

RESEARCH ARTICLE

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

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

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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 \pm 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.

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

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 (<i>Erignathus barbatus</i>)	Siku	M	2	158.0	21.8	100.4
	Noatak	M	1	150.1	17.9	89.7
Harbor seal (<i>Phoca vitulina</i>)	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
	Nayak	F	5	116.2	14.4	23.8
Ringed seal (<i>Pusa hispida</i>)	RS1	M	21	108.7	15.8	41.0
	Pimniq	M	3	89.2	13.2	28.5
	Amak	M	6	138.3	27.6	55.4
Spotted seal (<i>Phoca largha</i>)	Tunu	M	5	138.9	27.1	68.4

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.

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 nmlme packages: Halekoh and Højsgaard, 2014; Bates et al., 2015; <https://CRAN.R-project.org/package=nmlme>). 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 ($\text{CV} = \text{standard deviation}/\text{mean}$) 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/>).

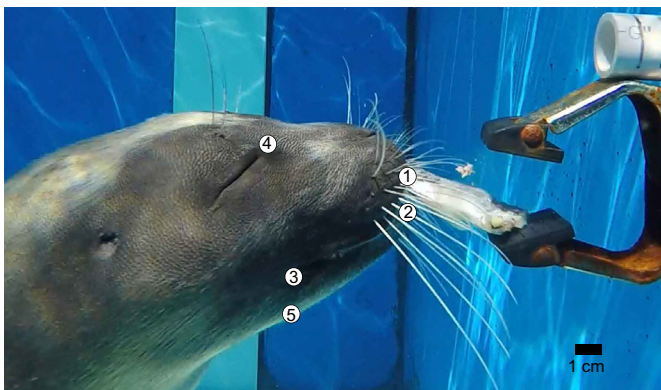


Fig. 1. Anatomical landmarks digitized during frame-by-frame video analyses, shown on the lateral profile of a ringed seal (RS1). Landmarks are as follows: (1) rostral tip of the upper jaw, (2) rostral tip of the lower jaw, (3) caudal-most point at the corner of the mouth, (4) rostral-most point of the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

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 (Hiimae 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 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.

Table 2. Summary of kinematic data for each species

Kinematic variable	Bearded seals (n=2)		Harbor seals (n=3)		Ringed seals (n=3)		Spotted seals (n=2)	
	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	280.60±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	0.17±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

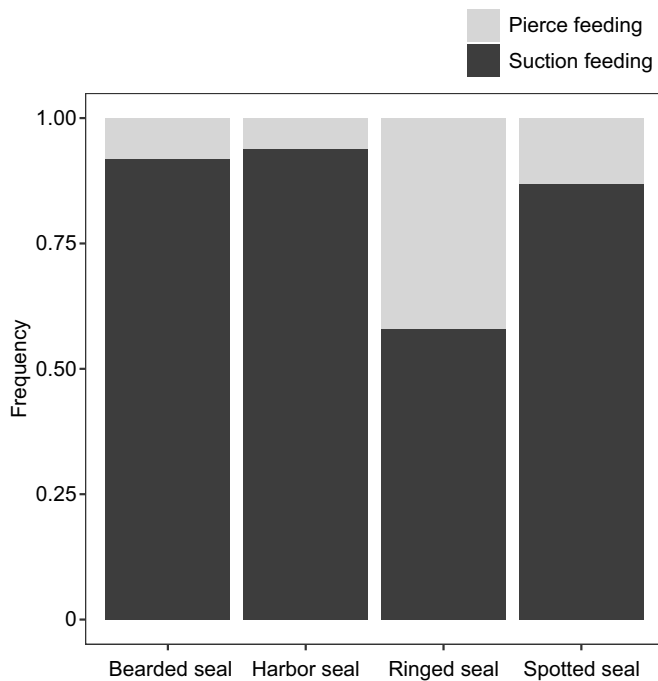


Fig. 2. Frequency of each mutually exclusive feeding strategy (suction feeding or pierce feeding) used by bearded ($n=2$), harbor ($n=3$), ringed ($n=3$) and spotted ($n=2$) seals.

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, $n=57$; 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 ($\chi^2=22.26$, $P<0.01$), shorter times to initial jaw closure ($\chi^2=8.32$, $P<0.01$) and shorter times to maximum gular depression ($\chi^2=19.21$, $P<0.01$) compared with pierce feeding.



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.

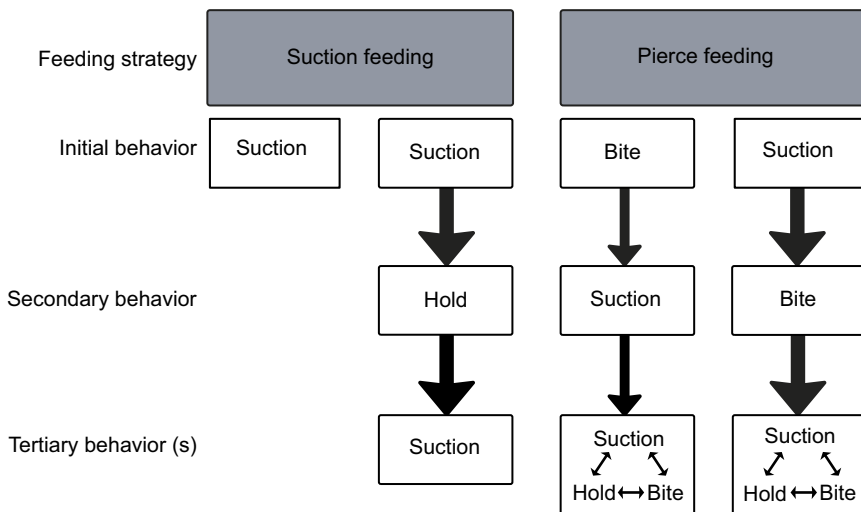


Fig. 4. Flow chart of feeding behaviors associated with pierce feeding and suction feeding strategies. The size of the arrows indicates how frequently each path was used within each feeding strategy. In pierce feeding, after the initial and secondary feeding behavior (suction and biting), seals used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

Furthermore, suction feeders exhibited significantly smaller maximum gapes ($\chi^2_1=23.18$, $P<0.01$), smaller maximum gape angles ($\chi^2_1=10.38$, $P<0.01$), smaller maximum gular depressions ($\chi^2_1=6.15$, $P<0.02$) and a reduced number of jaw motions ($\chi^2_1=10.71$, $P<0.01$). 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 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

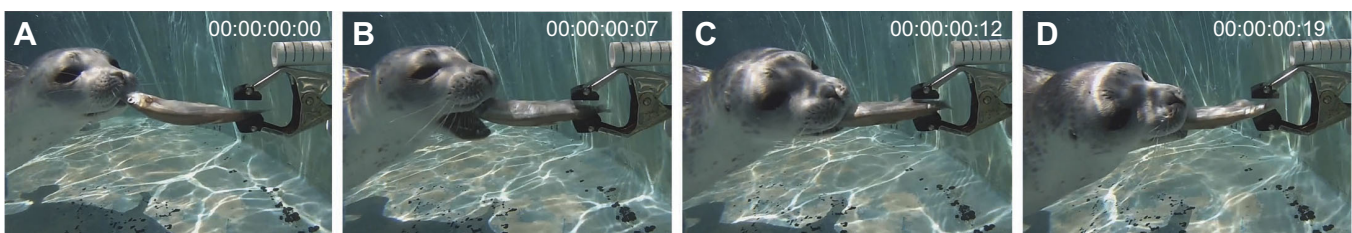


Fig. 5. Sequence of behaviors associated with the pierce feeding strategy exemplified by a single feeding trial with a ringed seal (Nayak). (A) Seal approaches the prey with vibrissae actively spread. (B) Jaws are opened to maximum gape and gape angle with teeth visible as seal engulfs the prey with 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.

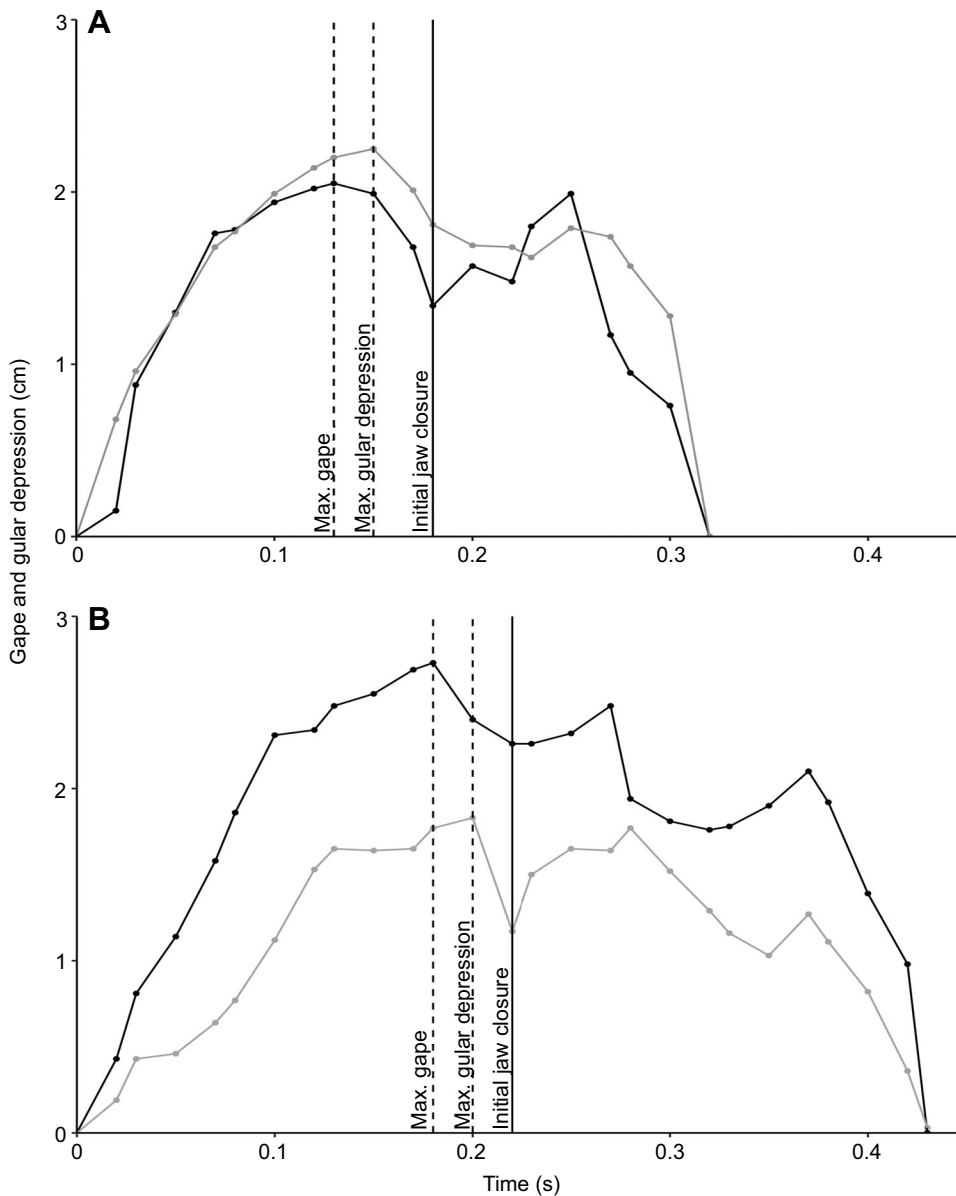


Fig. 6. Representative kinematic profiles of gape and gular depression when suction feeding and pierce feeding in a ringed seal (RS1). The black line represents gape and the gray line represents gular depression. With the exception of pierce feeding in harbor seals, all species showed similar timing 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.

gape angle closing velocity were highly variable in most species ($CV=0.19\text{--}0.87$), while maximum gape and maximum gape angle opening velocity were the most stereotyped ($CV=0.14\text{--}0.38$). When suction feeding, bearded seals had the highest kinematic variability of all species ($CV=0.47\pm 0.21$), and ringed seals had the most stereotyped kinematics ($CV=0.39\pm 0.14$). 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 ($CV=0.24\pm 0.20$).

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, 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

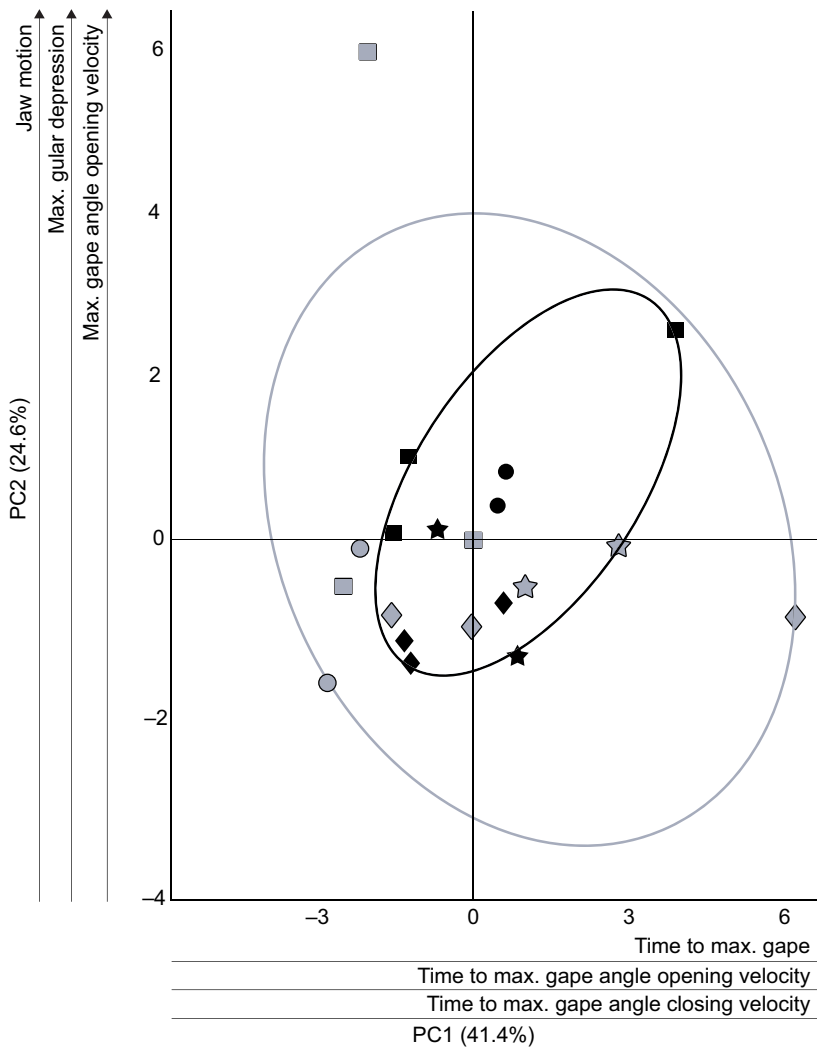


Fig. 7. Axes of kinematic variation in feeding as revealed by principal components analysis for all four phocid species. Symbols on the scatterplot represent individuals of each species. Circles represent bearded seals ($n=2$), squares represent harbor seals ($n=3$), diamonds represent ringed seals ($n=3$) 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.

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; 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

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

Kinematic variables	Bearded seals ($n=2$)		Harbor seals ($n=3$)		Ringed seals ($n=3$)		Spotted seals ($n=2$)	
	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

(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 et al., 2016) and well-developed muscular–vibrissal complexes (Fay, 1982; Marshall et al., 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

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

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Supplementary information

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Summary: Behavioral and kinematic differences exist between suction feeding and biting in seals. Suction feeding is common in seals and can occur without specialized skull morphology.

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