

## RESEARCH ARTICLE

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

Sarah S. Kienle<sup>1,\*</sup>, Aliya Cacaindin<sup>1</sup>, Traci Kendall<sup>1</sup>, Beau Richter<sup>1</sup>, Courtney Ribeiro-French<sup>1,2</sup>, Leann Castle<sup>3</sup>, Gwen Lentes<sup>3</sup>, Daniel P. Costa<sup>1</sup> and Rita S. Mehta<sup>1</sup>

## 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 walrus) 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

<sup>1</sup>Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Ecology and Evolutionary Biology, Santa Cruz, CA 95060, USA. <sup>2</sup>Monterey Bay Aquarium, Monterey, CA 93940, USA. <sup>3</sup>University of Hawaii at Manoa, Waikiki Aquarium, Honolulu, HI 96815, USA.

\*Author for correspondence (skienle@ucsc.edu)

 S.S.K., 0000-0002-8565-2870

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

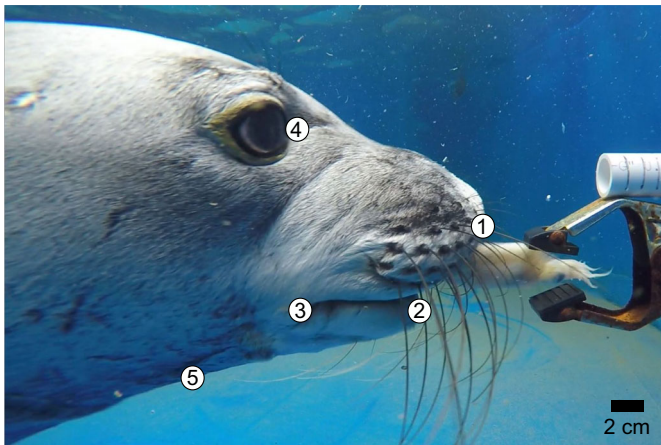
We built a feeding apparatus of PVC pipe that presented the Hawaiian monk seals with individual prey in a controlled and repeatable setting. A metal clamp held the prey and was attached to the feeding apparatus frame. A rope was attached to the clamp and tethered up the PVC pipe, which allowed the prey 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  $59.94 \text{ frames s}^{-1}$  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)= $10.00 \pm 0.57$  cm, body depth (BD)= $2.00 \pm 1.18$  cm], capelin [*Mallotus villosus*; SL= $13.85 \pm 0.58$  cm, BD= $2.16 \pm 0.20$  cm], squid (*Loligo* sp.; SL= $14.92 \pm 2.10$  cm, BD= $2.92 \pm 0.62$  cm) and herring (*Clupea pallasii*; SL= $20.63 \pm 4.12$  cm, BD= $4.15 \pm 0.38$ ). 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](http://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
Opuia	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 ( $\text{deg s}^{-1}$ ): 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 ( $\text{deg s}^{-1}$ ): 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 ( $\text{CV} = \text{standard deviation}/\text{mean}$ ) 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 variance 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)**

Kinematic variable	Capelin ( <i>n</i> =6)		Night smelt ( <i>n</i> =1)		Squid ( <i>n</i> =7)		Herring ( <i>n</i> =7)	
	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 <sup>-1</sup> )	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 <sup>-1</sup> )	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

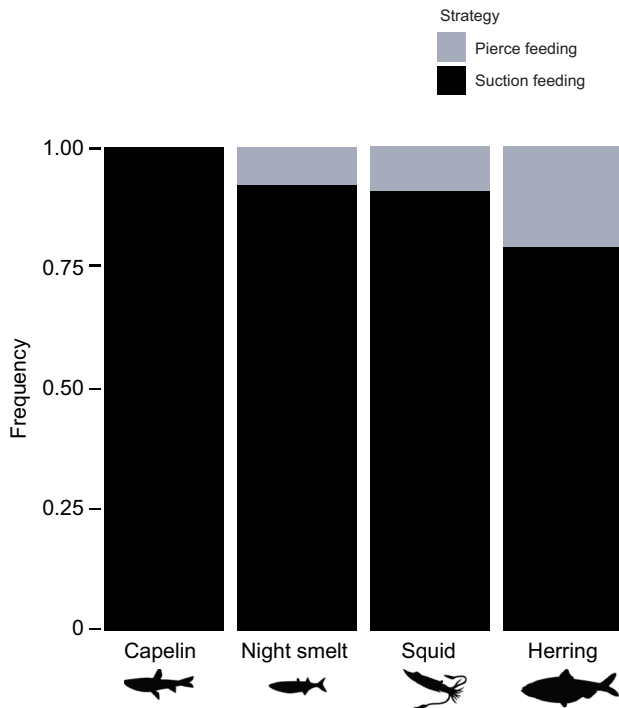
Values are means±s.d.

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

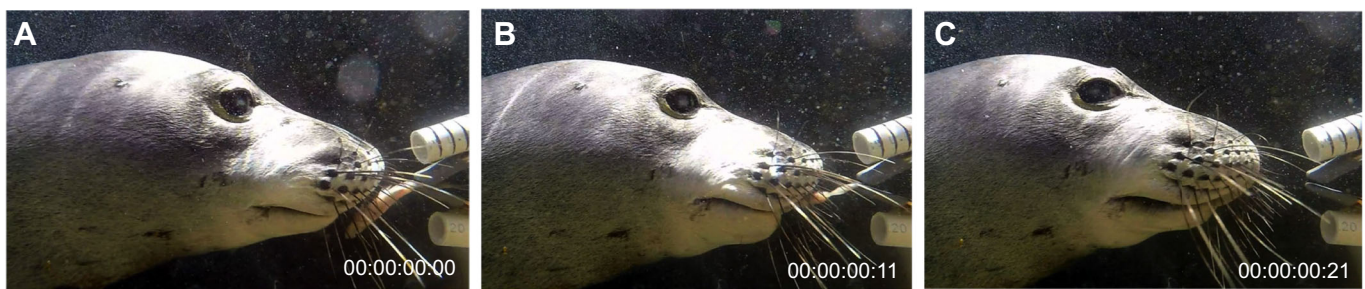
**Table 3.** Principal component loadings for each kinematic variable for principal components (PCs) 1 and 2

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

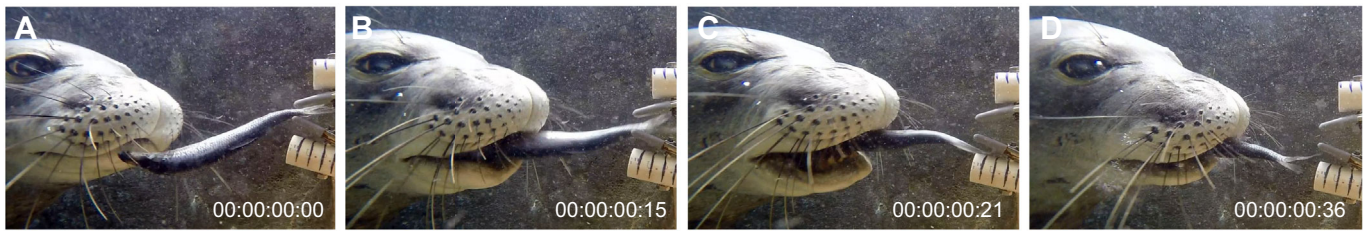
Bold values indicate kinematic variables that were significantly correlated with each PC axis.

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 ( $n=7$ ,  $F_1=4.09$ ,  $P=0.04$ ).

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<sup>-1</sup>, and the time is displayed as hours:minutes:seconds:frames.

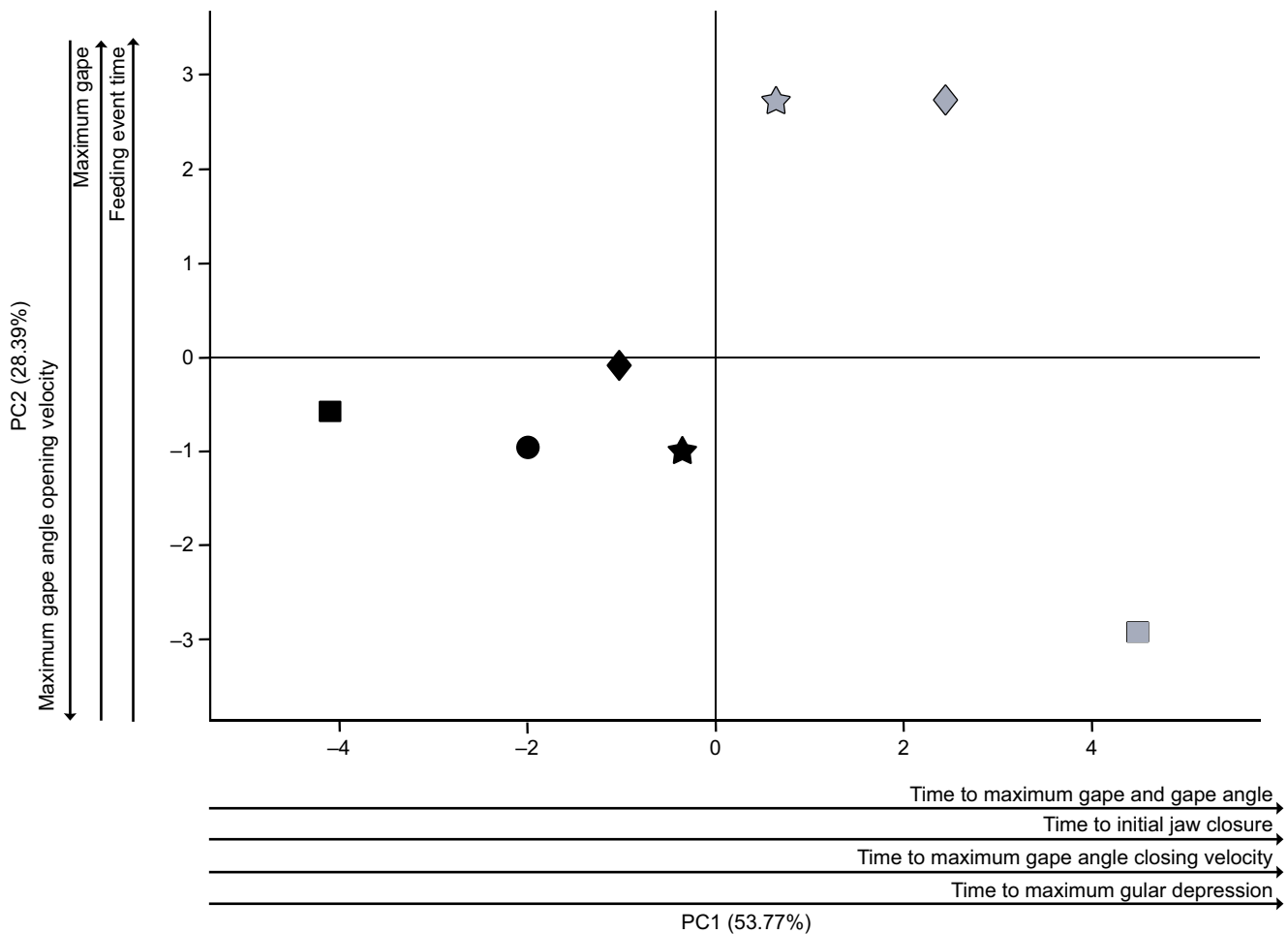


**Fig. 4. Sequence of feeding behavior associated with pierce feeding, exemplified by a Hawaiian monk seal (Ho'ailona).** (A) Seal approaches prey (herring) with the vibrissae actively engaged. (B) Seal forms the lips into a small circular opening, opens the lower jaw to maximum gape and gape angle, 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  $59.94 \text{ frames s}^{-1}$ , 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)**

Kinematic variable	Capelin ( <i>n</i> =6)		Night smelt ( <i>n</i> =1)		Squid ( <i>n</i> =7)		Herring ( <i>n</i> =7)	
	Suction	Pierce	Suction	Pierce	Suction	Pierce	Suction	Pierce
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 <sup>-1</sup> )	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 <sup>-1</sup> )	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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#### References

- Abrahms, B., Hazen, E. L., Bograd, S. J., Brashares, J. S., Robinson, P. W., Scales, K. L., Crocker, D. E. and Costa, D. P. (2017). Climate mediates the success of migration strategies in a marine predator. *Ecol. Lett.* **21**, 63–71.
- Adam, P. J. and Berta, A. (2002). Evolution of prey capture strategies and diet in Pinnipedimorpha (Mammalia, Carnivora). *Oryctos* **4**, 83–107.
- Alfaro, M. E., Janovetz, J. and Westneat, M. W. (2001). Motor control across trophic strategies: muscle activity of biting and suction feeding fishes. *Am. Zool.* **41**, 1266–1279.
- Bates, D., Maechler, M., Bolker, B. and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48.
- Berta, A., Churchill, M. and Boessenecker, R. W. (2018). The origin and evolutionary biology of pinnipeds: seals, sea lions, and walruses. *Annu. Rev. Earth Planet. Sci.* **46**, 203–228.
- Bowen, W. D., Tully, D., Boness, D. J., Bulheier, B. M. and Marshall, G. J. (2002). Prey-dependent foraging tactics and prey profitability in a marine mammal. *Mar. Ecol. Prog. Ser.* **244**, 235–245.
- Breed, G. A., Jonsen, I. D., Myers, R. A., Bowen, W. D. and Leonard, M. L. (2009). Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state–space analysis. *Ecology* **90**, 3209–3221.
- Cahoon, M. K., Littnan, C. L., Longenecker, K. and Carpenter, J. R. (2013). Dietary comparison of two Hawaiian monk seal populations: the role of diet as a driver of divergent population trends. *Endanger. Species Res.* **20**, 137–146.
- Chaves, Ó. M. and Bicca-Marques, J. C. (2016). Feeding strategies of brown howler monkeys in response to variations in food availability. *PLoS ONE* **11**, e0145819.
- Churchill, M. and Clementz, M. T. (2015). Functional implications of variation in tooth spacing and crown size in Pinnipedimorpha (Mammalia: Carnivora). *Anat. Rec.* **298**, 878–902.
- Cotté, C., d'Ovidio, F., Dragon, A. C., Guinet, C. and Lévy, M. (2015). Flexible preference of southern elephant seals for distinct mesoscale features within the Antarctic Circumpolar Current. *Prog. Oceanogr.* **131**, 46–58.
- Dill, L. M. (1983). Adaptive flexibility in the foraging behavior of fishes. *Can. J. Fish. Aquat. Sci.* **40**, 398–408.
- Fox, J. and Weisberg, S. (2011). *An R Companion to Applied Regression*, 2nd edn. Thousand Oaks, CA: Sage. <http://socserv.socsci.mcmaster.ca/~fox/Books/Companion>.
- Gerhardt, H. C. (1991). Female mate choice in tree frogs: static and dynamic acoustic criteria. *Anim. Behav.* **42**, 615–635.
- Goodman-Lowe, G. D. (1998). Diet of the Hawaiian monk seal (*Monachus schauinslandi*) from the Northwestern Hawaiian Islands during 1991 to 1994. *Mar. Biol.* **132**, 535–546.
- Gordon, K. R. (1984). Models of tongue movement in the walrus (*Odobenus rosmarus*). *J. Morphol.* **182**, 179–196.
- Greenwood, A. G. (1985). Prevalence of ocular anterior segment disease in captive pinnipeds. *Aquat. Mamm.* **1**, 13–15.
- Hanson, M. T., Alonso Aguirre, A. and Braun, R. C. (2009). *Clinical Observations of Ocular Disease in Hawaiian Monk Seals (Monachus schauinslandi)*. US Department of Commerce, NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC-18.
- Harding, A. M. A., Piatt, J. F., Schmutz, J. A., Shultz, M. T., Van Pelt, T. I., Kettle, A. B. and Speckman, S. G. (2007). Prey density and the behavioural flexibility of a marine predator: the common murre (*Uria aalge*). *Ecology* **88**, 2024–2033.
- Hocking, D. P., Evans, A. R. and Fitzgerald, E. M. G. (2012). Leopard seals (*Hydrurga leptonyx*) use suction and filter feeding when hunting small prey underwater. *Polar Biol.* **36**, 211–222.
- Hocking, D. P., Salverson, M., Fitzgerald, E. M. and Evans, A. R. (2014). Australian fur seals (*Arctocephalus pusillus doriferus*) use raptorial biting and suction feeding when targeting prey in different foraging scenarios. *PLoS ONE* **9**, e112521.
- Hocking, D. P., Fitzgerald, E. M., Salverson, M. and Evans, A. R. (2015). Prey capture and processing behaviors vary with prey size and shape in Australian and subantarctic fur seals. *Mar. Mamm. Sci.* **32**, 568–587.
- Hocking, D. P., Ladds, M. A., Slip, D. J., Fitzgerald, E. M. G. and Evans, A. R. (2016). Chew, shake, and tear: prey processing in Australian sea lions (*Neophoca cinerea*). *Mar. Mamm. Sci.* **33**, 541–557.
- Hocking, D. P., Marx, F. G., Park, T., Fitzgerald, E. M. and Evans, A. R. (2017). A behavioural framework for the evolution of feeding in predatory aquatic mammals. *Proc. R. Soc. B* **284**, 20162750.
- Jones, K. E. and Goswami, A. (2010). Quantitative analysis of the influences of phylogeny and ecology on phocid and otariid pinniped (Mammalia: Carnivora) cranial morphology. *J. Zool.* **280**, 297–308.
- Josse, J. and Husson, F. (2016). missMDA: a package for handling missing values in multivariate data analysis. *J. Stat. Softw.* **70**, 1–31.
- Juárez-Ruiz, A., Elorriaga-Verplancken, F. R., Moreno-Sánchez, X. G., Aguiniga-García, S., Amador-Capitanachi, M. J. and Gálvez, C. (2018). Diversification of foraging habits among Guadalupe fur seals from their only well-established breeding colony, Guadalupe Island, Mexico. *Mar. Biol.* **165**, 86.
- Kastelein, R. A. and Mosterd, P. (1989). The excavation technique for molluscs of Pacific walruses (*Odobenus rosmarus divergens*) under controlled conditions. *Aquat. Mamm.* **15**, 3–5.
- Kastelein, R. A., Muller, M. and Terlouw, A. (1994). Oral suction of a Pacific walrus (*Odobenus rosmarus divergens*) in air and under water. *Z. Saugtierkunde* **59**, 105–115.
- Kienle, S. S. and Berta, A. (2016). The better to eat you with: the comparative feeding morphology of phocid seals (Pinnipedia, Phocidae). *J. Anat.* **228**, 396–413.
- Kienle, S. S., Law, C. J., Costa, D. P., Berta, A. and Mehta, R. S. (2017). Revisiting the behavioural framework of feeding in predatory aquatic mammals. *Proc. R. Soc. B* **284**, 20171035.
- Kienle, S. S., Hermann-Sorensen, H., Costa, D. P., Reichmuth, C. and Mehta, R. S. (2018). Comparative feeding strategies and kinematics in phocid seals: suction without specialized skull morphology. *J. Exp. Biol.* **221**, jeb-179424.
- King, J. E. (1983). *Seals of the World*, 3rd edn. New York: Cornell University Press.

- Krüger, O., Wolf, J. B., Jonker, R. M., Hoffman, J. I. and Trillmich, F. (2014). Disentangling the contribution of sexual selection and ecology to the evolution of size dimorphism in pinnipeds. *Evolution* **68**, 1485–1496.
- Lê, S., Josse, J. and Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* **25**, 1–18.
- Lenth, R. V. (2016). Least-squares means: the R package lsmeans. *J. Stat. Softw.* **69**, 1–33.
- Littnan, C., Harting, A. and Baker, J. (2015). *Neomonachus schauinslandi*. The IUCN Red List of Threatened Species 2015: e.T13654A45227978. <http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T13654A45227978.en>.
- Longenecker, K. (2010). Fishes in the Hawaiian monk seal diet, based on regurgitate samples collected in the Northwestern Hawaiian Islands. *Mar. Mamm. Sci.* **26**, 420–429.
- Marshall, C. D., Kovacs, K. M. and Lydersen, C. (2008). Feeding kinematics, suction and hydraulic jetting capabilities in bearded seals (*Erignathus barbatus*). *J. Exp. Biol.* **211**, 699–708.
- Marshall, C. D., Wieskotten, S., Hanke, W., Hanke, F. D. and Marsh, A. (2014). Feeding kinematics, suction, and hydraulic jetting performance of harbor seals (*Phoca vitulina*). *PLoS ONE* **9**, 1–11.
- Marshall, C. D., Rosen, D. and Trites, A. W. (2015). Feeding kinematics and performance of basal otariid pinnipeds, Steller sea lions (*Eumetopias jubatus*), and northern fur seals (*Callorhinus ursinus*): implications for the evolution of mammalian feeding. *J. Exp. Biol.* **218**, 3229–3240.
- McHuron, E. A., Peterson, S. H., Hückstädt, L. A., Melin, S. R., Harris, J. D. and Costa, D. P. (2018). The energetic consequences of behavioral variation in a marine carnivore. *Ecol. Evol.* **8**, 4340–4351.
- Mehta, R. S. and Wainwright, P. C. (2007). Biting releases constraints on moray eel feeding kinematics. *J. Exp. Biol.* **210**, 495–504.
- Miller, A. K., Karnovsky, N. J. and Trivelpiece, W. Z. (2009). Flexible foraging strategies of gentoo penguins *Pygoscelis papua* over 5 years in the South Shetland Islands, Antarctica. *Mar. Biol.* **156**, 2527–2537.
- Miller, S., Colitz, C. M., St Leger, J. and Dubielzig, R. (2013). A retrospective survey of the ocular histopathology of the pinniped eye with emphasis on corneal disease. *Vet. Ophthalmol.* **16**, 119–129.
- Páez-Rosas, D., Riofrío-Lazo, M. and Aurióles-Gamboa, D. (2014). Flexibility in the foraging strategies of the Galapagos sea lion inferred from a multiple approach analysis. In *The Galapagos Marine Reserve* (ed. J. Denking and L. Vinuesa), pp. 71–80. Cham: Springer.
- Parrish, F. A. and Abernathy, K. (2006). Movements of monk seals relative to ecological depth zones in the lower Northwestern Hawaiian Islands. *Atoll Res. Bull.* **543**, 115–130.
- Parrish, F. A., Craig, M. P., Ragen, T. J., Marshall, G. J. and Buhleier, B. M. (2000). Identifying diurnal foraging habitat of endangered Hawaiian monk seals using a seal-mounted video camera. *Mar. Mamm. Sci.* **16**, 392–412.
- Parrish, F. A., Abernathy, K., Marshall, G. J. and Buhleier, B. M. (2002). Hawaiian monk seals (*Monachus schauinslandi*) foraging in deep-water coral beds. *Mar. Mamm. Sci.* **18**, 244–258.
- Parrish, F. A., Marshall, G. J., Littnan, C., Heithaus, M., Canja, S., Becker, B., Braun, R. and Antoneijs, G. A. (2005). Foraging of juvenile monk seals at French Frigate Shoals, Hawaii. *Mar. Mamm. Sci.* **21**, 93–107.
- Pauly, D., Trites, A. W., Capuli, E. and Christensen, V. (1998). Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci.* **55**, 467–481.
- Porter, H. T. and Motta, P. J. (2004). A comparison of strike and prey capture kinematics three species of piscivorous fishes: Florida gar (*Lepisosteus platyrhincus*), redbfin needlefish (*Strongylura notata*), and great barracuda (*Sphyraena barracuda*). *Mar. Biol.* **145**, 989–1000.
- Riedman, M. (1990). *The Pinnipeds: Seals, Sea Lions, and Walruses*. University of California Press.
- Rita, D., Drago, M., Galimberti, F. and Cardona, L. (2017). Temporal consistency of individual trophic specialization in southern elephant seals *Mirounga leonina*. *Mar. Ecol. Prog. Ser.* **585**, 229–242.
- Schoen, S. K., Piatt, J. F., Arimitsu, M. L., Heflin, B. M., Madison, E. N., Drew, G. S., Renner, M., Rojek, N. A., Douglas, D. C. and DeGange, A. R. (2018). Avian predator buffers against variability in marine habitats with flexible foraging behavior. *Mar. Biol.* **165**, 47.
- Schoener, T. W. (1971). Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**, 369–404.
- Schwenk, K. (2000). *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*. San Diego, CA: Academic Press.
- Simmons, S. E., Crocker, D. E., Hassrick, J. L., Kuhn, C. E., Robinson, P. W., Tremblay, Y. and Costa, D. P. (2010). Climate-scale hydrographic features related to foraging success in a capital breeder, the northern elephant seal *Mirounga angustirostris*. *Endanger. Species Res.* **10**, 233–243.
- Taylor, M. A. (1987). How tetrapods feed in water: a functional analysis by paradigm. *Zool. J. Linnean Soc.* **91**, 171–195.
- Villegas-Amtmann, S., Costa, D. P., Tremblay, Y., Salazar, S. and Aurióles-Gamboa, D. (2008). Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus wollebaeki*. *Mar. Ecol. Prog. Ser.* **363**, 299–309.
- Villegas-Amtmann, S., McDonald, B. I., Páez-Rosas, D., Aurióles-Gamboa, D. and Costa, D. P. (2017). Adapted to change: low energy requirements in a low and unpredictable productivity environment, the case of the Galapagos sea lion. *Deep Sea Res. II Top. Stud. Oceanogr.* **140**, 94–104.
- Wainwright, P. C., Mehta, R. S. and Higham, T. E. (2008). Stereotypy, flexibility, and coordination: key concepts in behavioral functional morphology. *J. Exp. Biol.* **211**, 3523–3528.
- Werth, A. J. (2000). Feeding in marine mammals. In *Feeding: Form, Function and Evolution in Tetrapods* (ed. K. Schwenk), pp. 487–526. San Diego, CA: Academic Press.
- Wilson, K., Littnan, C., Halpin, P. and Read, A. (2017). Integrating multiple technologies to understand the foraging behaviour of Hawaiian monk seals. *R. Soc. Open Sci.* **4**, 160703.