

RESEARCH ARTICLE

Durophagous biting in sea otters (*Enhydra lutris*) differs kinematically from raptorial biting of other marine mammals

Lori L. Timm-Davis^{1,2}, Randall W. Davis^{1,2,*} and Christopher D. Marshall^{1,2}**ABSTRACT**

Sea otters represent an interesting model for studies of mammalian feeding evolution. Although they are marine mammals, sea otters returned to the sea relatively recently and feed at the surface. Therefore, they represent a transitional stage of aquatic adaptation. Currently no feeding performance studies of sea otters have been conducted. The main objective of this study was to characterize the feeding kinematic profile in sea otters. It was hypothesized that sea otters would exhibit a terrestrial feeding behavior and that they forcefully crush hard prey at large gapes. As a result, biting kinematics would be congruent with biting behavior reported for their terrestrial ancestors, thus providing additional evidence that raptorial biting is a conserved behavior even in recently aquatic mammals. Sea otters consistently used a durophagous raptorial biting mode characterized by large gapes, large gape angles and lack of lateral gape occlusion. The shorter skulls and mandibles of sea otters, along with increased mechanical advantages of the masseter and increased bite force, form a repertoire of functional traits for durophagy. Here we consider durophagy to be a specialized raptorial biting feeding mode. A comparison of feeding kinematics of wild versus captive sea otters showed no significant differences in lateral kinematic profiles, and only minor differences in three frontal kinematic profiles, which included a slower maximum opening gape velocity, a slower maximum gape opening velocity, and a slower maximum closing gape velocity in captive sea otters. Data indicate functional innovations for producing large bite forces at wide gape and gape angles.

KEY WORDS: Feeding kinematics, Durophagy, Morphometrics, Craniodental morphology

INTRODUCTION

Among aquatic vertebrates and secondarily aquatic tetrapods, prey capture is achieved by raptorial biting, inertial suction, filtration or ram feeding (Schwenk, 2000; Motta et al., 2002; Mehta and Wainwright, 2007; Wilga et al., 2007; Marshall et al., 2008, 2015; Kane and Marshall, 2009; Timm-Davis et al., 2015; Marshall and Goldbogen, 2016), all of which are not mutually exclusive. Although there are exceptions, most aquatic vertebrates use suction as their primary feeding mode or are capable of incorporating suction in their feeding repertoire (Lauder, 1985; Summers et al., 1998; Grubich, 2001; Werth, 2006a). Therefore, the

mechanics of suction has been a major focus of study in aquatic vertebrates (e.g. Muller et al., 1982; Muller and Osse, 1984; Alfaro and Westneat, 1999; Alfaro et al., 2001; Alfaro and Herrel, 2001; Motta et al., 2002, 2008; Carroll et al., 2004; Wilga and Sanford, 2008). However, raptorial biting is also an important feeding mode in aquatic vertebrates, particularly among some marine mammals (Marshall et al., 2008, 2014, 2015; Kane and Marshall, 2009; Timm-Davis et al., 2015). Biting is defined as forceful contact of the jaws onto prey and can occur after a fast approach towards prey (Alfaro and Herrel, 2001; Alfaro et al., 2001; Motta et al., 2002).

Feeding mechanisms differ between aquatic and terrestrial environments (Shaffer and Lauder, 1988; Reilly and Lauder, 1990; Liem, 1990; Summers et al., 1998). In bony fishes, the versatile feeding apparatus allows for extensive dietary switching and reduced resource partitioning depending on resources (Liem, 1990; Case et al., 2008; Correa and Winemiller, 2014). In teleost fishes, the buccal cavity is often modeled as a truncated cone that expands to create negative pressures inside the oral cavity, drawing in prey and water (Liem, 1990; Day et al., 2005; Higham et al., 2005, 2006; Wainwright et al., 2007; Day et al., 2015). The versatility of this cone mode, however, is not restricted to prey capture. There are differences in pressure within different areas of the oral cavity. These differences are predicted to be generated by modulating muscle actions that change the shape of the cone, thus food can be moved or turned (Liem, 1990; Gerking, 1994; Higham et al., 2006).

Due to density differences between water and air, terrestrial vertebrates rely heavily on a biting feeding mode and tongue movements to manipulate prey within the oral cavity (e.g. Reilly and Lauder, 1990; Markey and Marshall, 2007). There are five stages in terrestrial feeding: (1) ingestion; (2) stage I transport to teeth; (3) mastication or food processing; (4) stage II transport to the oropharynx; and (5) swallowing (Hiimae, 2000). The jaw musculature and the hyolingual apparatus must be coordinated for prey to be transported and manipulated in the jaws of terrestrial vertebrates (Hiimae, 1978, 2000; Hiimae and Crompton, 1985; Herring, 1985; Reilly and Lauder, 1990; Liem, 1990; Alfaro and Herrel, 2001). In terrestrial vertebrates, the feeding apparatus (i.e. jaws) is operated by a relatively conserved pattern of muscle activity and results in an increase in resource partitioning and decrease in the degree of prey switching (Schoener, 1974; Morse, 1980; Vrba, 1980; Grant, 1986; Liem, 1990). Therefore, the terrestrial feeding apparatus is often more specifically matched to its biological role (Schoener, 1974; Liem, 1990).

After prey is acquired, food processing in terrestrial mammals begins with simple chopping or puncture-crushing and is followed by a rhythmic mastication cycle (Ahlgren, 1966; Hiimae and Crompton, 1971). This chopping behavior breaks the food into smaller manageable pieces in preparation for mastication prior to swallowing. Although sirenians do masticate, cetaceans and pinnipeds have lost this ability and possess a simplified dentition (e.g. the homodont dentition of odontocetes) and either swallow

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prey whole or in large pieces (Greaves, 1983; Adam and Berta, 2002; Berta et al., 2006; Field et al., 2010; Marshall and Goldbogen, 2016). Some pinnipeds may use a head shaking behavior, swinging prey around and using centrifugal force to break prey into smaller pieces for swallowing (Hocking et al., 2016) followed by some chopping behavior. Sea otters (*Enhydra lutris*) are marine mammals that have more recently returned to the sea and it is predicted that they retain mastication. When consuming soft-prey (e.g. fat innkeeper worms, sea cucumbers), flesh is removed with incisors, canines or premolars (Timm, 2013). When feeding on giant Pacific octopus, sea otters have been observed to swing the prey back and forth in the air to help break pieces off to be swallowed (Timm, 2013), as described for some pinnipeds (Hocking et al., 2016). Hard prey (i.e. bivalves) are cracked with molars or tools (e.g. rocks) and contents are removed with incisors and canines, and then swallowed. While consuming crabs, sea otters remove legs first by biting down and crushing them, then the carapace is cracked with the molars and incisors are used to scrape out the contents, which are then swallowed (Timm, 2013).

Sea otters are interesting in the context of mammalian feeding evolution as they have secondarily returned to the sea relatively recently (~5 million years ago; Berta and Morgan, 1985) compared with cetaceans (~50 million years ago; Thewissen et al., 2006) and pinnipeds (~27 million years ago). Sea otters capture prey with their forepaws but still use a predominantly biting feeding mode once prey is captured. Sea otters are durophagous (Taylor, 2000) marine mammals that feed on a variety of hard, benthic invertebrates including molluscs, crustaceans and echinoderms (Calkins, 1978; Garshelis, 1983; Garshelis et al., 1986; Doroff and Bodkin, 1994; Wolt et al., 2012) and their underlying craniodental morphology and biomechanics supports this crushing capability (Timm-Davis et al., 2015). Kinematic and performance studies provide a link between morphology and ecology (Wainwright, 1994) and can provide novel insights into the animal's trophic ecology and evolution (Anderson et al., 2008). As an individual's phenotype determines the limits of its performance (e.g. prey capture and food processing) (Wainwright, 1994), craniodental morphology provides valuable insights into the primary feeding mode of vertebrates. For example, biters are hypothesized to maximize force production rather than velocity, which also influences head shape (Barel, 1983; Westneat, 1994; Alfaro et al., 2001; Timm-Davis et al., 2015). Odontocetes (toothed whales) exhibit a dichotomy of craniodental phenotypes that correspond to feeding modes. Those that primarily use a raptorial biting or ram feeding mode possess long and narrow skulls (Bloodworth and Marshall, 2005; Kane and Marshall, 2009; McCurry et al., 2017) that maximize jaw tip velocity as an adaptation for piscivory. Odontocetes that use suction as a primary feeding mode possess skulls that are short, blunt and possess fewer teeth (Werth, 2006a,b; Kane and Marshall, 2009). However, shortening of the skull can also function synergistically for raptorial biting, particularly in durophagous species such as sea otters. Craniodental morphometrics of otters demonstrate a biomechanical trade-off between long fast jaws versus short powerful jaws, resulting in trophic specialization in this group (Timm-Davis et al., 2015).

However, how do such morphological innovations manifest behaviorally? Currently, there are no feeding kinematic or performance studies of sea otters. Feeding kinematic studies are a successful method to study feeding in marine mammals, and can be used to begin to elucidate the cost of foraging. Although sea otters forage underwater, they manipulate and ingest food at the surface, making them an ideal model system to study biting kinematics in

marine mammals. The main objective of this study was to characterize the kinematics of a biting mode in sea otters and compare their profile with terrestrial mammals. It was hypothesized that sea otters forcefully bite and crush hard benthic prey in a manner that is consistent with terrestrial durophagous mammals, but with large gapes, despite their return to an aquatic environment.

MATERIALS AND METHODS

Feeding kinematics

A video of wild and captive sea otter feeding was recorded for frame-by-frame motion analysis to characterize their kinematic profile. Only adult otters were used in this study. Feeding behavior of wild adult sea otters [*Enhydra lutris* (Linnaeus 1758)] ($N=31$) was video-recorded in Simpson Bay, Alaska (60.4°N, 145.5°W) in northeastern Prince William Sound (Gulf of Alaska); and for captive sea otters during controlled feeding trials at the Audubon Aquarium of the Americas in New Orleans, LA, USA. The captive otters were one adult male (body mass 28.2 kg, 128 cm in length) and one adult female (body mass 23.8 kg, 120.2 cm in length). We used captive sea otters to demonstrate that kinematic profiles in wild populations could be accurately measured. Kinematic profiles were recorded for wild sea otters feeding on the following hard prey (hard calcareous shell or test): clams, mussels, shrimp, sea stars, sea urchins and crabs. Hard prey for captive otters included shrimp, crab legs and ice treats. No kinematic profiles were recorded with soft prey.

Wild sea otters were recorded using a Sony TRV950 video camera (Sony Corporation, New York, NY, USA) at 30 frames per second (frames s^{-1}) from a 6-m aluminum skiff or 5-m fiberglass skiff in June 2009 and July 2010. Feeding trials were recorded in both lateral and frontal views. During a feeding event, the distance between the observer and sea otter was determined with a laser range finder with an inclinometer (LaserAce 300, Measurement Devices Ltd). Peak Motus (version 9; Vicon, Denver, CO, USA) was used to analyze the motion of the head and jaws during feeding. Projective scaling was determined by video recording a 20×20 cm square made from PVC pipe at all known distances. A video was obtained of wild sea otters feeding on clams, mussels, shrimp, sea stars, sea urchins and crabs. Only feeding events in which hard prey were consumed were analyzed kinematically.

Captive sea otters were recorded using the same camera during feeding sessions that involved a single presentation of various food items. Kinematic profiles were measured during the otter's normal feeding times. Otters were not satiated and were always motivated to feed. Otters were fed shrimp, crab legs and ice treats (clam and shrimp frozen in large ice blocks), which elicited large gapes and strong biting performance to crush the ice. The presentation of a food item and subsequent crushing and ingestion event defined a single feeding trial ($N=10$ for the male and $N=18$ for the female). Feeding trials were recorded in both lateral and frontal views. A 20×20 cm calibration square was placed in the same plane as the otter immediately following the feeding trial for projective scaling and calibration of the measurements.

Video recordings were imported into Peak Motus and cropped to one frame prior to jaw opening and one frame following jaw closing. Peak Motus separates video frames into fields resulting in a 60 Hz record. To characterize the movement of the jaws, four lateral and five frontal homologous anatomical landmarks (Fig. 1) were digitized throughout the entire gape cycle. This enabled us to calculate nine lateral and five frontal kinematic variables: (1) maximum gape; (2) time to maximum gape; (3) maximum gape angle (upper jaw just anterior to canine, tip of lower jaw just anterior to canine), commissure of lips; (4) time to maximum gape

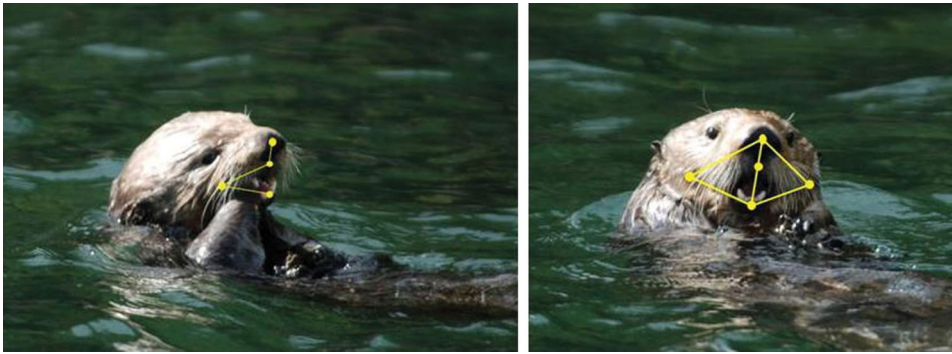


Fig. 1. Anatomical landmarks for

kinematic analysis in sea otters. Lateral landmarks include the nose, tip of upper jaw, tip of lower jaw and corner of mouth. Frontal landmarks include center of nose, center of upper jaw, center of mandible, corner of left side of mouth, and corner of right side of mouth.

angle; (5) maximum opening gape angle velocity; (6) time from lower jaw opening to maximum gape angle velocity; (7) maximum closing gape velocity; (8) time to the maximum closing gape angle velocity; and (9) total gape cycle duration (following Marshall et al., 2008, 2014, 2015) (Table 1).

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Statistical analyses

Normality of data was tested using a Shapiro–Wilk test. Kinematic variables were \log_{10} transformed and used in multivariate analysis (MANOVA) for wild kinematic profiles and an ANOVA for captive kinematic profiles. A MANOVA was used to determine whether kinematic variables differed among wild individuals using kinematic variables as the dependent factors and individuals as the independent factors. A MANOVA was used to determine whether kinematic variables differed across prey types for wild otters (clams, mussels, shrimp, sea stars, sea urchins and crabs) and an ANOVA was performed for captive otters (shrimp, crab legs and ice treats), using kinematic variables as the dependent factors and

prey types as the independent factors. For both captive and wild sea otters, lateral and frontal kinematic variables were analyzed separately. A MANOVA was then used to test for significant differences in kinematic variables between captive and wild sea otters, using kinematic variables as the dependent factors and captive versus wild as the independent factor. All statistical tests were performed using JMP 9.0 (SAS Institute, Cary, NC, USA). Kinematic profiles for hard prey only were used for this study.

RESULTS

Biting was the only feeding mode observed in both wild and captive sea otters and was characterized by a large gape, large gape angle, presentation of teeth and lack of lateral gape occlusion (Table 2). Hard prey was placed as far posterior into the mouth as possible over the molars. Location and positioning of the prey in the jaws was dependent on the prey type (hard versus soft) and size. The positioning of large, hard prey (e.g. clams or ice treats) in the posterior-most location of the jaws, over the molars, required a markedly increased gape. Despite the large gape and large gape angle compared with other carnivores, sea otters easily produced a bite force large enough to crush the food item (Fig. 2). In the wild, once prey was cracked open by the molars, the flesh was removed, or scooped out, at the anterior jaw using incisors or canines. Smaller, softer prey (e.g. sea cucumbers, fat innkeeper worms) were positioned more anteriorly and incisors, canines or premolars were used in conjunction with forelimbs to tear the flesh into smaller pieces and masticated prior to consumption. Wild sea otters were observed feeding on 15 different prey types (from 160 feeding

Table 1. Kinematic variables for captive and wild performance kinematics

Kinematic variable	Abbreviation	Description
Maximum gape	GAPE	Distance from the upper jaw tip to the lower jaw tip
Time to maximum gape	t_{GAPE}	Time from when the lower jaw began to open until the maximum gape
Maximum gape angle	GANG	Maximum angle from the maxillary tip to the corner of the mouth
Time to maximum gape angle	t_{GANG}	Time from lower jaw opening to maximum gape angle
Maximum gape angle opening velocity	GAOV (GLOV*)	Greatest angular [or linear (L) for frontal] rate of lower jaw opening
Time to maximum gape angle opening velocity	t_{GOAV} (t_{GLAV}^*)	Time elapsed from gape opening to maximum gape opening
Maximum gape angle closing velocity	GACV (GLCV*)	Greatest angular velocity [or linear (L) velocity for frontal] during lower jaw closure
Time to maximum gape angle closing velocity	t_{GACV} (t_{GLCV}^*)	Time from when the lower jaw began to close until the maximum gape angle [or linear (L) velocity for frontal] velocity
Total duration	t_{dur}^*	Elapsed time from the onset of gape opening to the last frame of gape closing

*Frontal kinematic variables.

Table 2. Summary of mean kinematic variables for captive and wild sea otters

	Captive	Wild
Lateral	(N=2)	(N=31)
GAOV (deg s ⁻¹)	416.9±186.9	519.2±226.7
t_{GOAV} (s)	0.10±0.04	0.06±0.03
GAPE (cm)	5.8±1.3	5.4±1.5
t_{GAPE} (s)	0.20±0.05	0.15±0.056
GANG (deg)	61.4±21.4	66.50±16.30
t_{GANG} (s)	0.17±0.04	0.15±0.06
GACV (cm s ⁻¹)	267.2±106.0	387.6±197.6
t_{GACV} (s)	0.06±0.01	0.07±0.05
t_{dur} (s)	0.33±0.06	0.29±0.07
Frontal	(N=2)	(N=21)
GLOV (deg s ⁻¹)	35.6±11.3	54.4±25.9
t_{GLOV} (s)	0.07±0.03	0.06±0.02
GLCV (cm s ⁻¹)	19.4±12.7	47.1±23.4
t_{GLCV} (s)	0.05±0.02	0.08±0.05
t_{dur} (s)	0.32±0.11	0.28±0.09

See Table 1 for definitions.



Fig. 2. Wild sea otter (*Enhydra lutris kenyoni*) in Simpson Bay, Alaska, placing a butter clam posteriorly in the mouth over the carnassials.

events), but kinematic profiles were created and analyzed using only hard prey (clams, mussels, shrimp, sea stars, sea urchins and crabs). The gape angle for soft prey was too small to obtain accurate kinematic profiles for comparison and they are provided here to represent the behavioral feeding repertoire observed.

Feeding kinematics among wild sea otters was conserved, and crushing appeared stereotypical, as predicted by the biomechanical arrangement of the masseter muscles and merging of the superficial and deep masseter muscles (Timm, 2013). The lateral feeding kinematic profile for both wild and captive sea otters is as follows: the mean feeding cycle duration (t_{dur}) in wild sea otters was

0.29 ± 0.07 s and in captive sea otters was 0.33 ± 0.06 s, respectively (Table 2). The jaws reached maximum gape angle opening velocity (GAOV) rapidly in wild (519.2 ± 226.7 deg s^{-1}) and captive (416.9 ± 186.9 deg s^{-1}) sea otters, respectively (Table 2). Maximum gape (GAPE) and maximum gape angle (GANG) occurred almost simultaneously in wild sea otters (5.4 ± 1.5 cm; 66.5 ± 16.3 deg; Table 2, Fig. 3). The jaws then closed slowly [gape angle closing velocity (GACV): wild, 387.6 ± 197.6 cm s^{-1} ; captive, 267.2 ± 106.0 cm s^{-1} ; Table 2]. Fig. 3 is a representative profile for wild sea otters.

In the frontal kinematic profile, the mean feeding cycle duration (t_{dur}) was also faster in wild sea otters (0.28 ± 0.09 s) compared with captive sea otters (0.32 ± 0.11 s; Table 2). The jaws reached maximum gape linear opening velocity (GLOV) more rapidly in wild (54.4 ± 25.9 deg s^{-1}) than captive otters (35.6 ± 11.3 deg s^{-1}). The jaws then closed slowly [gape linear closing velocity (GLCV): wild, 47.1 ± 23.4 cm s^{-1} ; captive, 19.4 ± 12.7 cm s^{-1}].

Lateral feeding kinematic variables of wild sea otters did not significantly differ among individuals ($F=0.98$, $P>0.05$, MANOVA) or prey types (clams, crabs, mussels, sea stars, sea urchins, shrimp) ($F=1.40$, $P>0.05$, MANOVA). No significant differences were found among these same subjects for the frontal feeding kinematic variables ($F=2.11$, $P>0.05$, MANOVA) or among prey type (clams, mussels, sea stars, shrimp) ($F=0.64$, $P>0.05$, MANOVA). Likewise, feeding kinematic variables of captive sea otters were also conserved. Lateral kinematic variables did not differ significantly between the two subjects ($F=5.81$, $P>0.05$, ANOVA) or among food items (ice treats, crab legs, shrimp) ($F=2.67$, $P>0.05$, ANOVA), nor did frontal feeding kinematics between these subjects differ significantly ($F=1.82$,

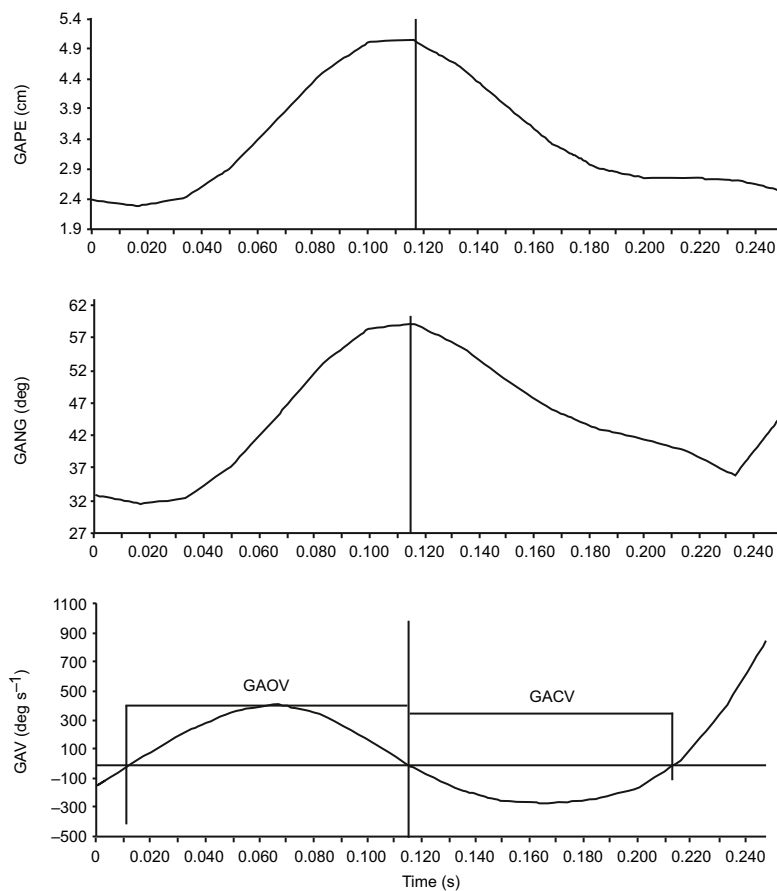


Fig. 3. Kinematic profile (lateral perspective) from a wild sea otter (*Enhydra lutris kenyoni*). GAPE, maximum gape; GANG, maximum gape angle; GAV, gape angle velocity (opening and closing); GAOV, maximum gape angle opening velocity; GACV, maximum gape angle closing velocity.

$P > 0.05$, ANOVA) or among prey (ice treats, crab legs, shrimp) ($F = 1.71$, $P > 0.05$, ANOVA). Furthermore, a comparison of all kinematics of wild versus captive sea otters feeding on various types of prey demonstrated no significant differences among kinematic variables ($F = 2.16$, $P > 0.05$, MANOVA) with the exception of three frontal kinematic variables. These significant differences in frontal kinematic variables between wild and captive sea otters included a slower maximum opening velocity (GAOV), a slower time to maximum gape opening velocity (t_{GAOV}), and a slower maximum closing gape velocity (GACV) in captive sea otters.

DISCUSSION

Sea otters are marine mammals that acquire prey from the sea floor with their forelimbs but consume prey at the surface (Estes et al., 1982, 2003; Bodkin et al., 2004; Tinker et al., 2008). Our results show that sea otter feeding is consistent with a typical carnivorous biting kinematic profile (*sensu* Hiimeae, 1978, 2000). The primitive terrestrial mammalian feeding begins with a fast opening of the jaw with some translational (side-to-side) movement of the mandible followed by slow closing of the jaws in which prey is masticated or crushed (Hiimeae and Crompton, 1985; Liem, 1990; De Vree and Gans, 1994). The jaw closing velocity is slower than jaw opening because prey is already positioned between the upper and lower jaws and therefore has a shorter distance to close.

The primary feeding mode of sea otters is biting, characterized by large gape, large gape angle and fast gape angle opening velocity. Sea otters open their jaws rapidly, and once maximum gape and gape angles are reached, the jaws slowly close and prey is either masticated (soft prey) or crushed (hard prey) for further processing. Both captive and wild sea otters positioned their food in precise locations of the jaw depending on the prey type. When consuming hard prey (clams, crabs, urchins), prey was positioned far back in the jaws where it was crushed with the blunt molars, which required an increased maximum gape and gape angle. When consuming soft prey, such as Pacific giant octopus (*Enteroctopus dofleini*), sea cucumbers or fat innkeeper worms (*Urechis caupo*), flesh was torn apart with the incisors or canines and the forelimbs.

A significant finding is that sea otters display extremely wide gape angles during forceful biting. Large gapes are necessary when a major food source, such as clams, has a high-centered shell that must be positioned over the large, blunt molars. A high bite force would also be needed to crack the shells open. The mammalian jaw is a third-class lever system, and bite force increases as the resulting force (e.g. bite point) is positioned closer to the jaw joint (Greaves, 1985, 2000; Herring et al., 2001; Dumont and Herrel, 2003; Santana et al., 2010; Pfaller et al., 2011), and is maximum when located in the posterior third of the jaw where carnassials are located (Greaves, 1982, 1985, 2000). Although gape angles typically ranged from 61 to 66 deg, gape angles up to 82 deg were commonly observed. This is a wide gape angle among mammals. The range of gape angles of most carnivores is much lower, approximately 55–65 deg (Herring and Herring, 1974; Christiansen and Adolphsen, 2007). Sea otters consistently and forcefully crushed hard prey at these large gape angles. The gape angle at which sea otters crush prey is larger than several other mammals, such as Egyptian fruit bats (*Rousettus aegyptiacus*, 47.1 deg), Pallas' long tongued bat (*Glossophaga soricina*, 46.5 deg) (Dumont and Herrel, 2003) and dingos (*Canis lupus dingo*, 35 deg) (Bourke et al., 2008). The maximum gape of sea otters approximates to that of domestic cats (*Felis catus*), which exhibit gape angles up to 80 deg (Türker and Mackenna, 1978), and approaches the gape of clouded leopards (*Neofelis nebulosa*), which are reported to have gapes up to 90 deg (Christiansen and Adolphsen,

2007). As a reference, the maximum gape reported for any mammal when biting is the extinct sabretooth cat (*Smilodon* sp.) at 95 deg owing to its divergent or extreme size and shape of dentition (e.g. large, blunt molars and carnassials) (Emerson and Radinsky, 1980; Christiansen, 2006, 2011; Christiansen and Adolphsen, 2007). Muscle tension in domestic cats appears to be greatest at maximum gape (Türker and Mackenna, 1978). It is suggested that the same may be true of sea otters and that the jaw closing musculature has biomechanical innovations for large bite forces at large gapes.

Even though there was no significant difference in total gape cycle duration between captive and wild sea otters, wild sea otters tended to demonstrate a slightly shorter cycle duration. The timing of the jaw opening occurred earlier in the profile for wild sea otters than for captive otters and the jaw closing velocity was more rapid in wild otters than in captive otters. The time to reach maximum gape for wild sea otters also occurred earlier than in captive sea otters. One possible explanation is that these differences relate to the foraging behavior of wild sea otters versus scheduled feeding events for captive sea otters. In general, most sea otter populations consume large, high caloric prey first, then as preferred prey decline, the diet diversifies to include smaller, less caloric-rich prey (Garshelis et al., 1986; Kvitek et al., 1988, 1993; Ralls and Siniff, 1990; Estes and Duggins, 1995; Laidre and Jameson, 2006). Therefore, wild sea otters must spend more time foraging to obtain the same amount of energy (Ralls and Siniff, 1990). This could explain the quicker opening velocity and more rapid closing velocity in wild sea otters. Wild sea otters also experience intraspecific competition, which may correspond to an earlier gape opening velocity and a more rapid closing velocity, in order to avoid having prey stolen from them. It is common behavior for males to steal prey from females (Cohn, 1998). In contrast, captive sea otters had a regular feeding routine and did not have to forage or compete for food. However, there were no statistical differences in lateral kinematic profiles and only minor differences in frontal profiles. An alternative hypothesis is that captive otters are more satiated than wild otters due to scheduled daily feedings, which could produce slower kinematic profiles (Sass and Motta, 2002). However, we made sure the animals were hungry during each event.

The crushing capability of sea otters at large gapes is partly a consequence of extreme mandibular bluntness. The mandibular bluntness index (MBI) is the ratio of jaw width to jaw length. Sea otters possess an MBI that is greater than 1.0, demonstrating that the mandible is wider than long (Timm-Davis et al., 2015). This is considered to be extreme among species for which bluntness data are available (Werth, 2006a). Significant differences in the craniodental morphometrics of sea otters (i.e. a large interorbital distance, rostral width at the molars, braincase width, palate width, skull width and zygomatic length) is a consequence of this extreme blunt phenotype. Based on preliminary and ongoing work, it is predicted that sea otters possess physiological innovations of their adductor muscles that allow them to bite forcefully at wide gapes. A large zygomatic length allows muscles to attach more anteriorly, thus improving bite force while allowing a larger gape. Longer muscle fibers of the masseter and temporalis can increase maximum muscle excursion, or the distance a muscle fiber can shorten (Taylor et al., 2009). Such innovations are reported for common marmosets (*Callithrix jacchus*) and pygmy marmosets (*Cebuella pygmaea*), both tree-gouging primates, in which masseter fiber lengths are elongated compared with non-gouging tree primates. These longer masseter fiber lengths are correlated with increased gape (Taylor et al., 2009). Similar results have been reported in pigs (Herring and Herring, 1974; Herring et al., 1979), mice (Satoh and Iwaku, 2006)

and many bats (Herrel et al., 2008). In addition, sea otters exhibit a significantly large masseteric mechanical advantage (MA) (Timm-Davis et al., 2015), which allows a large bite force capability for their small size relative to other durophagous mammals (Timm, 2013; Law et al., 2016). The blunt, robust skull and mandible, increased masseteric MA, increased carnassial surface area, and increased bite force capability at large gape angles all support a specialized durophagous capability in sea otters.

The kinematic data from this study support the functional hypotheses generated by traditional and geometric morphometrics, as well as biomechanical measures (Timm, 2013; Timm-Davis et al., 2015; Law et al., 2016). The combined dataset (i.e. morphological, shape, biomechanical and kinematic) is also consistent with other durophagous terrestrial carnivores, in which the skull and mandible tends to be short and blunt, with wide jaws and zygomatic breadths and enlarged adducting muscles (Dumont and Herrel, 2003; Nogueira et al., 2005; Tanner et al., 2010). For example, durophagous bats possess skulls that are taller, with wider palates and lower coronoid and condyles (designed for robust muscle attachment points) than bats feeding on softer fruits (Dumont and Herrel, 2003). Spotted hyenas (*Crocuta crocuta*) specializing in bone cracking possess robust dentition, larger jaw adductor muscles, larger sagittal crest, vaulted forehead and wider zygomatic breadths (skull width) than hyenas not specializing in bone cracking (Binder and Van Valkenburg, 2000; Van Valkenburg, 2007; Tanner et al., 2010).

Biting in sea otters differs from feeding kinematic profiles observed in other marine mammals that use biting as their primary feeding mode (Bloodworth and Marshall, 2005; Marshall et al., 2008, 2015; Kane and Marshall, 2009). Although Steller sea lions (*Eumetopias jubatus*) use both suction and biting feeding modes, they primarily display kinematic profiles distinctive of a suction feeder (Marshall et al., 2015). Steller sea lions display relatively small gapes (4.1 ± 1.26 cm), small gape angles (20.0 ± 5.6 deg), large depressions of the hyolingual apparatus, and lip pursing. In contrast, northern fur seals (*Callorhinus ursinus*) are biting specialists and display kinematic profiles most similar to that of sea otters. Despite their smaller size, sea otters are able to produce a much greater gape (captive: 5.8 ± 1.3 cm; wild: 5.4 ± 1.5 cm) compared with northern fur seals (4.4 ± 0.94 cm). It is difficult to directly compare gape among mammals of different sizes. However, gape angle is independent of size and sea otters have a much larger maximum gape angle (81 deg) than northern fur seals (55 deg). Northern fur seals have a faster GAOV (766.8 ± 243.19 s) and GACV (443.4 ± 156.53 s) compared with sea otters. These kinematic differences characterize and define durophagous biting (sea otters) versus raptorial biting (fur seals) for the first time. Clearly, durophagy is also a specialized biting feeding mode.

In conclusion, sea otters are marine mammals that often feed on hard, benthic invertebrates at the surface and possess kinematic profiles that coincide with a typical terrestrial carnivorous durophagous biting feeding mode. Sea otters crush their prey at extremely large gapes and gape angles. Shorter, blunter skulls and mandibles in sea otters, along with increased mechanical advantages at the masseter (Timm-Davis et al., 2015), and increased bite force capability (Timm, 2013) correlate with the kinematics of a durophagous biting mode of sea otters.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.L.T.-D., C.D.M.; Methodology: L.L.T.-D., C.D.M.; Formal analysis: L.L.T.-D.; Investigation: L.L.T.-D.; Resources: R.W.D., C.D.M.; Writing - original draft: L.L.T.-D.; Writing - review & editing: L.L.T.-D., R.W.D., C.D.M.; Supervision: R.W.D., C.D.M.; Project administration: C.D.M.

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