# Hawaiian monk seals (*Neomonachus schauinslandi*) exhibit behavioral flexibility when targeting prey of different shapes and sizes

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## SUMMARY STATEMENT

Hawaiian monk seals use biting and suction feeding strategies, which are behaviorally and kinematically distinct. While Hawaiian monk seals primarily use suction feeding, biting was used more frequently on larger prey.

ABSTRACT

Animals use diverse feeding strategies to capture and consume prey, with many species switching between strategies to accommodate different prey types. 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 critically 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) but also used biting, specifically pierce feeding (9% of all feeding trials), across all prey types. 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 kinematics to particular feeding contexts. Hawaiian monk seals are opportunistic marine predators and their ability to adapt their feeding strategy, behavior, and kinematics to specific foraging scenarios allows them to target diverse prey resources.

## 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, as 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 combat spatial and temporal heterogeneity in prey resources (Dill, 1983; Schoen et al., 2018; McHuron et al., 2018). For example, many species of pinnipeds (seals, sea lions, and walruses) change their foraging behavior in response to abiotic and biotic conditions, including prey (Bowen et al., 2002; Hocking et al., 2015, 2016), feeding context (Marshall et al. 2008, 2014, 2015; Hocking et al., 2014), habitat (Páez-Rosas et al., 2014), season (Breed et al., 2009; Cotté et al., 2015), and oceanographic conditions (Simmons et al., 2010; Villegas-Amtmann et al., 2016; Abrahms et al., 2017), and this often results 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; Juarez-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 is characterized by using the jaws and/or teeth to puncture and capture prey, often 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 (e.g., pierce feeding; 'suction'). Pinnipeds use these feeding strategies 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 fifteen 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 one of the most endangered pinnipeds on the planet (IUCN, 2018). These studies have shown that Hawaiian monk 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 et al., 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). While 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 this 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 critically 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 that suction feeding is a common pinniped feeding strategy, 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 seals 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) with seven subadult (n=1) and adult Hawaiian monk seals (n=6, Table 1). Data collection occurred from June 2016 to May 2017. The Hawaiian monk seals in this study had different 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 were able to fully participate 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 put into the clamp tail or tentacles first, 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 before the seal reached the apparatus. The seal consumed the prey and then returned to the trainer. The feeding trials took advantage of the seal's natural feeding behavior, and minimal

training was used to maintain the seal's position at the water's surface before the apparatus was submerged. Two GoPro cameras in underwater housings recording at 59.94 frames per second (fps) were mounted to the feeding apparatus to record anterior and lateral views of the feeding events.

Hawaiian monk seals were fed freshly thawed whole night smelt (*Spirinchus starksi*; standard length (SL)=10.00 ± 0.57 cm, body depth (BD)=2.00 ± 1.18 cm), capelin (*Mallotus villosus*; SL=13.85 ± 0.58 cm, BD=2.16 ± 0.20 cm), squid (*Loligo* sp.; SL=14.92 ± 2.10 cm, BD=2.92 ± 0.62 cm), and herring (*Clupea pallasii*; SL=20.63 ± 4.12 cm, BD=4.15 ± 0.38). Ho'ailona was the only seal fed night smelt rather than capelin as part of his regular diet. 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, feeding strategy, prey manipulation, and movement of the vibrissae and eyes. Suction feeding and biting were mutually exclusive strategies. A feeding trial was classified as suction feeding if the seal formed a small, circular opening with the mouth, teeth were not used, and prey moved fluidly into the mouth; in contrast, a feeding trial was classified as biting if the seal curled back the lips, had a wide gape, and teeth contacted the prey (Marshall et al. 2008, 2014, 2015; Kienle et al., 2018).

We used five homologous anatomical landmarks to quantify kinematic variables: rostral tip of the upper jaw, rostral tip of the lower jaw, caudal-most point at the corner of the mouth, rostral-most point of the eye, and rostral border of the hyoid apparatus (Fig. 1). Each landmark was digitized frame-by-frame for kinematic analysis in Tracker v. 4.92 (www.opensourcephysics.org). The kinematic variables measured in our study are as follows: (1) feeding event time (s): duration of the entire feeding event, from when the seal began to open its jaws (start of the feeding event) to when the entire prey was inside the mouth (end of the feeding event); (2) maximum gape (cm): maximum distance measured between the rostral tips of the upper and lower jaws during the feeding event; (3) time to maximum gape (s): time from the start of the feeding event to maximum gape; (4) maximum gape angle (deg): maximum angle measured between the rostral tips of the upper and lower jaws and the corner of the mouth during the feeding event; (5) time to maximum gape angle (s): time from the start of the feeding event to

maximum gape angle; (6) time to initial jaw closure (s): time from the start of the feeding event to when the jaws and/or teeth first closed over the prey; (7) maximum gape angle opening velocity (deg $s^{-1}$): maximum angular rate of lower jaw opening during the feeding event; (8) time to maximum gape angle opening velocity (s): time from the start of the feeding event to maximum gape angle opening velocity; (9) maximum gape angle closing velocity (deg $s^{-1}$): maximum angular rate of lower jaw closing during the feeding event; (10) time to maximum gape angle closing velocity (s): time from the start of the feeding event to maximum gape angle closing velocity; (11) maximum gular depression (cm): greatest distance measured between the rostral corner of the eye and the rostral edge of the hyoid apparatus; (12) time to maximum gular depression (s): time from the start of the feeding event to maximum gular depression; (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.

Flexibility is a measure of variation in a behavior between different experimental conditions (e.g., prey; Wainwright et al., 2008). To determine whether the feeding strategies and

kinematics varied between prey, we ran analyses of variance (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 kinematic performance in response to prey and inflexible if there was not a significant change in kinematic performance.

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

We conducted a principal components analysis (PCA) to determine the major axes of variation between each feeding strategy and prey type (FactoMineR and missMDA packages: Le 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. Principal components that explained 10% or more of the variation were retained, as determined from a scree plot of the variance contribute by each eigenvalue. All statistical analyses were conducted in R v. 3.3.3 (R Core Team, 2017).

## RESULTS

We conducted 1,367 feeding trials with Hawaiian monk seals (night smelt: 44 trials, capelin: 663 trials, squid: 242 trials, herring: 418 trials). Hawaiian monk seals showed behavioral flexibility in their use of different feeding strategies. Seals primarily used suction feeding with all prey types (79-100% of all feeding trials) but also used pierce feeding with all prey types (0.01-21% of all feeding trials; Table 2, Fig. 2). Suction feeding was characterized by a similar sequence of behaviors for all seals and prey types (Fig. 3, Movie 1S). 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 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 1S). 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 postcanine teeth 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 the 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, 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 is sometimes referred to as chewing (Hocking et al., 2014, 2015, 2016; Kienle et al., 2018).

*Feeding Kinematics*

Across the 1,367 feeding trials, 939 trials were analyzed for kinematics (68.69% of all feeding trials; night smelt=37, capelin= 508, squid=153, herring=243). The linear mixed effects models confirmed that pierce and suction feeding were kinematically distinct strategies, significantly differing across eight of the thirteen kinematic variables (Table 2). Suction feeding was characterized by significantly smaller maximum gapes ($F_1$=4.59, p=0.03) and gape angles ($F_1$=6.31, p=0.01), larger maximum gular depressions ($F_1$=4.88, p<0.01), and fewer numbers of jaw motions ($F_1$=274.43, p<0.01) compared to pierce feeding. Additionally, compared to pierce feeding, suction feeding resulted in shorter feeding event times ($F_1$=118.81, p<0.01), as well as shorter times to the following: jaw closure ($F_1$=6.49, p=0.01), maximum gape angle closing velocity ($F_1$=5.18, p=0.02), and maximum gular depression ($F_1$=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 ($F_3$=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 to pierce feeding for both the prey size ($F_1$=4.10, p=0.04) and shape ($F_1$=3.98, p=0.05) models. There was also a significant interaction between feeding strategy and prey shape for maximum gape angle closing velocity ($F_1$=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 ($p \leq 0.01$): time to maximum gape and gape angle, time to initial jaw closure, time to maximum gape angle closing velocity, and time to maximum gular depression. Principal component 1 was associated with the separation of pierce and suction feeding kinematics. Three kinematic variables were significantly correlated with PC2 ($p \leq 0.03$); feeding event time and maximum gape were positively correlated and maximum gape angle opening velocity was negatively correlated. Principal component 2 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).

*Behavioral Flexibility in Feeding Kinematics*

Suction feeding was used most frequently (>99.99% of suction 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).

The linear mixed effects models showed that 11 kinematic variables significantly differed between prey types: feeding event time ($F_3$=61.43, $p<0.01$), maximum gape ($F_3$=7.72, $p<0.01$) and gape angle ($F_3$=5.95, $p<0.01$), time to maximum gape ($F_3$=5.97, $p<0.01$) and gape angle ($F_3$=5.86, $p<0.01$), time to initial jaw closure ($F_3$=14.38, $p<0.01$), maximum gape angle closing velocity ($F_3$=3.41, $p=0.02$), time to maximum gape angle opening ($F_3$=3.20, $p=0.02$) and closing velocities ($F_3$=7.89, $p<0.01$), time to maximum gular depression ($F_3$=7.33, $p<0.01$), and the number of jaw motions ($F_3$=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.

For each of the 11 kinematic variable 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 to the other prey types (Tukey post-hoc, $p \leq 0.02$). When suction feeding, seals also had larger maximum gapes and gape angles when consuming herring compared to capelin (Tukey post-hoc, $p<0.01$) and night smelt (Tukey post-hoc, max gape: $p=0.02$, max gape angle: $p=0.05$); additionally, seals had longer times to maximum gape and gape angle when consuming squid compared to capelin (Tukey post-hoc, $p<0.01$) and herring (Tukey post-hoc, $p<0.01$). Seals had shorter times to initial jaw closure when suction feeding capelin compared to squid (Tukey post-hoc, $p<0.01$) and herring (Tukey post-hoc, $p=0.05$); similarly, seals had shorter times to initial jaw closure when suction feeding on squid compared to herring (Tukey post-hoc, $p<0.01$). Seals had faster times to maximum gape angle opening velocity when consuming capelin compared to squid (Tukey post-hoc, $p=0.01$); similarly, maximum gape angle closing velocity was faster when seals targeted squid compared to herring (Tukey post-hoc, $p=0.01$). Seals showed longer times to maximum gape angle closing velocity when targeting squid with suction feeding compared to capelin and herring (Tukey post-hoc, $p<0.01$). Seals also had longer times to maximum gular depression when consuming squid compared to capelin (Tukey post-hoc, $p<0.01$) and herring (Tukey post-hoc, $p=0.03$). The number of jaw motions significantly differed between prey types (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.

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 to 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. 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 those described for other pinnipeds (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014; Kienle et al., 2018), which shows 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 to 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 to other seal species for which comparable data exists (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 species, as Hawaiian monk seals are considerably larger (Kruger et al., 2014). In addition, Hawaiian monk seals exhibited larger maximum gular depressions when suction feeding compared to pierce feeding, which was not observed in bearded, harbor, ringed, and 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. This study on Hawaiian monk seals contributes to a growing behavioral dataset that suggests 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).

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 based on their skull and dental morphology. We found that Hawaiian monk seals are primarily suction feeders, regardless of prey size or shape. 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. However, as their skull and dental morphology predicts, Hawaiian monk seals also used pierce feeding. Pierce feeding followed a similar behavioral sequence as those described for other pinnipeds (Marshall et al., 2008, 2014, 2015; Hocking et al., 2014; Kienle et al., 2018). 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 to suction feeding. Hawaiian monk seal pierce feeding kinematics are concordant with those described for other 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), while 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 to 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 pierce and suction feeding in terms of the mean feeding event times observed in this study, 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 feeding 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 suction feeding 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. While 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 use pierce and suction feeding, as seals used both strategies with all prey types. The only exception was that most seals only used suction feeding when consuming capelin. Hawaiian monk seals also 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 strategy. In contrast, pierce feeding was the most stereotyped, which was also observed by Kienle et al. (2018), and pierce feeding appears to be a more conserved pinniped feeding strategy. 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 to suction feeding (Collar et al., 2014).

*Comparison with Foraging Behavior in the Wild*

Hawaiian monk seals in our controlled feeding studies showed similar behaviors to those observed in the wild. Available Crittercam video footage has shown that Hawaiian monk seals consume both small and large prey (Parrish et al., 2000; Wilson et al., 2017). Small prey are captured quickly and often not visible because of their size and quick handling time (~1 s) compared to larger prey that involve more processing and handling time (up to 1.5 min; Parrish et al., 2000; Wilson et al., 2017). While the feeding strategies used by wild Hawaiian monk seals are not described, we would predict from our observations of Hawaiian monk seals in this study that the small to medium sized prey are primarily consumed by suction feeding, while the larger prey are consumed by biting.

Two subpopulations of Hawaiian monk seals exist; the main Hawaiian Islands (MHI) subpopulation is smaller but increasing in size, while the northwestern Hawaiian Islands (NWHI) subpopulation is larger and decreasing (Baker et al., 2011). It is hypothesized that one of the main reasons for these opposite trends is because of differential foraging success between the two subpopulations. Some have suggested that the MHI subpopulation is increasing because the seals are more effective at finding and consuming prey, expending less effort when foraging,

and/or have greater prey resource availability than the NWHI population, all of which can result in greater foraging success (Cahoon et al., 2013; Wilson et al., 2017). The results from our study show that Hawaiian monk seals exhibit behavioral flexibility in feeding, which matches observations of their generalist diet and foraging behavior. Therefore, Hawaiian monk seals should be able to adapt their foraging behavior to different feeding scenarios. However, when environmental conditions are extremely poor, even species that exhibit behavioral flexibility are unable to buffer against changes in prey resources (Ronconi and Burger, 2008; Burke and Montevecchi, 2009; Chinn et al., 2016). Future work should focus determining the feeding strategies, handing times, and search effort from video footage collected from wild Hawaiian monk seals and on understanding the energetic costs of the different feeding strategies, which may better explain differences in foraging success between the two populations.

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**FIGURES**

**Figure 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.

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

**Figure 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 per second, and the time is displayed as hours: minutes: seconds: frames.

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

**Figure 5. Principal component axes of feeding kinematic variation across prey types.** Symbols on the plot represent prey types. 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. Circles indicate the 95% confidence intervals for each feeding strategy.

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## TABLES

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

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

**Table 2.** Summary of Hawaiian monk seal kinematic data for each prey type (capelin, night smelt, squid, and herring).

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

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

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

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

**Table 4**. Coefficient of variation for each prey type for each feeding strategy.

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