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Do differences in skull morphology and bite performance explain dietary specialization in sea otters?

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Intraspecific studies of morphology and performance are essential for understanding the factors that enable resource partitioning within ecological communities. The sea otter (*Enhydra lutris*) is one of the few mammal species in which individual-level dietary specialization has been documented, making them an ideal system to investigate the morphological basis of food resource partitioning. Here, we test if differences in food resource use within and between sea otter subspecies can be explained by differences in ecologically relevant metrics of bite performance that are mainly the product of variation in size, cranial morphology, or a combination of these traits. We use geometric morphometrics to evaluate variation in cranium size and morphology, and 2-dimensional models to estimate bite performance differences between 2 sea otter subspecies that differ in dietary ecology: the northern sea otter (*Enhydra lutris kenyoni*, a facultative generalist) and the southern sea otter (*E. l. nereis*, a specialist). We found significant differences in cranium shape and size between subspecies and between male and female sea otters. These differences were subtle yet consistent with most subspecies classifications and known sexually dimorphic traits. Cranial morphological differences did not translate into differences in estimated bite force between subspecies or sexes, but dentary strength differed significantly between male and female sea otters. Sea otters have short, blunt crania with pronounced sagittal and lambdoidal crests, and strong mandibles. These traits combine to produce high bite forces for their size. We propose that high bite performance capacity in sea otters enables resource-use variation by widening the diversity of available food resources they can procure from their environment; this allows them to behave as either generalists or specialists within different habitats.

Key words: bite force, Carnivora, geometric morphometrics, intraspecific variation, Mustelidae, resource-use specialization, sea otter, skull morphology

Intraspecific studies of morphology and performance are essential for understanding the factors that enable resource partitioning within populations and ecological communities. Variation in feeding performance and behavior across populations is expected to determine the breadth of the trophic niche explored by a species, and is the target of natural selection during morphological evolution. The sea otter (*Enhydra lutris*) is one of the smallest marine mammals, a keystone species in nearshore communities, and one of the few marine mammal species in which individual-level dietary specialization has been quantified and linked to ecological factors and processes (Estes et al. 2003; Tinker et al. 2008; Tinker et al. 2012; Newsome et al. 2015). These unique features make *E. lutris* an ideal system to investigate how morphological and behavioral traits affect intraspecific food resource partitioning.

Three subspecies of sea otter are currently recognized; the Asian sea otter, *Enhydra lutris lutris*, ranging from the Commander Islands of Russia to the Kuril Islands of Russia and Japan; the northern sea otter, *Enhydra lutris kenyoni*, ranging from the Aleutian Islands of Alaska south to Oregon; and the southern sea otter, *Enhydra lutris nereis*, of southern California and San Nicholas Island, California. Southern sea otters forage in rocky nearshore marine environments and have diverse diets consisting of sea urchin, abalone, snails, large decapods, and other prey items (Hines and Pearse 1982; Kvitek and Oliver 1988). Northern sea otters forage in mixed substrate habitats consisting of both soft-sediment and rocky substrates (Kvitek and Oliver 1988; Newsome et al. 2015). Their diet consists of a wide spectrum of marine invertebrates, but they tend to consume a higher proportion of infaunal bivalves than southern sea otters (Kvitek and Oliver 1988; Kvitek et al. 1992). Less is known about the diet of Asian sea otters.

While sea otter diets are diverse at a population or subspecies level, they are less so at an individual level (e.g., individuals can specialize on a few prey types—Estes et al. 2003). Recent studies have shown that competition drives variation in food resource use within and among sea otter populations (Estes et al. 2003; Tinker et al. 2008; Tinker et al. 2012). Habitat characteristics (e.g., sediment type) and the diversity and abundance of prey play an important role in whether sea otters function as dietary generalists or specialists when faced with increased competition (Newsome et al. 2015). Southern sea otter individuals in rocky nearshore environments tend to specialize their diet, alleviating competition by foraging for specific prey types (Estes et al. 2003; Newsome et al. 2015). In sharp contrast, northern sea otters in mixed-sediment habitats quickly deplete preferred prey, such as sea urchins and decapods, then move on to consume predominately infaunal bivalves, ultimately becoming more generalist foragers (Newsome et al. 2015). When compared to specialists, generalist foragers are expected to exhibit less-specialized morphologies or physiologies that are often linked to lower levels of feeding performance on specific prey items (e.g., Reudler et al. 2011). Thus, variation in food resource specialization, such as that observed within and among sea otter subspecies, could be associated with differences in cranial morphology and feeding performance (Bolnick et al. 2003).

The feeding apparatus of sea otters appears to be specialized for hard-object feeding; they have short, blunt crania (Riley 1985), bunodont dentition (Constantino et al. 2011), and fracture-resistant dental enamel (Ziscovici et al. 2014). As durophagous predators, sea otters rely on crushing bites to handle and process hard-bodied prey items (Riley 1985; Christiansen and Wroe 2007). Sea otters must consume nearly 25% of their body weight each day; they lack blubber and rely on an elevated metabolic rate in order to thermoregulate (Kenyon 1975; Williams et al. 1988). As a consequence, variation in morphological and behavioral traits that enhance bite performance and reduce competition could be critical for a sea otter's survival. Sexual dimorphism is one of the best-understood aspects of intraspecific morphological variation in this species. In southern sea otter populations, males exhibit much larger body sizes and cranial dimensions than females (Law et al. 2016a, 2016b). Larger heads directly translate into higher jaw adductor mass and ultimately higher theoretical bite forces in male southern sea otters (Law et al. 2016a, 2016b). Consistent with this trend, males and females differ in dietary preferences within southern sea otter populations (Newsome et al. 2015).

Variation in body size and cranial morphology among sea otter subspecies is moderate and, historically, has been a source of contention on the current designation of the 3 subspecies (Roest 1973; Riedman and Estes 1990; Wilson et al. 1991). Overall, northern sea otters are slightly larger than southern sea otters, although they vary in size geographically (Roest 1973). Southern sea otters have shorter, narrower skulls with blunt mandibles, whereas northern sea otters have longer skulls with a wider braincase and a wider zygomatic fossa (Wilson et al. 1991; Timm 2013; Timm-Davis et al. 2015). Differences in skull shape, especially those associated with morphological traits of the masticatory system, are expected to result in differences in bite force (e.g., Greaves 2002).

Here, we test whether and how differences in food resource use within and between sea otter subspecies can be explained by differences in ecologically relevant metrics of bite performance that are largely the product of variation in size and skull shape (or both via allometry—Christiansen and Adolfssen 2005). We predict that the specialized foraging strategy observed in southern sea otters is associated with a skull morphology that enables higher feeding performance metrics. Additionally, we predict that male sea otters of both subspecies will have higher bite forces than females due to known sexually dimorphic traits of the skull and differences in overall skull size (Roest 1973; Riley 1985; Law et al. 2016a; Wilson et al. 2016). To test our hypothesis, we applied 2-dimensional models (Thomason 1991; Therrien 2005) to estimate differences in bite performance between the 2 sea otter subspecies that are known to differ in dietary ecology (*E. l. kenyoni* and *E. l. nereis*), and conducted geometric morphometric analyses that allowed us to examine how independent and joint variation in cranial shape and size may underlie bite performance differences. These analyses allowed us to evaluate whether differences in size, cranial morphology, and bite performance are associated with dietary variation among sea otter populations.

MATERIALS AND METHODS

We took lateral, ventral, and dorsal-posterior digital photographs (Fig. 1) of 79 dry crania of adult individuals representing 2 subspecies of sea otter, *E. l. kenyoni* ($n = 47$; 17 males, 30 females) and *E. l. nereis* ($n = 30$; 19 males, 11 females) from the Burke Museum of Natural History and Culture (University of Washington, Seattle, Washington; Supplementary Data SD1). To standardize the position of the specimens in each of the 3 photographed views, we placed a Canon 5D Mark II digital camera on a stand at a fixed height and aligned the cranium to a centimeter grid in the plane of the zygomatic arch. Both the camera and the grid were leveled using a bubble level to avoid any distortion in the images due to misalignment. We used ImageJ (NIH, Bethesda, Maryland) to estimate the linear dimensions and muscle cross-sectional areas used in the bite performance calculations below.

To inform bite performance models based on mandible strength, we took linear measurements of the dry mandibles of 76 adult individuals representing 2 subspecies of sea otter, *E. l. kenyoni* ($n = 49$; 17 males, 32 females) and *E. l. nereis* ($n = 27$; 17 males, 10 females) from the Burke Museum of Natural History and Culture (University of Washington, Seattle, Washington; Supplementary Data SD1). All measurements were taken using digital calipers to the nearest hundredth of a millimeter. We chose a landmark immediately posterior to the second molar, and measured the height and width of the mandible at the center of the dentary, and the distance from the mandibular condyle to the landmark (Fig. 2).

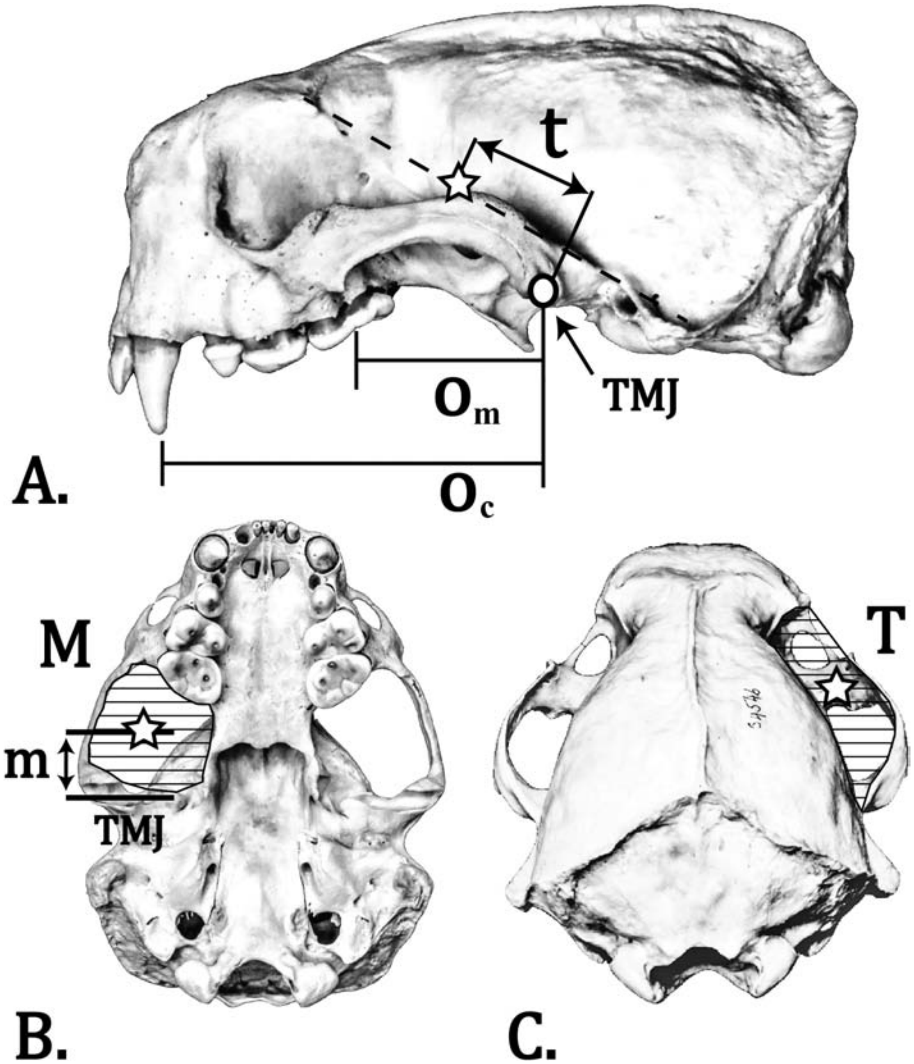

Fig. 1.—Linear measurements for estimating bite force (Thomason 1991): (A) Lateral view of *Enhydra lutris* cranium showing the temporomandibular joint (TMJ); the length of the moment arm of the temporalis muscle (t), measured from the TMJ to the centroid (★) of the cross-sectional area of the temporalis muscle along the plane of the muscle group; and the out levers (o), measured from the center of the first molar (o_m) to the TMJ and from the tip of the canine (o_c) to the TMJ. (B) Ventral view of *Enhydra lutris* cranium showing the TMJ; the cross-sectional area of the masseter/pterygoid muscle group (M); and the length of the moment arm of the masseter/pterygoid muscle group (m), measured from the TMJ to the centroid (★) of the cross-sectional area of the masseter/pterygoid muscle group. (C) Dorsal-posterior view of *Enhydra lutris* cranium showing the cross-sectional area of the temporalis muscle used to calculate the force of the temporalis muscle (T); and the centroid of the temporalis muscle (★).

Bite performance.—We used 2-dimensional models to estimate 2 proxies of feeding performance that are associated with differences in diet in vertebrates: bite force and maximum bending force of the mandible (Thomason 1991; Therrien 2005). We estimated bite force at the molars and the canines using the following equation:

$$\text{Bite Force} = 2*(M*m+T*t)/o$$

where M is the masseter + pterygoid muscle force, m is the moment produced about the temporomandibular joint (TMJ) by the masseter + pterygoid, T is the temporalis muscle force, t is the moment about the TMJ produced by the temporalis, and o is the out lever (Thomason 1991; Christiansen and Adolfssen 2005). We calculated the forces produced by the temporalis (T) and the masseter + pterygoid (M) by estimating each of their cross-sectional areas from photographs (Fig. 1) following Thomason (1991), and scaling these values by an isometric force value of 25 N/cm^2 (Herzog and Nigg 1994). To calculate the length of the moment arm for the temporalis (t), we first located the centroid of the cross-sectional area of this muscle in the lateral view (following Thomason 1991). We then measured the distance from the centroid to the center of the TMJ (Fig. 1A). Similarly, we estimated the moment arm for the masseter + pterygoid (m) in the ventral view as the distance from the centroid of their cross-sectional area to the TMJ (Fig. 1B). We defined the lever arm (o) as the distance from the center of the first upper molar to the center of the TMJ for molar bites, and the distance from the tip of the upper canine to the TMJ for canine bites (Fig. 1A).

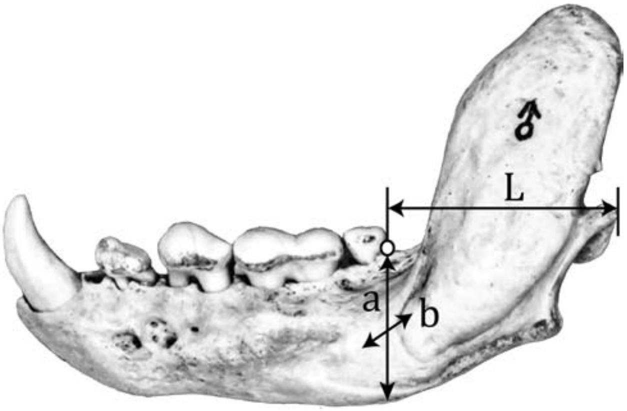

Fig. 2.—Linear measurements used for estimating the maximum bending force of the mandible and the ratio of section modulus (Therrien 2005). A landmark was chosen posterior to the last, lower molar of the mandible (open circle). Measurements of the height (a) and width (b) of the dentary were taken at the plane of section modulus on the dentary at the landmark. The length (*L*) from the landmark to the mandibular condyle was measured.

As a second proxy for feeding performance, we estimated the maximum bending force of the mandible by modeling the ramus as an elliptical beam (Therrien 2005). This method is more accurate than modeling the mandible as a rectangular beam, and enables more straightforward bite force interpretations that are not sensitive to size differences and other factors (Therrien et al. 2016). We calculated the maximum bending force at a landmark immediately posterior to the second molar using a series of equations. First, we calculated the distribution of bone about the labiolingual axis (*Ix*) and the dorsoventral axis (*Iy*) on the mandible using the following equations:

$$Ix = \pi ba^3 / 4$$

$$Iy = \pi ab^3 / 4$$

where *a* represents the height of the mandible and *b* represents the width of the mandible at the chosen landmark (Fig. 2; Biewener 1992; Therrien 2005). Next, we calculated the section modulus (*Z*), a measure of strength in bending, for the dorsoventral plane (*Zx*) and the labiolingual plane (*Zy*) using the following equations:

$$Zx = Ix / a$$

$$Zy = Iy / b$$

The maximum force applied (*F*) at the landmark is proportional to the ratio of the section modulus of the mandible (*Z*) and the distance from the mandibular condyle to the landmark immediately posterior to the second molar (*L*) (Fig. 2; Therrien 2005) and is represented by the following equation:

$$F = Zx / L$$

The ratio of the section modulus in the dorsoventral plane (*Zx*) and the section modulus in the labiolingual plane (*Zy*) is proportional to the ratio of the dorsoventral and mediolateral diameters of the mandibular corpus (Therrien 2005). We calculated this ratio to compare specialization for different loading regimes between subspecies and sexes using the following equation:

$$\text{Section modulus ratio} = Zx / Zy$$

A ratio greater than 1 indicates specialization toward dorsoventral loads via mandibles that are deeper than wide at the landmark. A ratio smaller than 1 indicates adaptation toward labiolingual loads via mandibles that are wider than deep at the landmark (Therrien 2005).

Cranial shape.—To assess differences in cranium size and shape, we used photographs and TPSdig2 (v. 2.10—Rohlf 2006) to place 15 homologous landmarks and 20 sliding semi-landmarks in the lateral view of the cranium, and 19 landmarks and 14 sliding semi-landmarks on the left side of the ventral view of the cranium (Fig. 3; Supplementary Data SD2). The square root of the mean square error of our landmark placement was 0.87 mm in the lateral view and 0.39 mm in the ventral view. We then performed a generalized Procrustes analysis of landmark coordinates using functions within the package *geomorph* (Adams et al. 2009) to extract variables representing cranium size (centroid size) and shape (Procrustes coordinates). We performed a principal component analysis (PCA) on shape coordinates to illustrate patterns of morphological variation.

Statistical analyses.—We conducted a 2-way analysis of variance (ANOVA) to test for statistical differences in bite force, maximum bending force of the mandible, and section modulus ratio between subspecies and sexes. We used 2-way ANOVAs to test for statistical differences in cranium centroid size between subspecies and sexes, and multivariate analyses of variance (MANOVAs) to test for statistical differences in shape coordinates between subspecies and sexes. To test if trends in cranial shape were dependent on size, we tested for allometry by calculating the common allometric component (CAC—Mitteroecker et al. 2004) and performed an ANOVA with a permutation test of Procrustes coordinates on centroid size while accounting for within-group patterns of covariation (10,000 iterations). All statistical analyses were conducted in R 3.3.2 (R Core Team 2012).

RESULTS

Bite performance.—Molar and canine bite forces estimated from cranial measurements are presented in Table 1. Sea otters are expected to produce molar bite forces that are 2.09 ± 0.17 (mean ± *SD*) times stronger than canine bites (Table 1). Bite force estimates did not differ significantly between subspecies or sexes at either the canine or molar bite points (Table 2). Using the average surface area of the distal tip of the upper canine (4 mm^2, calculated from photographs), we estimated a mean bite pressure of 43.9 ± 9.27 N/mm^2 in *E. l. nereis* and 43.4 ± 7.87 N/mm^2 in *E. l. kenyoni* when these animals bite with both canines.

We did not find statistical differences in the maximum bending force of the mandible between *E. l. kenyoni* and

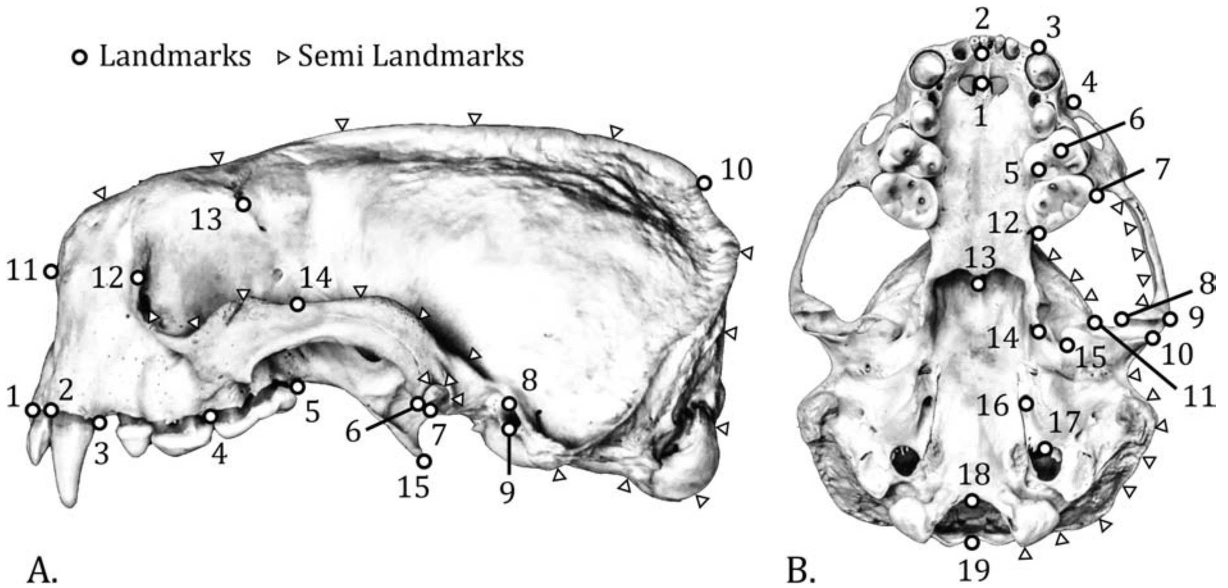

Fig. 3.—Landmarks (open circles) and semi-landmarks (triangles) digitized from the lateral cranium (A) and ventral cranium (B) for geometric morphometric analysis. See Supplementary Data SD2 for descriptions of landmarks.

E. l. nereis ($F_{1,73} = 1.11$, $P = 0.295$). However, we did find a statistically significant difference in the maximum bending force of the mandible between males and females of each subspecies ($F_{1,73} = 15.31$, $P < 0.001$; Table 3). Males had a greater maximum bending force of the mandible (*E. l. nereis*: 1.18 ± 0.15 cm^2; *E. l. kenyoni*: 1.15 ± 0.23 cm^2) than females (*E. l. nereis*: 0.98 ± 0.08 cm^2; *E. l. kenyoni*: 0.94 ± 0.19 cm^2). The interaction term between sex and subspecies was not significant in this ANOVA. We obtained similar results when we modeled the mandible as a rectangular beam (Freeman and Lemen 2010; Supplementary Data SD3).

We did not find significant differences between sexes in the section modulus ratio of the mandible (*Zx/Zy*). However, we found significant differences in the section modulus ratio of the mandible between subspecies, *E. l. nereis* and *E. l. kenyoni* ($F_{1,73} = 11.552$, $P = 0.001$; Table 4). *Enhydra lutris nereis* had a slightly greater section modulus ratio (2.01 ± 0.21) than *E. l. kenyoni* (1.84 ± 0.25). Section modulus ratios greater than 1, as seen in both subspecies, are indicative of specialization for dorsoventral loads on the mandible. These ratios also indicate mandibles that are deeper than they are wide at the second molar.

Cranial shape.—We found statistically significant differences in cranial shape (Procrustes coordinates) in both the lateral and ventral views between both subspecies (lateral view: $F_{1,57} = 4.639$, $P = 0.002$; ventral view: $F_{1,66} = 4.103$, $P < 0.001$; Table 5; Supplementary Data SD4 and SD5) and between sexes when these were pooled across subspecies (lateral view: $F_{1,57} = 2.32$, $P = 0.0179$; ventral view: $F_{1,66} = 4.64$, $P = 0.032$; Table 5; Supplementary Data SD6 and SD7). Within each subspecies, differences between sexes remained significant for *E. l. kenyoni* (lateral view: $F_{1,35} = 2.26$, $P = 0.025$; ventral view: $F_{1,46} = 1.97$, $P = 0.046$), but not for *E. l. nereis* (lateral view: $F_{1,24} = 1.02$, $P = 0.408$; ventral view: $F_{1,22} = 1.11$, $P = 0.324$).

Table 1.—Estimated molar and canine bite forces (mean ± *SD*) for 2 subspecies of sea otter, *Enhydra lutris kenyoni* and *Enhydra lutris nereis*.

Subspecies	*n*	Molar Mean ± *SD*	Canine Mean ± *SD*
Enhydra lutris kenyoni	43	365.6 ± 65.5	172.6 ± 31.9
Males	17	368.6 ± 55.6	177.8 ± 32.9
Females	26	363.6 ± 72.2	169.2 ± 31.5
Enhydra lutris nereis	25	356.3 ± 78.9	175.6 ± 37.1
Males	17	349.8 ± 81.7	172.1 ± 35.9
Females	8	370.1 ± 76.3	183.1 ± 40.8

Table 2.—Results from a 2-way analysis of variance (ANOVA) of molar and canine bite forces between sexes and 2 sea otter subspecies, *Enhydra lutris kenyoni* and *Enhydra lutris nereis* (*d.f.*: degrees of freedom; SS: sum of squares; MS: mean squares).

	d.f.	*SS*	*MS*	*F*	*P*-value
Molar bite force					
Sex	1	608	607.8	0.119	0.730
Subspecies	1	993	993.3	0.195	0.659
Sex * subspecies	1	2,275	2,275	0.445	0.507
Residuals	65	329,514	5,069.4		
Canine bite force					
Sex	1	104	103.6	0.089	0.767
Subspecies	1	94	93.7	0.080	0.778
Sex * subspecies	1	1,367	1,366.8	1.740	0.283
Residuals	65	75,907	11,167.8		

Morphological differences between the 2 subspecies appeared to be subtle and distributed among several axes in morphospace (Supplementary Data SD4 and SD5). Southern sea otters (*E. l. nereis*) had overall shorter crania and narrower braincases than northern sea otters (*E. l. kenyoni*). Additionally, southern sea otters were wider between the postorbital process than northern sea otters. Within each subspecies, the crania of males tended to have taller braincases at the midpoint with a slightly concave surface at the posterior end of the cranium. This shape is characteristic of taller sagittal crests (dorsally) and lambdoidal crests (posteriorly). However, we noted that some females also had prominent sagittal and lambdoidal crests, although not as developed as those found in males. We also noted females had smaller braincases than males, and these were narrow toward the anterior end. Males had zygomatic arches that were taller at the midpoint and thicker mediolaterally at the posterior end, whereas zygomatic arches of females were rounded dorsoventrally and gently sloped toward the external auditory meatus. Additionally, the zygomatic fossa was more square-shaped (i.e., wide both anteriorly and posteriorly) in males versus more narrow anteriorly and widened posteriorly in females.

Table 3.—Results from a 2-way analysis of variance (ANOVA) on the maximum bending force of the mandible between sexes and 2 sea otter subspecies, *Enhydra lutris kenyoni* and *Enhydra lutris nereis*. Bold *P*-values indicate significance (α = 0.05).

	d.f.	*SS*	*MS*	*F*	*P*-value
Sex	1	0.909	0.909	15.31	**< 0.001**
Subspecies	1	0.066	0.066	1.11	0.295
Residuals	73	4.335	0.059		

Table 4.—Results from a 2-way analysis of variance (ANOVA) on the section modulus ratio of the mandible between sexes and 2 sea otter subspecies, *Enhydra lutris kenyoni* and *Enhydra lutris nereis*. Bold *P*-values indicate significance (α = 0.05).

	d.f.	*SS*	*MS*	*F*	*P*-value
Sex	1	0.022	0.022	0.397	0.53
Subspecies	1	0.625	0.625	11.552	**< 0.001**
Residuals	73	43.951	0.054		

Table 5.—Results from 2 multivariate analyses of variance (MANOVAs) on Procrustes coordinates of the lateral and ventral views of the cranium. Sex and sea otter subspecies, *Enhydra lutris kenyoni* and *Enhydra lutris nereis*, were predictor variables. Bold *P*-values indicate significance (α = 0.05).

	d.f.	*SS*	*MS*	*F*	R^2	*P*-value
Lateral view						
Subspecies	1	0.009	0.009	4.639	0.071	**< 0.001**
Sex	1	0.004	0.004	2.325	0.036	**0.018**
Subspecies * sex	1	0.002	0.002	1.016	0.016	0.390
Residuals	57	0.113	0.001		0.877	
Ventral view						
Subspecies	1	0.005	0.005	4.103	0.056	**< 0.001**
Sex	1	0.003	0.003	2.093	0.028	**0.032**
Subspecies * sex	1	0.002	0.002	1.738	0.023	0.068
Residuals	66	0.096	0.001		0.892	

We found statistical differences in cranium size (centroid size) between subspecies in both the lateral and ventral views (Table 6). The crania of southern sea otters (*E. l. nereis*) were slightly larger than those of northern sea otters (*E. l. kenyoni*). We also found statistically significant size differences between sexes in the lateral and ventral views (Table 6), with males having larger crania than females. We found positive allometry in cranial shape with respect to centroid size (Supplementary Data SD8 and SD9), so that larger crania were longer, had taller braincases at the midpoint, larger sagittal and lambdoidal crests, taller, wider, and more robust zygomatic arches at the midpoint, and taller rostra at their most anterior point.

DISCUSSION

The nearly range-wide extirpation of sea otters during the 19th century left only a few isolated populations in Alaska, California, and eastern Asia (Roest 1973; Riedman and Estes 1990; Larson et al. 2012). Modern sea otters are remnants of those few populations, with a loss of over one-half of their genetic diversity (Larson et al. 2012). This bottleneck event likely had an effect on the cranial morphological diversity among and within sea otter subspecies today. Consistent with this scenario, biogeographic studies (Larson et al. 2012), and previous taxonomic descriptions (Roest 1973; Wilson et al. 1991; Timm 2013), we found subtle, quantitative differences in the size and shape of the cranium and mandible between *E. lutris* subspecies. Our results further highlight that these differences are linked via an allometric relationship in which cranial shape changes in tandem with size. Southern sea otters appear to have slightly larger skulls than northern sea otters, which contradicts the findings of Timm-Davis et al. (2015) and Timm (2013) but supports the notion that northern sea otters vary in size throughout their range (as observed by Roest 1973). A considerable proportion of the northern sea otter skulls used in this study came from adult specimens collected during the 1989 Exxon Valdez oil spill in Prince William Sound, Alaska. If sea otters in this area or time period had consistently smaller skulls than more

Table 6.—Results from 2-way analyses of variance (ANOVAs) on centroid size between sexes and 2 sea otter subspecies, *Enhydra lutris kenyoni* and *Enhydra lutris nereis*. Bold *P*-values indicate significance (α = 0.05).

	d.f.	*SS*	*MS*	*F*	*P*-value
Lateral view					
Subspecies	1	10.34	10.33	5.61	**0.021**
Sex	1	24.51	24.52	13.29	**< 0.001**
Subspecies * sex	1	0.57	0.286	0.156	0.856
Residuals	58	106.96	1.87		
Ventral view					
Subspecies	1	0.14	0.13	0.14	0.713
Sex	1	12.13	12.14	12.07	**< 0.001**
Subspecies * sex	1	5.38	5.37	5.73	**0.020**
Residuals	67	67.31	1.00		

western or recent populations, it is possible that our data were biased toward smaller individuals. As there is no evidence that this is the case, future studies should investigate if there is a substantial and functionally significant degree of size variation within the full geographic range of northern sea otters.

Based on skull morphometrics, Timm-Davis et al. (2015) hypothesized that northern sea otters would have higher bite forces than southern sea otters due to a higher mechanical advantage of the masseter and overall larger temporalis attachment area. However, our findings suggest that the subtle differences in skull shape and size between northern and southern sea otters do not translate into significant differences in bite force. Our 2-dimensional bite force model uses dry skulls to estimate the cross-sectional area of the temporalis and masseter-pterygoid muscle groups in order to calculate bite forces. Although this may lead to underestimation (Davis et al. 2010), the model-generated predictions of bite force are comparable to previously published estimates (Thomason 1991; Christiansen and Adolfssen 2005; Christiansen and Wroe 2007; Law et al. 2016b) and produced greater values for molar than for canine bite forces (consistent with mammalian jaw lever mechanics—Greaves 2002). High molar bite forces and broad, rounded-cusped molars allow sea otters to crush hard-bodied benthic invertebrates (Riley 1985; Constantino et al. 2011; Timm 2013; Law et al. 2016b), whereas high canine bite forces allow them to pry open bivalves and pierce mechanically challenging prey (Timm 2013; Law et al. 2016b). Our bite force estimates further support the prediction that sea otters have forceful bites relative to their body size (as in other mustelids—Christiansen and Adolfssen 2005), and these values are well above the pressure required to puncture the exoskeleton of marine invertebrates commonly found in their diet (e.g., crabs: 30.14 ± 5 N/mm^2—Hepburn et al. 1975).

Our analyses revealed sexual dimorphism in the size and shape of the cranium in northern sea otters. We found that adult male sea otters of both subspecies have crania that are larger overall, taller, and wider behind the orbits, all of which corroborate findings and predictions from previous studies (Roest 1973; Riley 1985; Wilson et al. 1991; Law et al. 2016a, 2016b). Although we only detected sexual dimorphism in the cranial shape of northern sea otters, previous studies have documented sexual dimorphism in southern sea otters as well (Law et al. 2016a, 2016b). This lack of statistical significance for southern sea otters could reflect differences in sample size, and emphasizes the potential need for larger samples in these types of intraspecific studies.

Bite performance also appears to be sexually dimorphic in both sea otter subspecies. Male sea otters have a stronger, more robust mandible at the second molar, as indicated by a greater maximum bending force. This estimate of maximum bending force can be used as a proxy for bite force, and has been shown to be more accurate in providing estimates of bite force than Thomason's (1991) dry skull method (Therrien et al. 2016). This may explain why we did not find differences in estimated bite forces between male and female sea otters using the dry skull method. Consistent with our results, Law et al. (2016b) found significant differences in theoretical bite forces between adult males and females in *E. l. nereis.* Their study measured jaw adductor mass from fresh specimens, which is a superior approach to estimating cross-sectional areas and bite forces from dry skulls (albeit constrained by specimen availability). Therefore, it is likely that male sea otters of both subspecies do exhibit greater in vivo bite forces than females, in addition to stronger mandibles. It is unclear, however, if robust jaws and forceful bites in male sea otters are the product of intraspecific diet specialization. These traits may be the result of sexual selection on size and, via allometry, cranial shape. Forceful bites are advantageous to males because they bite each other during fights to establish territories and increase reproductive opportunities with females (Riedman and Estes 1990).

Regardless of the selective pressures causing sexual dimorphism in cranial morphology and feeding performance, male sea otters have the potential to consume more mechanically challenging prey than females just by virtue of their skull size and morphology. This might be important for expanding resource use or diminishing competition. Females, on the other hand, may also overcome bite performance disadvantages by processing tough prey through tool use; sea otters use rocks and other objects to crack open tough prey, and females use tools more frequently than males (Fujii et al. 2015). Tool use in female sea otters is thus a valuable behavioral strategy that eases the processing of otherwise inaccessible prey (e.g., marine snails and bivalves—Fujii et al. 2015).

Several cranial features underlie a durophagous diet in sea otters, including blunt skulls with a shortened rostrum (Riley 1985; Law et al. 2016b), robust and widened zygomatic arches (Timm 2013), pronounced sagittal and lambdoidal crests (Law et al. 2016a, 2016b), and bunodont molars with rounded cusps (Constantino et al. 2011). Together, these features enable more forceful bites via a shorter outlever and increased attachment sites for the jaw adductors, and concentration of bite forces on smaller areas without risking tooth fracture (Crofts 2015). In addition to these features, we found specializations for durophagy in the shape of the mandible. Both northern and southern sea otters have section modulus ratios (*Zx/Zy*) that reflect a deeper than wide mandibular corpus. This shape is more resistant to dorsoventral loads, and likely allows sea otters to consume tough prey. Southern sea otters exhibit a greater section modulus ratio than northern sea otters, which could enable them to consume relatively tougher prey as predicted. However, despite significant cranial and mandibular shape differences, we did not find any theoretical bite performance differences (bite force or mandible strength) between sea otter subspecies. Instead, their high performance capacity seems to enable either subspecies to switch prey types under specific conditions. Consistent with this idea, sea otters can exhibit high dietary plasticity; some individuals have been reported to consume over 150 different species of prey including echinoderms, large decapods, bivalves, snails, squid, and occasionally fish (Kvitek and Oliver 1988; Estes et al. 2003). We postulate that high performance ability enables northern and southern sea otters to act as generalists or specialists depending on prey availability, habitat characteristics, and competition.

Our results further support previous findings (Estes et al. 2003; Tinker et al. 2008; Tinker et al. 2012; Fujii et al. 2015; Newsome et al. 2015) that variation in resource use within sea otter populations may be linked to individual foraging behavior, physiological adaptations, and habitat characteristics, all of which likely influence the diversity and abundance of consumed prey more than morphological and bite force differences in this species. When foraging, factors other than cranial morphology are more likely to reduce intraspecific competition, such as age and sexual maturity, foraging experience and skill, and established territories (Estes et al. 2003; Tinker et al. 2008; Tinker et al. 2012; Lafferty and Tinker 2014).

In conclusion, we used geometric morphometrics to evaluate variation in cranial size and morphology and 2-dimensional models to estimate bite performance differences between 2 subspecies of sea otter, *E. l. nereis* and *E. l. kenyoni*. We found size and shape differences in cranial morphology between subspecies and sexes. These cranial morphological differences were consistent with most subspecies classifications and known sexual dimorphic traits of the skull, yet they were subtle and did not translate into differences in estimated bite force. Sea otters have cranial and dental features that combine to produce forceful bites that in turn allow them to efficiently process prey and satisfy elevated metabolic rates necessary for thermoregulation. We hypothesize that high bite forces in sea otters enables variation in resource use by increasing the diversity of mechanically challenging prey sea otters can procure from their environment, allowing them to behave as either generalists or specialists within their habitat. We further postulate that northern and southern sea otters could both act as specialists, depending on habitat characteristics and prey availability. When faced with increased intraspecific competition, it is likely that factors such as age and sexual maturity, foraging skill, tool use, and established territories prove more advantageous to individual sea otters than intraspecific morphological or bite performance differences.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—A list of specimens used in this study. All specimens were obtained from the Burke Museum of Natural History and Culture. The Burke Museum ascension number (UWBM), sex, subspecies, and geographic location of the specimen are given.

Supplementary Data SD2.—Description of landmarks and semi-landmarks used in this study.

Supplementary Data SD3.—Relative index of dentary strength in which the dentary is modeled as a rectangular beam (Freeman and Lemen 2010).

Supplementary Data SD4.—Shape variation in the lateral cranium between 2 subspecies of sea otter (*Enhydra lutris nereis* and *E. l. kenyoni*).

Supplementary Data SD5.—Shape variation of the ventral cranium between 2 subspecies of sea otter (*Enhydra lutris nereis* and *E. l. kenyoni*).

Supplementary Data SD6.—Shape variation in the lateral cranium between males and females of 2 subspecies of sea otter (*Enhydra lutris nereis* and *E. l. kenyoni*).

Supplementary Data SD7.—Shape variation of the ventral cranium between males and females of 2 subspecies of sea otter (*Enhydra lutris nereis* and *E. l. kenyoni*).

Supplementary Data SD8.—Results from 1-way analyses of variance (ANOVAs) for allometry in skull shape with respect to centroid size in sea otter (*Enhydra lutris*) skulls in the lateral and ventral views.

Supplementary Data SD9.—Positive allometry in the lateral cranium of 2 sea otter subspecies, *Enhydra lutris kenyoni* and *Enhydra lutris nereis*.

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