to turn it before swallowing. One harbor seal (Sprouts) reoriented the prey in the majority of pierce feeding trials, preferring to consume it side-first or tail-first.

Feeding strategy kinematics

Across the 994 trials, 231 trials (23% of all feeding trials) were analyzed for kinematics (bearded seals, *n*=45; harbor seals, *n*=57;

Fig. 3. Sequence of behaviors associated with the suction feeding strategy exemplified by a spotted seal (Tunu). (A) Seal approaches the prey with vibrissae actively spread and lips pursed to form a small, circular opening. (B) The prey is pulled into the oral cavity by suction as jaws are opened to maximum gape and gape angle. (C) Mouth closes over the prey during initial jaw closure. Video was filmed at 59.94 frames s^{-1}, and time is displayed as h:min:s:frames.

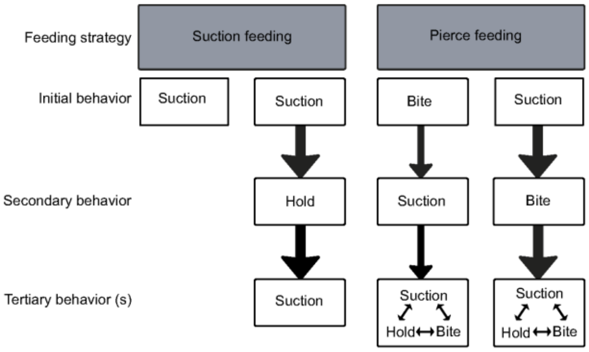

Fig. 4. Flow chart of feeding behaviors associated with pierce feeding and suction feeding strategies. The size of the arrows indicates how frequently each path was used within each feeding strategy. In pierce feeding, after the initial and secondary feeding behavior (suction and biting), seals used a variable combination of tertiary behaviors (e.g. suction, holding and biting) to pull prey entirely inside the mouth.

ringed seals, *n*=69; spotted seals, *n*=60). Seven kinematic variables significantly differed between the pierce and suction feeding strategies. Suction feeding was characterized by significantly shorter feeding event times (χ_1^2=22.26, *P*<0.01), shorter times to initial jaw closure (χ_1^2=8.32, *P*<0.01) and shorter times to maximum gular depression (χ_1^2=19.21, *P*<0.01) compared with pierce feeding. Furthermore, suction feeders exhibited significantly smaller maximum gapes (χ_1^2=23.18, *P*<0.01), smaller maximum gape angles (χ_1^2=10.38, *P*<0.01), smaller maximum gular depressions (χ_1^2=6.15, *P*<0.02) and a reduced number of jaw motions (χ_1^2=10.71, *P*<0.01). In contrast, pierce feeding was characterized by longer feeding event times, longer times to initial jaw closure and longer times to maximum gular depression compared with suction feeding. Additionally, pierce feeders had larger maximum gapes and gape angles, larger maximum gular depressions, faster gape angle opening velocities and an increased number of jaw motions.

The sequence of kinematic events for suction feeding was consistent across species: maximum gape and gape angle were followed by maximum gular depression and subsequently by initial jaw closure (Fig. 6A). The kinematics associated with pierce feeding followed a similar sequence to the kinematics for suction feeding (Fig. 6B); this was also consistent across species, with the exception of the harbor seal. In harbor seals, maximum gular depression preceded maximum gape and initial jaw closure (Table 2).

The first three PCs explained 75.8% of the variation in feeding kinematics (Table S1). The correlation coefficient matrix identified eight significantly correlated variables with PC1. High positive PC1 loadings were associated with time to maximum gape, time to maximum gape angle opening velocity and time to maximum gape angle closing velocity. The correlation coefficient matrix identified six variables significantly correlated with PC2. High positive PC2 loadings were associated with maximum gape angle opening velocity, maximum gular depression and the number of jaw motions. PC3 was significantly associated with a high positive loading for maximum gape. All significant variables for PCs 1–3 were positively correlated. Species were more clustered in kinematic space based on the suction feeding kinematics compared with the pierce feeding kinematics (Fig. 7). PC1 was associated with pierce feeding, and PC2 was associated with suction feeding.

Intraspecific variation in feeding kinematics

Maximum gape was significantly smaller when suction feeding in bearded (*t*-ratio=2.39, *P*<0.02), ringed (*t*-ratio=4.10, *P*<0.01) and spotted seals (*t*-ratio=2.36, *P*<0.01). Feeding event time was significantly shorter in harbor (*t*-ratio=2.87, *P*<0.01) and ringed seals (*t*-ratio=4.09, *P*<0.01) when suction feeding; there were also fewer jaw motions in harbor (*t*-ratio=2.70, *P*<0.01) and ringed seals (*t*-ratio=3.07, *P*<0.01). In harbor seals, maximum gape angle closing velocity was faster (*t*-ratio=−2.15, *P*<0.03) and time to maximum gular depression was longer (*t*-ratio=−6.08, *P*<0.01) when suction feeding. In ringed seals, time to initial jaw closure was shorter (*t*-ratio=2.83, *P*<0.01), maximum gape angle (*t*-ratio=3.91, *P*<0.01) and maximum gular depression (*t*-ratio=2.14, *P*<0.04) were smaller, and maximum gape angle opening velocity was slower (*t*-ratio=2.52, *P*<0.01) during suction feeding.

To quantify overall feeding variability, we averaged the CV for all kinematic variables for each feeding strategy. Suction feeding was associated with a higher overall CV than pierce feeding for all species, with the exception of spotted seals. Spotted seals had the same average CV for both pierce and suction feeding strategies (Table 3). Suction feeding trials exhibited the highest variability in

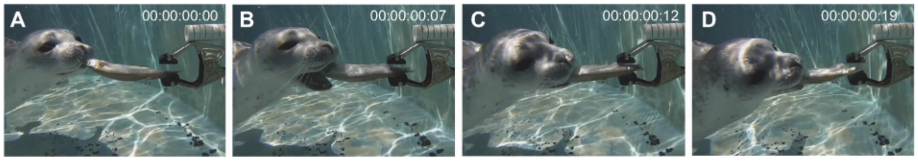

Fig. 5. Sequence of behaviors associated with the pierce feeding strategy exemplified by a single feeding trial with a ringed seal (Nayak). (A) Seal approaches the prey with vibrissae actively spread. (B) Jaws are opened to maximum gape and gape angle with teeth visible as seal engulfs the prey with the mouth. (C) Mouth closes over the prey during initial jaw closure. (D) Lips are pursed to form a small, circular opening, and the prey is drawn farther into the mouth via suction.

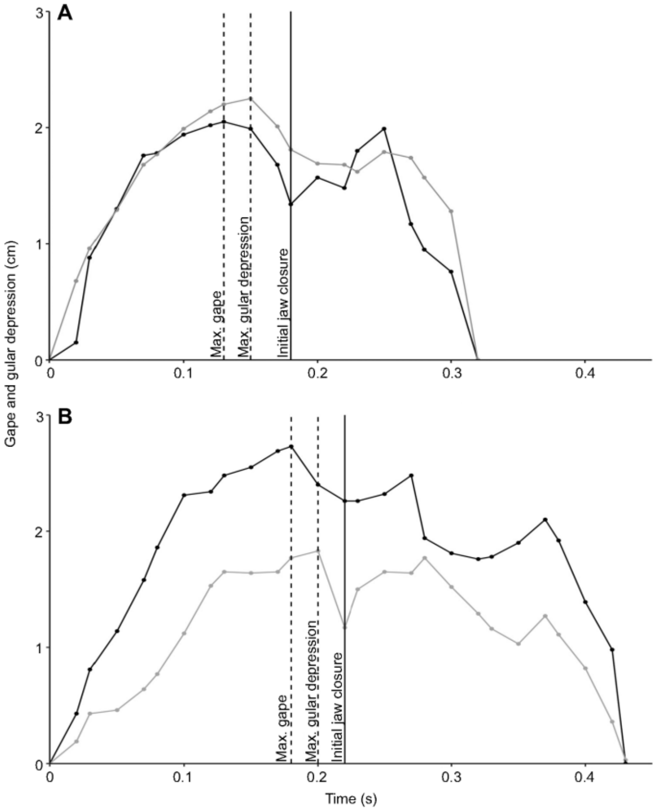

Fig. 6. Representative kinematic profiles of gape and gular depression when suction feeding and pierce feeding in a ringed seal (RS1). The black line represents gape and the gray line represents gular depression. With the exception of pierce feeding in harbor seals, all species showed similar timing in feeding events. Maximum gape was followed by maximum gular depression and then initial jaw closure. (A) Example of multiple bouts of suction. The seal used suction to pull the prey partially into the mouth, closed the jaws, and then used another round of suction to pull the prey entirely inside the oral cavity. (B) Example of pierce feeding. The seal used biting to get the prey partially into the mouth, closed the jaws, used another round of biting, closed the jaws, and then used suction to pull the prey entirely inside the oral cavity.

time to maximum gape angle opening velocity for most species (CV=0.72–0.98), while maximum gular depression was the most stereotyped (CV=0.11–0.17). When pierce feeding, time to maximum gape angle opening velocity and time to maximum gape angle closing velocity were highly variable in most species (CV=0.19–0.87), while maximum gape and maximum gape angle opening velocity were the most stereotyped (CV=0.14–0.38). When suction feeding, bearded seals had the highest kinematic variability of all species (CV=0.47±0.21), and ringed seals had the most stereotyped kinematics (CV=0.39±0.14). When pierce feeding, spotted seals had the highest kinematic variability of all species (0.40±0.18), and harbor seals had the most stereotyped kinematics (CV=0.24±0.20).

DISCUSSION

Captive bearded, harbor, ringed and spotted seals in controlled feeding trials primarily used suction feeding and some pierce feeding when targeting prey underwater. These results add to the larger comparative behavioral dataset showcasing the importance of suction feeding to pinnipeds in the aquatic environment (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014, 2015). Suction feeding in bearded, harbor, ringed and spotted seals was characterized by a similar sequence of behavioral and kinematic events, including pursing of the lips to form a small circular opening, rapid lower jaw depression and maximum gular depression following maximum gape. Overall, suction feeding was characterized by shorter feeding event times and times to initial jaw closure, smaller maximum gapes and gape angles, lower gape angle opening velocities, smaller gular depressions and fewer jaw motions compared with pierce feeding.

Pierce feeding, a form of biting, was the only other feeding strategy observed in this study. Pierce feeding pinnipeds have a greater diversity of cranial and mandibular shapes than grip and tear, filter and suction feeders (Jones et al., 2013; Kienle and Berta, 2016). As evidenced by the seals in this study, biting was associated with different ingestion behaviors, including prey capture, external prey processing and prey manipulation. Pierce feeding was characterized by curling back the lateral sides of the lips to expose the teeth and quickly depressing the lower jaw to open the mouth. The jaws closed after the prey was partially inside the mouth,

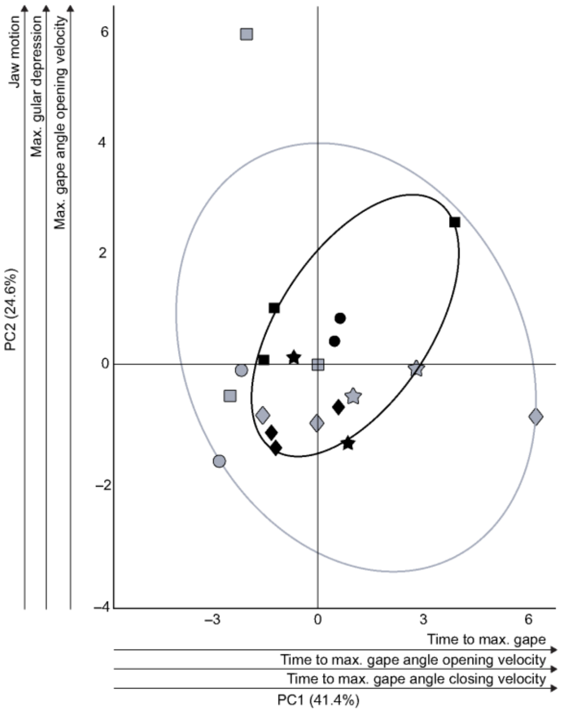

Fig. 7. Axes of kinematic variation in feeding as revealed by principal components analysis for all four phocid species. Symbols on the scatterplot represent individuals of each species. Circles represent bearded seals (*n*=2), squares represent harbor seals (*n*=3), diamonds represent ringed seals (*n*=3) and stars represent spotted seals (*n*=2). Colors indicate feeding strategy, where black indicates suction feeding and gray indicates pierce feeding. Variables that loaded strongly on each axis are represented by arrows indicating the direction in which the variables increased along the axis. Circles indicate the 95% confidence intervals for each feeding strategy.

resulting in direct contact of the teeth on the prey. Suction was used together with biting in different combinations to pull prey inside the oral cavity. Overall, pierce feeding was characterized by longer feeding event times and times to initial jaw closure, larger maximum gapes and gape angles, faster gape angle opening velocities, larger gular depressions and more jaw motions compared with suction feeding. Grip and tear feeding, another type of biting used by pinnipeds, was not observed, likely due to the relatively small prey relative to head size used in this study; grip and tear feeding is often associated with prey that are too large to swallow whole (Taylor, 1987; Hocking et al., 2014, 2015, 2016).

Skull morphology and feeding strategies

Pinnipeds are hypothesized to exhibit morphological adaptations for particular feeding strategies (Adam and Berta, 2002; Jones and Goswami, 2010; Jones et al., 2013; Churchill and Clementz, 2015;

Table 3. Coefficient of variation for each species for each feeding strategy

	Bearded seals (*n*=2)		Harbor seals (*n*=3)		Ringed seals (*n*=3)		Spotted seals (*n*=2)	
Kinematic variables	Suction	Pierce	Suction	Pierce	Suction	Pierce	Suction	Pierce
Max. gape	0.25	0.32	0.27	0.14	0.23	0.21	0.30	0.38
Time to max. gape	0.64	0.47	0.45	0.30	0.38	0.38	0.35	0.62
Max. gape angle	0.32	0.34	0.37	0.14	0.28	0.20	0.29	0.20
Time to max. gape angle	0.58	0.35	0.50	0.34	0.45	0.37	0.38	0.62
Max. gape angle opening velocity	0.45	0.17	0.54	0.14	0.44	0.18	0.53	0.36
Time to max. gape angle opening velocity	0.98	0.87	0.80	0.74	0.72	0.44	0.72	0.36
Max. gape angle closing velocity	0.56	0.67	0.60	0.20	0.40	0.33	0.76	0.39
Time to max. gape angle closing velocity	0.46	0.48	0.37	0.19	0.42	0.36	0.21	0.46
Time to initial jaw closure	0.34	0.28	0.41	0.54	0.33	0.36	0.27	0.33
Max. gular depression	0.12	0.25	0.11	0.06	0.13	0.13	0.17	–
Time to max. gular depression	0.51	0.09	0.53	0.00	0.41	0.48	0.37	–
Feeding cycle duration	0.52	0.31	0.57	0.16	0.39	0.51	0.54	0.33
No. of jaw movements	0.42	0.35	0.44	0.24	0.48	0.42	0.36	0.35
Mean	0.47	0.38	0.46	0.24	0.39	0.33	0.40	0.40

Kienle and Berta, 2016). For example, suction generation in pinnipeds is often associated with a distinct suite of morphological traits, including the loss of teeth or reduced tooth complexity (Fay, 1982; King, 1983; Churchill and Clementz, 2015), broad and flat rostrums (Jones and Goswami, 2010), wide, arched palates (Kastelein and Gerrits, 1990; Adam and Berta, 2002; Kienle and Berta, 2016), robust orofacial musculature (Fay, 1982; Marshall, 2016) and well-developed muscular–vibrissal complexes (Fay, 1982; Marshall, 2016). In this study, bearded seals were the only species for which there was strong correspondence between skull and dental morphology and feeding strategy. Intriguingly, while bearded seals are the most ancestral phocine lineage (Berta et al., 2018), their primary feeding strategy, suction, differs from the ancestral pinniped biting strategy (Werth, 2000a; Adam and Berta, 2002; Churchill and Clementz, 2015). Bearded seals may have diverged from the ancestral feeding mode over the course of their long, independent evolutionary history, although the evolution of feeding strategies in pinnipeds is not well known (Adam and Berta, 2002). Bearded seals generate strong subambient pressures, exhibiting values comparable to those of the walrus, another specialized suction feeder (Kastelein et al., 1994; Born et al., 2003; Marshall et al., 2008). These powerful suction pressures are likely aided by their specialized skull, orofacial and dental morphology (Churchill and Clementz, 2015; Kienle and Berta, 2016; Marshall, 2016). Bearded seals also had the highest average variability for the suction feeding kinematics of any species in this study, and this variability may allow bearded seals to modify their suction feeding behaviors and kinematic performance to particular feeding contexts.

The three species in this study historically classified as pierce feeders (i.e. harbor, ringed and spotted seals) used more suction feeding than pierce feeding, suggesting that pinnipeds are capable of generating suction without specialized skull and dental morphologies. Pierce feeding is associated with skull and dental adaptations, including large postcanines with unequal but limited postcanine spacing (Churchill and Clementz, 2015), enlarged orbits (Adam and Berta, 2002; Kienle and Berta, 2016), and enlarged pterygoid bones and long toothrows (Kienle and Berta, 2016). The present study, supported by the results of Marshall et al. (2008, 2014, 2015) and Hocking et al. (2012, 2014, 2015), reveals the prevalence of suction feeding in secondarily aquatic marine mammals and suggests that skull and dental morphology do not accurately reflect the diversity of feeding strategies for many pinnipeds. However, there may be a trade-off between species that have specialized morphologies associated with suction feeding and those that do not. For example, harbor seals are unable to generate high subambient pressures like those of suction feeders with specialized morphologies (e.g. bearded seal, walrus: Kastelein et al., 1994; Marshall et al., 2008, 2014). We speculate that, like the harbor seal, ringed and spotted seals may be unable to generate high subambient pressures comparable to those of the bearded seal. The inability to generate powerful subambient pressures while suction feeding may limit the type and size of prey that pinnipeds without specialized suction morphologies can target.

We predicted that, as specialized suction feeders, bearded seals would be kinematically distinct from the other species in this study. However, all four species had similar kinematic profiles when using the same feeding strategy within the same feeding context. Rather, the larger differences resulted from feeding strategy and not species, further showing that suction feeding and biting are kinematically distinct strategies. These findings continue to showcase the importance of functional studies in testing hypotheses generated from comparative morphology (Collar and Wainwright, 2006; Kane and Marshall, 2009).

Variability and flexibility in feeding strategies

Many pinnipeds can alter their behavior depending on the feeding context (Werth, 2000b; Marshall et al., 2008, 2014, 2015; Hocking et al., 2014, 2015). However, some species are invariant in their feeding behavior, regardless of context (Marshall et al., 2015). In this study, we demonstrate that bearded, harbor, ringed and spotted seals can vary feeding behavior within the same feeding context, as all species use both pierce and suction feeding. Additionally, our results show behavioral flexibility in feeding for two species (bearded and harbor seals) for which there are comparable data from previous work. For example, bearded seals in this study used biting (pierce feeding) in addition to suction feeding underwater, whereas no biting was observed underwater in a previous study of bearded seals (Marshall et al., 2008). Biting feeding strategies are more often observed when animals feed on larger prey (Hocking et al., 2014, 2015, 2016), and seals in this study were fed whole capelin (∼15 cm in length) that were more than three times the length of the herring pieces used by Marshall et al. (2008). The larger prey in this study may represent the beginning of a threshold where bearded seals are more likely to use a biting strategy. Additionally, we never observed bearded or harbor seals using hydraulic jetting (the forceful and directed movement of water from the mouth used in ingestion: Fay, 1982; Kastelein and Mosterd, 1989; Marshall et al., 2008; Hocking et al., 2012) in combination with suction, which differs from previous observations of these two species (Marshall et al., 2008, 2014). In the previous studies, some prey were placed in recessed wells and it was found that seals sometimes complemented suction with hydraulic jetting; this behavior has been documented in other pinnipeds, including harbor seals (Marshall et al., 2014), leopard seals (Hocking et al., 2012) and walruses (Kastelein and Mosterd, 1989), and is typically observed when pinnipeds feed on difficult-to-access or buried prey (Fay, 1982; Kastelein and Mosterd, 1989). Previous studies have emphasized how pinnipeds alter feeding strategies and behavior under different scenarios (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014) and with changes in prey size and shape (Hocking et al., 2015, 2016). Individuals in this study would likely exhibit additional behaviors in other feeding contexts than those examined here, as has been shown for bearded and harbor seals (Marshall et al., 2008, 2014).

The use of multiple feeding strategies that are behaviorally flexible is thought to be advantageous for species feeding in spatially and temporally dynamic ecosystems (Dill, 1983). Many pinnipeds – including the seals studied here – can alter feeding strategies in response to the abiotic and biotic environment (Schoener, 1971), such as changes in prey type/size (Boveng et al., 2009; Kelly et al., 2010; Cameron et al., 2010; Hocking et al., 2014, 2015) and seasonal and/or spatial variation (Lowry and Frost, 1981; Pierce et al., 1991). In addition to environmental contexts, feeding behaviors in pinnipeds can differ as a result of life history, including body size and ontogeny (Lowry and Frost, 1981; Dehn et al., 2007; Boveng et al., 2009; Jones and Goswami, 2010). Bearded, harbor, ringed and spotted seals have been documented using diverse feeding behaviors (Bowen et al., 2002; Marshall et al., 2008, 2014). For example, harbor seals change their feeding behaviors when targeting different prey (Bowen et al., 2002). When feeding on cryptic prey, seals swam near the bottom ('cruising'), thrusting their heads at prey or into the sand to find prey; alternatively, when targeting conspicuous prey (e.g. schools of fish), seals darted from behind the school to isolate individual fish

(Bowen et al., 2002). Having multiple feeding behaviors and variability within each feeding strategy is likely advantageous for these pinnipeds and may allow them to adapt to different foraging scenarios and prey resources.

Convergence in feeding strategies

Pinnipeds have converged on similar feeding strategies – biting, filter feeding and suction feeding – as observed in other fully aquatic vertebrates (Taylor, 1987; Werth, 2000a; Schwenk, 2000; Hocking et al., 2017; Kienle et al., 2017). Suction feeding, which is well studied in fishes, follows an extremely conserved sequence of events (Muller and Osse, 1984; Lauder, 1985; Motta et al., 2002; Gibb and Ferry-Graham, 2005) irrespective of morphology. Suction feeding in pinnipeds is generated by the rapid depression and retraction of the tongue via the hyoid apparatus and associated with large gape opening and closing velocities and a large gular depression (Gordon, 1984; Heyning and Mead, 1996; Marshall et al., 2008). This hypothesis is supported by controlled feeding studies of several species of marine mammals, including odontocetes (Heyning and Mead, 1996; Kastelein et al., 1997; Werth, 2000b; Bloodworth and Marshall, 2005; Kane and Marshall, 2009) and pinnipeds (Gordon, 1984; Kastelein et al., 1994; Marshall et al., 2008, 2014, 2015). However, all four seal species in our study had feeding kinematics that differed from the typical suction feeding pattern observed in other marine mammals, often displaying slower gape angle opening and closing velocities and smaller gular depressions when suction feeding compared with pierce feeding in the same individuals. These findings are similar to those recently reported for Steller sea lions (*Eumetopias jubatus*: Marshall et al., 2015) and harbor seals (Marshall et al., 2014).

Collectively, the available data suggest that suction generation in pinnipeds is not as conserved as in fishes. In phocids, suction feeding kinematics are more variable than pierce feeding kinematics. In fishes, biting has been found to be highly variable in certain clades, such as Anguilliformes (eels: Collar et al., 2014). Our findings and those of Marshall et al. (2015) show that biting in seals is more stereotyped. Evolutionary history may play a key role in determining variability and flexibility within a particular feeding strategy. It is worth considering that while pinnipeds evolved from terrestrial carnivores that likely used biting (Taylor, 1987; Werth, 2000a; Adam and Berta, 2002; Berta et al., 2018), suction feeding, the derived feeding strategy, is more variable. In contrast, suction feeding is the ancestral feeding strategy for Elopomorph fishes (bone fish, tarpon and eels), and biting, the derived feeding strategy, is more variable (Collar et al., 2014). These comparisons, albeit in phylogenetically disparate groups, suggest that understanding the evolutionary transitions of feeding behavior may provide insight into how variability within feeding strategies evolves.

Conclusions

The results of this study highlight the feeding strategies and kinematics used by bearded, harbor, ringed and spotted seals, which are consistent with observations of other pinnipeds as well as other marine mammals. Additionally, we show that feeding context, such as those posed by experimental treatments, may influence the prevalence of different feeding strategies. Overall, our findings reveal that feeding strategies are not always accompanied by skull and dental morphological specializations. Pierce and suction feeding are the primary feeding strategies used by bearded, harbor, ringed and spotted seals, and each feeding strategy is associated with distinct behaviors and kinematic profiles. The myriad adaptations for underwater feeding and the ability of many pinnipeds to exhibit context-dependent feeding strategies have enabled these taxa to survive and flourish as apex and mesopredators in aquatic ecosystems worldwide.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

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CHAPTER 3

SUPPLEMENTARY INFORMATION

TABLE S1. Principal component loadings for each kinematic variable for principal components (PCs) 1-3.

Kinematic variable	PC1 (41.4%)	PC2 (24.6%)	PC3 (9.8%)
Feeding event time (s)	**0.673**	0.269	-0.250
Maximum gape (cm)	0.349	0.298	**0.864**
Time to maximum gape (s)	**0.924**	-0.191	-0.143
Maximum gape angle (deg)	**0.737**	-0.206	0.348
Time to initial jaw closure (s)	**0.573**	**0.538**	-0.066
Maximum gape angle opening velocity (deg s^{-1})	0.158	**0.836**	0.057
Time to maximum gape angle opening velocity (s)	**0.926**	0.001	0.133
Maximum gape angle closing velocity (deg s^{-1})	**0.574**	**0.490**	0.022
Time to maximum gape angle closing velocity (s)	**0.911**	0.076	0.098
Maximum gular depression (cm)	0.042	**0.822**	0.272
Time to maximum gular depression (s)	**0.771**	**0.453**	0.073
Number of jaw movements	0.164	**0.775**	-0.331

*Bolded numbers indicate kinematic variables that were significant correlated with each PC axis.

MOVIE 1. Examples of suction feeding and biting (pierce feeding) for bearded, harbor, ringed, and spotted seals.

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CHAPTER 4

HAWAIIAN MONK SEALS EXHIBIT BEHAVIORAL FLEXIBILITY WHEN TARGETING PREY OF DIFFERENT SIZE AND SHAPE

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RESEARCH ARTICLE

Hawaiian monk seals exhibit behavioral flexibility when targeting prey of different size and shape

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ABSTRACT

Animals use diverse feeding strategies to capture and consume prey, with many species switching between strategies to accommodate different prey. Many marine animals exhibit behavioral flexibility when feeding to deal with spatial and temporal heterogeneity in prey resources. However, little is known about flexibility in the feeding behavior of many large marine predators. Here, we documented the feeding behavior and kinematics of the endangered Hawaiian monk seal (*Neomonachus schauinslandi*, *n*=7) through controlled feeding trials. Seals were fed multiple prey types (e.g. night smelt, capelin, squid and herring) that varied in size and shape to examine behavioral flexibility in feeding. Hawaiian monk seals primarily used suction feeding (91% of all feeding trials) across all prey types, but biting, specifically pierce feeding, was also observed (9% of all feeding trials). Suction feeding was characterized by shorter temporal events, a smaller maximum gape and gape angle, and a fewer number of jaw motions than pierce feeding; suction feeding kinematic performance was also more variable compared with pierce feeding. Seals showed behavioral flexibility in their use of the two strategies. Suction feeding was used most frequently when targeting small to medium sized prey and biting was used with increasing frequency on larger prey. The feeding kinematics differed between feeding strategies and prey types, showing that Hawaiian monk seals adjusted their behaviors to particular feeding contexts. Hawaiian monk seals are opportunistic marine predators and their ability to adapt their feeding strategy and behavior to specific foraging scenarios allows them to target diverse prey resources.

KEY WORDS: Suction, Biting, Foraging, Feeding, Pinniped, Kinematics

INTRODUCTION

Animals use diverse feeding strategies to capture and consume prey, and this diversity is shaped by the interplay of behavior, morphology and physiology (Schoener, 1971; Schwenk, 2000). Species that use multiple feeding strategies often tailor their behaviors to specific feeding contexts, which can result in increased foraging success (Dill, 1983; Taylor, 1987; Villegas-Amtmann et al., 2008; Chaves and Bicca-Marques, 2016). Behavioral flexibility, or the ability to alter behavior in response to changing stimuli (Wainwright et al., 2008), is thought to be advantageous for animals feeding in variable environments. Animals with greater flexibility can modulate their behavior in response to changes in prey abundance and distribution (Dill, 1983; Harding et al., 2007; Miller et al., 2009).

Many marine animals exhibit behavioral flexibility when feeding to overcome spatial and temporal heterogeneity in prey resources (Dill, 1983; Schoen et al., 2018; McHuron et al., 2018). For example, many species of pinnipeds (seals, sea lions and walruses) change their foraging behavior in response to abiotic and biotic conditions, including prey (Bowen et al., 2002; Hocking et al., 2015, 2016), feeding context (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014), habitat (Páez-Rosas et al., 2014), season (Breed et al., 2009; Cotté et al., 2015) and oceanographic conditions (Simmons et al., 2010; Villegas-Amtmann et al., 2017; Abrahms et al., 2017), resulting in increased foraging success. However, other pinnipeds show little flexibility when feeding and appear constrained to a particular feeding strategy (e.g. northern fur seal, *Callorhinus ursinus*; Marshall et al., 2015). Specialization for a particular feeding strategy may allow animals to efficiently target specific prey but may also limit their ability to adapt to changes in prey resources (Villegas-Amtmann et al., 2008; Rita et al., 2017; Abrahms et al., 2017; Juárez-Ruiz et al., 2018).

Pinnipeds use multiple feeding strategies to capture and consume prey – biting, filter feeding and suction feeding (Taylor, 1987; Werth, 2000; Hocking et al., 2017; Kienle et al., 2017) – and each strategy is associated with cranial, mandible and dental adaptations (Jones and Goswami, 2010; Churchill and Clementz, 2015; Kienle and Berta, 2016). The two most common pinniped feeding strategies are biting (specifically pierce feeding) and suction feeding. Pierce feeding, characterized by using the jaws and/or teeth to puncture and capture prey, is often used in combination with suction, and prey are swallowed whole with little to no processing (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014; Kienle et al., 2018). Suction feeding is characterized by the generation of a subambient pressure differential that draws water and prey into the mouth (Gordon, 1984; Marshall et al., 2008). Suction can be used as a feeding strategy ('suction feeding') or as a mechanism that aids in prey capture and processing and is integrated with other feeding strategies ('suction'). These strategies allow pinnipeds to consume diverse prey in aquatic ecosystems worldwide (King, 1983; Riedman, 1990; Pauly et al., 1998).

Here, we examined the feeding strategies and kinematics of Hawaiian monk seals (*Neomonachus schauinslandi*), one of the oldest phocid (seal) lineages (Berta et al., 2018). Over the last 15 years, several studies have focused on understanding the feeding ecology of this species (Parrish et al., 2002, 2005; Longenecker, 2010; Cahoon et al., 2013; Wilson et al., 2017), as Hawaiian monk seals are one of the most endangered pinnipeds on the planet (Littnan et al., 2015). These studies have shown that Hawaiian monk

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seals are benthic foragers that actively search for prey in the benthos by digging, pushing and/or overturning sand, rocks and corals (Parrish et al., 2002; Parrish and Abernathy, 2006; Wilson et al., 2017). In addition, Hawaiian monk seals are categorized as generalist predators, consuming fish, cephalopods and crustaceans (Goodman-Lowe, 1998; Parrish et al., 2005; Longenecker, 2010; Cahoon et al., 2013). Although their skull and dental morphology suggests a biting strategy (Adam and Berta, 2002; Churchill and Clementz, 2015; Kienle and Berta, 2016), little is known about how Hawaiian monk seals capture or consume prey.

The goal of the present study was to examine the feeding strategies of Hawaiian monk seals and test for behavioral flexibility in feeding; this information is important for understanding the feeding capabilities and limitations of this endangered species. The first objective of this study was to document the feeding strategies of Hawaiian monk seals through controlled feeding trials. Previous studies have demonstrated the prevalence of suction feeding in pinnipeds, regardless of skull or dental morphology (Marshall et al., 2008, 2014, 2015; Hocking et al., 2012, 2014, 2015; Kienle et al., 2018). Based on these studies, we tested whether skull morphology corresponds with feeding strategy in Hawaiian monk seals. We predicted that Hawaiian monk seals would use both biting and suction feeding and that the feeding kinematics would differ between the strategies. The second objective was to examine behavioral flexibility in Hawaiian monk seals when fed on different prey types that varied in shape and size. We hypothesized that Hawaiian monk seals would show behavioral flexibility in their feeding strategies and kinematics when targeting different prey. We predicted that Hawaiian monk seals would primarily use biting when consuming larger prey and suction feeding when consuming smaller prey.

MATERIALS AND METHODS

Study animals

The study was conducted at the Long Marine Laboratory (University of California, Santa Cruz, Santa Cruz, CA, USA), the Minnesota Zoo (Apple Valley, MN, USA) and the Waikiki Aquarium (Honolulu, HI, USA). We examined the feeding behavior of seven sub-adult (n=1) and adult (n=6) Hawaiian monk seals [*Neomonachus schauinslandi* (Matschie 1905)] (Table 1). Data collection occurred from June 2016 to May 2017. The Hawaiian monk seals in this study had varying degrees of visual impairment (no impairment, n=2; partial impairment, n=4; full impairment, n=1). Visual impairment is relatively common in captive and wild pinnipeds, including Hawaiian monk seals (Greenwood, 1985; Hanson et al., 2009; Miller et al., 2013). All seals participated in the feeding trials, and there was no statistical effect of visual acuity on feeding performance. Seals were conditioned using positive reinforcement and voluntarily participated in the feeding trials. Behavioral research was approved by the Animal Care and Use Committee at each institution and conducted under federal authorizations for marine mammal research under National Marine Fisheries Service permits 15453, 17967 and 19590-01.

Feeding trials and kinematic variables

We built a feeding apparatus of PVC pipe that presented the Hawaiian monk seals with individual prey in a controlled and repeatable setting. A metal clamp held the prey and was attached to the feeding apparatus frame. A rope was attached to the clamp and tethered up the PVC pipe, which allowed the prey to be released from the clamp when the apparatus was underwater. The prey was clamped by the tail or arms, in the case of squid, and the feeding apparatus was submerged approximately 1 m underwater. The seal was stationed with a trainer across the pool at the beginning of each feeding trial. Once the apparatus was underwater, the seal was cued to swim to the apparatus. The clamp was then released so that the prey was floating in the water column before the seal reached the apparatus. The seal consumed the prey and then returned to the trainer. The feeding trials took advantage of the seal's natural feeding behavior, and minimal training was used to maintain the seal's position at the water's surface before the apparatus was submerged. Two GoPro cameras in underwater housings recording at 59.94 frames s^{-1} were mounted to the feeding apparatus to record anterior and lateral views of the feeding events.

Hawaiian monk seals were fed freshly thawed whole night smelt [*Spirinchus starksi*; standard length (SL)=10.00±0.57 cm, body depth (BD)=2.00±1.18 cm], capelin (*Mallotus villosus*; SL=13.85±0.58 cm, BD=2.16±0.20 cm), squid (*Loligo* sp.; SL=14.92±2.10 cm, BD=2.92±0.62 cm) and herring (*Clupea pallasii*; SL=20.63±4.12 cm, BD=4.15±0.38). The seal at the Waikiki Aquarium was fed night smelt, squid and herring as part of his regular diet; all other seals were fed capelin, squid and herring. Prey lengths ranged from 30% to 80% of the seals' head lengths, and prey were within the size range of prey consumed by Hawaiian monk seals in the wild (Goodman-Lowe, 1998; Parrish et al., 2005; Cahoon et al., 2013).

Each feeding trial was viewed frame-by-frame in GoPro Studio v. 2.5.7 or QuickTime Player to determine the sequence of feeding behavior, movement of the vibrissae and eyes, and identify feeding strategy and prey manipulation. We used five homologous anatomical landmarks to quantify kinematic variables: rostral tip of the upper jaw, rostral tip of the lower jaw, caudal-most point at the corner of the mouth, rostral-most point of the eye and rostral border of the hyoid apparatus (Fig. 1). Each landmark was digitized frame-by-frame for kinematic analysis in Tracker v. 4.92 (www.opensourcephysics.org). The kinematic variables measured in our study are as follows: (1) feeding event time (s): duration of the entire feeding event, from when the seal began to open its jaws (start of the feeding event) to when the entire prey was inside the mouth (end of the feeding event); (2) maximum gape (cm): maximum distance measured between the rostral tips of the upper and lower jaws during the feeding event; (3) time to maximum gape (s): time

Table 1. Life history information for the Hawaiian monk seals (*Neomonachus schauinslandi*, n=7) that participated in the feeding trials

Individual	Sex	Estimated age (years)	Mass (kg)	Standard head length (cm)	Standard body length (cm)	Institution
Ho'ailona	M	8	164	33	216	Waikiki Aquarium
KE-18	M	15	198	28	217	Long Marine Laboratory
Koa	F	22	214	38	214	Minnesota Zoo
Nani	F	22	191	25	208	Minnesota Zoo
Ola	F	22	195	31	214	Minnesota Zoo
Opua	F	22	171	34	204	Minnesota Zoo
Paki	F	22	205	40	228	Minnesota Zoo

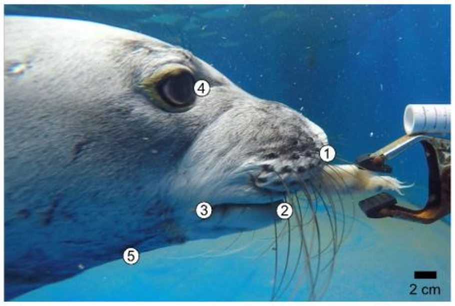

Fig. 1. Digitized anatomical landmarks illustrated on the lateral profile of a Hawaiian monk seal (KE-18). Landmarks are as follows: (1) rostral tip of upper jaw, (2) rostral tip of lower jaw, (3) caudal-most point at the corner of the mouth, (4) rostral-most point at the corner of the eye and (5) rostral border of the hyoid apparatus.

from the start of the feeding event to maximum gape; (4) maximum gape angle (deg): maximum angle measured between the rostral tips of the upper and lower jaws and the corner of the mouth during the feeding event; (5) time to maximum gape angle (s): time from the start of the feeding event to maximum gape angle; (6) time to initial jaw closure (s): time from the start of the feeding event to when the jaws and/or teeth first closed over the prey; (7) maximum gape angle opening velocity (deg s^{-1}): maximum angular rate of lower jaw opening during the feeding event; (8) time to maximum gape angle opening velocity (s): time from the start of the feeding event to maximum gape angle opening velocity; (9) maximum gape angle closing velocity (deg s^{-1}): maximum angular rate of lower jaw closing during the feeding event; (10) time to maximum gape angle closing velocity (s): time from the start of the feeding event to maximum gape angle closing velocity; (11) maximum gular depression (cm): greatest distance measured between the rostral corner of the eye and the rostral edge of the hyoid apparatus; (12) time to maximum gular depression (s): time from the start of the feeding event to maximum gular depression; and (13) number of jaw motions: number of dorso-ventral jaw movements throughout the feeding event. The seal's head had to be in lateral view throughout the feeding event and the entire prey had to be consumed in frame for a trial to be included in the kinematic analyses. For this reason, more feeding trials were conducted than were included in the kinematic dataset.

Statistical analyses

We ran linear mixed-effects models to investigate the relationship between feeding strategy, prey type and the 13 kinematic variables (lme4 package; Bates et al., 2015). In the full model, feeding strategy and prey type were the fixed effects, and we included an interaction between feeding strategy and prey. Individual, head length and visual acuity were included as random effects. We ran all combinations of variables in our models and used an Akaike information criterion (AIC) to rank the candidate models. We examined residual plots for each kinematic variable for obvious deviations from normality or homoscedasticity, but none were observed. We ran two additional sets of linear mixed-effects models to examine how characteristics of the prey, specifically prey size and shape, affected feeding kinematics. These models were identical to those described above, but either prey size (represented by the mean standard length for each prey type) or prey shape (measured by the geometric mean of prey standard length and prey body depth) were included as a fixed effect with feeding strategy instead of prey type.

We quantified flexibility, a measure of variation in a behavior between different experimental conditions (e.g. prey; Wainwright et al., 2008). A behavior was considered flexible if there was a statistically significant response to the experimental treatment (i.e. prey type), whereas a behavior was considered inflexible if there was not a statistically significant response (Wainwright et al., 2008). To determine whether the feeding strategies and kinematics were flexible between treatments, we ran ANOVAs with *F*-tests for each fixed effect to test the significance of each predictor variable (car and lme4 packages; Fox and Weisberg, 2011; Bates et al., 2015). Next, we used least-squares means to perform Tukey *post hoc* contrasts for each kinematic variable within each feeding strategy and prey type to determine which kinematic variables differed among prey (lsmeans package; Lenth, 2016). Hawaiian monk seals were considered flexible if there was a significant change in their kinematic performance in response to prey and inflexible if there was not a significant change in kinematic performance.

Based on the ANOVA results, we further examined variability within feeding strategies and between treatments by quantifying the coefficient of variation (CV=standard deviation/mean) for each kinematic variable. The CV is a measure of variation in a behavior under a particular set of experimental conditions. A low CV (values close to 0) indicates stereotypy, and a high CV (values close to 1) indicates high variability (Gerhardt, 1991; Wainwright et al., 2008).

We conducted a principal components analysis (PCA) to determine the major axes of variation between each feeding strategy and prey type (FactoMineR and missMDA packages; Lê et al., 2008; Josse and Husson, 2016). We used a correlation coefficient analysis to determine the positive and negative contributions of each kinematic variable to each principal component (PC) axis. PCs that explained 10% or more of the variation were retained, as determined from a scree plot of the variance contribute by each eigenvalue. All statistical analyses were conducted in R v. 3.3.3 (https://www.r-project.org/).

RESULTS

We conducted 1367 feeding trials with Hawaiian monk seals (night smelt: 44 trials, capelin: 663 trials, squid: 242 trials, herring: 418 trials). Seals primarily used suction feeding across all prey types (79–100% of all feeding trials) but were also observed pierce feeding with all prey types (0.01–21% of all feeding trials; Table 2, Fig. 2). Suction feeding was used most frequently (>99.99% of feeding trials) when seals targeted capelin, one of the smallest prey types in this study, and least frequently (79% of suction feeding trials) when seals targeted herring, the largest prey type (Table 2, Fig. 2). Conversely, pierce feeding was used most frequently when seals consumed herring (21% of herring feeding trials) and least frequently when seals consumed capelin (<0.01% of capelin feeding trials). One Hawaiian monk seal used more pierce feeding than suction feeding, but this was only observed when the seal consumed herring (73% of herring trials).

Suction feeding was characterized by a similar sequence of behaviors for all seals and prey types (Fig. 3, Movie 1). First, the seal approached the prey and pursed its lips to form a small, round opening. The lateral facial muscles tightened so that the sides of the mouth were drawn tightly together. The rostral-most portion of the jaws separated as the seal depressed its lower jaw. The prey was then

Table 2. Summary of Hawaiian monk seal kinematic data for each prey type (number of kinematic trials analyzed for each prey type: capelin=508, night smelt=37, squid=153 and herring=243)

	Capelin (*n*=6)		Night smelt (*n*=1)		Squid (*n*=7)		Herring (*n*=7)	
Kinematic variable	Suction	Pierce	Suction	Pierce	Suction	Pierce	Suction	Pierce
Proportion	1.00	0.00	0.92	0.08	0.91	0.09	0.79	0.21
Feeding event time (s)	0.19±0.12	0.43	0.19±0.16	0.36±0.22	0.29±0.30	0.65±0.18	0.40±0.31	0.94±0.53
Maximum gape (cm)	2.86±0.81	–	2.56±0.81	2.75±0.27	3.24±1.05	4.00±0.65	3.28±0.69	4.04±1.51
Time to maximum gape (s)	0.11±0.08	–	0.09±0.05	0.19±0.05	0.13±0.08	0.13±0.06	0.11±0.07	0.14±0.09
Maximum gape angle (deg)	17.13±5.06	–	14.98±3.81	22.20±0.98	17.98±6.44	29.17±6.36	20.01±6.86	24.06±7.56
Time to maximum gape angle (s)	0.12±0.08	–	0.08±0.05	0.19±0.05	0.13±0.08	0.13±0.06	0.11±0.07	0.15±0.11
Time to initial jaw closure (s)	0.20±0.10	–	0.16±0.05	0.32±0.03	0.22±0.12	0.23±0.07	0.23±0.10	0.28±0.17
Maximum gape angle opening velocity (deg s^{-1})	139.15±108.30	–	130.02±82.41	198.95±4.17	149.13±73.76	95.95±56.65	159.61±93.04	123.22±56.10
Time to maximum gape angle opening velocity (s)	0.07±0.06	–	0.01±0.01	0.12	0.08±0.07	0.05±0.01	0.07±0.05	0.04±0.02
Maximum gape angle closing velocity (deg s^{-1})	96.46±72.29	–	90.33±72.23	241.55±11.53	129.05±87.40	173.00±35.16	75.79±71.93	83.83±96.78
Time to maximum gape angle closing velocity (s)	0.16±0.09	–	0.11±0.05	0.24±0.05	0.17±0.11	0.16±0.06	0.17±0.09	0.22±0.15
Maximum gular depression (cm)	12.82±2.14	–	9.84±1.47	9.06	11.31±1.78	11.66	13.03±1.88	10.67±3.07
Time to maximum gular depression (s)	0.13±0.06	–	0.08±0.04	0.22	0.18±0.10	0.13	0.17±0.08	0.25±0.19
Number of jaw motions	1.11±0.34	2.00	1.21±0.41	2.33±0.58	1.24±0.60	3.13±0.84	1.49±0.84	3.40±1.16

Values are means±s.d.

drawn partly or entirely inside the mouth in a rapid, fluid motion. After the initial prey capture, the lower jaw was elevated, trapping the prey partly or entirely in the mouth. Jaw closure was frequently followed by water expulsion from the sides of the mouth (88.66% of suction feeding trials). In the majority of suction feeding trials (73.71%), the prey was pulled entirely inside the mouth during initial prey capture, and this was referred to as pure suction. In some suction feeding trials (26.29%), seals pulled the prey partly inside the mouth during initial prey capture, held it in the mouth, and then used another bout of suction (following the sequence described above) to pull the prey entirely inside the oral cavity; this was referred to as multiple bouts of suction. Multiple bouts of suction were used more frequently when seals fed on larger prey (capelin: 11.66%; night smelt: 20.59%; squid: 56.57%; herring: 43.65% of suction feeding trials).

Pierce feeding was characterized by a more variable combination of behaviors than suction feeding for Hawaiian monk seals (Fig. 4, Movie 1). Seals varied in whether biting or suction was used as the initial mode of prey capture. When seals used biting as the initial mode of prey capture (20.93% of pierce feeding trials), the seal approached the prey and the lips were curled back, exposing the incisors, canines and postcanines in lateral view. The lower jaw was quickly depressed, and the seal moved its head so that the prey was positioned between the upper and lower jaws. The lower jaw was then quickly elevated, resulting in the seal biting down on the prey, trapping it between the teeth and jaws. Sometimes seals used biting to manipulate or reorient the prey before it entered the mouth. When suction was used initially (79.07% of pierce feeding trials), it followed the same pattern described in suction feeding trials, but the prey was never pulled entirely inside the mouth during initial prey capture. Regardless of whether the initial feeding behavior was biting or suction, after the seal closed its mouth over the prey, the seal used variable sequences of suction and biting to pull the prey entirely inside the oral cavity. When pierce feeding, seals never consumed the prey with only one jaw motion. Also, suction was always used in combination with biting to pull the prey inside the mouth.

All individuals showed similar patterns in their use of the two feeding strategies, with the exception of one Hawaiian monk seal that never used pierce feeding. All seals actively engaged their vibrissae in all feeding trials, and this was characterized by flexing the supraorbital and mystacial vibrissae forward when approaching the prey and keeping the vibrissae protracted throughout the feeding event. Hawaiian monk seals kept their eyes open in the majority of feeding trials (95.22% of suction feeding trials; 94.34% of pierce feeding trials). Although seals were always presented with the prey head-first relative to their approach, seals varied in whether they consumed the prey head-, side- or tail-first. Seals consumed prey head-first most often when suction feeding (55.73% of suction feeding trials) and side-first most often when pierce feeding (46.75% of pierce feeding trials). When consuming the prey side- or tail-first, the seal would either approach from the side and push the prey with the rostrum to reposition it, or use suction and/or biting to turn the prey side- or tail-first before consuming it. Two seals were occasionally observed blowing bubbles out of their noses during the feeding trials. One seal was occasionally observed making repeated dorso-ventral motions of the lower jaw and gular region when using suction feeding to consume night smelt (5.88% of night smelt suction feeding trials) after prey was inside the mouth prior to swallowing. This behavior has been observed in other pinnipeds and

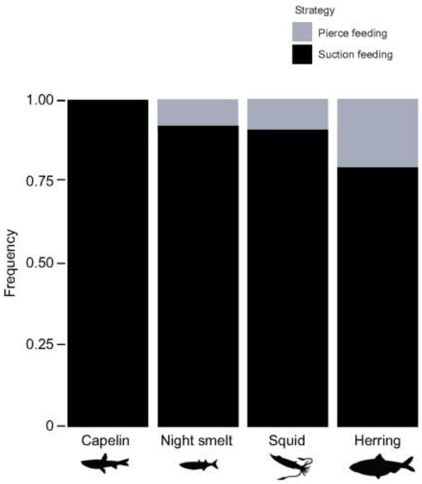

Fig. 2. Frequency of pierce feeding and suction feeding strategies used by Hawaiian monk seals (n=7) when consuming different prey (e.g. capelin, night smelt, squid or herring).

is sometimes referred to as chewing (Hocking et al., 2014, 2015, 2016; Kienle et al., 2018).

Feeding kinematics

Across the 1367 feeding trials, 939 trials were analyzed for kinematics [68.69% of all feeding trials; night smelt=37 (n=1), capelin=508 (n=6), squid=153 (n=7), herring=243 (n=7); here we define n as the number of Hawaiian monk seals that were fed each prey type]. The linear mixed-effects models confirmed that pierce and suction feeding were kinematically distinct strategies, significantly differing across eight of the 13 kinematic variables (Table 2). Suction feeding was characterized by significantly smaller maximum gapes (n=7, F_1=4.59, P=0.03) and gape angles (n=7, F_1=6.31, P=0.01), larger maximum gular depressions (n=7, F_1=4.88, P<0.01) and fewer numbers of jaw motions (n=7, F_1=274.43, P<0.01) compared with pierce feeding. Additionally, compared with pierce feeding, suction feeding resulted in shorter feeding event times (n=7, F_1=118.81, P<0.01), as well as shorter times to the following: jaw closure (n=7, F_1=6.49, P=0.01), maximum gape angle closing velocity (n=7, F_1=5.18, P=0.02) and maximum gular depression (n=7, F_1=11.36, P<0.01). There was no interaction between feeding strategy and prey type for most of the kinematic variables, with the exception of feeding event time (n=7, F_3=2.16, P=0.02). We found similar results from linear mixed-effects models when we incorporated prey size and shape. The only exceptions were that the maximum gape angle closing velocity was significantly slower when suction feeding compared with pierce feeding for both the prey size (n=7, F_1=4.10, P=0.04) and shape models (n=7, F_1=3.98, P=0.05). There was also a significant interaction between feeding strategy and prey shape for maximum gape angle closing velocity (n=7, F_1=4.09, P=0.04).

Table 3. Principal component loadings for each kinematic variable for principal components (PCs) 1 and 2

Kinematic variable	PC1 (53.77%)	PC2 (28.39%)
Feeding event time (s)	0.21	**0.41**
Maximum gape (cm)	0.14	**0.46**
Time to maximum gape (s)	**0.36**	−0.14
Maximum gape angle (deg)	0.24	0.33
Time to maximum gape angle (s)	**0.37**	−0.10
Time to initial jaw closure (s)	**0.37**	−0.04
Maximum gape angle opening velocity (deg s^{-1})	0.15	**−0.45**
Time to maximum gape angle opening velocity (s)	0.24	−0.31
Maximum gape angle closing velocity (deg s^{-1})	0.26	−0.19
Time to maximum gape angle closing velocity (s)	**0.36**	−0.05
Maximum gular depression (cm)	−0.15	0.15
Time to maximum gular depression (s)	**0.32**	0.03
Number of jaw movements	0.26	0.35

Bold values indicate kinematic variables that were significantly correlated with each PC axis.

The first two PCs explained 82.16% of the variation in the feeding kinematics (PC1: 53.77%, PC2: 28.39%; Table 3, Fig. 5). Based on the correlation coefficient analysis, five timing variables were identified as significantly and positively correlated with PC1 (P≤0.01): time to maximum gape, time to maximum gape angle, time to initial jaw closure, time to maximum gape angle closing velocity and time to maximum gular depression. PC1 was associated with the separation of pierce and suction feeding kinematics. Three kinematic variables were significantly correlated with PC2 (P≤0.03); feeding event time and maximum gape were positively correlated and maximum gape angle opening velocity was negatively correlated. PC2 resulted in three clusters: (1) pierce feeding kinematics for small prey (i.e. night smelt), (2) suction feeding kinematics for all prey types and (3) pierce feeding kinematics for larger prey (i.e. squid and herring).

Fig. 3. Sequence of feeding behavior associated with suction feeding, exemplified by a Hawaiian monk seal (Ho'ailona). (A) Seal approaches prey (night smelt) with the vibrissae actively engaged. (B) Seal forms the lips into a small circular opening, opens the lower jaw to maximum gape and gape angle and pulls prey into the mouth by suction. (C) Seal closes mouth over prey during initial jaw closure. The video was filmed at 59.94 frames s^{-1}, and the time is displayed as hours:minutes:seconds:frames.

Fig. 4. Sequence of feeding behavior associated with pierce feeding, exemplified by a Hawaiian monk seal (Ho'ailona). (A) Seal approaches prey (herring) with the vibrissae actively engaged. (B) Seal forms the lips into a small circular opening, opens the lower jaw to maximum gape and gape angle, and pulls prey into the mouth by suction. (C) Jaws opened to maximum gape and gape angle with teeth visible as seal engulfs prey with the mouth. (D) Mouth closes over prey during jaw closure. The video was filmed at 59.94 frames s^{-1}, and the time is displayed as hours:minutes:seconds:frames.

Behavioral flexibility in feeding kinematics

The linear mixed-effects models showed that 11 of the 12 kinematic variables significantly differed between prey types: feeding event time (n=7, F_3=61.43, P<0.01), maximum gape (n=7, F_3=7.72, P<0.01) and gape angle (n=7, F_3=5.95, P<0.01), time to maximum gape (n=7, F_3=5.97, P<0.01) and gape angle (n=7, F_3=5.86, P<0.01), time to initial jaw closure (n=7, F_3=14.38, P<0.01), maximum gape angle closing velocity (n=7, F_3=3.41, P=0.02), time to maximum gape angle opening (n=7, F_3=3.20, P=0.02) and closing velocities (n=7, F_3=7.89, P<0.01), time to maximum gular depression (n=7, F_3=7.33, P<0.01) and the number of jaw motions (n=7, F_3=36.05, P<0.01). These results were largely concordant with the linear mixed-effects models for prey size and prey shape, with a few exceptions. Five kinematic variables that significantly differed among the prey types were not significantly different for either prey size or prey shape: time to maximum gape and gape angle, time to maximum gape angle opening and closing velocity, and time to maximum gular depression. Additionally, time to initial jaw closure did not significantly differ in the prey size model.

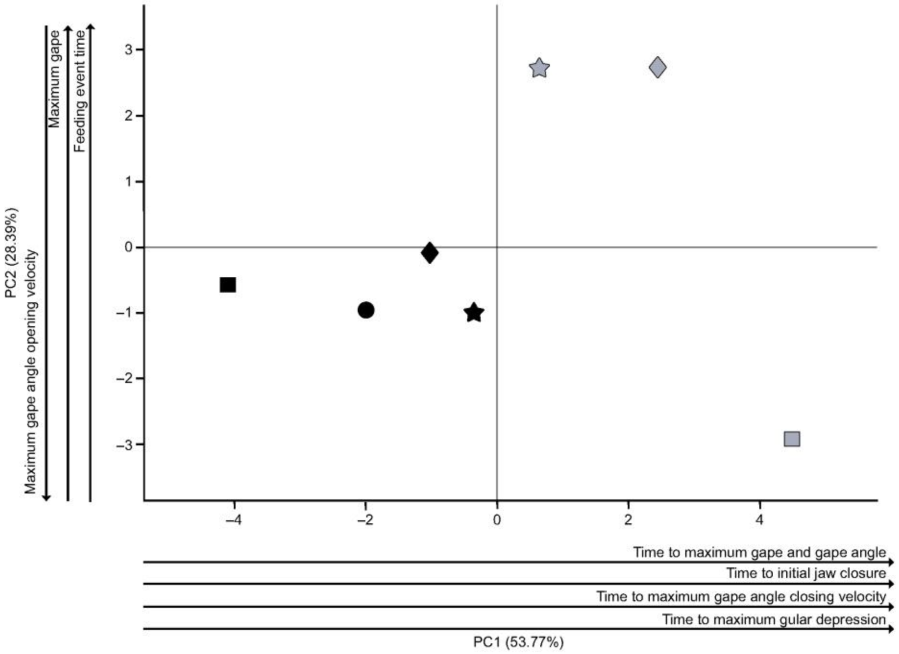

Fig. 5. Principal component axes of feeding kinematic variation across prey types. Symbols on the plot represent prey types, where circles represent capelin trials, squares represent night smelt trials, stars represent squid trials and diamonds represent herring trials. Colors indicate feeding strategy, where black is suction feeding and gray is pierce feeding. Variables that loaded strongly on each axis are represented by arrows that indicate the direction in which the variables increase along the axis.

Table 4. Coefficient of variation for each prey type for each feeding strategy (number of kinematic trials analyzed for each prey type: capelin=508, night smelt=37, squid=153 and herring=243)

	Capelin (n=6)		Night smelt (n=1)		Squid (n=7)		Herring (n=7)	
Kinematic variable	Suction	Piece	Suction	Pierce	Suction	Piece	Suction	Piece
Feeding event time (s)	0.51	–	0.83	0.61	0.62	0.20	0.59	0.40
Maximum gape (cm)	0.28	–	0.32	0.10	0.24	0.16	0.19	0.33
Time to maximum gape (s)	0.55	–	0.53	0.28	0.54	0.45	0.53	0.22
Maximum gape angle (deg)	0.28	–	0.25	0.04	0.24	0.22	0.29	0.28
Time to maximum gape angle (s)	0.55	–	0.53	0.28	0.52	0.45	0.52	0.22
Time to initial jaw closure (s)	0.44	–	0.34	0.09	0.33	–	0.38	–
Maximum gape angle opening velocity (deg s^{-1})	0.66	–	0.63	0.02	0.53	0.59	0.50	0.06
Time to maximum gape angle opening velocity (s)	0.71	–	0.47	–	0.70	0.29	0.62	0.47
Maximum gape angle closing velocity (deg s^{-1})	0.69	–	0.80	0.05	0.37	0.20	0.87	0.29
Time to maximum gape angle closing velocity (s)	0.45	–	0.41	0.20	0.49	0.35	0.45	0.47
Maximum gular depression (cm)	0.13	–	0.15	–	0.10	–	0.13	0.07
Time to maximum gular depression (s)	0.40	–	0.44	–	0.42	–	0.34	0.00
Number of jaw motions	0.28	–	0.34	0.25	0.41	0.21	0.37	0.31
Mean	0.46	–	0.46	0.19	0.42	0.31	0.44	0.26

For each of the 11 kinematic variables that significantly differed among prey types, we then determined which prey types drove these patterns using Tukey *post hoc* contrasts. Seals had significantly longer feeding event times when suction feeding on herring compared with the other prey types ($n=7$, Tukey *post hoc*, $P\leq 0.02$). When suction feeding, seals also had larger maximum gapes and gape angles when consuming herring compared with capelin ($n=7$, Tukey *post hoc*, $P<0.01$) and night smelt ($n=7$, Tukey *post hoc*, maximum gape: $P=0.02$, maximum gape angle: $P=0.05$); additionally, seals had longer times to maximum gape and gape angle when consuming squid compared with capelin ($n=7$, Tukey *post hoc*, $P<0.01$) and herring ($n=7$, Tukey *post hoc*, $P<0.01$). Seals had shorter times to initial jaw closure when suction feeding capelin compared with squid ($n=7$, Tukey *post hoc*, $P<0.01$) and herring ($n=7$, Tukey *post hoc*, $P=0.05$); similarly, seals had shorter times to initial jaw closure when suction feeding squid compared with herring ($n=7$, Tukey *post hoc*, $P<0.01$). Seals had faster times to maximum gape angle opening velocity when consuming capelin compared with squid ($n=7$, Tukey *post hoc*, $P=0.01$); similarly, maximum gape angle closing velocity was faster when seals targeted squid compared with herring ($n=7$, Tukey *post hoc*, $P=0.01$). Seals showed longer times to maximum gape angle closing velocity when targeting squid with suction feeding compared with capelin and herring ($n=7$, Tukey *post hoc*, $P<0.01$). Seals also had longer times to maximum gular depression when consuming squid compared with capelin ($n=7$, Tukey *post hoc*, $P<0.01$) and herring ($n=7$, Tukey *post hoc*, $P=0.03$). The number of jaw motions significantly differed between prey types ($n=7$, Tukey *post hoc*, $P<0.01$); seals used the fewest numbers of jaw motions when consuming capelin and the largest numbers of jaw motions when consuming herring using both pierce and suction feeding.

Variability in feeding kinematics

We quantified variability in feeding kinematics for each prey type by averaging the CV across all seals within each feeding strategy for each prey type (Table 4). Suction feeding kinematics had the highest average CV within all prey types compared with the pierce feeding kinematics. When suction feeding, seals had the most variability in kinematic performance when consuming capelin and night smelt and were the most stereotyped when consuming squid. When suction feeding, the highest variability was observed in the time to maximum gape angle opening velocity for the capelin and squid trials, feeding event time for the night smelt trials, and maximum gape angle closing velocity for the herring trials. In contrast, when suction feeding, maximum gular depression was the most stereotyped kinematic variable when seals consumed all prey types. When pierce feeding, seals had the most variability in kinematic performance when consuming squid and were the most stereotyped when consuming night smelt. The most variable kinematics when pierce feeding were feeding event time for the night smelt trials, maximum gape angle opening velocity for the squid trials, and time to maximum gape angle opening and closing velocities for the herring trials. In contrast, when pierce feeding, the most stereotyped kinematics were maximum gape angle opening velocity for the night smelt trials, maximum gape for the squid trials, and time to maximum gular depression for the herring trials.

DISCUSSION

Hawaiian monk seals used two feeding strategies, suction feeding and biting (specifically pierce feeding), and exhibited behavioral flexibility when targeting whole prey in controlled feeding trials with four prey treatments. Suction feeding and biting are common pinniped feeding strategies (Werth, 2000; Hocking et al., 2017; Kienle et al., 2017) and are widely used by many diverse aquatic taxa, including sharks, fish, sea otters and cetaceans (Taylor, 1987; Schwenk, 2000; Werth, 2000). The prevalence of these feeding strategies among many phylogenetically distinct lineages, especially those that have secondarily entered the aquatic environment, suggests that the physical properties of water have led to a strong convergence in feeding strategies.

Feeding strategies and kinematics

Hawaiian monk seals primarily used suction feeding, regardless of prey size and shape. Their suction feeding behavior is similar to that described for other pinnipeds (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014; Kienle et al., 2018), showing that suction feeding in pinnipeds follows a conserved sequence of behaviors. Suction feeding was kinematically distinct from pierce feeding and characterized by shorter temporal events, such as jaw closure, maximum gape angle closing velocity, maximum gular depression and overall feeding times, as well as smaller maximum gapes and gape angles, larger maximum gular depressions and fewer jaw motions when compared with pierce feeding. Maximum gape occurred first, followed by maximum gular depression and then finally jaw closure. This kinematic sequence matches that described for other pinnipeds (Marshall et al., 2008, 2014, 2015; Kienle et al., 2018). Compared with other seal species for which comparable data exist (i.e. bearded, harbor, ringed and spotted seals), Hawaiian monk seals had faster feeding event times, smaller maximum gapes and gape angles, smaller maximum gape angle opening and closing velocities, larger maximum gular depressions, and fewer numbers of jaw motions when suction feeding (Kienle et al., 2018). These kinematic differences may be related to differences in body size between the different species, as Hawaiian monk seals are considerably larger (Krüger et al., 2014). Hawaiian monk seals also exhibited larger maximum gular depressions when suction feeding compared with pierce feeding, which was not observed in bearded, harbor, ringed or spotted seals (Kienle et al., 2018). However, large gular depressions when suction feeding have been reported for other pinnipeds (Marshall et al., 2008, 2014, 2015), indicating that gular depression is variable among and within species. The present study on Hawaiian monk seals contributes to a growing behavioral dataset that demonstrates that suction feeding is an important and widespread pinniped feeding strategy (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014, 2015; Kienle et al., 2018).

Based on their skull and dental morphology, Hawaiian monk seals (as well as their close relatives, Caribbean monk seals, *Neomonachus tropicalis*, and Mediterranean monk seals, *Monachus monachus*) are classified as pierce feeders. However, here we show that Hawaiian monk seals primarily use suction feeding. Previous studies of other pinniped taxa have observed similar patterns (Marshall et al., 2014, 2015; Hocking et al., 2014, 2015; Kienle et al., 2018), providing strong evidence that pinnipeds do not require specialized skull or dental morphologies to generate suction. Nevertheless, as their skull and dental morphologies predict, Hawaiian monk seals also used pierce feeding across all four prey treatments. Pierce feeding was characterized by longer temporal events (including jaw closure, maximum gape angle closing velocity and maximum gular depression) and overall feeding times, as well as larger maximum gapes and gape angles, smaller gular depressions and more jaw motions compared with suction feeding. Hawaiian monk seal pierce feeding kinematics are concordant with those described for other pinniped taxa (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014; Kienle et al., 2018), and suggest that, like suction feeding, pierce feeding and its associated kinematics are conserved among pinnipeds.

Behavioral flexibility and variability

Hawaiian monk seals showed behavioral flexibility in feeding strategies and kinematics when consuming different prey. Suction feeding was most prevalent when capturing small prey (e.g. capelin, night smelt), whereas pierce feeding was more common when consuming larger prey (e.g. squid, herring). There appears to be a threshold where it is more efficient for predators to switch between biting and suction feeding, and this threshold is likely based on predator head size relative to prey size and shape. For example, Australian and subantarctic fur seals switched from suction feeding to biting when prey had a body depth greater than 7.5 cm (Hocking et al., 2015). We documented the beginning of this prey size relative to predator head size threshold, as Hawaiian monk seals used more biting as both prey size and body depth increased. The largest prey (herring) was ~80% of the Hawaiian monk seal's head length, and seals used more pierce feeding on herring compared with the smaller prey types. If we had presented Hawaiian monk seals with even larger prey (>80% of the seal's head length), we predict that the seals would have switched to using more biting than suction feeding, which has been observed in other pinnipeds (Hocking et al., 2014, 2015, 2016). Hawaiian monk seals also showed behavioral flexibility in their feeding kinematics. Several kinematic variables changed as Hawaiian monk seals consumed different prey, including all timing variables, maximum gape and gape angle, maximum gape angle closing velocity and the number of jaw motions. Hawaiian monk seals can therefore modulate their feeding kinematics in response to prey, which is advantageous for this generalist predator that consumes many different prey types (Goodman-Lowe, 1998; Parrish et al., 2005; Longenecker, 2010; Cahoon et al., 2013).

Suction feeding and pierce feeding are associated with trade-offs in terms of efficiency, as measured by timing events. When we compare mean feeding event times for pierce and suction feeding, Hawaiian monk seals can consume 1.2 to 2.4 times more prey using suction feeding than pierce feeding over the same time period. Suction feeding also requires fewer jaw motions and is associated with smaller gapes and gape angles. Suction feeding is likely a highly efficient feeding strategy when seals are targeting small to medium sized prey that can be consumed quickly with little to no processing. Suction feeding is the primary strategy used by benthic foraging pinnipeds (e.g. bearded seals; Hawaiian monk seals; walruses, *Odobenus rosmarus*; Australian fur seals, *Arctocephalus pusillus*; Kastelein and Mosterd, 1989; Kastelein et al., 1994; Marshall et al., 2008; Hocking et al., 2014; Kienle et al., 2018), suggesting that this feeding mode is highly effective when targeting cryptic and/or concealed benthic prey. In contrast, pierce feeding is less efficient in terms of timing, as it takes longer to consume prey; it also requires seals to open their mouths wider and use more jaw motions to pull prey entirely inside the mouth. Although pierce feeding may not be an efficient strategy for consuming small to medium prey, it becomes important when seals target larger prey that cannot be consumed by suction feeding alone. Larger prey may also have increased energy densities that compensate for the increased time and energy required to consume them.

Hawaiian monk seals showed variability in their feeding kinematics when targeting different prey. The suction feeding kinematics were the most variable, suggesting that Hawaiian monk seals can adjust their suction feeding kinematic performance to particular feeding scenarios. A similar pattern was observed in bearded, harbor, ringed and spotted seals (Kienle et al., 2018), indicating that suction feeding is a highly variable pinniped feeding strategy. In contrast, pierce feeding was the most stereotyped; this was also observed by Kienle et al. (2018). Pierce feeding appears to be a more conserved pinniped feeding strategy than suction feeding. These patterns of variability for pinnipeds differ from those in other aquatic vertebrates, such as fishes, where biting is often the most variable strategy compared with suction feeding (Alfaro et al., 2001; Porter and Motta, 2004; Mehta and Wainwright, 2007).

Comparison with foraging behavior in the wild

Hawaiian monk seals in our controlled studies showed feeding behaviors similar to those observed in the wild. Crittercam video footage collected from wild Hawaiian monk seals has shown that seals consume small to large prey; small prey are captured quickly and are often not visible because of their size and quick handling time (~1 s), while larger prey involve more processing and handling time (up to 1.5 min; Parrish et al., 2000; Wilson et al., 2017). Although the feeding strategies used by wild Hawaiian monk seals have not been described, we predict that small to medium sized prey are primarily consumed by suction feeding, whereas larger prey are consumed by biting. There is potential in the future for determining feeding strategies, handling times and search effort for different prey types, and quantifying the energetic costs of different feeding strategies using Crittercam video footage collected from wild Hawaiian monk seals to understand the trade-offs between suction feeding and biting.

Hawaiian monk seals in our study exhibited behavioral flexibility in feeding, changing their behavior and kinematics to consume different prey types; this matches descriptions of wild Hawaiian monk seal foraging behavior. Hawaiian monk seals in the wild are opportunistic foragers, consuming a range of prey that vary in size and shape, from parrotfish and congrid eels to Hawaiian bobtail squid and day octopus (Goodman-Lowe, 1998; Parrish et al., 2005; Longenecker, 2010; Cahoon et al., 2013). To be successful foragers, Hawaiian monk seals must adapt their feeding behavior to particular feeding contexts, from benthic foraging on demersal prey to pelagic foraging on mid-water prey (Parrish et al., 2002; Parrish and Abernathy, 2006; Wilson et al., 2017). Therefore, behavioral flexibility in feeding is likely advantageous, allowing Hawaiian monk seals to take advantage of the diverse prey resources in their tropical habitat.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.S.K., R.S.M.; Methodology: S.S.K., R.S.M.; Software: S.S.K.; Validation: S.S.K., A.C.; Formal analysis: S.S.K., A.C.; Investigation: S.S.K., T.K., B.R., C.R., L.C., G.L.; Resources: T.K., B.R., C.R., L.C., G.L.; Data curation: S.S.K., A.C.; Writing - original draft: S.S.K.; Writing - review & editing: S.S.K., D.P.C., R.S.M.; Visualization: S.S.K., R.S.M.; Supervision: D.P.C., R.S.M.; Project administration: S.S.K., D.P.C., R.S.M.; Funding acquisition: S.S.K., D.P.C., R.S.M.

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Supplementary information

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CHAPTER 4

SUPPLEMENTARY INFORMATION

MOVIE 1. Examples of suction feeding and biting (pierce feeding) for Hawaiian monk seals targeting different types of prey (night smelt, capelin, squid, and herring).

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SUMMARY

Animals have evolved diverse strategies for capturing and consuming prey, as foraging success is intrinsically linked to fitness (Schoener, 1971; Taylor, 1987; Schwenk, 2000; Werth, 2000a). Intraspecific variation in foraging strategies is widespread, with individuals switching between strategies in response to intrinsic and extrinsic factors, including life history (e.g., sex, age), geography, environmental fluctuations, and prey availability (Tremblay and Cherel, 2003; Vander Zanden et al., 2010; Weise et al., 2010; Peckham et al., 2011; Patrick and Weimerskirch, 2014; Kernaléguen et al., 2015). Intraspecific variation when feeding can have cascading consequences, from altering population dynamics to changing ecosystem functioning (Bolnick et al., 2003, 2011; Araújo et al., 2011), Additionally, the ability of species to use multiple foraging strategies results in increased behavioral flexibility, and this flexibility is advantageous for adapting and responding to changing abiotic and biotic conditions. This dissertation builds upon some foundational studies that have highlighted the importance of understanding and examining intraspecific variation in ecological processes. This dissertation focuses on examining intraspecific variation and behavioral flexibility in the foraging strategies of seals, a diverse group of marine carnivores that occupy the role of top predators in aquatic ecosystems worldwide.

In Chapter 1 of this dissertation, I compare the foraging strategies of adult northern elephant seals from multiple breeding colonies across the species range and examine the different factors that drive intraspecific variation in the species. I find

that northern elephant seals use multiple strategies on their biannual at-sea foraging trips, within individuals differing in their movement patterns, dive behavior, and foraging success. Northern elephant seals occupy a wide ecological niche that includes continental shelf ecosystems from Baja California to the Aleutian Islands and mesopelagic ecosystems from the California Current to the Subarctic Pacific. Intraspecific variation is driven by the combination of sex, season, and breeding colony. The results of this chapter highlight the importance of sex-specific and seasonal differences in foraging behavior, and these findings are supported by studies of northern elephant seals from a single breeding colony (Le Boeuf et al., 2000; Simmons et al., 2010; Robinson et al., 2012). This chapter also adds breeding colony as an important factor contributing to intraspecific variation in northern elephant seal foraging strategies. These different foraging strategies may have arisen to reduce competition with conspecifics, and/or to balance trade-offs between foraging success and energy expenditure. This widespread variation has likely contributed to continued success of northern elephant seals as marine predators in the North Pacific Ocean.

Chapter 1 demonstrates the importance of comparative, range-wide studies in biology, as individuals from a single population are not representative of the entire species. Building on the findings of Chapter 1, future studies should continue to examine intraspecific variation of northern elephant seals across the species range. There are numerous projects that could be developed comparing the life history, behavior, ecology, and physiology of northern elephant seals across their range, from examining thermoregulatory strategies along a latitudinal gradient to comparing predator-prey dynamics at different colonies. Using northern elephant seals as a model system,

In Chapter 2 of this dissertation, I examine intraspecific niche divergence in the foraging strategies of northern elephant seals. In this chapter, I find that male and female northern elephant seals use different foraging strategies. Males are benthic continental shelf predators, while females are mesopelagic predators. Contrary to previous studies that have shown potential overlap between male and female at-sea behavior (Simmons et al, 2010; Robinson et al., 2012; Peterson et al., 2015), I document little to no overlap between the male and female strategies. My results show that the sexes occupy different ecological niches in North Pacific ecosystems. The male strategy is associated with higher foraging success and higher mortality compared to the female strategy. Similar trade-offs between foraging success and survival have been documented in other sexually dimorphic species (Spidle et al., 1998; Mooring et al., 2003; Bunnefeld et al., 2006). In northern elephant seals, this trade-off between foraging success and survival is likely related to sex-specific life histories. Females maximize their fitness by reproducing early and having a long life in which to reproduce (Reiter et al., 1981). Pelagic habitats allow females to meet their energetic needs, while also being relatively safe. In contrast, males maximize fitness by surviving to maturity, attaining large body sizes quickly, and successfully reproducing in the 1-2 years an adult male has access to breeding opportunities (Le Boeuf, 1974). Continental shelf ecosystems provide the resources males need to reach and sustain their large body sizes, even though feeding in these areas result in higher mortality. Northern elephant seals are extreme examples of sexual dimorphism (Bartholomew, 1970; Ralls, 1977), and this dimorphism is reflected in their sex-specific strategies for maximizing fitness. Chapter 2 highlights that intraspecific niche divergence, along with sexual selection, are responsible for the maintenance of sexual dimorphism in this species.

Based on the finding of Chapter 2, there are several future research projects that would be interesting to explore. In light of the dramatic differences in survival between male and female northern elephant seals, it would be interesting to investigate the different causes of at-sea mortality. While in Chapter 2 we hypothesize that male seals have higher mortality rate due to predation, this needs to be explicitly tested. Future work should also examine the relationship between foraging success and reproductive success in northern elephant seals, specifically focusing on male seals that operate in one of the most competitive breeding systems among mammals (Bartholomew, 1970). Furthermore, future studies should explicitly examine the role of intraspecific niche divergence in the evolution and maintenance of sexual dimorphism in other sexually dimorphic species.

In Chapter 3 of this dissertation, I compare inter- and intraspecific variation in feeding strategies of four species of seals: bearded, harbor, ringed, and spotted seals. In this chapter, I find that all four species primarily used a suction feeding strategy but were also observed using a biting strategy. Suction feeding and biting were associated with distinct kinematic profiles, suggesting strong convergence in the underwater feeding strategies used by seals. All four species showed intraspecific variation in their feeding behavior and kinematics and had the ability to switch between biting and suction feeding depending on the context. The results of this study are largely concordant with previous studies of bearded and harbor seals (Marshall et al., 2008, 2014), and this is the first study to document feeding strategies in ringed and spotted seals. The ability of all four species to use multiple feeding strategies is likely advantageous when foraging in dynamic marine ecosystems that favor opportunistic predators.

Based on the findings of Chapter 3, future studies should document and examine the feeding strategies of other pinnipeds, as well as other clades of marine mammals. Currently, little is known about the feeding strategies of many marine mammal taxa; without these data, comparative studies of feeding strategies are difficult. Additional work is needed to understand the relationship between morphology, physiology, ecology, and behavior in the evolution and use of different feeding strategies. Furthermore, it is currently unclear what are the benefits and constraints associated with different feeding strategies, and research efforts should focus on understanding the prevalence of different strategies and examining trade-offs between strategies.

In Chapter 4 of this dissertation, I examine intraspecific variation and behavioral flexibility in the feeding strategies of Hawaiian monk seals. Building on Chapter 3, I examined how individuals change their feeding behavior and kinematics in response to changes in prey size and shape. In Chapter 4, I conducted controlled feeding trials with seven Hawaiian monk seals that were fed different prey types.

Similar to Chapter 3, I find that Hawaiian monk seals primarily used a suction feeding strategy across all prey types, but sometimes use a biting strategy. Together, Chapters 3 and 4 add to a growing body of literature showing that suction feeding is an important and common pinniped feeding strategy (Marshall et al., 2008, 2014, 2015; Hocking et al., 2012, 2014, 2015); this differs from the predictions made from studies of skull and tooth morphology (Adam and Berta, 2002; Churchill and Clementz, 2016; Kienle and Berta, 2016). In Chapter 4, I also document that Hawaiian monk seals exhibit behavioral flexibility in their use of the two feeding strategies. Suction feeding is used most frequently when targeting small to medium sized prey and biting is used with increasing frequency on larger prey. Hawaiian monk seals can change their feeding behavior and kinematics when using different feeding strategies and targeting different prey types. This behavioral flexibility is advantageous as it allows Hawaiian monk seals to target diverse prey resources in their tropical habitat.

Building on the results of Chapter 4, future studies should integrate both captive feeding trials and studies of feeding in wild animals to understand the feeding strategies of different species. Specifically, it would be interesting to determine feeding strategies, handling times, and search effort for different prey types and quantifying the energetic costs of different feeding strategies. For many species, the increasing use of video camera footage collected from instruments deployed on wild animals will provide a novel platform for understanding trade-offs between different strategies and behaviors.

This dissertation is an investigation of the foraging strategies of seals and examines intraspecific variation and behavioral flexibility at different scales, from individuals to species. This work advances our understanding of how individuals, populations, and species use different suites of behaviors to maximize foraging success in response to different abiotic and biotic factors. The ability to switch between different foraging strategies depending on the context was likely important as early pinnipeds transitioned from feeding on land to feeding in the water. And, in an era of widespread and rapid environmental change, flexibility and intraspecific variation in feeding are going to be a critical to these species' continued survival.

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