FEEDING BIOMECHANICS & CRANIODENTAL MORPHOLOGY IN OTTERS (LUTRINAE)

A Dissertation

by

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ABSTRACT

Variation in terrestrial mammalian craniodental morphology and skull shape is known to constrain feeding performance, which in turn influences dietary habits and ultimately fitness. Otters have evolved two feeding specializations: underwater raptorial capture of prey (mouth-oriented) and capture of prey by hand (hand-oriented), which likely correspond to craniodental morphology and bite performance. However, feeding biomechanics and performance data for otters, aquatic mustelids that consume prey above water, are sparse. The first goal of the study was to investigate the relationship between feeding morphology and bite performance between two mouth-oriented piscivores (giant river otters and North American river otters) and two hand-oriented invertebrate specialists (sea otters and Asian small-clawed otters) using morphometric approaches. The second goal was to investigate fluctuating asymmetry in the cranium of otters. The third goal was to characterize feeding mechanisms (kinematics and jaw musculature) and role of bite performance in the trophic ecology of sea otters. Mouth-oriented piscivores possessed longer skulls and mandibles, with jaws designed for increased velocity at the expense of bite capability. Hand-oriented possessed more blunt skulls and mandibles designed for increased bite capability. Sea otters displayed a greater degree of fluctuating asymmetry of the skull, which is likely linked to environmental stresses. Bite performance and durophagous feeding behavior in sea otters was characterized in detail in the feeding kinematics. Estimated bite forces of sea otters were large enough to crush all size classes of butter and littleneck clams tested in

the lab. However, sea otters are size selective predators and generally choose bivalves of small to medium size. Medium sized butter and littleneck clams required an intermediate breaking force, and are buried at a shallower depth than larger clams. Clams requiring an intermediate breaking force could decrease consumption time, thus overall handling time.

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CHAPTER I

INTRODUCTION

Evolution of Otters

The masticatory apparatus and specialized bite capability of mustelids, particularly otters, is a result of a long history of mammalian evolution centered on the development of heterodonty, changes in jaw biomechanics, and mastication. Early mammals demonstrated an extensive diversification and ecomorphological specialization (Luo, 2007). Currently there are 5,416 extant mammal species and 1,229 genera (Wilson & Reeder, 2005; Luo, 2007). Mammals are a monophyletic group of vertebrate tetrapods that originated from synapsids (Dilkes & Reisz, 1996; Oftedal, 2002). Due to numerous new synapsid fossil-finds, our knowledge of these mammalian ancestors has broadened considerably, particularly the evolutionary transitions of therapsids to cynodonts to modern mammals (Luo, 2007). Therapsids that survived the Permian-Triassic extinction event displayed morphological trends that formed the basis of modern mammalian anatomical plan of the skull, such as a reduction of the temporal shield and an enlargement of the single temporal opening or fenestration (Rubidge & Sidor, 2001). This enlargement of this single temporal fenestration produced a sagittal crest and zygomatic arches, which became new attachment points for the lateral adductor muscles (temporalis and masseter muscles). The upper canines became wider and longer. An external auditory meatus (passageway from outer ear to tympanic membrane of middle ear) formed in the squamosal bone. Cynodonts (derived therapsids and the sister group to mammals) possessed additional derived characteristics, including a masseteric fossa of the dentary bone, laterally flared zygomatic arches, reduced angular bone on the lower jaw, and heterodont dentition (Rubidge & Sidor, 2001). The development of this masseter muscle is an important functional refinement to the masticatory apparatus; true mastication is restricted to Mammalia. The new masseter muscle provided more control of transverse jaw movements, increased bite force, and reduced the stress placed on the jaw joint. Unlike the pelycosaurs (basal Synapsids) and therapsids, cynodonts developed two occipital condyles that articulated with the atlas (cervical vertebrae 1 or C1). The maxillary and palatine bones also expanded caudally and toward the midline, forming a secondary hard palate; an important mammalian adaptation for nursing and breathing during feeding events (Vaughan et al., 2000). By the late Triassic (250 mya) and early Jurassic (200 mya) true mammals emerged (Mammalia) and radiated into numerous groups (Vaughan et al., 2000). Morganucodontidae, a multituburculate, represents the earliest known mammals and appeared in the fossil record in the late Triassic or early Jurassic (250-200mya) (Vaughan et al., 2000; Luo, 2007). Heterdonty had arisen and premolars most likely had predecessors or deciduous teeth, an indication of diphydonty. Evidence suggests that these early mammals exhibited unilateral occlusion (anisognathy); chewing occurring on a single side at a time, as do many extant mammals do today (Vaughan et al., 2000).

The three modern mammalian clades, prototheria, metatheria, and eutheria, arose and underwent major diversification in the Mesozoic Era (250-65 mya) (Ji et al., 2002; Veron et al., 2008). Metatherians (marsupials) and eutherians (placentals) diverged into two different phylogenetic lineages in the middle Cretaceous (approximately 144 mya) (Cifelli & Davis, 2003; Luo, 2007). Eutherians (placentals) and metatherians (marsupials) currently comprise up to 99% of all extant mammalian species and show great diversification in ecomorphological characteristics, including unique ecological specializations, such as predation and scavenging (e.g., moving away from generalized insectivorous diets) (Smith, 1997; Luo et al., 2003; Luo, 2007). The extinction of non-avian dinosaurs at the K-T boundary opened up new niches for mammals. Fossils reveal that the first mammals were small, shrew to marmot size (Godinot, 1994; Alroy, 1999; Catania, 2000). The braincase was long and narrow. Three molars were present and were typically tribosphenic, possessing a protocone on the upper molars which fit into the talonid basin and three cusps on the lower molars (Cifelli, 1999). The molars of eutherians (and metatherians) are derived from this basal tribosphenic form in earlier mammals (Hiiemae & Crompton, 1985; Luo et al., 2001). Symmetrodonts (mammal-like synapsids) also developed a triposphenic tooth pattern (molars with three primary cusps arranged in an isosceles triangle), but there was no direct occlusion present because of the lack of a talonid posterior to the trigonid (Luo et al., 2001; Rougier et al., 2003; Luo et al., 2007). Pantotherians (a clade of Mesozoic mammals) also evolved a tribosphenic dentition with the addition of a talonid on the lower molars for direct occlusion between the upper and lower molars (Crompton & Jenkins, 1967). It has been suggested that tribosphenic molars of eutherians and metatherians were derived from pantotheres (Crompton & Jenkins, 1967; Dashzeveg & Kielan-Jaworowska. 1984; Schmidt-Kittler, 2002). Eutherians also possess this direct occlusion due to the presence of the talonid. An inspection of dentition morphology reveals that eutherians display a diverse feeding ecology and adaptations across numerous feeding categories such as: insectivory, carnivory, frugivory, and herbivory (Vaughan et al., 2000; Schmidt-Kittler, 2002). This dental diversity, in addition to mastication, allowed therian mammals to radiate into open niches and exploit new habitats and prey in a rapidly changing environment.

The Order Carnivora appeared approximately 60 million years ago during the Paleocene (Van Valkenburgh, 2007). Miacids are thought to represent the basal stock from which all modern Order Carnivora evolved (Radinsky, 1982; Ewer, 1998; Van Valkenburgh, 1999; Wesly-Hunt & Flynn, 2005; Smith & Smith, 2010). Miacids coexisted with other carnivorous mammals: Order Creodonta (which include the families Oxyaenidae and Hyaenodontidae) and Order Condylarthra (particularly the family Mesonychidae) (Radinsky, 1982). However, while miacids underwent rapid evolutionary radiation by the end of the Eocene, oxyaenids, hyaenodontids, and mesonychids went extinct. Miacids gave rise to the modern families of Order Carnivora that we see today. The best evidence that demonstrates miacids as the first carnivoran representatives is the development of P^4 and M_1 as the carnassials (Van Valen, 1969). This functional complex has two advantages: carnassials can become functional prior to the shedding of the deciduous carnassials and it provides a greater potentiality for adaptive differentiation (Ewer, 1998). The lower first molar is the only molar involved in both shearing and piercing as a carnassial tooth. There are three major pathways for the evolution of this molar, producing either purely flesh consuming carnivores (hypercarnivores), herbivores, or omnivores (Ewer, 1998). In hypercarnivores (such as members of the Family Felidae), the posterior molars are reduced or lost and the carnassials are modified as shearing blades. The jaws are shortened so that the maximum force operating on the jaw muscles is exerted at the level of the carnassials (Greaves, 1982; Greaves, 1985; Christiansen & Wroe, 2007; Van Valkenburgh, 2007). Omnivores, or mixed feeders, have modified molars designed for crushing and the shearing edges are reduced. Herbivores represent departure from this mixed feeding morphology. The carnassials secondarily lose their blade-like cusps and become more blunt and designed for grinding (Ewer, 1998). Sea otters are exceptional in that the carnassials are broad and flat, designed for durophagy (e.g., crushing hard, benthic prey). Sea otters are the only members of Lutrinae that possess bunodont dentition for such a dietary specialization (Lewis, 2008). Therefore, Miacids had dentition which held the potential for producing highly successful carnivorous predators, omnivores, or secondarily herbivores (Ewer, 1998). With such wide variation in dentition miacids could exploit new resources in a changing environment (Ewer, 1998).

During the late Eocene, Order Carnivora radiated rapidly (Valkenburgh, 1999; Wesley-Hunt, 2005), and became ecologically diverse, spannnig a wide range of feeding spectrums. This suggests significant differences in craniodental morphology (Sacco & Valkenburgh, 2004; Christiansen & Wroe, 2007). The Order Carnivora is composed of two independent lineages or suborders: Caniformia (dog-like carnivores) and Feliformia (cat-like carnivores) (Van Valkenburgh, 1999; Delisle & Strobeck, 2005; Vaughn, et al., 2011), which rapidly radiated in the late Eocene and early Oligocene (35 mya) (Van

Valkenburgh, 1999). Caniformia is subdivided into two infraorders (Bininda-Emonds & Russell, 1996; Delisle & Strobeck, 2005) or superfamiles (Flynn et al., 1988): Canidae (dogs and foxes) and Arctoidea (bear-like carnivores). Arctoidea is subdivided further into 8 families: Canidae (dogs), Felidae (cats), Ursidae (bears), Mustelidae (weasels), Procyonidae (raccoons), Herpestidae (mongoose), Hyaenidae (hyenas), Viverridae (civets) (Binida-Emonds et al., 1999; Christiansen & Wroe, 2007). Carnivoran families are distinguished taxonomically from each other based on skull morphology (e.g., middle ear and basicranial anatomy; Radinsky, 1981a; Radinsky, 1981b; Radinsky, 1982; Van Valkenburgh, 1999; Goswami, 2006; Wroe & Milne, 2007; Van Valkenburgh, 2007) and more recently using molecular data (e.g., Mauda & Yoshida, 1994; Sato et al., 2004; Spaulding et al., 2009; Eizirik et al., 2010). Although data on gene structure and function are numerous, there are few data regarding how phenotypes evolved (Schwenk, 2000b; Relyea, 2002). Phenotype is what performs in the environment and is what natural selection acts on (Schwenk, 2000b; Schwenk & Wagner, 2001; Nussey et al., 2005). However, phenotypes alone do not explain functional significances. Therefore to examine feeding performance (e.g., prey capture), biomechanically relevant morphology (e.g., mechanical advantages, craniodental morphology, and jaw mechanics) and genetic data are used to provide information about dietary specializations (Radinsky, 1981a; Sacco & Van Valkenburgh, 2004, Van Valkenburgh, 2007). Therefore a combination of morphological, molecular, and functional data are needed to provide a comprehensive understanding of organismal evolution (Schwenk, 2000b).

Otters and their allies are grouped within Family Mustelidae, which is composed of 22 genera and 59 species (Koepfli et al., 2008). Mustelidae is a monophyletic group that appeared in the fossil record approximately 35 million years ago (Riley, 1985; Marmi et al., 2004). It includes four to seven subfamilies (Dragoo & Honeycutt, 1997), with five being the most recognized: Mephitinae (skunks), Melinae (badgers), Lutrinae (otters), Mustelinae (rest of the mustelids), and Mellivorinae (honeybadgers) (Dragoo & Honeycutt, 1997). Mustelidae is the most species- and diversity-rich in the order Carnivora, but also (Sato et al., 2003; Lee & Mill, 2004). Morphological characteristics of extant mustelids include the loss of the carnassial notch on the P^4, the loss of M^2, and enlarged scent glands (Marmi et al., 2004). However, there are a number of specialized feeders and exploiters of all types of habitats, making this an excellent family to study and understand the significance of mechanical diversity (Lee & Mill, 2004). For example, geographic variation in craniodental morphology has been shown in species of *Mustela* (weasels) (Lee & Mill, 2004) and sexual dimorphism in cranial features has been described in North American weasels, badgers, and otters (Dayan et al., 1989; Lynch & O'Sullivan, 1993).

Otters diverged from other mustelid lineages 20-25 mya during the Miocene (Koepfli & Wayne, 1998). There are 7 genera and 13 species that range from Europe, Asia, Africa, North America, and South America (Koepfli & Wayne, 1998). The genus *Mionictus* is the oldest known otter fossil dating back approximately 20 mya (Koepfli & Wayne, 1998). Three monophyletic groups of otters have been distinguished (Figure 1-1; Carss, 1995; Koepfli et al., 2008). Clade 1 contains the Old World river otters and sea otters and includes: cape clawless otters (*Aonyx capensis*), Asian small-clawed otters (*Aonyx cinereus*), smooth-coated otter (*Lutrogale perspicillata*), Eurasian otters (*Lutra lutra*), hairy-nosed otter (*Lutra sumatrana*), sea otters (*Enhydra lutris*), and spotted-necked otters (*Hydrictis maculicollis*). Although sea otters are difficult to place in Lutrinae due to their unique semi-aquatic lifestyle and geographic distributions, sea otters have been shown to be the earliest lineage to diverge within the Old World otters (Koepfli & Wayne, 1998). Clade 2 contains the New World otters: North American river otters (*Lontra canadensis*), marine otters (*Lontra felina*), and Neotropical river otters (*Lontra longicaudis*). Ancestors of North American river otters are thought to have crossed the Bering land bridge into North America by the Pliocene (Serfass et al., 1998). Once in North America, otters evolved and expanded their range to exploit a wide range of habitat (Serfass et al., 1998). Due to the morphological differences observed in North American river otters compared to Old World otters, the generic name was changed from *Lutra* to *Lontra* (Serfass et al., 1998). Clade 3 consists of the giant otter (*Pteronura brasiliensis*).

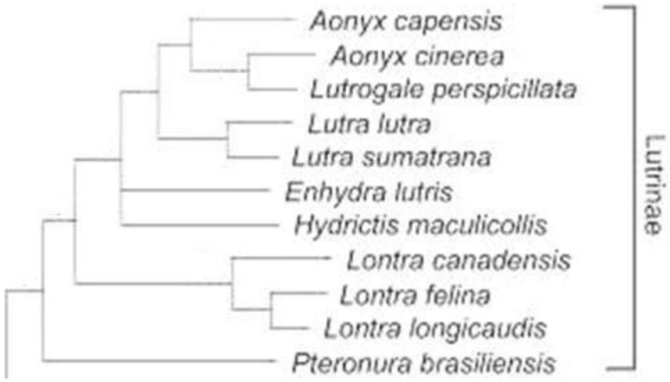

Figure 1-1. Phylogenetic relationships of otters (Koepfli et al., 2008).

Three subspecies of sea otters are recognized based on geographic distribution (Cronin et al., 1996; Doroff & Burdin, 2011) and all three demonstrate variations in their skull morphology and diet (Wilson et al., 1991). By the Miocene (20-5mya), the genus *Enhydra* diverged from the basal lutrinae species (Berta & Morgan, 1985). According to molecular (Masuda & Yoshida, 1994) and morphological (Berta and Morgan, 1985) data, *Lutra* is the closest extant relative of sea otters. According to a phylogenetic analysis by Berta and Morgan (1986), sea otters have two lineages. One leads to the extinct *Enhydriodon* and the second lineage leads to the extinct *Enhydritherium* and extant *Enhydra*. *Enhydritherium* appeared in the fossil record during the Miocene (Europe and North America). This extinct species was exclusively found in or near the coastal marine environments. *Enhydritherium* and *Enhydra* lineage originated within the Old World. The most widely accepted hypothesis of how sea otters reached the new world was presented by Berta and Morgan (1985). They predicted that *Enhydritherium* dispersed from Europe around the rim of the North Atlantic and into the Pacific Ocean through the Central American Seaway during the Miocene. *Enhydra* diverged from basal Lutrinae in late Miocene or early Pliocene (7-5 mya). Modern *Enhydra* arose in North Pacific during the Pleistocene (1-3 mya) and have been confined to this region. Before the international fur trade (early 1700s), the worldwide population of sea otters was estimated to be between 150,000 (Kenyon, 1969) and 200,000 (Johnson, 1982) individuals. Worldwide, sea otter populations have declined to approximately 2,000 individuals by the end of the commercial fur trade in 1911 (Kenyon, 1969; Ralls & Siniff, 1990; Larson et al., 2002). Although populations have recovered in parts of

Russia (Bering Island, Kamchatka Peninsula, and Kuril Islands), Alaska (specifically along the Aleutian Islands, Alaska Peninsula, the Kodiak archipelago, and Prince William Sound), and central California, populations are now small and widely dispersed resulting in low genetic diversity (Ralls et al., 1983). Russian sea otters (*Enhydra lutris lutris*) are distributed from the Kuril Islands to the Kamchatka Peninsula and the Commander Islands. Alaskan sea otters (*Enhydra lutris kenyoni*) range from the Aleutian Islands to Prince William Sound and along the Pacific coast of Canada south into Washington and Oregon. In Alaska, three stocks are recognized: southeast (Dixon Entrance to Cape Yakataga), south central (Prince William Sound, Kenai Peninsula, and Kachemak Bay), and southwestern (Alaska Peninsula, Aleutian Islands, Kodiak Islands, and Cook Inlet) (Doroff & Burdin, 2011). California sea otters (*Enhydra lutris nereis*) have a small range in central California, from Point Conception near Santa Barbara to Año Nuevo in San Mateo County (Hanni et al., 2003; Doroff & Burdin, 2011).

In addition to isolation and low genetic diversity, sea otters are exposed to several environmental stressors and threats, such as oil spills (Garrott et al., 1993; Monson et al., 2000), fisheries interactions (Wild & Aimes, 1974; Johnson, 1982; Garshelis et al., 1986), and disease (Miller et al., 2002; Kreuder et al., 2003). After commercial hunting of sea otters was banned, the California sea otter population increased at a rate of 5% per year until the 1970's when the population plateaued (Ralls & Siniff, 1990). Due to the lack of increased population growth (likely due to anthropogenic factors and disease), California sea otters have been listed as a threatened species on the U.S. Endangered Species list (Ralls & Siniff, 1990; Doroff & Burdin, 2011). Diseases, such as protozoal encephalitis caused by protozoan parasites (*Toxoplasma gondii* and *Sacrocystis neurona*) have been identified as a major contributor to sea otter mortality in California (Conrad et al., 2005; Johnson et al., 2009). In Alaska, sea otter populations in the Kodiak archipelago and lower Cook Inlet remain stable (Doroff & Burdin, 2011). However, Alaskan sea otters in Southwest Alaska (Aleutian Islands) are listed as threatened due to the rapid population declines from the late 1980s through 2005 (Doroff et al., 2003, Estes et al., 2005, Burn et al., 2003). The most likely cause of the decline in the Aleutian Islands is predation by killer whales (*Orcinus orca*) (Estes et al., 1998; Williams et al., 2004; Reisewitz et al., 2006). In 1989, sea otter populations in northern Prince William Sound (PWS) declined due to the Exxon Valdez oil spill, which killed thousands of sea otters (Garrott et al., 1993; Monson et al., 2000). However, sea otters in Simpson Bay (northeastern PWS) were relatively unaffected by the oil spill (Lee et al., 2009). The increase in sea otter population size in PWS after the fur trade has created conflict with the shellfish fisheries at a local scale (e.g., Cordova) (Garshelis et al., 1986).

Sea otters in northeastern PWS are thought to be responsible for the decline of the Dungeness crab fishery (Garshelis et al., 1986; Lee et al., 2009). Historically, the diet of sea otters changes rapidly when they reoccupy an area (Ostfeld, 1982; Kvitek et al., 1992; Estes & Duggins, 1995; Watt et al., 2000; Lee et al., 2009). Sea otters are generalists and will first prey on the most calorically rich prey (e.g., clams, abalone, urchins), then diversify once the preferred prey declines (Estes et al., 1978; Estes et al., 1981; Ostfeld, 1982; Kvitek et al., 1993; Kvitek et al., 1988; Estes & Duggins, 1995;

Laidre & Jameson, 2006). Therefore, once the preferred prey (e.g., Dungeness crab) is depleted sea otters will switch to a less preferred prey. The populations in Russia appear to be stable around Bering and Medney Islands, but have shown recent decline in the Commander and Kuril Islands (Doroff & Burdin, 2011). The cause of the decline is unknown, but poaching is not out of the question (Doroff & Burdin, 2011).

Craniodental morphology and bite performance of otters have not been investigated within a phylogenetic and biomechanical approach and can provide invaluable information regarding the adaptive radiation of mustelids and specifically Lutrinae. Therefore, members of each Lutrinae clade were chosen to investigate this variation. Two New World species (North American river otters and giant river otters) are primarily piscivores and two Old World species (sea otters and Asian small-clawed otters) primarily feed on benthic invertebrates, allowing for a comparison between craniodental morphology and dietary specializations within a phylogenetic context.

Feeding Adaptations and Dietary Differences of Otters

Otters have evolved two trophic specializations, mouth-oriented piscivory and hand-oriented invertebrate predation, both of which likely correspond to cranial morphology and bite performance (Carss, 1995; Medina-Vogel et al., 2004). North American river otters (*Lontra canadensis*), Neotropical river otters (*Lontra longicaudis*), giant river otters (*Pteronura brasilliensis*), smooth coated otters (*Lutrogale perspicillata*), Eurasian river otters (*Lutra lutra*), and hairy-nosed otters (*Lutra sumatrana*) are considered mouth-oriented piscivores, and this mode of feeding is considered to be pleisomorphic (Toweill, 1974; Berta & Morgan, 1986; Sivasothi and Nor, 1994; Pardini, 1998; Lariviere & Walton, 1998). Sea otters (*Enhydra lutris*), Asian small-clawed (*Aonyx cinerea*), African clawless (*Aonyx capensis*) are hand-oriented species that primarily feed upon benthic invertebrate prey (Wade, 1975; Ostfeld, 1982; Sivasothi & Nor, 1994; Carss, 1995; Estes & Duggins, 1995; Tinker et al., 2007).

Feeding behavior, dentition, and brain morphology related to sensory systems differ between the two feeding modes (Radinsky, 1968; Carss, 1995). Mouth-oriented otters, which tend to specialize in piscivory, exhibit enlarged somatosensory region of the brain that corresponds to the lips, jaws, and muzzle (Carss, 1995). In addition to brain morphology, it is predicted that skull morphology will differ between the two feeding modes, as demonstrated with the family Ursidae (Sacco & Van Valkenburgh, 2004). Ursidae is comprised of eight species with varying diets, including hypercarnivory, herbivory, and insectivory (Sacco & Van Valkenburgh, 2004; Christiansen, 2007; Figueirido et al., 2009). As in ursids, it is predicted that otters with longer skulls and mandibles will exhibit a decreased biting capability, but increased jaw velocity. Increased jaw velocity would be advantageous for capturing elusive prey, such as fish. Such adaptations are present in the extreme in piscivore specialists such as gharials, river dolphins, and certain extinct marine reptiles. Although extreme elongation of the skull and mandible does not occur in otters, the biomechanical tradeoff in favor of jaw velocity over bite force still applies. In piscivorous otters, the carnassials (P^4 and M_1) are sharp and are presumed to function for shearing and tearing flesh of fish. This is in contrast to otters specializing on hard, benthic invertebrates. These species are hand-oriented predators and possess further modified (blunt) carnassials (Carss, 1995). The carnassials in this group of otters are broad and flattened, designed for crushing their prey (Riley, 1985; Carss, 1995; Popowics, 2003). In addition to these modified carnassials, it is hypothesized that the skulls and mandibles of hand-oriented otters will be shorter and more blunt compared to piscivorous otters. It is also hypothesized that these craniodental differences will increase the biting capability necessary for breaking open hard prey, at the expense of jaw velocity.

Overall Research Objectives

The first objective was to investigate the relationships between feeding morphology (i.e., craniodental morphometrics; Chapter II) and bite performance (estimated bite forces; Chapter III) of two mouth-oriented piscivore specialists (North American river otters and giant river otters) and two hand-oriented invertebrate specialists (Asian small-clawed otters and 3 subspecies of sea otter). The second objective was to characterize feeding mechanisms (jaw musculature (Chapter III) and kinematics (Chapter IV)) and role of bite performance in the trophic ecology of sea otters to begin to elucidate foraging costs (dive time, consumption time, and overall handling time; Chapter V).

CHAPTER II

CRANIAL MORPHOMETRICS

Introduction

The fossil record of the order Carnivora extends back 60 million years (Radinsky, 1981a; Van Valkenburgh, 2007) and Carnivora is the most ecologically diverse mammalian order (Christiansen & Wroe, 2007; Meiri et al., 2005; Van Valkenburgh, 2007). Variation in cranial morphology and skull shape constrains feeding performance in many terrestrial mammals (Sacco & Van Valkenburgh, 2004; Lee & Mill, 2004; Goswami, 2006; Christiansen & Wroe, 2007; Van Valkenburgh, 2007; Wroe & Milne, 2007; Figueirido et al., 2009), which in turn influences dietary habits, survival, and ultimately fitness (Arnold, 1983). The feeding apparatus is used to capture, subdue, and process prey, as well as to capture mates for reproduction and as a defense against predators (Anderson et al., 2008). Mustelids (weasels, otters, badgers and skunks) are one of the most diverse families in the order Carnivora and are a good model system to explore the morphological and biomechanical diversity of their feeding adaptations (Lee & Mill, 2004).

Although craniodental morphology and dietary adaptations have been examined to some extent in terrestrial mustelids (Riley, 1985; He et al., 2002; Popowics, 2003; Lee & Miller, 2004; Abramov & Puzachenko, 2005), few data exist for aquatic mustelids such as otters (Lutrinae). Morphological and behavioral diversity among otters is reflected in their diet and foraging behaviors (Radinsky, 1981a; Radinsky, 1981b; Kruuk et al., 1994; Hussain et al., 1997; Lee & Mill, 2004; Sacco & Van Valkenburgh, 2004; Meiri et al., 2005; Goswami, 2006; Wroe & Milne, 2007; Van Valkenburgh, 2007). For example, in river otters, the digastric muscles are enlarged (compared to terrestrial carnivores), which enables the rapid jaw closure necessary for catching fast moving fish with their mouths underwater (Lee & Mill, 2004). This is also reflected in their cranial morphology. Concomitantly, river otters possess broad mastoid processes, which is necessary for attachment of the enlarged digastric muscles (Lee & Mill, 2004). River otters also possess sharp carnassials necessary for piercing and shearing fish (Popowics, 2003). In contrast, sea otters possess short, blunt skulls with bunodont dentition, used for crushing hard, benthic prey (Popowics, 2003; Lewis, 2008). However, there are no data on the functional feeding morphology of otters. Otters have evolved one of two trophic specializations: mouth-oriented piscivory or hand-oriented invertebrate specialists (Carss, 1995; Medina-Vogal et al., 2004). North American river otters (*Lontr*a canadensis), Neotropical river otters (*Lontra longicaudis*), giant river otters (*Pteronura brasiliensis*), smooth coated otters (*Lutrogale perspicillata*), European river otters (*Lutra lutra*), and hairy-nosed otters (*Lutra sumatrana*) are mouth-oriented predators (Radinsky, 1968) and feed primarily on fish (Medina-Vogal et al., 2004), which is the basal feeding mode (Berta & Morgan, 1986; Carrs, 1995). Based on diet, it is predicted that spotted-necked otters (*Hydrictis maculicollis*) are mouth-oriented predators, since they feed primarily on fish, frogs, and amphibians (Somers & Purves, 1996). Sea otters (*Enhydra lutris*), Asian small-clawed otters (*Aonyx cinerea*), and African clawless otters (*Aonyx capensis*) primarily feed on invertebrate prey (Medina-

Vogal et al., 2004) and are hand-oriented predators (Radinsky, 1968; Sivasothi & Nor, 1994; Jacques et al., 2009). Although Asian small-clawed otters primarily feed on invertebrates, they will on occasion incorporate fish into their diets (Sivasothi and Nor, 1994), as will some populations of sea otters (Riedman & Estes, 1988). We predict that the underlying cranial morphology and biomechanics will explain the feeding performance of these two feeding specializations (mouth-oriented piscivore specialists vs. hand-oriented invertebrate specialists). The first goal of this chapter was to compare craniodental morphology among two mouth-oriented, piscivore specialists (North American river otters and giant river otters) and two hand-oriented invertebrate specialists (Asian small-clawed otters and sea otters) through traditional and geometric morphometrics to determine the functional significance of their mechanical diversity (Lee & Miller, 2004) and dietary adaptations and specializations (Wilson et al., 1991). It was hypothesized that cranial morphology and biomechanics would differ between the two predatory behaviors (mouth-oriented vs. hand-oriented), and that mouth-oriented piscivore specialists would possess long and narrow skulls indicative of high velocity jaws. In contrast, hand-oriented durophagous specialists are hypothesized to possess short, blunt skulls with a greater mechanical advantage (MA) of the jaw adducting muscles for biting, as the expense of jaw velocity. Durophagous specialists are predicted to possess a greater occlusal surface area of the postcanine teeth for crushing hard, benthic prey.

The second goal of this chapter was to investigate variation in cranial morphology among the three sea otter subspecies (Alaskan sea otters, Enhy*dra lutris* *kenyoni*; California sea otters, *Enhydra lutris nereis*; and Russian sea otters, *Enhydra lutris lutris*). These subspecies are based on geographically isolated populations (Wilson et al., 1991) and are managed separately by United States Geological Survey (USGS) (Gorbic & Bodkin, 2001; Lance et al., 2004). Although sea otters are generally durophagous predators that feed on hard, benthic prey, Alaskan (Aleutian Islands) and Russian sea otters incorporate fish into their diets (Riedman & Estes, 1988). This is in contrast to California sea otters that specialize on hard benthic invertebrates such as clams, abalone, and sea urchins (Estes et al., 2003b; Tinker et al., 2007; Tinker et al., 2008). Therefore due to dietary differences and geographic isolation, how does cranial morphology differ among subspecies? It was hypothesized that the magnitude of mandibular bluntness and mechanical advantage would vary among subspecies concomitant with their primary prey source (fish vs. hard invertebrates). That is, California sea otters, which tend to specialize on hard benthic invertebrates, should possess shorter and blunter skull morphology and shapes with a higher MA. Russian sea otters, which tend to have a greater proportion of fish in their diets, should demonstrate longer, narrower skull morphology and shapes with a lower MA, which would be consistent with increased jaw velocity.

In addition to diet, environmental stresses (e.g., inbreeding, habitat destruction, prey sensitivity to pollutants) can affect developmental stability of individuals and thus increase phenotypic variation in populations (Parsons, 1990; Swaddle, 1994; Badyaev et al., 2000; Hoffmann & Hercus, 2000). Individuals are affected differently, depending on their ability to buffer stress (Badyaev et al., 2000). Groups of individuals and certain traits may also have different sensitivity to stresses. For example, if a species is sexually dimorphic, one sex may be under stronger directional selection to grow and develop faster and thus be more sensitive to environmental stresses (Badyaev et al., 2000). Fluctuating asymmetry (FA) has been used as an indicator of environmental stress (Clarke, 1993; Allenbach et al., 1999; Leung et al., 2000). Fluctuating asymmetry refers to non-directional deviations from bilateral symmetry and has been demonstrated to impact fitness (Leung et al., 2000). Although, most individuals within a population are not perfectly symmetrical in shape, large FA has been shown to increase with increasing environmental stress. Organisms under stress require energy to compensate for stress, which should reduce energy for more important functions such as growth and reproduction, negatively impacting the population (Koehn & Bayne, 1989; Leung et al., 2000). Fluctuating asymmetry has received much attention in the last decade as a bioindicator of stress (Leung et al., 2000) because it is more cost-effective than monitoring environmental fauna and it is relatively easy to measure (Clarke, 1993; Leung et al., 2000). Fluctuating asymmetry is also biologically relevant since it is related to the quality of the organism (Clarke, 1993; Leung et al., 2000), that is, a proxy for fitness. Asymmetry of the crania can influence the size, shape, and weight of masticatory muscles, and therefore may affect, feeding biomechanics, bite force and kinematics (Roest, 1993; Berta & Sumich, 1999). Although FA has been shown to affect the reproductive fitness of an individual, it is unknown what the consequences of asymmetrical skulls have on the feeding biomechanics. It is predicted that FA has a negative impact on feeding performance and increases the costs of foraging through increased handling time or processing prey. Fluctuating asymmetry and feeding performance data are sparse for aquatic mammals. If sea otters are experiencing fluctuating asymmetry, it is predicted that California sea otters (*Enhdyra lutris nereis*) may be the most affected due to the small range and small population size, which would increase the probability of inbreeding and the risk of asymmetric features.

Objectives and Hypotheses

The main objectives of this chapter were to examine the interspecific morphological diversification of four species of otters: Asian small-clawed otters (*Aonyx cinerea*), North American river otters (*Lontra canadensis*), giant river otters (*Pteronura brasiliensis*), and three subspecies of sea otters (*Enhydra lutris*) with traditional and geometric morphometrics to examine craniodental adaptations to specialized diets and feeding behaviors (e.g., mouth-oriented vs. hand-oriented). Unlike traditional morphometrics, which uses linear distances between pairs of landmarks to analyze shape variation, geometric morphometrics analyzes the geometry among locations of all landmarks simultaneously (Parsons et al., 2003). Geometric morphometrics is a multivariate methodology based on homologous Cartesian landmark coordinates. Once landmarks are scaled, rotated and a Procrustes superimposition of landmarks applied, only pure shape variables remain. The resulting procrustes shape coordinates can be used for statistical analysis (Mitteroecker & Gunz, 2009). Landmarks capture more shape information and thus have a higher statistical power than traditional morphometrics (Rohlf, 2003). Geometric morphometrics also provides a visualization of the variation within the shape of the skull and mandible (Lynch et al., 1996). By using both traditional and geometric morphometrics to quantify shape variation, we can increase the power of our statistical analyses and can provide a more detailed description to the morphological variation. It was hypothesized that (1) mouth-oriented otters would possess long, narrow skulls indicative of high velocity jaws and hand-oriented otters would possess short, blunt skulls with a greater occlusal surface area for increased bite force and crushing capability, (2) skull shape and craniodental morphology of sea otters would vary significantly among subspecies based on diet and geographical location, (3) sea otters would possess a higher mandibular bluntness index (MBI; Werth, 2006a) than river otters and Asian small-clawed otters, and (4) sea otters would possess a greater MA of the masseter than other otter species. Fluctuating asymmetry was also measured for each species. It was hypothesized that (1) sea otters would show the greatest deviation from cranial symmetry and (2) California sea otters would show the highest degree of fluctuating asymmetry among sea otter subspecies.

Materials and Methods

Taxonomic Sampling

Four otter species (2 mouth-oriented and 2 hand-oriented) were selected. North American river otters (*Lontra canadensis*, n=43) and giant river otter (*Pteronura brasiliensis*, n=17) represented mouth-oriented piscivore specialists. Hand-oriented otters were represented by Asian small clawed otters (*Aonyx cinerea*, n=23), and all 3 subspecies of sea otters (Alaskan, *Enhydra lutris kenyoni*, n=40; Russian, *E. l. lutris*, n=8; California, *E. l. nereis, n=20*)). Specimens were obtained through loans courtesy of the Burke Museum of Natural History at the University of Washington (Seattle, Washington), Smithsonian National Museum of Natural History (Washington, D.C.), and the American Museum of Natural History (New York, New York).

Traditional Morphometrics and Biomechanical Measurements

Twenty-three standard cranial measurements (Figs. 2-1 and 2-2; Table 1; following Roest, 1985; Lynch & O'Sullivan, 1993; Hattori et al., 2003; Sacco & Van Valkenburgh, 2004) were collected using digital calipers. Occlusal surface area was measured by capturing scaled digital images using Image J (NIH, Bethesda, MD).

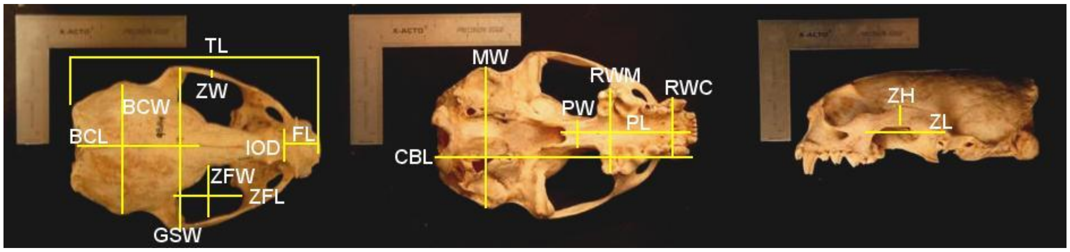

Figure 2-1. Cranial morphometric variables (Giant river otter; *Pteronura brasiliensis*).

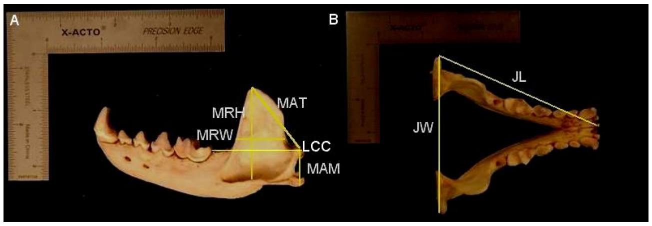

Figure 2-2. Cranial morphometric variables for mandible. (Giant river otter; *Pteronura brasiliensis*).

Table 2-1. Definitions of standard cranial morphometric variables

Total length (TL)	Max length of skull from tip of rostrum to the nuchal crest	**Greatest squamosal width (GSW)**	Max width of zygomatic arches dorsal to glenoid fossa
Braincase length (BCL)	Apex of nuchal crest to postorbital constriction	**Zygomatic width (ZW)**	Max width or thickness of zygomatic arch at jugal-squamosal suture
Braincase width (BCW)	Greatest width across braincase posterior to zygomatic arches and dorsal to tympanic bullae	**Zygomatic length (ZL)**	Max length including squamosal and jugal
Condylobasal length (CBL)	Distance from posterior-most projections of the occipital condyles to anterior edge of the premaxilliary bones	**Zygomatic height (ZH)**	Max height of zygomatic arch at jugal-squamosal suture
Facial length (FL)	Fronto-nasal suture to anterior most tip of premaxilla	**Zygomatic fossa width (ZFW)**	Max width of zygomatic fossa from directly posterior to molar fossa near frontal bone across to zygomatic arch
Interorbital distance (IOD)	Least distance across orbits, anterior to post-orbital process	**Zygomatic fossa length (ZFL)**	Max length of zygomatic fossa from posterior/lateral of molar fossa to anterior of glenoid fossa
Palatal length (PL)	From alveolus of first incisors to anteriormost point on posterior edge of palate	**Jaw width (JW)**	Distance from most posterior part of condyle to posterior part of condyle
Palatal width (PW)	Width across palate posterior to last upper molars	**Jaw length (JL)**	Distance from the anterior tip of the mandibular symphysis to the posterior edge of the mandibular condyle
Rostral width at canine (RWC)	Max width of rostrum at the canines; including the canines	**Max height of ramus (MRH)**	Max height of ramus from apex of coronoid process to deepest point of masseteric fossa
Rostral width at molars (RMW)	Max rostral width at last upper molars; including the molars	**Max width of ramus (MRW)**	Max width of ramus from interior condyle process to edge of coronoid process
Mastoid width (MW)	Width from mastoid to mastoid	**Moment of arm of massester (MAM)**	Distance from ventral border of angular process to dorsal tip of condyle process
Occlusal surface area (OSA)	Surface area of postcanine too row	**Moment of arm of temporalis (MAT)**	Distance from dorsal coronoid process to dorsal tip of condyle

Mandibular bluntness index (MBI) was calculated for each otter species and subspecies using scaled digital photographs and Image J following Werth (2006a; Figure 2-2). The MBI calculates a ratio of jaw width (JW) to jaw length (JL), which is more reliable than skull to length ratios (Werth, 2006a). The distance between the two condylar edges (JW) and the distance from the anterior tip of the mandibular symphysis to the posterior edge of the mandibular condyle (JL) were measured. This calculation provides a dimensionless value, which is useful for comparative studies.

The mechanical advantages (MA) of the masseter and temporalis muscles were calculated for each specimen (following Radinsky, 1981a; Gittleman & Van Valkenburgh, 1997). The in-lever arm length (moment arm of masseter, moment arm of temporalis) was measured as the distance from the jaw joint to the insertion points of each muscle (Radinsky, 1981a; Gittleman & Van Valkenburgh, 1997; Tanner et al., 2010). The out-lever was measured as the distance from the jaw joint to the bite point (posterior carnassials) on the mandible (Radinsky, 1981a). More specifically, the moment arm of masseter (MAM) was measured as the distance between the dorsal surface of the mandibular condyle to the ventral border of the angular process (Figure 2-2). Therefore, the mechanical advantage of the masseter ($MA_{masseter}$) was measured by dividing the MAM by the distance from the posterior-most condyle process edge to the posterior of the lower carnassial (LCC) as follows:

$$\mathbf{MA_{masseter} = MAM / LCC}$$

The moment arm of temporalis (MAT) was measured as the distance between the dorsal surface of the mandibular condyle to the apical tip of the coronoid process (Figure 2-2).

The mechanical advantage of the temporalis ($MA_{temporalis}$) was measured by dividing the MAT by LCC as follows:

$$\mathbf{MA_{temporalis} = MAT / LCC}$$

Statistical Analyses for Traditional Morphometrics

Statistical analyses of traditional morphometric data were performed with JMP Version 9 software (SAS Institute Inc., Cary, NC) and Microsoft Excel 2003 (Microsoft Corporation) to determine skull variation among otter species using 17 of the 23 variables (Figure 2-1). Normality of data was tested using a Shapiro-Wilk test. Levene's test was used to test the assumption of homogeneity of variances. All data were $\log_{10}$ transformed to normalize variances. To analyze variations in cranial morphology corrected for the effect of size, a MANOVA was performed on transformed data. Geometric mean (geomean size), the product of the 17 skull variables taken to the 17th root for each individual, was used as the size variable. Geometric mean provides a volume value which is highly correlated with body mass (personal dataset, 97% correlation). Therefore, when body mass values are limited, one can use geometric mean to replace it as the size factor. Traditional morphometric data were tested for effects due to species and geomean size. Following a MANOVA, a discriminant function analysis on $\log_{10}$ transformed data, with species as the covariate, was performed to demonstrate craniodental morphometric differentiation of the skulls. To test for variations in MBI among species, a MANOVA was performed, with mean MBI values as the dependent variable and species as the independent variable. Student Newman-

Keuls post-hoc tests were performed to test which group(s) were significantly different. To test for significant differences in mechanical advantage at the masseter and temporalis, the in-lever/out-lever ratios were arcsine transformed to control for size. A MANOVA was then executed on the mechanical advantage of the temporalis and masseter to test for significant variation among species. To test which group(s) was significantly different, Student Newman-Keuls post-hoc tests were performed. To test for significant differences in occlusal surface areas (OSA), OSA was first regressed against condylobasal length to remove the effect of size. Residuals were then saved and used to test for significant differences among species. A MANOVA test was performed with the regressed OSA values as the dependent variable and species as the covariate. Post hoc (Student-Newman-Keuls) tests were performed to determine which species significantly differed from the others.

Geometric Morphometrics

Scaled digital images skulls from each species were taken from the left, lateral side (AK sea otters, N=28; CA sea otters, N=19; Russian sea otters, N=8; North American river otters, N=31; giant river otters, N=15; Asian small-clawed otters, N=22), the dorsal perspective (AK sea otters, N=45; CA sea otters, N=19; Russian sea otters, N=8; North American river otters, N=34; giant river otters, N=16; Asian small-clawed otters, N=23), ventral perspective (AK sea otters, N=40; CA sea otters, N=18; Russian sea otters, N=8; North American river otters, N=29; giant river otters, N=15; Asian small-clawed, N=22) using a Nikon D200 SLR camera stationed on a copy stand

(Figure 2-3). Scaled digital images of mandibles were taken of the left lateral side (AK sea otters, N=32; CA sea otters, N=10; Russian sea otters, N=7; North American river otters, N=49; giant river otters, N=16; Asian small-clawed otters, N=23) and in the dorsal perspective. The same skulls were used for both traditional morphometrics and landmark-based geometric morphometrics. Only skulls in which all landmarks could be observed were used in geometric morphometric analysis. A total of 87 landmarks were point digitized using TpsDig2 (Rohlf, 2009). Twenty-one landmarks were digitized on the dorsal side, 30 landmarks on the ventral side, 21 landmarks on the left lateral side, and 15 on the left lateral side of the mandible (Figure 2-3). Shape variables were separated from overall size, position, and orientation of landmark configurations by translating, scaling, and rotating the coordinates (Zelditch et al., 2004) to obtain Procrustes shape coordinates, which were then used in the statistical analyses. Each configuration of landmarks was centered at the origin by subtracting coordinates of its centroid from the corresponding x, y coordinates of each landmark (Zelditch et al., 2004). This translates each centroid to the origin. Landmark configurations were scaled to unit centroid size by dividing each coordinate of each landmark by centroid size. All configurations were then rotated to a referenced configuration to minimize Procrustes distance (e.g., summed squared distance between homologous landmarks) (Zelditch, 2004).

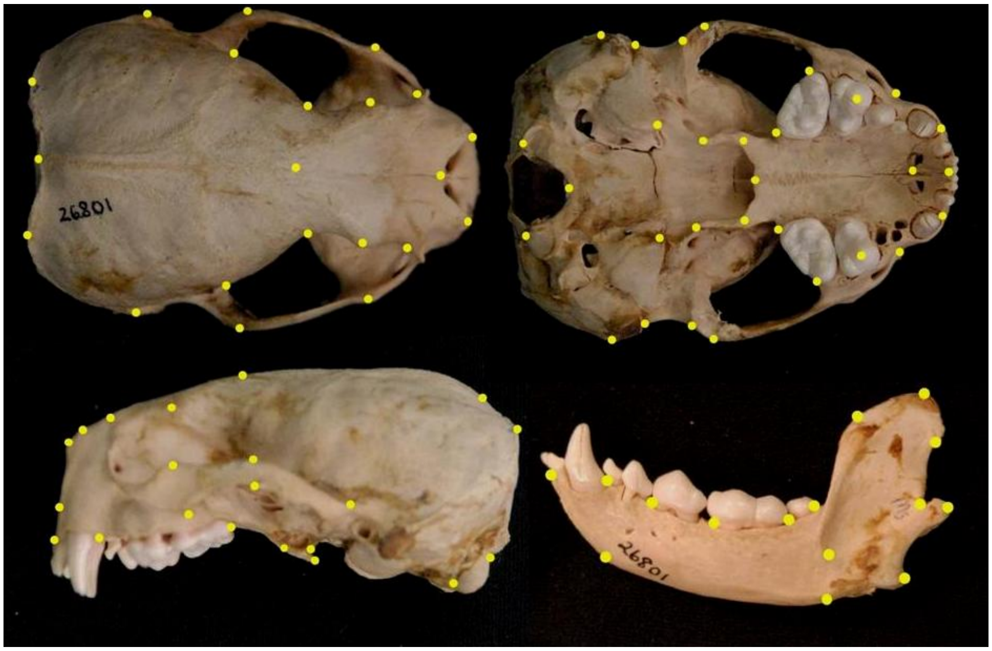

Figure 2-3. Homologous landmarks for geometric morphometrics (Sea otter, *Enhydra lutris*).

Statistical Analysis for Geometric Morphometrics

To analyze variation among groups, the Canonical Variates Analysis program within the software IMP (Integrate Morphometric Package; CVAGen7b; Sheets, 2004, http://www.canisius.edu/~sheets/morphsoft.html) was used (following Zelditch et al., 2004) to compute partial warp scores and a MANOVA followed by a canonical variates analysis (CVA). Canonical variates scores were also computed using Mahalanobis distances.

Fluctuating Asymmetry with Geometric Morphometrics

Fluctuating asymmetry (FA) was measured using existing geometric morphometric data, a method based on the Procrustes technique (Klingenberg & McIntyre, 1998). Geometric morphometrics is a powerful multivariate statistical procedure that uses patterns of covariance among landmarks to detect localized shape variation and, therefore, asymmetries (Klingenberg & McIntyre, 1998). The same scaled digital images and landmarks used for geometric morphometrics analysis were used and uploaded to TpsDig2 (Rolf 2009) to test for asymmetry. Landmarks were digitized on the left and right corresponding sides in the dorsal perspective (Alaskan sea otters n=32; California sea otters n=19; Russian sea otters n=8; North American river otters n=34; giant river otters n=16; Asian small-clawed otters n=19). Landmark coordinates were then uploaded to Microsoft Excel 2007 (Microsoft Corporation, Redmond, WA) where they were scaled to their common centroid size, superimposed so that they have the same centroid, and rotated against each other around their common centroid so that only shape differences remained. For each individual, x and y coordinates were centered by subtracting the grand mean (of each x and y separately) from the x and y coordinates and multiplied by its scale. Covariance was then measured to show how much the two variables changed together. This is also called the sum of squares and cross products (SSCP) matrix and was calculated by multiplying the centered, scaled data matrix by the centered, scaled matrix. This gives a 2x2 SSCP matrix. The centered, scaled configurations were then rotated using eigenvectors calculated from the covariance. In excel, this was done by multiplying centered scaled data by eigenvectors and then dividing it by centroid size. Centroid size was calculated by taking the square root of SSCP matrix. Superimposing and rotating coordinates aligns all the left and right landmarks simultaneously, which provides an overall consensus configuration (Klingenberg & McIntyre, 1998). The consensus configuration is the mean coordinates of corresponding landmarks in aligned configurations, and makes up the new set of variables that contain all the shape information (Klingenberg & McIntyre, 1998). Deviations were measured for left and right corresponding sides by taking the square root of the sum of the centered, scaled, and rotated x and y configurations. Asymmetry was then measured as the deviations between x and y pairs of corresponding left and right sides (Klingenberg & McIntyre, 1998). The sum of the deviations is the calculated fluctuating asymmetry.

Statistical Analysis for Fluctuating Asymmetry (FA)

A MANOVA was performed on the measured FA values to statistically test for variations in fluctuating asymmetry among species in the dorsal perspective. Student Newman-Keuls post-hoc tests were performed to test which group(s) were significantly different. All statistical analyses were performed in JMP Version 9 software (SAS Institute Inc., Cary, NC).

Results

Traditional Morphometrics and Biomechanics

There were significant differences in skull morphology among species (Figure 2-4; F=25.6; p<0.01). In the discriminant data analysis, Canonical Axis 1 separated sea otters from Asian small-clawed otters, North American river otters, and giant river otters. Sea otters and giant river otters were larger in size as indicated by the larger geomean (Figure 2-4). In addition, sea otters possessed the greatest interorbital distance (IOD), greatest rostral width at the molar (RMW), greatest braincase width (BCW), greatest palate width (PW), greatest skull width (GSW), and greater zygomatic length (ZL) than all other otters investigated (Figure 2-4). Canonical Axis 2 separated giant river otters from all other otter species (Figure 2-4) and was strongly influenced by total skull length (TL) and palate length (PL). Asian small-clawed otters and North American river otters possessed greater facial lengths (FL) and zygomatic fossa lengths (ZFL) than the remaining otter species. When size effect was eliminated, OSA was greater in sea otters (F=246.9; p<0.01) than any other otter species investigated (Figure 2-5). California sea otters possessed the greatest OSA compared to Alaskan or Russian sea otters (F=13.3; p=0.0004). Alaskan and Russian sea otters possessed the next greatest OSA compared to other otter species investigated but were not significant different from each other (F=1.3; p=0.257). Asian small-clawed otters possessed intermediate OSA (Figure 2-5) and North American river otters possessed the smallest OSA (F=177.8; p<0.01) (Figure 2-5).

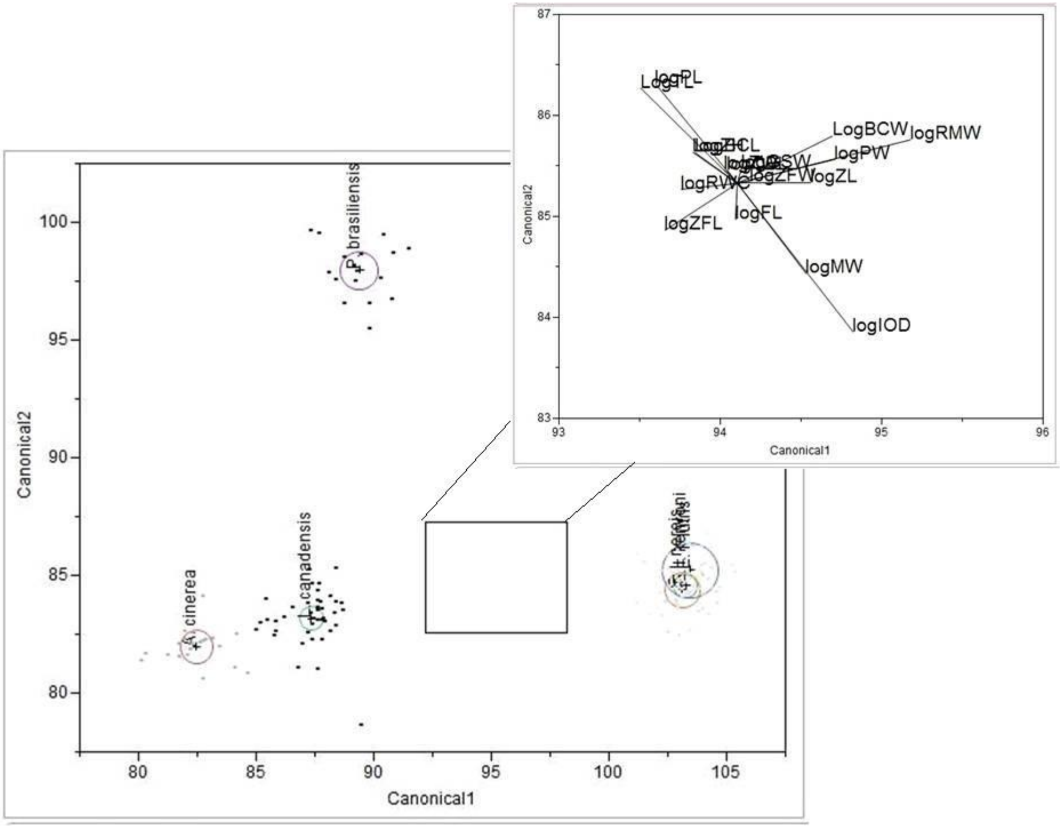

Figure 2-4. Discriminant analysis with $\log_{10}$ transformed skull morphometric variables. Four groups separated out based on 17 biomechanically relevant skull morphometrics.

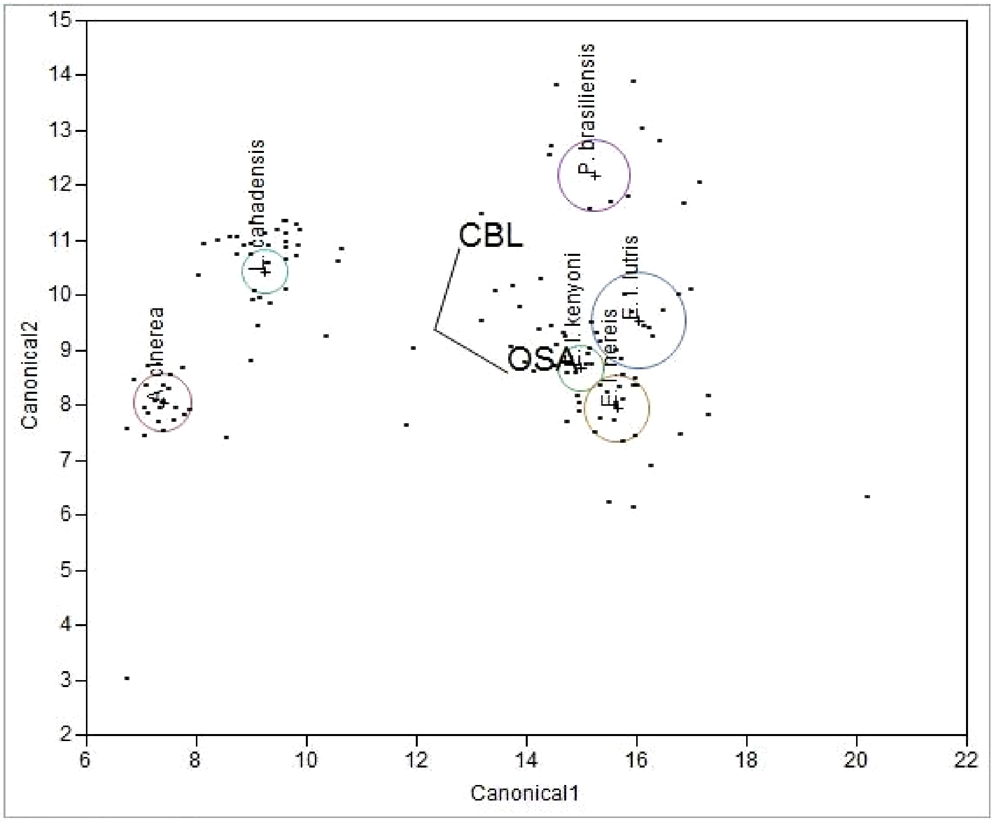

Figure 2-5. Discriminant function analysis with occlusal surface area (OSA) of postcanine dentition on upper left jaw and condylobasal length (CBL).

Significant mandibular shape differences were observed among species (F=31.8; p<0.01) and geomean size (F=7.33; p<0.01) (Figure 2-6). Canonical Axis 1 separated giant river otters from the rest of the otter species and was strongly influenced by mandibular length (Figure 2-6). Giant river otters possessed the greatest mandible length (ML) of the otter species examined, regardless of size, whereas North American river otters and Asian small-clawed possessed greater coronoid process lengths (CPL).

Canonical Axis 2 separates sea otters from the remaining otter species and was strongly influenced by a greatest mandibular ramus height (MRH) (Figure 2-6).

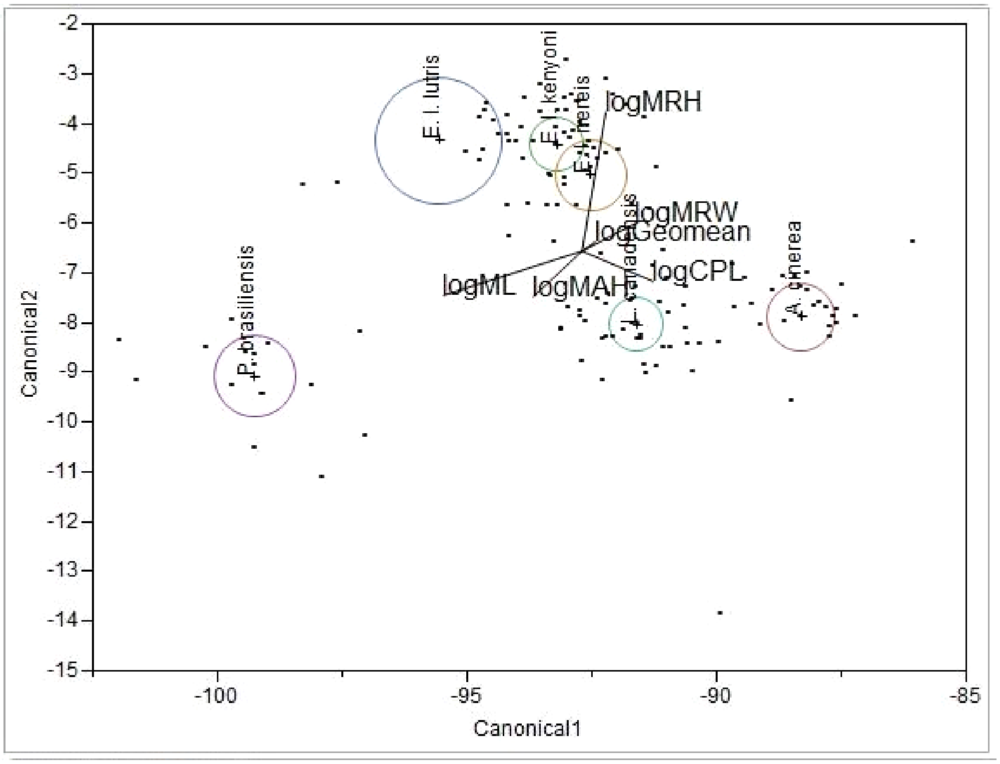

Figure 2-6. Discriminant analysis of otter mandible morphometrics.

Among sea otters, a separate discriminant analysis on demonstrated significant skull morphometric variable among all 3 subspecies was conducted (Figure 2-7; F=3.1; p<0.01). Canonical Axis 1 separated Russian sea otters from California sea otters and Alaskan sea otters and was strongly influenced by zygomatic fossa length (ZFL) and rostral width at molars (RMW) (Figure 2-7). In addition, Russian sea otters possessed the greatest palate length (PL) and geomean size. Alaskan sea otters possessed the largest braincase width (BCW) and California sea otters possessed the greatest zygomatic length (ZL) and palate width (PW). Canonical Axis 2 separated Alaskan sea otters from California sea otters, and was strongly influenced by zygomatic fossa width (ZFW) and mastoid width (MW) (Figure 2-7). Alaskan sea otters possessed the greatest ZFW and California sea otters possessed the greatest ZL, MW, and PW.

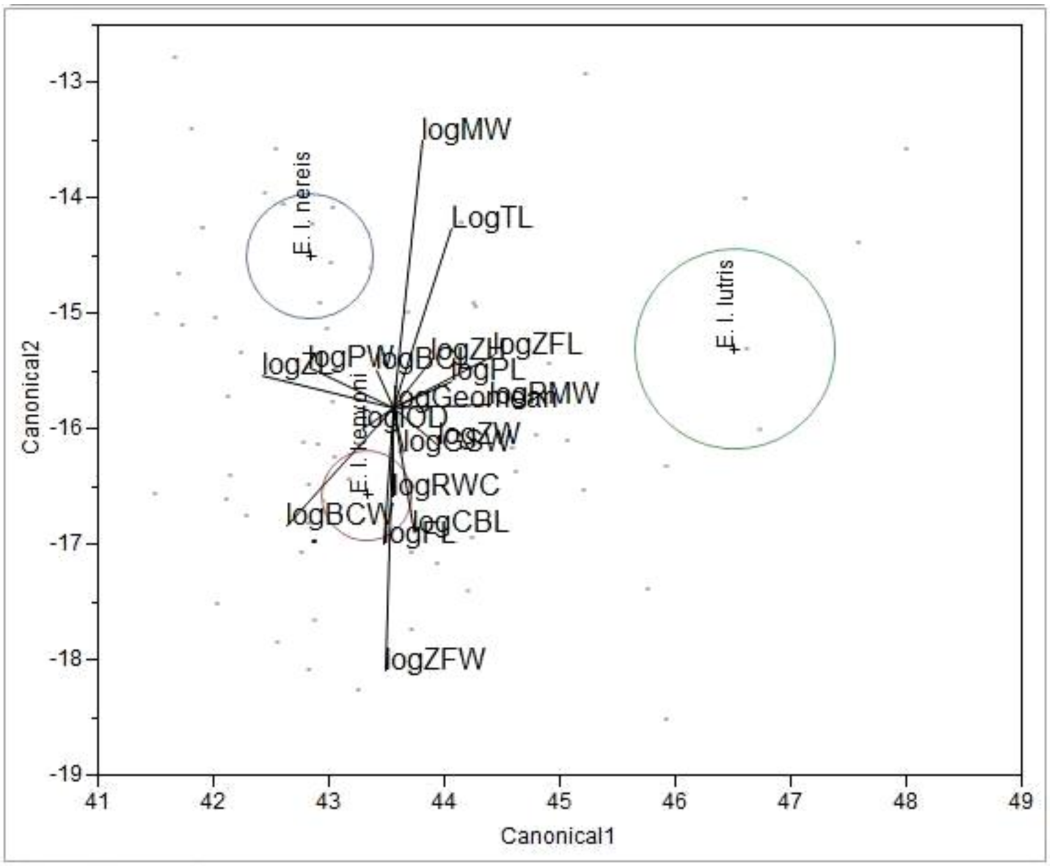

Figure 2-7. Discriminant analysis with $\log_{10}$ transformed skull morphometric variables. Three subspecies of sea otter separated out based on skull morphology.

Mandibular Bluntness Index and Mechanical Advantage

Significant differences in the mandibular bluntness index (MBI) was demonstrated among otter species (Figure 2-8; F=117.02; $p<0.01$). Asian small-clawed otters, North American river otters, and giant river otters possessed a mandibular bluntness index less than 1.0, demonstrating that mandibles are longer than they are wide. Asian small-clawed otters possessed greater MBIs than giant river otters and North American river otters (F=4.9; $p<0.05$), however no significant difference was shown between giant river otters and North American river otters (F=1.14; p=0.29). In contrast, sea otters possessed MBIs greater than 1.0, demonstrating very blunt mandibles that were wider than they were long. Sea otters possessed significantly larger MBIs than all the other otter species (F=433.0; $p<0.0001$). Among sea otters, California sea otters possessed greater MBIs than Russian and Alaskan sea otters (F=5.81; $p<0.05$), but no difference was detected between Alaskan and Russian sea otters (F=0.028; p=0.87).

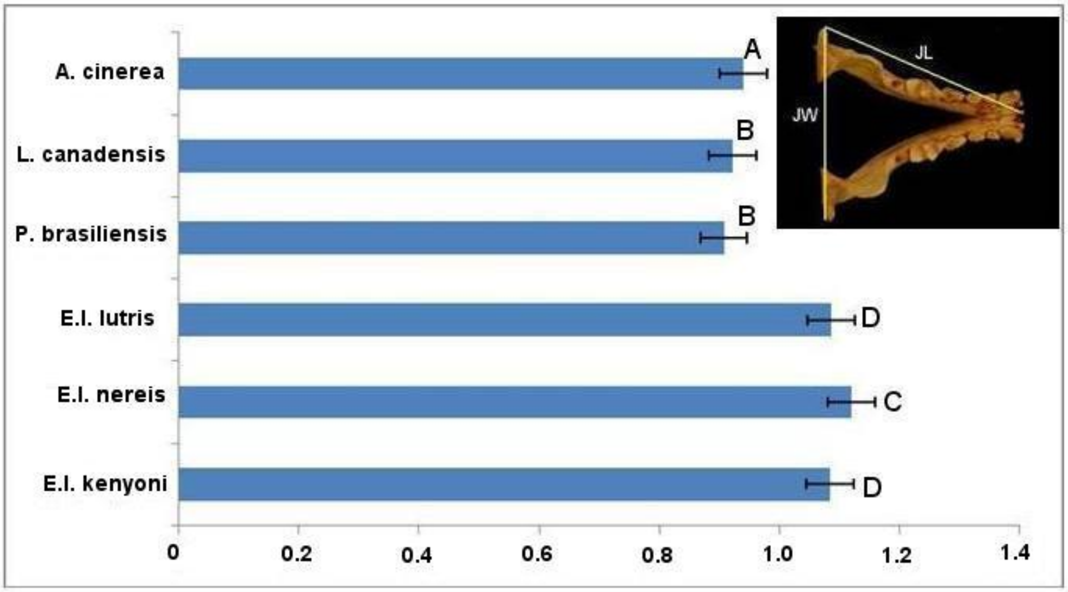

Figure 2-8. Mandibular bluntness index (MBI). Same letters represent no significant difference and different letters represent significant differences.

Significant differences were shown in the mechanical advantage of the masseter among species (Figure 2-9; F=41.6; p<0.01). Giant river otters and Asian small-clawed otters possessed the lowest masserteric MA (F=152.0; p<0.01). There were no differences in the masseteric MA between giant river otters and Asian small-clawed otters (F=1.3; p=0.26). Alaskan sea otters possessed the greatest masseteric MA compared to all other otters (F=81.5; p<0.01). Among sea otter subspecies, Alaskan sea otters possessed greater masseteric MA than both California and Russian sea otters (F=6.1; p=0.01). However, no significant difference was observed between California and Russian sea otters (F=0.30; p=0.59).

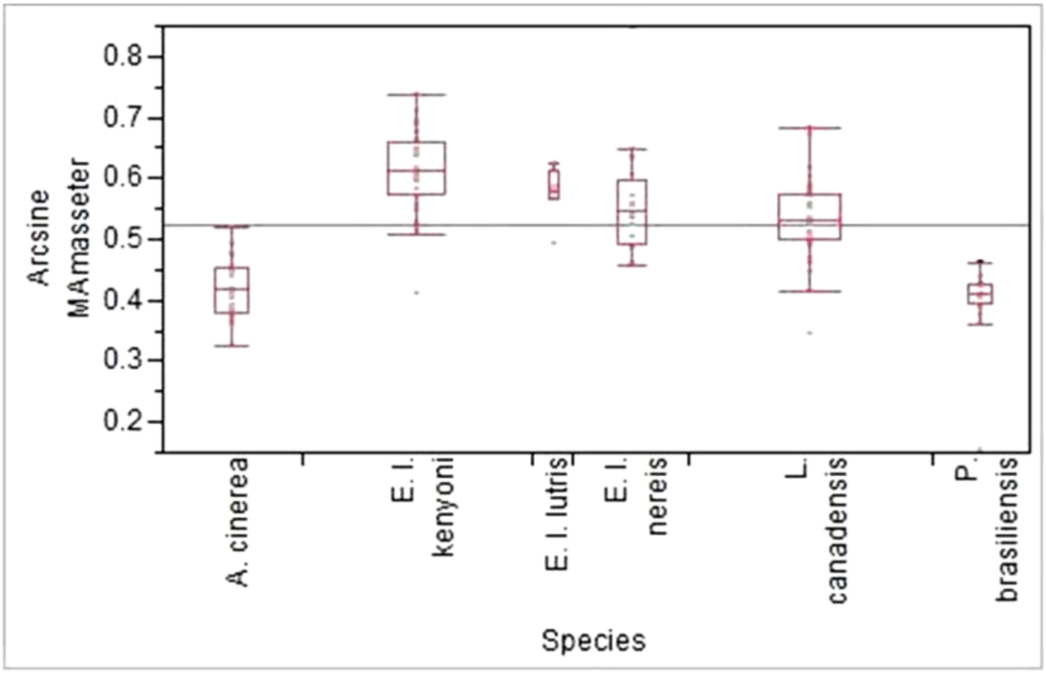

Figure 2-9. Mechanical advantage of masseter (MAmasseter).

Variation in the mechanical advantage of the temporalis was demonstrated among species (Figure 2-10; F=9.2; p<0.01). North American river otters possessed the greatest temporalis MA (F=23.6; p<0.01) and giant river otters possessed the lowest MA (F=23.7; p<0.01). Asian small-clawed otters possessed an intermediate temporalis MA (Figure 2-10). No significant differences were observed among sea otter subspecies (F=0.82; p=0.45) and no significant difference was found between Asian small-clawed otters and Alaska and California sea otters (F=1.0; p=0.32).

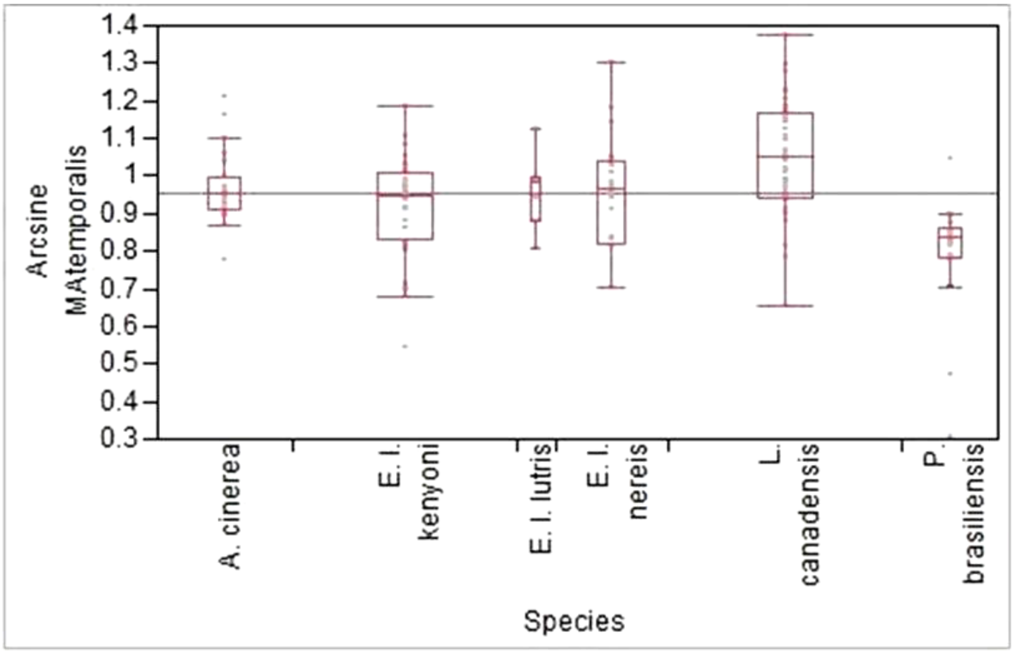

Figure 2-10. Mechanical advantage of temporalis muscle in all otters.

Geometric Morphometrics

Significant shape differences were demonstrated in both the skull and mandible among otter species (MANOVA and Mahalanobis D^2 tests ($p<0.01$)) for each axis. In the dorsal perspective, Canonical Axis 1 separated all three subspecies of sea otters from all other otters (Figure 2-11A). Canonical Axis 2 separated North American river otters from the Asian small-clared and giant river otters (Figure 2-11A). The greatest variation observed in the dorsal perspective was the interorbital distance (IOD) (Figure 2-11B). Sea otters possessed a wider skull anterior to the braincase than Asian small-clawed otters, giant river otters, and North American river otters. Giant river otters had the most narrow IOD, followed by Asian small-clawed otters and North American river otters.

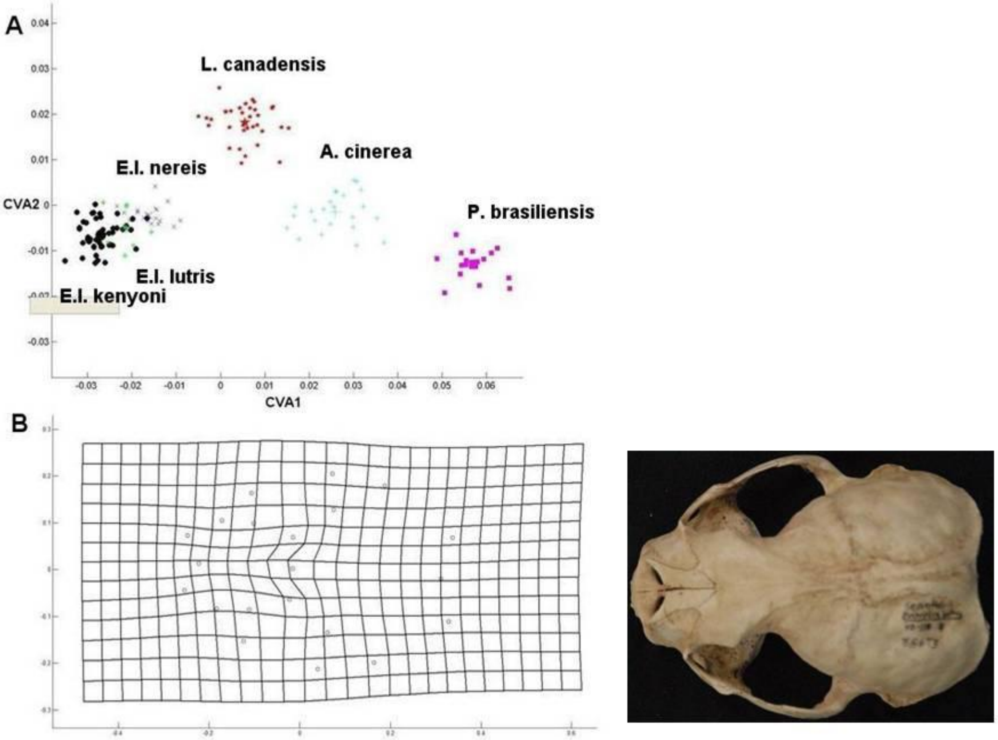

Figure 2-11. Dorsal perspective (n=145). (A) Canonical variates analysis of 4 species of otters. (B) Thin plate spline showing nonuniformity. ● *Enhydra lutris kenyoni* × , *E. l. nereis*; ✱ , *E. l. lutris*; ★*Lontra canadensis*;■, *Pteronura brasiliensis*; + , *Aonyx cinerea*.

In the ventral perspective, Canonical Axis 1 separated sea otters from giant river otters, Asian small-clawed otters, and North American river otters (Figure 2-12A). Canonical Axis 2 separated North American river otters from the remaining otter species (Figure 2-12A). The most variation in the ventral perspective was observed in the pterygoid hamulus and tip of the rostrum (Figure 2-12B). The distance between the left and right hamuli was greatest in sea otters than all other otters investigated. Giant river otters possessed the longest rostra, followed by North American river otters, Asian small-clawed otters; sea otters had the shortest rostra.

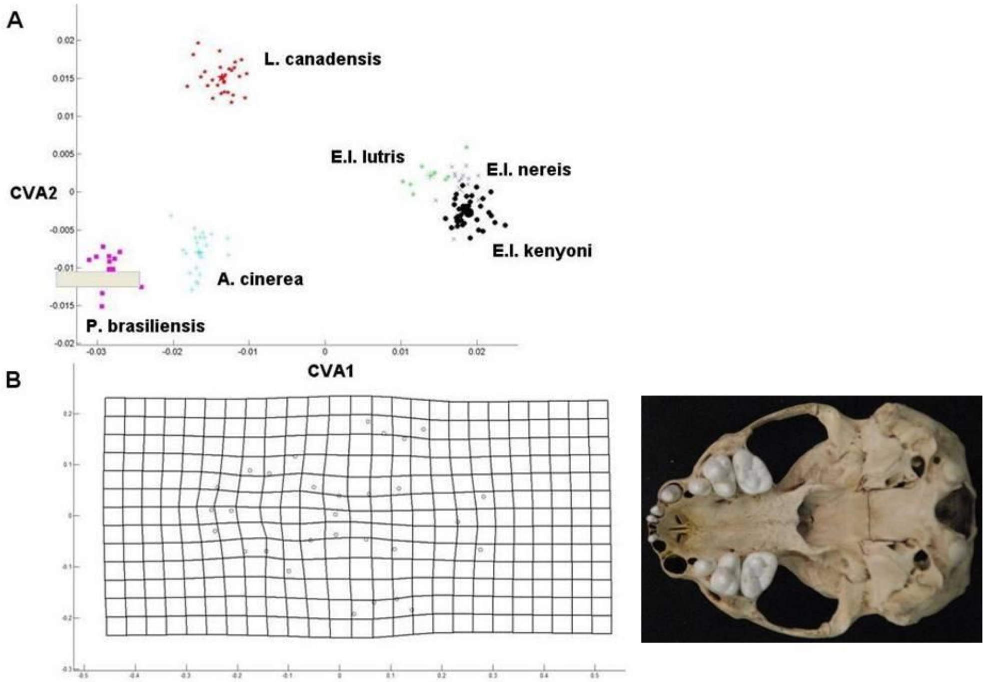

Figure 2-12. Ventral perspective (n=132). (A) Canonical variates analysis of 4 species of otters. (B) Thin plate spline showing nonuniformity. ● *Enhydra lutris kenyoni*; ×, *E. l. nereis*; ✱, *E. l. lutris*; ★*Lontra canadensis*; ■, *Pteronura brasiliensis*; +, *Aonyx cinerea*.

Significant variation was observed in the lateral perspective among otters (Figure 2-13). Canonical Axis 1 separated sea otters from all other otter species (Figure 2-13A). Canonical Axis 2 separated Asian small-clawed otters and giant river otters from North American river otters and sea otters (Figure 2-13A). The most variation in the lateral perspective was observed in the pterygoid hamulus length and rostrum height (Figure 2-13B). North American river otters and giant river otters possessed longer and more gracile pterygoid hamuli than other otters investigated. Sea otters possessed a robust and short pterygoid hamuli and greater rostrum height than the other otters investigated.

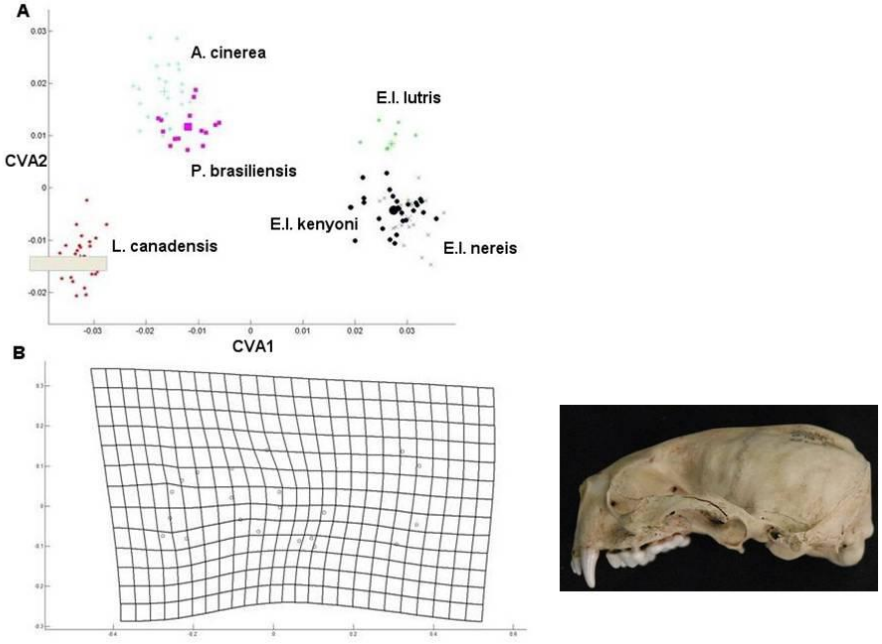

Figure 2-13. Lateral perspective (n=123). (A) Canonical variates analysis of 4 species of otters. (B) Thin plate spline showing nonuniformity. ● *Enhydra lutris kenyoni*; × , *E. l. nereis*; ✳ , *E. l. lutris*; ★ *Lontra canadensis*; ■, *Pteronura brasiliensis*; + , *Aonyx cinerea*.

The shape of the mandible differed significantly among species (Figure 2-14). Canonical Axis 1 separated sea otters from all other otters (Figure 2-14A). Canonical Axis 2 separated North American river otters and giant river otters from Asian small-clawed otters (Figure 2-14A). The most variation was observed in the coronoid process and depth of the masseteric fossa (Figure 2-14B).

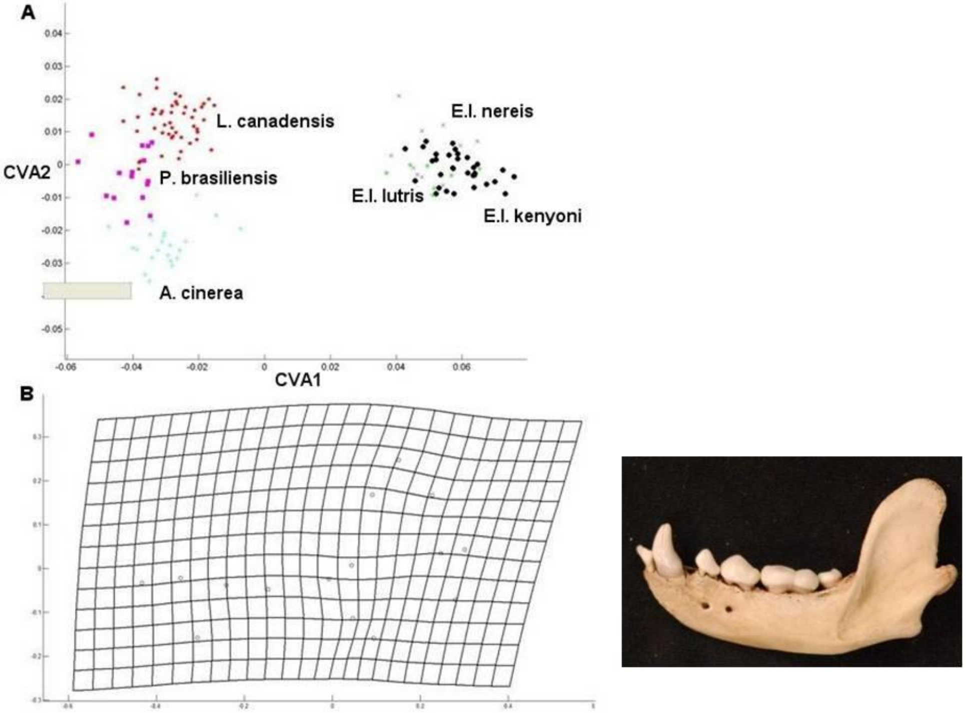

Figure 2-14. Mandible perspective (n=137). (A) Canonical variates analysis of 4 species of otters. (B) Thin plate spline showing nonuniformity. ● *Enhydra lutris kenyoni*; × , *E. l. nereis*; ✳ , *E. l. lutris*; ★ *Lontra canadensis*; ■ , *Pteronura brasiliensis*; + , *Aonyx cinerea*.

The tip of the coronoid process was higher and projected more posteriorly in sea otters. The masseteric fossa depth was greatest in the sea otters. The length of the mandible was greatest in giant river otters, followed by Asian small-clawed otters, and North American river otters and sea otters.

Fluctuating Asymmetry

Significant variation in dorsal cranial symmetry among species was demonstrated (F=9.4; p<0.01). Among all otter species in the study, sea otters showed the highest degree of asymmetry (F=34.5; p<0.01; Figure 2-15). Among sea otters, there were no significant differences in FA between Russian and Alaskan sea otters (F=0.0004; p=0.98). However, Russian sea otters and Alaskan sea otters showed the greatest amount of asymmetry among the sea otter subspecies, followed by California sea otters. No significant differences were observed between giant river otters and North American river otters (F=0.044; p=0.83), Asian small clawed otters and North American river otters (F=0.87; p=0.35), or Asian small clawed otters and giant river otters (F=0.94; p=0.33).

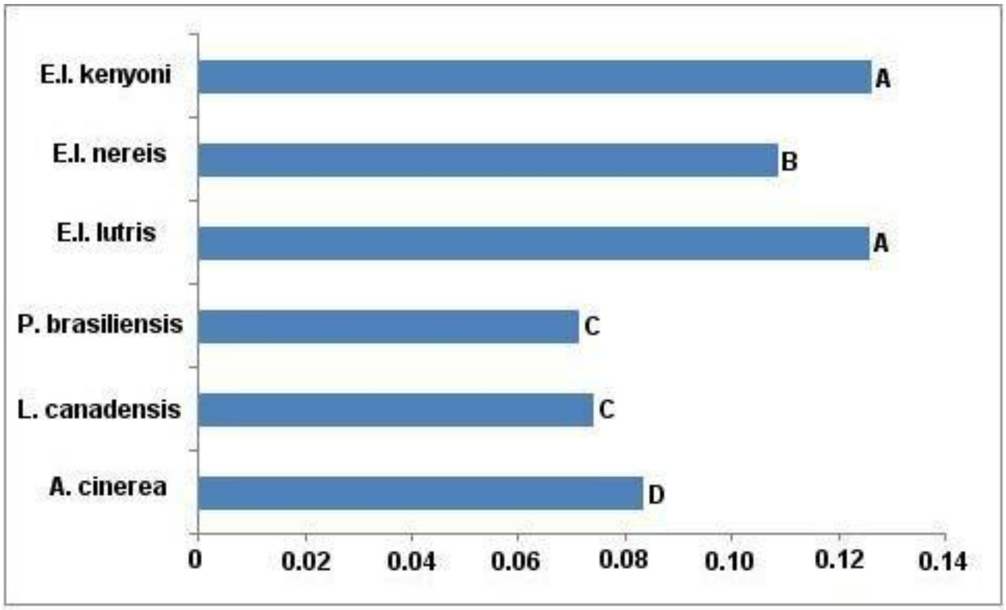

Figure 2-15. Fluctuating asymmetry with dorsal images. Greatest asymmetry was observed in all three subspecies of sea otters. Same letters represent no signficant differences and different letters represent significant differences.

Discussion

In addition to reduced dentition and variation in carnassial morphology (Wilson et al., 1991; Riley, 1985; Carss, 1995; Lariviere & Walton, 1998), analyses of craniodental morphology of several species of otters demonstrate many differences that support divergent feeding modes (mouth-oriented vs. hand-oriented) in relation to diet. Giant river otters possessed the greatest total skull length, palate length, rostrum length, and mandibular length compared to any other otter species investigated, regardless of geomean size. Longer skulls are correlated with longer mandibles and a bite point positioned further away from the temporal-mandibular joint (TMJ). This produces jaws with greater velocity. There is a mechanical tradeoff in any lever system (Westneat, 1994; Westneat et al., 2005; Vogel, 2003; Herrel et al., 2008) that allows for jaws to either maximize force or velocity, but not both simultaneously (Westneat, 1994; Levinton & Allen, 2005; Herrel et al., 2008). That is, high velocity jaws cannot maximize force, and forceful jaws sacrifice velocity. Giant river otters feed primarily on fish (Carter & Rosas, 1997; Rosas et al., 1999) and are mouth-oriented predators (Radinsky, 1968). This species possessed the smallest temporalis and masseteric MA, therefore reducing force output, but maximizing jaw velocity, which is advantageous for capturing fast and elusive fish (e.g., Characiformes, Perciformes, and Siluriformes) with the canines (Rosas et al., 1999). In addition to increasing jaw velocity, smaller mechanical advantages of jaw adducting muscles that should maximize gape (Greaves, 1982; Dumont & Herrel, 2003). There is a tradeoff between MA and gape (Herring & Herring, 1974; Greaves, 1985; Dumont & Herrel, 2003 Slater & Van Valkenburgh, 2009). In general, mammals with a large gape angle require muscles that stretch, which impacts the geometry of the mechanical advantage (Dumont & Herrel, 2003; Slater and Van Valkenburgh, 2009). However, there is an optimal range for sarcomere length. Human sarcomeres have a resting length of approximately 1.6-2.6μm (Martini, 1998). Within this optimal range, the maximum number of cross bridges can form during muscle contraction and the highest muscle tension is produced (Martini, 1998). However, when sarcomeres are completely shortened, the thick filaments are pressed against the Z-lines and the myosin heads cannot pivot or produce tension. Alternatively, if sarcomere lengths are greater than the optimal range, tension is reduced by the reduction of the size of the zone of overlap and the number of cross-bridge interactions between actin and myosin (Martini, 1998). The latter situation occurs at larger gapes unless certain other adaptations are in place. A simple solution to increase gape is to elongate the jaws. Longer jaws (Greaves, 1983; Binder & Van Valkenburgh, 2000) and larger body size (Greaves, 1983; Slater & Van Valkenburgh, 2009) correlate with larger gapes. Giant river otters are the largest and longest otter species. They possessed the greatest total skull and mandibular length compared to other otter species investigated in this study. If an animal requires a large gape, it will either increase its body size, which also increases its mandibular length through scaling, or the architecture of the jaw adducting muscles may be modified allowing for greater stretch (Greaves, 1983). The stretch factor is the ratio of L/l, where L is the length of the stretched muscle and l is the superficial masseter (Herring & Herring, 1974). The stretch factor can be varied by changing the origin-insertion ratio (e.g., origin may migrate forward) and lengthening of individual fibers (by reducing pennation), which allows for greater gape (Herring & Herring, 1974).

North American river otters primarily feed on fish, but also incorporate crustaceans (e.g., crayfish), amphibians, birds, and mollusks (Toweill, 1974), which places them in an intermediate position between piscivory and invertebrate specialists. Males form larger groups after the mating season concurrent with the availability of schooling fishes, such as salmon (Salmonidae), herring (Clupeidae), sandlance (Ammodytidae), and capelin (Osmeridae) (Blundell et al., 2002). These fast schooling fishes are more calorically rich and more desirable. Similar to giant river otters, North

American river otters possessed long mandibles (as demonstrated by MBI and geometric morphometric analyses), which should place the resulting force further away from the TMJ, providing the advantage of high velocity jaws to catch fast, schooling fishes, at the expense of force output. North American river otters possessed the highest MA at the temporalis than any other otter species investigated, but had lower masseteric MA. This correlated with a greater moment arm of the temporalis, which increases the force generated. North American river otters also possessed the greatest coronoid length, which is an insertion of the temporalis muscle, increasing surface area for muscle attachment. A greater coronoid length (and low condyle) also correlates to a larger moment arm of temporalis, or in-lever. Functionally this allows for an increase in temporalis moment arm and explains the higher temporalis MA (Freeman, 1979; Sacco & Van Valkenburgh, 2004; Figueirido et al., 2009). The increased temporalis MA provides increased force to the anterior mandible at the canines, and functions pull the jaw upwards and backwards (Herring, 1985). These traits are advantageous for a mouth-oriented predator catching fast, elusive prey.

Asian small-clawed otters, unlike giant river otters and North American river otters, are hand-oriented predators (Sivasothi & Nor, 1994; Jacques et al., 2009) and should not require high velocity jaws to capture prey. This correlation was supported by the traditional morphometric analysis as well as the blunter MBI values and skull shapes (geometric morphometric analyses). Asian small-clawed otters (hand-oriented predator) and North American river otters (mouth-oriented predator) consume broader and more diverse spectrum of prey than sea otters and giant river otters, which may be why these two species grouped together in the traditional morphometric analyses. Within Asian small-clawed otters the temporalis MA was significantly greater than the masseteric MA. Again this suggests increased force at the anterior jaws near the canines. This species also possessed the greatest zygomatic fossa length. The large zygomatic fossa length should allow for a larger temporalis muscle to attach to the coronoid process of the mandible.

Sea otters are hand-oriented, durophagous predators that almost exclusively prey on benthic invertebrates, with the exception of Alaskan sea otters that range along the Aleutian Islands and Russian sea otters that prey on epibenthic fish (Riedman & Estes, 1988). Much of the morphological traits correlated with this durophagous appear related to the very blunt and wide mandible. Wide mandibles are concomitant with wide skulls and a wide upper jaw. This correlation explains the increase in greatest interorbital distance, increased rostral width at the molars, braincase width, palate width, and greater skull width. The corresponding differences in jaw adductors likely explain increased zygomatic length. Sea otters also differed in that their masserteric MA was much higher than any other otter species investigated. Increased masserteric MA functions to increase force to the posterior jaw near the molars and should be considered an adaptation for durophagy. The masseter muscle originates along the entire length of the zygomatic arch. An enlarged arch should provide additional surface area for attachment of this major adducting muscle. An enlargement of the zygomatic arch should decrease the length that muscle fibers are pulled, thus increasing the force that each fiber can produce, as well as increase mechanical advantage of the masseter (Herring & Herring, 1974). Increasing the zygomatic length also increases the length of the masseter, which also increases mechanical advantage (Herring & Herring, 1974). A greater moment arm of masseter generates more control over chewing behavior (Radinsky, 1985). The masseter muscle inserts onto and into the masseteric fossa on the mandible. Therefore the height of the mandibular ramus and depth of the mandibular fossa conveys important functional significance to jaw biomechanics. The length and depth of the masseteric fossa was enlarged in sea otters, providing additional surface area for the masseter to insert as well as accommodating a masseter with a larger physiological cross-sectional area. I n addition, sea otters possessed a greater distance between the pterygoid hamuli than any otter species investigated. A greater distance between the pterygoids correlates to an enlarged muscle mass of the lateral and medial pterygoids, which are a one of the three pairs of adductor muscles.

Traditional and geometric cranial morphometric analyses of sea otters demonstrated that they exhibited a larger and deeper posterior mandibular ramus, and shorter, blunter skull shapes, which is consistent with increased bite force at the carnassials of other mammals (Sacco & Van Valkenburgh, 2004; Figueirido et al., 2009). An increase in the vertical height of the mandibular ramus results in an increase in vertical orientation for the masseter (Crompton & Hiiemae, 1969). This causes an increase in the moment arms of the masseter and medial pterygoids (Crompton & Hiiemae, 1969). A greater mandibular ramus height and a more anterior position of the masseter results in smaller gapes, unless the muscle architecture is modified by increasing muscle fiber length (Hylander, 1972). In addition to shorter facial lengths (which positions the masseter muscle more anteriorly), sea otters had a tall and vertical ramus and a large zygomatic length for masseter attachment. A large zygomatic length may allow muscles to attach more anteriorly, thus improving bite force while allowing a larger gape. Longer fibers can increase maximum muscle excursion, or distance a muscle fiber can shorten (Taylor et al., 2009). For jaw adducting muscles this likely translates to wider maximum gapes (Taylor et al., 2009). Common marmosets (*Callithrix jacchus*) and pygmy marmosets (*Cebuella pygmaea*), both tree gouging primates, displayed longer fiber lengths of the masseter than non-gouging tree primates which was correlated with greater gape (Taylor et al., 2009). Similar results were shown in pigs (Herring & Herring, 1974; Herring et al., 1979) and mice (Satoh & Iwaku, 2006). The object of these adaptations for force generation is the large occlusal surface area (OSA) of the upper postcanine teeth of sea otters. These broad flat molars provide a crushing surface upon which to crush prey. The wide postcanine teeth of sea otters is consistent with other mustelids that crush their prey (Popowics, 2003). When the effect of size was eliminated, the OSA of sea otters was the largest of all otters investigated, even larger than giant river otters, a species much larger in absolute body size (Morrison et al., 1974; Carter & Rosas, 1997). In more carnivorous otter species (e.g., giant river otters), the postcanine teeth are sharp and designed for slicing prey (Lewis, 2008). However, sea otters are the only extant otter that possesses bunodont dentition (Lewis, 2008). Unlike all other otter species that had long and narrower rostrums, sea otters also possessed a greater height of the rostrum (e.g., increasing area for muscle attachment) (Herrel et al., 2002) and shorter skull lengths providing a greater force (Nogueira et al., 2009). Increased rostral height increases the strength of the skull and minimizes bending due to increased bite force (Preuschoft & Witzel, 2002; Tanner et al., 2010). The more anteriorly positioned zygomatic arch and shortening of the rostrum are also characteristic of animals preying on hard prey (Nogueira et al., 2009). Shorter, blunter jaws (MBI > 1.0) place the resulting force closer to the TMJ, providing the advantage of increased MA and thus a greater bite force performance. Shorter and wider skulls also bring the canines closer to the fulcrum, which incresed the MA even at the tip of the jaw, resulting in increased bite force at this position as well (Nogueira et al., 2009). Therefore, skull (e.g., short, blunt skulls, wider than long jaws) and postcanine morphology of sea otters show numerous advantageous traits for a mouth-oriented predator specializing on hard, benthic prey. All craniodental morphologies and jaw biomechanics demonstrate that sea otter skulls are built to maximize bite performance and crush prey.

Variation was also observed in the cranial morphology among sea otter subspecies. Russian sea otters possessed greater palatal and zygomatic fossa lengths compared to the other two subspecies. California and Alaskan sea otters possessed greater zygomatic lengths than Russian sea otters, which increases the surface area for masseter attachment. As mentioned above, an increase in zygomatic length, decreases stretch of the masseter and increases its MA (Herring & Herring, 1974). Alaskan sea otters displayed the greatest masseteric MA, followed by California and Russian sea otters. Alaskan sea otters also exhibited greater braincase and zygomatic fossa width than California and Russian sea otters. A larger zygomatic fossa width correlates to a larger temporalis muscle cross-sectional area and mass connecting to the coronoid process. This should function to increase the in-force component of the jaw lever and potential increase the temporalis MA (Gans & de Vree, 1987; Antón, 1999; Herrel et al., 2008; Pfaller et al., 2011). The greater mechanical advantages of both the masseter and temporalis adductors should correspond to greater estimated bite forces (see Chapter III) but also influence jaw velocity. California sea otters and Alaskan sea otters consume a greater quantity of hard, benthic prey, (Kvitek et al., 1993; Green & Brueggeman, 1991; Ralls et al., 1995; Tinker et al., 2007; Estes et al., 2003b; Laidre & Jameson, 2006; Ostfeld, 1982; Garshelis et al., 1986; Estes & Duggins, 1995) which corresponds to a greater bite force. The prey of Russian and Alaskan sea otters (inhabiting parts of Southwest Alaska including Alaska Peninsula, Aleutian Islands, and Amchitka Island) include epibenthic fish such as flatfish (Pleuronectids) in their diet (Riedman & Estes, 1988; Green & Brueggeman, 1991; Watt et al., 2000). However, populations in Southwest Alaska still incorporate more benthic invertebrates than fish into their diets (Green & Brueggeman, 1991, Watt et al., 2000). Russian sea otters, on the other hand, incorporate a larger proportion of fish in their diets (Riedman & Estes, 1988), which may be congruent with smaller MA and estimated bite forces than California and Alaskan sea otters.

Sea otters showed the greatest FA compared to all other otters investigated. Stressful conditions in pregnant females are thought to cause disturbances in the developmental stability of offspring, as demonstrated in rodents (e.g., noise, temperature, behavior; Siegel et al., 1975), Baltic grey seals (e.g., environmental pollution; Zakharov & Yablokov, 1990) and cheetahs (e.g., low population size; Wayne et al., 1986). Sea otters have low genetic variability (Larson et al., 2002), low reproductive rates, weak dispersal rates, and are exposed to various infectious diseases (Estes et al., 1982; Linsday et al., 2000; Miller et al., 2002; Jessup et al., 2004; Goldstein et al., 2009). In addition, all sea otter subspecies are geographically isolated (Wilson et al., 1991; Cronin et al., 1996), making breeding among the three subspecies unlikely. The fur trade in the 18th and 19th centuries caused widespread reduction and extirpation of many sea otter populations (Garshelis & Garshelis, 1984; Larson et al., 2002). This reduction in population and reduced genetic variation may have led to inbreeding depression (Wayne et al., 1986; Larson et al., 2002). Historically, sea otters ranged from the Island of Hokkaido, Japan, through the Kuril Islands and the Kamchatka Peninsula of Russia, throughout the Aleutian Islands, and down along the North American west coast to Baja California (Larson et al., 2002). Sea otter populations remained in decline until their protection in 1911 by the international treaty (Ralls et al., 1996; Larson et al., 2002). Although several sea otter populations recovered by the 1970s (Larson et al., 2002) and translocation efforts were successful in Washington, Southeast Alaska, and British Columbia (Jameson et al., 1982; Larson et al., 2002), sea otter populations were still absent or remained in decline in much of their historic range (Larson et al., 2002). Recently, California sea otters and Alaskan sea otters populations in the Aleutian Islands have declined (Doroff et al., 2003; Hanni et al., 2003). California sea otters are found in a limited range from Point Conception near Santa Barbara, California, to Año Nuevo in San Mateo County, California and have recovered more slowly from the fur trade (Hanni et al., 2003) than other populations. California sea otters have been experiencing elevated mortality, which is causing a decline in this threatened species (Estes et al., 2003a). California sea otters may be experiencing developmental instability due to low population size, limited habitat range, infectious disease such as toxoplasmosis (Miller et al., 2002), and immune suppression from exposure to organochlorines (Kannan et al., 1998; Hanni et al., 2003). Fishing may also be causing stress to the California sea otter populations. The population decline observe from 1976 to 1984 was likely due to incidental mortality in fishing nets and the decline observed between 1995 and 1999 was likely due to a live-fish fishery (Estes et al., 2003a). Such numerous sources of stress can manifest as cranial asymmetry. Therefore, deviations from bilateral cranial morphology may be showing that the California population is under great stress (low population size, infectious diseases, and fishing). Alaskan and Russian sea otters possessed greater cranial asymmetry than California sea otters, which may likely be due to environmental stresses caused by increased predation (e.g., orca) (Estes et al., 1998), disease (Hanni et al., 2003), or greater bottlenecks from increased hunting historically. Since the 1980s, northern sea otters have been declining, along with other marine mammals (e.g., Northern fur seals, Steller's sea lions, and harbor seals; Goldstein et al., 2009). Predation by orcas may be the leading cause of sea otter decline in western Alaska (Estes et al., 1998; Doroff et al., 2003). However, certain portions of the Alaskan sea otter populations have been infected with phocine distemper virus (PDV) (Goldstein et al., 2009). PDV has been introduced to the North Pacific from the Atlantic in 2000, possibly contributing to the decline of several marine mammal populations in the Pacific Northwest (Goldstein et al., 2009). In 2006, a large number of sea otters in southcentral

Alaska (adjacent to the southwest stock which is listed as threatened) were found dead due to valvular endocarditis and septicemia, which are infections associated with *Streptococcus infantarius* subsp. *coli* (Goldstein et al., 2009). Due to the lack of bacterial infection or heart valve defects, necropsy reports concluded that this disease was most likely caused by a primary immunosuppressive viral infection, PDV (Goldstein et al., 2009). Alaskan sea otters (composed of three separate stocks: southeast, southcentral, and southwest) comprise up to 90% of the world's sea otter population (Hanni et al., 2003). A rapid decline in these stocks should be of main concern to management of this species, as signs of stress are apparent in the cranial morphology of their offspring.

In conclusion, the data demonstrated a divergent craniodental pattern in the two trophic specializations (mouth vs. hand-oriented) in otters that correlates with diet (fish, combination of fish, amphibians, crustaceans, or benthic invertebrates). North American river otters and giant river otters are mouth-oriented predators that possess long mandibles, rostrums, and long and gracile pterygoids hamuli. Longer, narrower skulls, and long mandibles position the resulting bite force further from the temporal-mandibular joint, providing jaws with greater velocity at the expense of bite force capability. High velocity jaws are an important adaptation for mouth-oriented species that catch fast moving prey, such as fish. Sea otters and Asian small-clawed otters are hand-oriented predators with further modified dentition and shorter skull and mandibular lengths (in relation to size) than North American river otters and giant river otters. Shorter mandibles, position the resulting bite force closer to the TMJ, providing a more forceful bite at the expense of velocity. The remaining suite of traditional morphometrics, biomechanical measurements and cranial shape analyses (geometric morphometrics) support and the functional dichotomy of mouth vs. hand oriented otter predators. Fluctuating asymmetry of the skull was most common in sea otters. Low population size, disease, fishing techniques, and predation are the most likely causes of population declines in sea otter populations, possibly causing females (due to stress) to produce offspring with asymmetrical skulls. This is a sign that sea otters are under great stress and should be monitored more closely.

CHAPTER III

ESTIMATED BITE FORCE OF OTTERS AND THE PHYSIOLOGY OF JAW MUSCULATURE IN SEA OTTERS

Introduction

Bite Force

The form and function of vertebrate skulls, mandibles, dentition, and jaw musculature have been widely investigated to examine their relationships with feeding performance and trophic ecology (e.g., Kiltie, 1982, 1984; Herring et al., 2001; Herrel et al., 2002; Dumont & Herrel, 2003; Huber & Motta, 2004; Christiansen & Adolfssen, 2005; Huber et al., 2005; Erickson et al., 2003; Christiansen & Wroe, 2007; Anderson et al., 2008). Among vertebrates increased bite performance and durophagy is an important adaptation that confers a trophic advantage (Wroe et al., 2005, Christiansen & Wroe, 2007) and is closely linked to the design and evolution of the cranial-mandibular system (Anderson et al., 2008; Herrel et al., 2009). The entire cranial system is often optimized to withstand mechanical forces as well as be able to exploit food resources (Herring 1985; Herring et al., 2001; Huber & Motta, 2004). The vertebrate cranium is complex and involves the integration of muscular and mechanical systems, which influences its morphology over evolutionary and ontogenetic time (Herring, 1980; Pérez-Barbería & Gordon, 1999; Huber & Motta, 2004; Bloodworth & Marshall, 2007). Variation in the skull and mandible shape and morphology translates into variations in bite force and feeding performance (Herrel et al., 2002; Christiansen & Adolfssen, 2005;

Wroe et al., 2005; Christiansen & Wroe, 2007; Van Valkenburgh, 2007). For example, in terrestrial durophagous vertebrates, the skull and mandible tends to be short and blunt, with wide jaws and zygomatic breadths, and enlarged jaw adducting muscles (Dumont, 2003; Nogueira et al., 2005; Tanner et al., 2010). This suite of characteristics functions to increase bite performance. In canids that consume large prey, dentition surface area is generally reduced, the canines and incisors are large, the snouts tend to be broad, the mandibles are more rigid and the mechanical advantages of the temporalis is increased (Van Valkenburgh & Koepfli, 1993). However, canids with an omnivorous diet, exhibit larger molar grinding areas, smaller incisors and canines less rigid mandibles, and more openly spaced premolars (Van Valkenburgh & Koepfli, 1993). Carnivorous ursids possess reduced molar grinding surface areas with small carnassial blades and low mandibular rigidity, similar to omnivorous canids (Sacco & Van Valkenburgh, 2004). In contrast, herbivores evolved forceful, large muscles to chew or grind food in the posterior of the jaws with strong transverse movements across the ridged teeth (Janis, 1995). The transverse pattern of mandibular movement requires large masseter muscles but also large lateral and medial pterygoid muscles, which is reflected in the large moment arm of the masseter, large angle of the mandible (e.g., to provide broad area of attachment for well-developed masseter and pterygoid muscles), high position of the jaw joint, large zygomatic arches for the origin of the masseter (Janis, 1995), and a large robust pterygoid hamulus. Bite force is affected by many morphological aspects, such as body size and skull morphometrics (e.g., gape angle, skull length and width), skull shape, adductor muscle architecture and physiology (i.e., muscle mass, muscle fiber types, pennation, and insertion/origination points), and bite point location on the jaw (i.e., anterior or posterior point along the length of the jaw) (Herring & Herring, 1974; Herring et al., 1979; Dumont & Herrel, 2003; Anderson et al., 2008). Bite force is also influenced by gape. There is a tradeoff among muscle tension, mechanical advantage and gape (Herring & Herring, 1974; Martini, 1998; Dumont & Herrel, 2003). Generally, mammals with large gape angles possess muscles that stretch, which lowers the mechanical advantage of the jaw adducting muscles (Dumont & Herrel, 2003). However, in specialized taxa (such as those found in the Order Chiroptera) changes in the insertion points of adducting muscles and their internal architecture have resulted in species that can produce a high bite forces with a high gape angle or species with a high bite force at a low gape angle (Dumont & Herrel, 2003). Sea otters are interesting in that they possess extreme short, blunt, jaws that are wider than they are long, and postcanine tooth morphology that show advantageous traits for a durophagous predator. Sea otters are known to increase gape widely to crush bivalves, but this has not been measured (but see Chapter IV). Therefore it is likely that they may possess muscular adaptations (i.e., changes in size, attachments, architecture and fiber length) that function to increase bite force at large gapes.. Sea otters possess a greater mandibular ramus height and a more anteriorly positioned masseter, which usually decreases gape. However, adductor muscle position and architecture can be modified by changing insertion points and increasing fiber length, which would increase gape. A more anteriorly located digastric (jaw opening muscle) insertion may also be an adaptation to a shorter, blunter skull that helps to maintain a wide gape (Scapino, 1976). For example, felids have short and blunt jaws (for increased bite force) that may necessitate a more anteriorly located digastrics insertion in order to preserves a wide gape (Scapino, 1976). Sea otters have been observed to feed on pismo clams (*Tivela stultorum*), a very large bivalves (Wade, 1975; Miller et al., 1975). Riley (1985) showed that sea otters had an increased surface area of digastric muscle origin and insertion relative to North American river otters, an arrangement similar to that found in felids. To place large clams posteriorly into the mouth over the carnassials (for maximum force), sea otters must exhibit a large maximum gape. We predict that the long zygomatic arch ,wide jaws, long fiber length of the masseter serve to increase gape while maintaining a large bite force. However, to date no comparative bite force data for sea otters exists and data regarding the anatomy and architecture of the jaw adductor system of otters are few (Riley, 1985). Therefore, our questions are: (1) How much force is produced by the masseter, pterygoids, and temporalis? And (2) Do sea otters indeed maintain a high bite force at wide gapes?

The mammalian jaw is a 3rd class lever system, in which the effort (in-force) is placed between the fulcrum and the load. In the case of the mammalian jaw, the tympanomandibular joint (TMJ) is the fulcrum, the adductor muscles (temporalis, masseter, and/or pterygoid complex) are the effort, and the load (out-force) is the bite force which can vary in location from the incisors to the molars. Simple lever mechanic principles dictate that bite force increases as the resulting force location (i.e., bite point) is positioned closer to the TMJ, or fulcrum (Greaves 1985; Greaves, 2000; Santana et al. 2010). Bite force is different at each resultant location along the jaw (e.g., canines vs. carnassials), and is at its maximum in many mammals when it is located in the posterior

1/3 of the jaw (Greaves 1982; Greaves, 1985; Greaves, 2000). Not coincidentally, the carnassial teeth are also located in the posterior 1/3 of the jaw, where maximum force is generated (Greaves, 1985). This arrangement allows for the maximum force to be applied to food items, while maintaining a reasonable gape (Greaves, 1983). The distance between the jaw joint and the carnassials is thought to be highly constrained within the Order Carnivora, indicating that concentrating bite force at this location is of importance in the evolution of carnivores (Greaves, 1982; Christiansen & Adolfssen, 2005; Christiansen & Wroe, 2007). However, carnassials are subject to selection pressure and have been modified in at least two ways. In specialized carnivorous species (such as hypercarnivores like felids), the carnassials are sharp and designed for shearing and slicing prey, whereas in omnivores, herbivores, or species specializing on hard prey, the carnassial morphology trend toward increasing bluntness and flatness (bunodont) for crushing and grinding (Christiansen & Adolfssen, 2005; Christiansen & Wroe, 2007). The overarching question is, “Does bite force differ between otters specializing on piscivorous, mouth-oriented otters vs. durophagous hand-oriented otters? It is predicted that giant river otters and North American river otters have sharp carnassials for shearing fish and long mandibles for increased jaw velocity, but at the expense of reduced bite force. It is also predicted that sea otters can generate a large bite force at a relatively larger gape.

Bite force is a whole-organism performance measure that can be used to examine the relationship between morphology and feeding performance (Herrel et al., 2002; Anderson et al., 2008; Davis et al., 2010). Variation among individual bite force may also be linked to variation in individual fitness (Herrel et al., 1996; Anderson et al., 2008) in addition to dietary differences (Herrel et al., 2002; Christiansen & Adolfssen, 2005; Christiansen & Wroe, 2007; Figueirido et al., 2009). By increasing bite force an organism can increase the proficiency of handling prey (decrease handling time), such as capturing, subduing, and crushing prey, and thus increase the net rate of energy intake while foraging (Huber & Motta, 2004; Mcbrayer, 2004; Anderson et al., 2008; Davis et al., 2010. This is important for sea otters since they have a high metabolic rate and must consume up to 30% of their body weight per day for survival (Riedman & Estes, 1990; Lairde & Jameson, 2006).

The relationship between bite performance and craniodental biomechanics has been investigated in numerous terrestrial species (Kiltie, 1984; Mcbrayer, 2004; Christiansen & Adolfssen, 2005; Wroe et al., 2005; Lappin & Husak, 2005; Christiansen & Wroe, 2007; Ellis et al., 2008), but few data are available for secondarily aquatic tetrapods, such as otters. Sea otters are durophagous predators (Kenyon, 1969; Garshelis et al., 1986; Kvitek et al., 1992, Kvitek et al., 1993; Ralls et al., 1995; Taylor, 2000; Estes et al., 2003b) that feed on a variety of hard, benthic invertebrates, including mollusks, crustaceans, and echinoderms (Kenyon, 1969; Calkins, 1978; Garshelis, 1983; Doroff & Bodkin, 1994; Garshelis et al., 1986; Estes et al., 2003b; Tinker et al., 2008; Wolt et al., 2012; see Chapter V). Although many studies have documented diet and foraging behaviors of otters (Toweill, 1974; Freeman, 1979; Kruuk et al., 1994; Sivasothi & Nor, 1994; Carter & Rosas, 1997; Hussain & Choudhury, 1997; Rosas et al., 1999; Blundell et al., 2002; Jacques et al., 2009), few data are available on the biomechanical performance of the jaws (e.g., bite force) and jaw musculature (Riley, 1985; Lynch & O'Sullivan, 1993; Christiansen & Wroe, 2007; Constantino et al., 2011). Investigating the ecomorphology of feeding in otters will provide new insights into the energetics of their foraging ecology.

*Jaw Adductor Musculature of Sea Otters (*Enhydra lutris*)*

Among mammalian jaws the resulting force is often placed further from the TMJ than the applied force by the jaw musculature (Crompton & Parker, 1978; Herring et al., 2001). Depending upon the jaw adductors and the length of the jaw this can negatively impact mechanical advantage. However, there are many ways to increase mechanical advantage and bite performance (Greaves, 1983; Pfaller et al., 2011). The animal can increase its bite force by either growing larger in size, by relative hypertrophy of the adductor muscles (via positive allometry), or by changing the architecture of the jaw adducting muscles (e.g., degree of pennation, change origination/insertion points) (Greaves, 1983). The magnitude of tension produced by a muscle is a function of muscle mass and physiological cross-sectional area, fiber length, and the pennation angle (Herrel et al., 2008). Pennation acts to increase the number of fibers in a given volume, at the cost of creating shorter fibers, and thus acts to increase the output force (Herring, 1980). An increase in the number of fibers packed next to each other increases the physiological cross-sectional area (PCSA) and therefore produces more force (but at the expense of velocity) than parallel fibers with longer fiber lengths (Taylor & Vinyard, 2009).

The TMJ and position of the adductor muscles establishes the basic mechanical environment of the mammalian feeding apparatus. Modifications of this basic system allows for the variation of mastication patterns simply by changing muscle location, proportions, and activation, as well as craniodental morphology, (Riley, 1985; Hiiemae & Crompton, 1985). Jaw muscles are morphologically linked to anatomical structures and mechanical advantage can be modulated by changing muscle insertion points, angles, or by repositioning the bite force point in the jaw (Herring & Herring, 1974; Herring, 1980; German & Franks, 1991; Fukunaga et al., 1997; Greaves, 2000; Pfeller et al., 2011). This connection would suggest a relationship in the timing of their movements (German & Franks, 1991). The anatomy, architecture, and physiology of jaw adducting muscles has been investigated in many terrestrial species (Herring & Herring, 1974; Herring et al., 1979; Dumont & Herrel, 2003; Herrel et al., 2008; Herrel et al., 2009; Taylor & Eng, 2009; Taylor & Vinyard, 2009), and a few marine mammals (Werth, 2000; Werth, 2006b; Bloodworth & Marshall, 2007); little is known regarding adductor jaw muscle of sea otters. This topic is central to understanding how sea otter jaws function, which in turn has ecological and energetic consequences.

Objectives and Hypotheses

The first objective of this chapter was to calculate an estimated bite force in giant river otters (*Pteronura brasiliensis*), North American river otters (*Lontra canadensis*), Asian small-clawed otters (*Aonyx cinerea*), California sea otters (*Enhydra lutris nereis*), Alaskan sea otters (*E. l. kenyoni*), and Russian sea otters (*E. l. lutris*). It was hypothesized that otters feeding on hard invertebrate prey (sea otters and Asian small-clawed otters) would possess greater estimated bite forces than primarily piscivorous otters (North American river otters and giant river otters). It is also predicted that increases in bite force would correspond with craniodental morphologies characterized in Chapter II. The second objective was to characterize the jaw adductor anatomy, architecture and muscle fiber length, estimate physiological cross-sectional area (PCSA), maximum theoretical muscle tension (MTMT) and bite force in sea otters. Due to time constraints and the lack of available specimens due to their remote distribution and protective status (e.g., giant river otters), only sea otters jaw musculature was characterized. It was hypothesized that sea otters would exhibit a large PCSA and MTMT of the masseter, temporalis, and pterygoid complex that results in a large in-force to mandibular lever system that approximates the estimated bite force from the dry skull method and exceeds the crushing force required to consume hard prey items (Chapter V).

Materials and Methods

Estimated Bite Force via Dry Skull Methodology

Bite forces of California sea otters (n=20), Alaskan sea otters (n=37), Russian sea otters (n=7), North American river otters (n=43), giant river otters (n=15), and Asian small-clawed otters (n=23) were estimated using a dry skull method following Thomason (1991). Scaled digital images of each skull were taken in dorsal, lateral, and ventral, perspectives. Each mandible was photographed in left lateral view with a Nikon

D200 SLR camera stationed on a copy stand (Figure 3-1). Image J (NIH, Bethesda, MD) was used to compute the cross-sectional areas of the zygomatic fossa where the masseter-medial pterygoid complex and temporalis muscles are located. The cross-sectional area of each adductor muscles (MT, masseter-pterygoid complex; TT, temporalis) was multiplied by the estimated isometric force value of 37 N/cm^2 (370 KPA; estimated value of mammalian muscle) (Christiansen and Wroe, 2007), which gave an estimated MTMT for each muscle group (Thomason, 1991). The direction of the force vectors for masseter-pterygoid complex and temporalis acts perpendicular to the plane of the area and through the centroid (Thomason, 1991). The in-lever of the masseter (ML) about the TMJ was computed from ventral images (Figure 3-1). The in-lever of the temporalis was measured with the centroid in the left lateral view (Figure 3-1). The out-levers for the temporalis and masseter-pterygoid complex were measured at the posterior of incisors, canines, and carnassials.

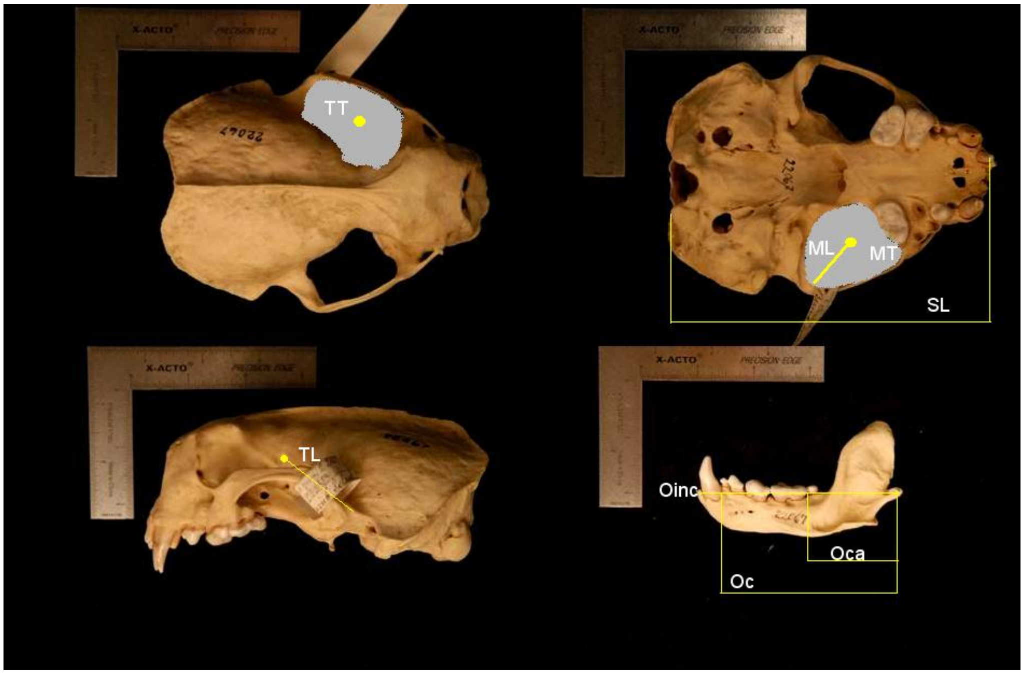

Figure 3-1. Illustration of morphometric variables used to calculate relative bite force estimates (following Thomason, 1991). *TT*, cross-sectional area of temporalis; *MT*, cross-sectional area of masseter; *ML*, lever arm of masseter and medial pterygoid; *TL*, lever arm of temporalis; *Oinc*, distance from condyle to incisors; *Oc*, distance from condyle to canines; *Oca*, distance from condyle to carnassials. A Russian sea otter, *Enhydra lutris lutris,* is depicted.

Bite force was estimated as follows:

Bite Force at Canine = 2(MT x ML + TT x TL)FPA/Oc

Bite Force at Carnassial = 2(MT x ML + TT x TL)FPA/Oca

Bite Force at Incisors = 2(MT x ML + TT x TL)FPA/Oinc where *MT* is the cross-sectional area of the masseter-pterygoid complex in ventral view, *ML* is the lever arm of the masseter and pterygoid complex about the TMJ, *TT* is the cross-sectional area of the temporalis muscle in dorsal view, and *TL* is the lever arm of the temporalis about the TMJ from its centroid to the line of action of the midpoint of the jaw joint, *FPA* is the estimated maximal isometric force per unit area of muscle tissue for mammals (370 KPA or 37 N (Wroe et al., 2005), *Oc* is the distance from the condyle to the posterior surface of the canines, *Oca* is the distance from the condyle to the posterior surface of the carnassials, and *Oinc* is the distance from the condyle to the posterior surface of the incisors. The in-lever is multiplied by 2 based on the assumption that both sides will contract maximally (Thomason, 1991).

Statistical Analyses

To remove the effects of size, bite force measurements were regressed against total skull length. A MANOVA was performed with bite force estimates as the dependent variables and total skull length as the independent variables. Residuals were then saved. MANOVA tests were performed from linear regressions, with residual bite force as the dependent variable and species as the covariate, to test for significant differences among otter species. Post hoc (Student-Newman-Keuls) tests were performed to determine which species significantly differed from the others. Statistical tests were performed using JMP Pro 9.0 (SAS Institute, Cary, NC, USA).

Jaw Musculature of Sea Otters

Gross Morphology

Alaskan sea otter salvage material (N=18; *Enhydra lutris kenyoni*) were obtained by the Alaskan Fish and Wildlife Service (Permit Number MA041309-3). Dissections of the head and jaw apparatus were conducted at Texas A&M University's Necropsy Laboratory. Sea otters heads were stored in a freezer at -20^{o}F until ready for analysis, then they were thawed in a refrigerator overnight prior to a dissection. Heads were dissected to characterize the origin and insertion of each jaw adducting muscle (temporalis muscle, masseter muscle and the lateral and medial pterygoid complex in total). Since these samples were recovered from stranded individuals, not all of the adductor muscles were in good condition in each individual. Five individuals were used to dissect all three adductor muscles, 8 individuals were used to analyze masseters and pterygoid complex only, 2 individuals were used to analyze temporalis and pterygoids only, 1 individual was used to analyze masseter and temporalis only, and 2 were used to analyze the pterygoid complex. The width, length, thickness, and mass of these muscles on both the left and right side of the jaw were measured. Width of muscles and maximum thickness were measured at the center for both the left and right sides.

Nitric Acid Dissections

Masseter (n=14), temporalis (n=8), and pterygoid muscle complexes (n=17) were removed from sea otters skulls. Fiber lengths were measured following nitric acid dissection (following Loeb & Gans, 1986). First, each muscle was fixed in 10%

formalin overnight before being placed in a glass dish containing 30% nitric acid in physiological buffered saline. Muscles were kept in this solution until connective tissues were digested and the muscle fascicles and fibers began to separate. This process took 3 days for masseters and pterygoids and 1 week for temporalis muscles. Once the fibers began to separate, the nitric acid-saline solution was decanted and replaced with a 50% glycerin/nitric acid mixture, followed by a 50% glycerin (in water) solution. These two solutions slowed and finally stopped the breakdown of the muscle tissue, respectively. Muscle fascicles were placed under a stereoscope in glycerin (Nikon 150, SMZ 1500, Nikon Instruments, Inc), and individual fibers were teased apart using glass probes. The length of 4 individual fibers were measured from 4 individuals (n=16 fiber lengths) for each muscle using a calibrated eye reticle. To calibrate the reticle, a scale was placed in the field of view at a specified magnification and the distance between the reticles was measured (1 mm).

Physiological Cross-Sectional Area (PCSA) and Maximum Theoretical Muscle Tension (MTMT)

Salvage material was dissected to remove skin and connective tissue so that origin and insertion points for each adductor could be visualized and photographed. After the origin and insertion of each adductor was characterized, each muscle was extracted and weighed with a digital scale. To calculate the maximum theoretical muscle tension (MTMT) for the temporalis, masseter, and lateral-medial pterygoid complex, physiological cross-sectional areas (PCSA) were obtained for each muscle (following Spector et al. 1980; Powell et al. 1984; Bloodworth & Marshall 2007). The following equation was used to estimate PSCAs:

$$\mathbf{PCSA = (muscle\ mass)\ x\ (\cos\theta)\ /\ (FL)\ x\ (muscle\ density)}$$

where cos θ is mean fascicle angle relative to the muscle's line of action, FL is the mean fiber length (cm) and muscle density is the estimated density of muscle is assumed to be $1.056 g/cm^3$ (Mendez & Key, 1960; Murphy & Beardsley, 1974).

The MTMT was estimated following Spector et al. (1980), Powell et al. (1984), and Bloodworth & Marshall (2007):

$$\mathbf{MTMT = (PCSA)\ x\ (specific\ tension)}$$

where specific tension is the assumed to be $22.5 N/cm^2$ (Powell et al., 1984).

To calculate the amount of force produced by each adducting muscle, MTMT was multiplied by the cos vector angle (angle of muscle and fascicles relative to palatal plane). The sum of forces calculated for the temporalis, masseter, and pterygoid complex was then compared to the mean estimated bite force at the incisors of Alaskan sea otters.

Statistical Analysis

To test for normality, a MANOVA was run with side (left vs. right) as the covariate. This was performed for vector angle (angle to palatal plane), length, and mass separately for temporalis, masseter, and the pterygoid complex. The residuals were saved and a distribution test was run with residuals. A normal continuous fit and Goodness of Fit (Shapiro-Wilk W test) were performed. All data were normally distributed. A one-way analysis of variances (ANCOVAs) was used to test for differences in muscle morphometric data (angle, length, and mass) between left and right sides. Temporalis, masseter and pterygoid complex data were performed separately.

Results

Estimated Bite Force

When the effect of size was removed by regressing estimated bite forces against total skull length, there were significant differences observed at the incisors (F=10.9; p<0.01), canines (F=9.1; p<0.01), and carnassials (F=10.0; p<0.01) among all species (Figure 3-2). All 3 subspecies of sea otters had significantly different estimated bite forces compared to all other otter species investigated (F=6.3; p<0.05). California sea otters possessed the greatest estimated bite force at the incisors (F=29.7; p<0.01) and canines (F=20.1; p<0.01) relative to the other otter species investigated. Russian sea otters possessed the lowest bite force at the incisors (19.6; p<0.01), canines (F=17.4; p<0.01), and carnassials (F=18.6; p<0.01) compared to other otter species investigated (Figure 3-2). There was no significant difference between Alaskan sea otters and North American river otters at the canines (F=0.19; p=0.66) or carnassials (F=2.7; p=0.10). Overall, there were no significant differences in estimated bite force at the incisors and canines (ANOVA, F=3.13; p>0.05). Estimated bite force for all species was greater at the carnassials than the incisors and canines (ANOVA, F=425.9; p<0.01). Asian small-clawed otters had high estimated bite forces, right below the values of California sea otters and giant river otters. Asian small-clawed otters had slightly greater estimated bite forces above North American river otters, however not significant.

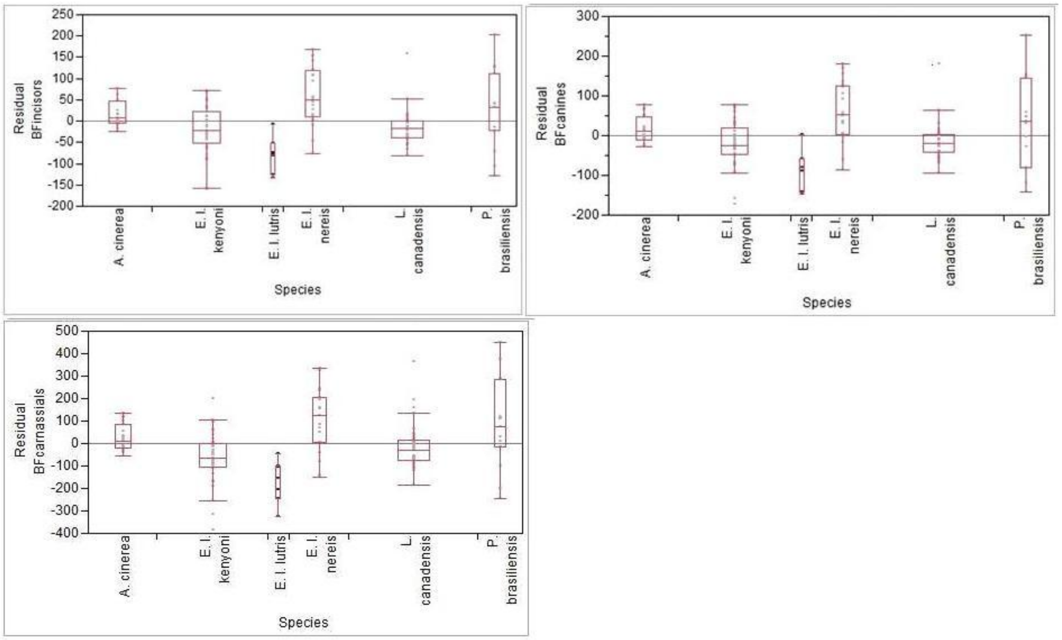

Figure 3-2. Residual bite forces for each species, with size effect removed.

There were differences in the relative bite forces at all three bite point locations among the 3 subspecies of sea otter (F=6.08; p<0.01). California sea otters possessed the greatest estimated bite forces at the incisors (F=37.9; p<0.01), canines (F=35.7; p<0.0001), and carnassials (F=34.7; p<0.01). Russian sea otters possessed the lowest estimated bite force at the incisors (21.7; p<0.01), canines (F=17.4; p<0.01), and carnassials (F=15.1; p<0.01).

Jaw Musculature of Sea Otters

<u>Gross Anatomy</u>

The temporalis (n=8), masseter (n=14), and pterygoid complex (n=17) muscles from 18 Alaskan sea otters were dissected and their morphological and physiological properties were characterized (Figure 3-3). The masseter originated on the zygomatic arch, where deep fibers overlapped with fibers of the temporalis. The masseter inserted on the masseteric fossa, ventrolateral surface of the mandibular ramus, and angular process. The pterygoid muscle complex originated within the pterygopalatine fossa and pterygoid hamulus and inserted on the medial surface and caudal margin of the mandibular ramus just ventral to the condyle. The temporalis muscle originated within the temporal fossa and inserted onto the coronoid process of the mandible. The temporalis and masseter muscles fused between the zygomatic arch and coronoid process. The temporalis was thinnest anteriorly and in the center, then thickened posteriorly near the jaw joint (posterior to zygomatic arch) (Table 3-1).

Figure 3-3. Left lateral view of (A) temporalis, (B) masseter (superficial layer), and (C) lateral-medial pterygoid complex in sea otters (*Enhydra lutris kenyoni*).

Physiological Cross-Sectional Area (PCSA) and Maximum Theoretical Muscle Tension (MTMT)

As expected, the temporalis muscle had the greatest mean width, length, and mass than the masseter and pterygoid complex muscles (Table 3-1). The vector angle (angle between the fiber line of action and the mandible) was greatest in the temporalis muscle, followed by the masseter and pterygoid complex muscles. The masseter muscle had the greatest thickness (center), followed by the pterygoid complex (center) and temporalis muscle (posterior). There were no significant differences in the vector angle (angle relative to palatal plane), length, or mass of the contralateral masseter (F=0.04, p=0.85; F=0.06, p=0.81; F=0.002, p=0.967), pterygoid complex (F=0.14, p=0.71;

F=1.02, p=0.32; F=0.79, p=0.38), or temporalis muscles (F=0.40, p=0.54; F=0.10, p=0.75; F=0.0001, p=0.9920). Therefore, PCSA and MTMT for each muscle were calculated for the left sides only.

Table 3-1. Mean widths (center), lengths, thickness (center), and angles of left and right adductor muscles in Alaskan sea otters (*Enhydra lutris kenyoni*).

	Left Width (cm)	**Right Width (cm)**	**Left Length (cm)**	**Right Length (cm)**	**Left Thickness (cm)**	**Right Thickness (cm)**	**Left Vector Angle**	**Right Vector Angle**
Masseter (n=14)	2.8±0.5	3.0±0.4	3.9±0.5	4.0±0.4	1.3±0.2	1.2±0.3	40.4±4.4	40.5±3.3
Pterygoid (n=17)	1.1±0.2	1.1±0.3	2.7±0.5	2.9±0.4	0.7±0.1	0.7±0.2	22.9±4.7	23.1±4.5
Temporalis (n=8)	6.3±0.8	6.1±0.6	9.1±1.1	9.3±0.7	0.5±0.3	0.5±0.4	131.4±7.2	133.6±0.7

The temporalis muscle had the greatest muscle mass followed by the masseter and lateral-medial pterygoid complex. The masseter muscle, which had a greater vector angle, mass, and fiber length than the lateral-medial pterygoid complex, produced a greater MTMT than the pterygoid complex (Table 3-2). The temporalis muscle possessed the greatest physiological cross sectional area (PCSA) and maximum theoretical muscle tension (MTMT) followed by the masseter muscle and the pterygoid complex (Table 3-2).

Table 3-2. Mean left angles, lengths (cm), mass (g), PCSA (cm^2), MTMT (N), and amount of force (N) produced for masseter, pterygoid, and temporalis of Alaskan sea otters (*Enhydra lutris kenyoni*). Fiber lengths were based on the mean fiber length from four individuals (N=4 per individual per muscle) and muscle density was 1.056 g/cm^2.

	Vector Angle	**Muscle Length (cm)**	**Fiber Length (cm)**	**Mass (g)**	**PCSA (cm^2)**	**MTMT (N)**	**Force produced (N)**
Masseter (n=14)	40.4±4.4	3.9±0.5	1.68	7.9±2.7	2.6±1.6	86.4±38.4	59.4±35.9
Pterygoid (n=17)	22.9±4.7	2.7±0.47	1.17	2.1±0.6	1.0±0.6	36.3±14.7	19.5±11.4
Temporalis (n=8)	131.4±7.2	9.1±1.1	2.30	53.6±24.1	13.2±8.7	496.2±233.3	313.0±192.6

The temporalis muscle is estimated to generate the greatest amount of force (313 N; Table 3-3) followed by the masseter muscle which is estimated to produced ~ 59 N and the lateral-medial pterygoid complex at ~ 20 N (Table 3-2). In Alaskan sea otters, the estimated bite force at the incisors (via dry skull method) was 376 N. The sum of the forces produces by each adducting muscle was 392 N (Table 3-2), which is a comparable value.

Discussion

Estimated Bite Force via the Dry Skull Method

Bite forces were positively correlated with increasing body size, which is common among vertebrates (Aguirre et al., 2002; Pfaller et al., 2011; Marshall et al., 2012). Estimated bite forces in all otter species investigated in this study changed in relation to length of the out-lever (bite point on the lower jaw) and was greatest at the carnassials, as anticipated. 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, or fulcrum (Greaves 1985; Greaves, 2000; Herring et al., 2001; Dumont & Herrel, 2003; Santana et al. 2010, Pfaller et al., 2011), and is maximum when located in the posterior 1/3 of the jaw (Greaves 1982; Greaves, 1985; Greaves, 2000). Carnassials are also located in the posterior 1/3 of the jaw, where maximum force is generated (Greaves, 1985, Greaves, 2000). Therefore as shown in other mammals, the maximum bite force of otters is demonstrated to be highest at the carnassials. The distance between the jaw joint and the carnassials is thought to be highly constrained within the Order Carnivora, thus indicating the bite force at this location is of importance in the evolution of carnivores (Greaves, 1982; Christiansen & Adolfssen, 2005; Christiansen & Wroe, 2007). This distance was not significantly different at the incisors or canines because the out-lever distance was not significantly different, and therefore did not produce different bite forces.

Significant differences were demonstrated in bite force across otter species. Giant river otters had a high estimated bite force (compared to other otter species). Giant river otters feed primarily on fish (Carter & Rosas, 1997; Rosas et al., 1999) and are mouth-oriented predators (Radinsky, 1968). In the previous chapter, data showed that giant river otters possessed the greatest skull length, palate length, and mandible length. Longer skulls correlate with longer mandibles and position the resulting bite point further from the jaw joint, producing jaws with greater velocity (Westneat et al., 2005). There is a biomechanical tradeoff between force and velocity in the musculo-skeletal system (Westneat, 1994, Herrel et al., 2002, Herrel et al., 2009). Therefore animals can specialize for either force or velocity, but not both. Small mechanical advantages at masseter and temporalis muscles and long cranial morphometrics (see Chapter II) suggest that this mouth-oriented predator is more dependent on fast closing jaws than increased bite force. Although giant river otters possessed low mechanical advantages at the masseter and temporalis muscles (higher at temporalis), they still possessed a slightly higher bite force than other otters. The greater bite force could be explained by a greater muscle mass of the temporalis muscle, rather than mechanical advantage. In lever mechanics, the force input (adductor muscles in this case) can be just as important as MA in generating the force output (bite force in this case). Therefore, it would appear that the jaw apparatus of giant river otters compensates for low MA (which provides a higher jaw tip velocity) by increasing the MTMT of the temporalis muscle. The fact that this is accomplished by larger temporalis muscle rather than the masseter muscles is biomechanically important, since it is known that functionally the temporalis muscle provides power to the anterior jaws (Hylander & Johnson, 1985; Ross & Hylander, 2000).

North American river otters had an intermediate estimated bite force. This species possessed the largest mechanical advantage of the temporalis muscle compared to other otter species investigated, but an intermediate mechanical advantage at the masseter muscle (see Chapter II). This would suggest that the temporalis muscle provides the greatest amount of force, at the anterior of the jaws, when closing the mouth and could be the result of an increased moment arm of the temporalis muscle. North American river otters primarily feed on fish, but also incorporate crustaceans (e.g., crayfish), amphibians, birds, and mollusks (Toweill, 1974). Similar to the giant river otter, North American river otters possess longer and narrower cranial morphology (see Chapter II), which likely places the resulting bite force points further from the jaw joint. This provides the advantage of jaws with a greater velocity. North American river otters also possessed the greatest coronoid length, upon which the temporalis muscle inserts and allows for an increase in leverage (e.g., increase in moment arm for temporalis) and jaw muscle area and volume (Freeman, 1979; Sacco & Van Valkenburgh, 2004; Figueirido et al., 2009). Therefore, the data suggests that the temporalis muscle provides the majority of the output force, at the anterior of the jaws, during the biting behavior. This is an advantageous trait for mouth-oriented predators.

Asian small-clawed otters possessed a high estimated bite force, similar to giant river otters. Asian small-clawed otters, unlike giant river otters and North American river otters, are hand-oriented predators (Sivasothi & Nor, 1994; Jacques et al., 2009) and are predicted to be more dependent on bite force in consuming prey. Asian small-clawed otters primarily feed on crabs (*P. smithianus*) and mollusks, but also incorporate giant scorpions (*Heterometrus longimanus*), millipedes (*Julidea* sp.), and fish into their diet (Sivasothi & Nor, 1994). Although the mechanical advantage of the masseter muscle as the smallest compared to all species investigated, this species possessed the second largest mechanical advantage at the temporalis muscle (see Chapter II), which would explain the greater estimated bite force. The moment arm of the temporalis was large, thus increasing the amount of force generated. The large zygomatic fossa length (see Chapter II) also provides a large space for the temporalis to attach to the coronoid process. Therefore, as shown in the giant river otters, Asian small-clawed otters rely heavily on the temporalis for jaw adducting forces.

Sea otters had a high estimated bite force. Among the sea otter subspecies, California sea otters possessed the greatest bite at each bite location, followed by Alaskan and Russian sea otters, which had the lowest estimated bite force at each bite location. Sea otters had the greatest masseteric mechanical advantage than all other otter species investigated when size effect was removed (see Chapter II). This suggests that the masseter muscle plays a greater role in bite performance and durophagy among the jaw adductor muscles, and compared to all other otter species. Sea otters are hand-oriented, durophagous predators that almost exclusively prey on benthic invertebrates, with the exception of Alaskan sea otters around the Aleutian Islands and Russian sea otters which prey on epibenthic fish (Riedman & Estes, 1988). Compared to other otter species investigated, sea otters had the greatest interorbital distance, rostral width at the molars, braincase width, palate width, and zygomatic arch length (see Chapter II). The zygomatic arch is an origination point for the masseter muscle. An enlarged zygomatic arch provides increased surface area for attachment of this major adducting muscle. Sea otters not only possessed the greatest mandibular ramus height, providing greater surface area for this jaw adducting muscle to attach, but also the greatest depth, which increases the physiological cross-sectional area of the masseter and the tension that this muscle can produce.

Estimated Maximum Theoretical Muscle Tension in Sea Otter Adductors

Not surpringly, the temporalis muscle in sea otters had a greater muscle surface area at its origin (temporal fossa) than the masseter muscle (zygomatic arch) or pterygoid complex (pterygo-palatine fossa), which also increases the muscle force generated in conjunction with an enlarged muscle mass (Herring & Herring, 1974). In sea otters, the temporalis muscle had the greatest PCSA of the three adductor muscle groups, thus it exhibited a greater maximum theoretical muscle tension (MTMT) than the masseter or pterygoids. The estimated bite force (via dry skull method) of Alaskan sea otters was 376.1±68.9 N. The temporalis is estimated to provide 313±192.6 N of that force. Fiber length in the temporalis muscle was greater than masseter. This is not too surprising since the masseter has some pennation to its architecture and the temporalis has no pennation. Shorter fiber lengths are associated with pennation and this organization increased MTMT (Askew & Marsh, 1998; Fukunaga et al., 1997). The longer fiber length in the temporalis muscle should increase contraction velocities, at the expense of force generation (Gans & de Vree, 1987; Taylor & Vinyard, 2009). This means that although the temporalis muscle can produce more force overall, the masseter can produce more force per unit area than the temporalis muscle.

The only significant differences demonstrated between sea otters and North American river otters (e.g., mouth-oriented predator) are that the superficial masseter muscle fascicles are at a greater angle relative to the palatal plane and the distinction between the superficial and deep masseter muscle is not as obvious in sea otters (Riley, 1985). This is likely an important feature in sea otters. While the alignment of the muscle fascicles of the superficial and deep masseter muscle may slightly limit variation of motion, it also functions to increase MTMT, thus increasing bite force at the carnassials where they are needed. The crushing behavior of sea otters is likely somewhat stereotypical, and other masticatory muscles likely allow for enough variation in the range of movement to compensate. Therefore the alignment of these two parts of the masseter should be considered an adaptation for durophagy. The masseter is estimated to provide 59.4±35.9 N to the overall estimated bite force (376.1±68.9 N). The masseter had a smaller mass than the temporalis, but had shorter fiber lengths and some degree of pennation, which provides a large PCSA relative to its size. The mechanical advantage of the masseter in sea otters was large compared to other otters investigated in this study (see Chapter II). This provides biomechanical evidence that the masseter plays a major role in increasing bite performance of this durophagous predator. In addition to an increase in the origin and insertion areas of the digastrics (Riley, 1985), sea otters show a more rostrally positioned masseter, similar to the North American river otters (Riley, 1985) and this may correlate to the ability to maintain a wide gape at a high bite force (Scapino, 1976). The pterygoid complex possessed the smallest PCSA and MTMT and is predicted to provide 19.5±11.4 N of the overall estimated bite force

In conclusion, bite force was greatest at the carnassials and there was no significant difference between incisors and canines. Although giant river otters possessed the smallest mechanical advantage at the temporalis and masseter muscles, they still possessed the greatest estimated bite for all otter species investigated. The greater estimated bite force could be explained by a greater body size and muscle mass of the temporalis muscle, rather than mechanical advantage. North American river otters had the largest mechanical advantage of the temporalis muscle and an intermediate bite force compared to other otters. As with giant river otters, North American river otters possessed longer skulls and mandibles, which would provide the advantage of faster moving jaws (e.g., greater velocity). Asian small-clawed otters possessed a high estimated bite force similar to giant river otters. Although the mechanical advantage of the masseter muscle was small, this species possessed the second largest mechanical advantage at the temporalis. This could explain the high estimated bite force. Overall, sea otters had a high estimated bite force. California sea otters possessed the greatest bite force at all bite locations, followed by Alaskan sea otters and then Russian sea otters. Sea otters possessed the greatest mechanical advantage at the masseter muscle compared to other otters, which support the premise that the masseter plays an important role in durophagy.

CHAPTER IV

FEEDING KINEMATICS

Introduction

The skull and feeding apparatus of vertebrates underwent many morphological and functional changes during the transition from water-to-land (Reilly & Lauder, 1990; Summers et al., 1998; Ahlberg & Clark, 2006). Feeding mechanisms differ between aquatic and terrestrial environments (Shaffer & Lauder, 1988; Reilly & Lauder, 1990; Liem, 1990; Summers et al., 1998; Lemell et al., 2002). Among aquatic vertebrates, such as bony and cartilaginous fishes, and secondarily aquatic tetrapods such as marine mammals, prey capture is achieved by biting (pierce biting), ram feeding, suction (inertial suction), or filtration (Schwenk, 2000a; Motta et al., 2002; Mehta & Wainwright, 2007; Wilga et al., 2007; Marshall et al., 2008; Kane & Marshall, 2009), all of which are not mutually exclusive. Although many chondrichthyans use feeding modes that incorporate biting, the primary feeding mode of most aquatic vertebrates (with notable exceptions) is suction (Lauder, 1985; Summers et al., 1998; Grubich, 2001) and has been a major focus of study in aquatic vertebrates (e.g., Muller et al., 1982; Muller & Osse, 1984; Alfaro & Westneat, 1999; Alfaro et al., 2001; Alfaro & Herrel, 2001; Carroll et al., 2004). There are two types of suction. Inertial suction feeding produces enough negative pressure within the intraoral cavity draw both water and prey into the mouth (Lauder, 1985; Norton & Brainerd, 1993; Summers et al., 1998). During inertial suction, most aquatic vertebrates depress the floor of the buccal cavity;

this often is accomplished by depression of the hyoid. The rapid increase in intraoral volume results in a drop in intraoral pressure thus generating suction (Lauder, 1980; Bemis & Lauder, 1986; Lauder & Reilly, 1988; Werth, 1989; Motta et al., 1997; Summers et al., 1998; Kane & Marshall, 2009). If an animal does not generate enough suction, the prey may be pushed away from the mouth from the bow wave as the predator approaches (Summers et al., 1998). Therefore, suction may only be sufficient enough to counter the motion of the predator as it approaches prey and allow it to grasp the prey in its jaws (Summers et al., 1998). This second type of suction is termed compensatory suction, and is often associated with ram feeding (Summers et al., 1998). Biting is a major prey acquisition mechanism in many groups of vertebrates, including fishes (e.g., sharks, rays, gars, cichlids) and marine mammals (Alfaro & Westneat, 1999; Kane & Marshall, 2009). Biting in both fishes and marine mammals can be defined as forceful contact of the jaws onto prey and can occur after fast approach towards prey (Alfaro & Herrel, 2001; Alfaro et al., 2001; Motta et al., 2002). Herbivory, carnivory, and molluscivory in fishes all use forceful biting with the oral jaws (Alfaro & Westneat, 1999). Since air is less dense than water, suction is not usually possible on land (Liem, 1990; Marrero & Winemiller, 1993) and biting is the primary feeding mode (Markey & Marshall, 2007).

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). 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, which 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). However due to density differences between water and air, terrestrial vertebrates rely heavily on tongue movements to manipulate prey within the oral cavity (Reilly & Lauder, 1990). The jaw musculature and the hyoid apparatus must be coordinated for prey to be transported and manipulated in the jaws of terrestrial vertebrates (Herring, 1985; Reilly & Lauder, 1990; Liem, 1990; Alfaro & Herrel, 2001; Motta et al., 2002). In aquatic vertebrates such as fishes, the versatile feeding apparatus (i.e., cone shaped buccal cavity) allows for extensive dietary switching and reduced resource partitioning depending on resources (Liem, 1990; Case et al., 2008). However, in terrestrial vertebrates, the feeding apparatus (i.e., jaws) is operated by a relatively constant muscle output and results in an increase in resource partitioning and decrease in the degree of prey switching (Liem, 1990). Therefore, the terrestrial feeding apparatus is often more specifically matched to its biological role (Liem, 1990). Sea otters represent an interest situation in the evolution of mammalian feeding. Although sea otters are marine mammals, they feed at the surface and should exhibit a more terrestrial feeding behavior.

Performance studies provide a link between morphology and ecology; this is the basis of ecological morphology (Wainwright, 1994). Ecomorphology, the study of covariation of morphology of the organism and its environment, can be used to provide information about the feeding mode and performance (e.g., prey capture) (Bock, 1994; Schwenk, 2000a). Performance measures associated with the vertebrate feeding apparatus can provide novel insights into the animal’s trophic ecology and evolution

(Anderson et al., 2008). Due to the lack of kinematic and physiological data for aquatic mammals, cranial morphology can provide valuable evidence regarding of the primary feeding mode of aquatic mammals as shown in Chapters II and III. Cranial morphology can be used to provide evidence of the primary feeding mode, because an individual's phenotype determines the limits of its performance (e.g., prey capture and food processing) (Wainwright, 1994). Although there is variation between form and function, the vertebrate feeding system represents modifications from the same basic model (Schwenk, 2000a). Biters are hypothesized to maximize force production rather than velocity, which also influences head shape (Barel, 1983; Westneat, 1994; Alfaro et al., 2001). Biters also possess robust oral jaws and adductor muscles (Bellwood & Choat, 1990; Turingan & Wainwright, 1993). However, odontocetes that use biting or ram feeding as the primary feeding mode possess long and narrow skulls (Bloodworth & Marshall, 2005; Kane & Marshall, 2009) as an adaptation for piscivory. In contrast to odontocete ram feeders, the skulls of marine mammals that use suction as a primary feeding mode are short, blunt and with fewer teeth (Werth, 2006a; Werth, 2006b; Kane & Marshall, 2009). Much of this dichotomy among odontocetes can be explained by the need for long fast jaws for piscivory, and the occlusion of lateral gape that a blunt and wide jaw and skull can provide for suction feeding (Bloodworth and Marshall, 2005; Marshall et al, 2006; Kane and Marshall, 2009).

There are several studies on the feeding apparatus in both marine and terrestrial vertebrates, such as ram and suction feeding in cetaceans (Bloodworth & Marshall, 2005; Werth, 2006a; Werth, 2006b; Marshall et al., 2008; Kane & Marshall, 2009), lingual feeding in lizards (Schwenk & Throckmorton, 1989; Meyers et al., 2002), and mastication in terrestrial mammals (e.g., Herring, 1985; Herring, 1993). However, there are currently no experimental studies on feeding performance of sea otters. Performance 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 conveniently feed at the surface, making them an ideal model system to study feeding performance in marine mammals.

Objectives and Hypotheses

The main objective of this chapter was to characterize the kinematic profile of feeding events and biting in sea otters. Kinematic profiles were measured in both wild and captive sea otters. Kinematics of captive sea otters provided the opportunity to ground-truth our work with sea otters in the wild and to demonstrate that kinematic profiles in wild populations could be accurately measured. It was hypothesized that otters forcefully bite and crush hard benthic prey at large gapes, and that biting kinematics would be congruent with the biting kinematics reported for other marine mammals, thus suggesting that the biting feeding mode is a conserved behavior.

Material and Methods

Feeding Kinematics of Sea Otters

Footage of feeding events of wild and captive sea otters were collected for frame-by-frame motion analysis and characterization of a kinematic profile. Feeding events of wild sea otters were recorded in Simpson Bay, AK (ca. 60.4° N, 145.5° W), located in northeastern Prince William Sound, Alaska, in June 2009 and July 2010. Footage of feeding events from captive sea otters were collected during controlled feeding trials at the Audubon Aquarium of the Americas in New Orleans, LA. During the time of the feeding trials, captive subject 1 (male) weighed 28.2 kg, and was 128 cm in length. Captive subject 2 (female) weighed 23.8 kg, and measured 120.2 cm in length.

Feeding events of wild Alaskan sea otters were documented by videotaping each event using a Sony TRV950 video camera (Sony Corp., New York, NY, USA) at 60 Hz, from a small 6 meter aluminum skiff or 5 m fiberglass skiff. During a feeding event, the distance between the observer and sea otter was recorded using a laser range finder with inclinometer (LaserAce®300, Measurement Devices Ltd.). Footage of wild otter feeding was later calibrated by recording additional footage of a 20 cm x 20 cm calibration square of at each observed distance of feeding sea otters in the field. Footage of the calibration square at each specific distance, for each feeding event, obtained in the wild was used for projective scaling calibration within the Peak Motus motion analysis system (v. 9; Vicon, Denver, CO, USA). Kinematic profiles of sea otters were measured when feeding on clams, mussels, shrimp, sea stars, sea urchins, and crabs.

Feeding events of the captive sea otters were filmed during feeding sessions that involved a single presentation of each food. Each presentation of a food item defined a feeding trial. Feeding trials (n=10 for subject 1 and n=18 for subject 2) were also recorded using a Sony TRV950 video camera at 60 Hz. Feeding trials were recorded in a lateral or frontal view. A 20 cm x 20 cm calibration square was placed in the same plane as the individual immediately following the feeding trial for projective scaling and calibration of the measurements. Kinematic profiles of captive sea otters were measured from feeding trials involving shrimp, crab legs, and ice treats with clam and shrimp, which elicited large gapes and strong biting behavior to crush the ice.

Video clips were imported into Peak Motus and cropped to one frame prior to jaw opening and one frame following jaw closing. That is, each feeding trials consisted of single gape cycle. To characterize the movement of the jaws, four lateral and five frontal homologous anatomical landmarks (Figure 4-1) were digitized throughout the entire gape cycle for each feeding trial across all subjects, both wild and captive. This allowed for nine lateral and five frontal kinematic variables (Table 4-1) to be calculated. Kinematic variables calculated included: (1) maximum gape, (2) time to maximum gape, (3) maximum gape angle, (4) time to maximum gape 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, (9) total gape cycle duration (following Marshall et al. 2008). All variables were measured in the frontal view, with the exception of maximum gape angle and time to maximum gape angle (Table 4-1). All variables measured were filtered using a cubic spline filter.

Figure 4-1. Anatomical landmarks for kinematic analysis. Lateral landmarks include the nose, tip of upper jaw, tip of lower jaw, 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. Images courtesy of Dr. Randy Davis.

Table 4-1. Kinematic variables for captive and wild performance kinematics. *Frontal kinematic variables.

Kinematic Variable	**Abbreviation**	**Description**
maximum gape	GAPE	distance from the upper jaw tip to the lower jaw tip
time to maximum gape	tGAPE	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 the mandibular tip
time to maximum gape angle	tGANG	time from lower jaw opening to maximum gape angle
maximum gape angle opening velocity	GAOV (GLOV*)	greatest angular (or linear for frontal) rate of lower jaw opening
time to maximum gape angle opening velocity	tGOAV (tGLOV*)	time elapsed from gape opening to maximum gape opening
maximum gape angle closing velocity	GACV (GLCV*)	greatest angular velocity (or linear velocity for frontal) during lower jaw closure
Time to maximum gape angle closing velocity	tGACV (tGLCV*)	time from when the lower jaw began to close until the maximum gape angle (or linear for frontal) velocity
total duration	tDUR*	elapsed time from the onset of gape opening to the last frame of gape closing

Statistical Analyses

Normality of data was tested using a Shipiro-Wilks' test. Kinematic variables were $\log_{10}$ transformed and used in multivariate analysis of variances (MANOVAs). A MANOVA was used to determine if kinematic variables differed among individuals using kinematic variables as the dependent factors and individuals as the independent factors. A MANOVA was used to determine if kinematic variables differed across prey types (captive: shrimp, crab legs, and ice treats with clam and shrimp; wild: clams, mussels, shrimp, sea stars, sea urchins, and crabs), using kinematic variables as the dependent factors and prey types as the independent factors. Captive and wild sea otters were tested separately. 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 vs. wild as the independent factors. All statistical tests were performed using JMP 9.0 (SAS Institute, Cary, NC, USA).

Results

Biting was the prominent feeding mode in both wild and captive sea otters. Biting was characterized by the large gape and presentation of teeth. Once sea otters had acquired prey (whether brought up to the surface on their own or handed to them by a trainer , they would either place the prey in the anterior of the jaws, or as far posterior into the mouth to place the food over the molars. Position of the prey in the jaws was dependent on the prey type (hard vs. soft) and size. Large, hard prey (e.g., clams or ice treats) were placed in the posterior of the jaws, which required an increased gape and a bite force great enough to crack the food item open (Figure 4-2). Once prey was cracked open by the molars (i.e., carnassials), flesh was removed with incisors or canines (see Chapter VI). Smaller, softer prey (e.g., shrimp, fat innkeeper worms) were positioned more anterior of the jaws where incisors or canines were used in conjunction with hands to tear flesh (Figure 4-3). Wild sea otters were observed feeding on 15 different prey types (160 feeding events).

Figure 4-2. Wild sea otter *(Enhydra lutris kenyoni*) placing a butter clam posteriorly in the mouth over the carnassials. (Simpson Bay, Alaska; Image courtesy of Dr. Randy Davis).

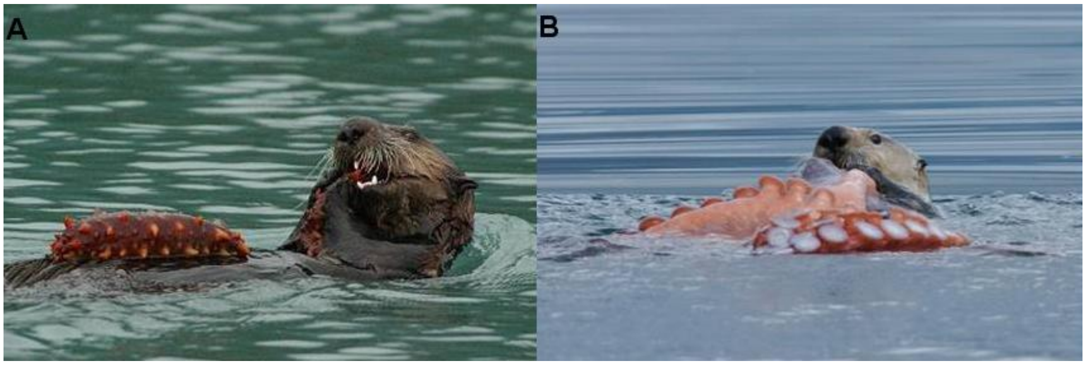

Figure 4-3. Wild sea otters (*Enhydra lutris kenyoni*) feeding on (A) sea cucumber and (B) giant Pacific octopus in Simpson Bay, Alaska. Both are soft bodied prey that did not require high consumption times or handling time at the surface. Images courtesy of Dr. Randy Davis (A) and Ryan Wolt (B).

Feeding kinematics among wild sea otters was conserved and crushing appeared stereotypical, as predicted by the merging of the superficial and deep masseter muscles (see Chapter III). Lateral feeding kinematic variables 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), nor did the frontal feeding kinematic variables among these subjects differ significantly (F=2.11; p>0.05, MANOVA) or among prey type (clams, mussels, sea stars, shrimp) (F=0.64, p>0.05, MANOVA). Feeding kinematic variables in captive sea otters were also conserved. Lateral kinematic variables did not differ significantly between the two subjects (F= 5.81; p>0.05, MANOVA) or among food items (ice treats, crab legs, shrimp) (F=2.67; p>0.05, MANOVA), nor did frontal feeding kinematics between these subjects differ significantly (F=1.82; p>0.05, MANOVA) or prey (ice treats, crab legs, shrimp) (F=1.71; p>0.05, MANOVA). Furthermore, a comparison of all kinematics of all wild vs. captive prey feeding on various types of prey and food items 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 slower maximum opening gape velocity (GLOV) (Table 4-2), a slower maximum gape opening velocity (tGOLV), and a slower maximum closing gape velocity (GLCV) in captive sea otters. These differences were not considered surprising since captive animals do not have a need to consume as much as their free-ranging counterparts.

The feeding kinematic profile for both wild and captive sea otters is as follows: the mean feeding cycle duration (tDUR) in wild sea otters was 0.29±0.07 s and in captive sea otters was 0.33±0.06 s respectively (Table 4-2). The jaws reached maximum gape angle opening velocity (GAOV) and maximum gape linear opening velocity (GLOV) rapidly in wild (519.2±226.7 deg. s^{-1}) and captive (416.9±186.9 deg. s^{-1}) sea otters, respectively (Table 4-2). 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 4-2; Figure 4-4). The jaws then closed slowly (GACV or GLCV) (wild, 387.6±197.6 s; captive, 267.2±106.0 cm s^{-1}; Table 4-2). The results demonstrate that if video footage is carefully collected, feeding kinematics of sea otters can be accurately measured in the wild, which opens up new research opportunities.

Table 4-2. Summary of mean kinematic variables for captive and wild sea otters.

	Captive sea otters	**Wild sea otters**
Lateral	(n=2)	(n=31)
GAOV (deg. s^{-1})	416.9±186.9	519.2±226.7
tGAOV (s)	0.10±0.04	0.06±0.03
GAPE (cm)	5.8±1.3	5.4±1.5
tGAPE(s)	0.20±0.05	0.15±0.056
GANG (deg)	61.4±21.4	66.50±16.30
tGANG(s)	0.17±0.04	0.15±0.06
GACV (cm s^{-1})	267.2±106.0	387.6±197.6
tGACV (s)	0.06±0.010	0.07±0.05
tDUR (s)	0.33±0.06	0.29±0.07
Frontal	(n=2)	(n=21)
GLOV (deg. s^{-1})	35.6±11.3	52.4±25.9
tGLOV (s)	0.07±0.03	0.06±0.02
GLCV (cm s^{-1})	19.4±12.7	47.1±23.4
tGLCV (s)	0.05±0.02	0.08±0.05
tDUR (s)	0.32±0.11	0.28±0.09

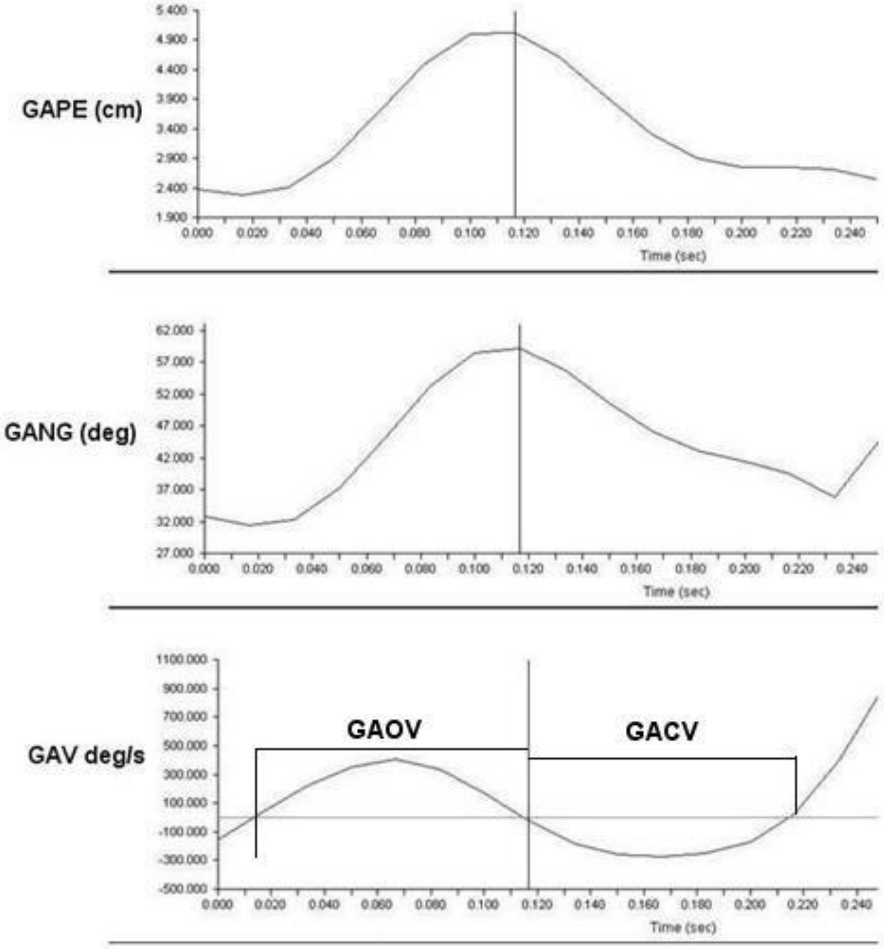

Figure 4-4. Kinematic profile (lateral perspective) from a wild sea otter (*Enhydra lutris kenyoni*). *GAPE*, maximum gape; *GANG*, maximum gape angle; *GAV*, gape angle velocity (opening and closing).

Discussion

The primary feeding mode of sea otters is biting, which was characterized by large gape, large gape angle, and fast gape angle velocity. This is similar to biting kinematic profiles observed in other marine mammals (Bloodworth & Marshall, 2005; Kane and Marshall, 2009; Marshall et al., 2008). Sea otters are marine mammals that forage on the seafloor but consume prey at the surface (Estes et al., 1982; Estes et al., 2003b; Bodkin et al., 2004; Tinker et al., 2008). Our data show that sea otters are consistent with a typical mammalian feeding kinematic profile of biters. The basic terrestrial feeding cycle begins with slow opening of the jaws with movement of the hyolingual apparatus to fit the prey, followed by fast opening of the jaw with the skull and mandible moving in opposite directions (Hiiemae & Crompton, 1985; Liem, 1990). The final stage involves a slow closing of the jaws in which prey is chewed or crushed. The jaw closing velocity is slower than jaw opening because prey was already positioned between the upper and lower jaws and therefore had a shorter distance to close. In both wild and captive sea otters, the jaws opened rapidly, and once maximum gape and gape angles were reached, the jaws slowly closed and prey was chewed (soft prey) or crushed (hard prey). Both captive and wild sea otters positioned the prey in precise locations of the jaw depending on the prey type (see Chapter VI). When consuming soft prey, such as Pacific giant octopus (*Enteroctopus dofleini*), sea cucumbers, or fat innkeeper worms (*Urechis caupo*), flesh was removed with the incisors or canines and the forelimbs. Hard prey (clams, crabs, urchins) were positioned further back in the jaws where prey was crushed with the blunt molars, which increased maximum gape and gape angle. In fact, the widest gape angle observed was 82.8 degrees. This is an extremely wide gape angle among mammals. The gape angle of most carnivorans range from ~55-65 deg (Christiansen & Adolfssen, 2005). Forceful biting is occurring at this gape angle since hard prey items were observed to be crushed. This value is larger than several other mammal that are considered to bite a large gape angles such as Eqyptian fruit bats (*Rousettus aegyptiacus,* 47.1 deg), Pallas' long tongued bat (*Glossophaga soricina*, 46.5 degrees) (Dumont and Herrel, 2003) and dingos (*Canis lupus dingo*, 35 degrees) (Bourke et al., 2008). The maximum gape of sea otters approximates that of the domestic cats (*Felis catus*), which have gapes up to 80 deg (Türker & Mackenna, 1978), and approaches the gape of clouded leopards (*Neofelis nebulosa*) which are reported to have gapes up to 90 degrees (Christiansen & Adolfssen, 2005). As a reference the maximum gape reported for any mammal when biting is the extinct sabretooth cat (*Smilodon sp.*) at a remarkable 95 degrees due to its divergent dentition (Emerson & Radinsky, 1980; Christiansen, 2006; Christiansen & Adolfssen, 2007; Christiansen, 2011). Interestingly, muscle tension in domestic cat appears to be greatest at maximum gape (Mackenna & Türker, 1978); the same may be true of sea otters. Once shells (e.g., clams or crabs) were crushed by sea otters the flesh was removed with incisors or canines (see Chapter VI). Wide gape is not always associated with biting. Balaenopterids are lunge feeders that use a wide gape angle (80 deg) to draw in a greater volume of water and prey (Goldbogen et al., 2011).

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. It is predicted that these differences are due to the fact that wild sea otters must consume 30% of their body weight per day due to a high metabolic rate (Riedman & Estes, 1990; Lairde & Jameson, 2006) and are exposed to intraspecific competition (Estes et al., 2003b), whereas captive sea otters face none of these challenges. 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; Ralls & Siniff, 1990; Kvitek et al., 1993; Estes & Duggins, 1995; Laidre & Jameson, 2006). Therefore, wild sea otters must spend more time foraging to obtain the same amount of energy (Ralls & Siniff, 1990). 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 minor differences in frontal profiles. Therefore, feeding kinematics of sea otters can still be accurately measured in the wild.

Sea otters are durophagous (Taylor, 2000) marine mammals that feed on a variety of hard, benthic invertebrates including mollusks, crustaceans, and echinoderms (Calkins, 1978; Garshelis, 1983; Doroff & Bodkin, 1994; Garshelis et al., 1986; Wolt et al., 2012; also see Chapter VI) and the underlying feeding morphology and biomechanics supports this crushing capability (Chapter II). The ability to perform behaviors is limited by the phenotype (Wainwright, 1994). As reported in Chapter II, skull of sea otter diverges from other otter species most likely as consequence of extreme mandibular bluntness. Sea otters possess a mandibular bluntness index greater than 1.0, demonstrating that the mandible is wider than long (Chapter II). This is considered to be the extreme among species for which bluntness data are available. Significant differences in morphometrics of sea otters (i.e., a large interorbital distance, rostral width at the molars, braincase width, palate width, skull width, and zygomatic length) are likely a functional consequence of this extreme blunt mandible. Further evidence of functional consequences of a blunt mandible is the significantly large masseteric mechanical advantage (see Chapter II) and a large bite force capability for its small size (see Chapter III). With their short, robust skull and mandible, increased masseteric MA, increased surface area of the carnassials, and increased bite force capability at extreme gape angles sea otters are well designed for durophagy. The kinematic data from live animals reinforce and support the functional hypotheses generated by traditional and geometric morphometrics, as well as biomechanical measures. The combined dataset (i.e., morphological, shape, biomechanical, and kinematic) are consistent with other durophagous carnivores. For example, in durophagous bats, the skulls are taller, with wider palates and lower coronoid and condyles (designed for robust muscle attachment points) than bats feeding on softer fruits (Dumont, 2003). Spotted hyenas specializing on bone cracking possess robust dentition, larger jaw adductor muscles, larger sagittal crest, vaulted forehead, and wider zygomatic breadths (skull width) than hyenas not specializing on bone cracking (Tanner et al., 2010). All durophagous species exhibit short, blunt skull shapes, with large jaw adducting muscles, increase MA, and dental adaptations for crushing.

In conclusion, sea otters are durophagous marine mammals that consume hard, benthic prey. However, when feeding on land, vertebrates display little to no hyoid depression (Summers et al., 1998; Marshall et al., 2008) an increase in gape, gape angle, and lack of lateral gape occlusion. Feeding sea otters also employed extremely large gapes, gape angles, and did not occlude lateral gape consistent with a biting feeding mode. Shorter, blunter skulls and mandibles in sea otters, along with increased mechanical advantages at the masseter (see Chapter II), and increased bite force capability (see Chapter III) also correlate to the biting mode of sea otters.

CHAPTER V

BREAKING FORCE OF BIVALVES AND OVERALL HANDLING TIME OF PREY IN ALASKAN SEA OTTERS (*ENHYDRA LUTRIS KENYONI*) IN SIMPSON BAY

Introduction

Foraging behaviors of sea otters greatly impact the benthic community in both rocky and soft-sediment environments and are of particular interest to ecologists and conservationists alike (Ostfeld, 1982; Kvitek et al., 1988; Estes & Palmisano, 1974; Ebeling & Laur, 1988; Estes and Harrold, 1988; Estes & Duggins, 1995; Laidre & Jameson, 2006; Lee et al., 2009). Sea otters are apex predators in coastal communities (Estes and Duggins, 1995). Sea otters increase metabolic rate as a thermoregulatory adaptation and must consume up to 30% of their body weight per day (Riedman & Estes, 1990; Lairde & Jameson, 2006). This need is met with increased foraging activity, which has drastic impacts to the benthic community (Laidre & Jameson, 2006). For example, in areas of reoccupation, sea otters have been shown to reduce abundance of large sea urchins, thus reducing grazing behaviors of urchins and keeping the kelp communities in check (Estes et al., 1978; Duggins, 1980; Ebeling and Laur, 1988; Estes & Duggins, 1995). In the absence of sea otters, sea urchin population increases, causing a drastic decline in macroalgae (Estes & Duggins, 1995) and substantially change the habitat and ecosystem. Therefore, sea otters and are considered keystone predators.

Foraging patterns of sea otters are consistent with optimal foraging theory (Stephen & Krebs, 1986; Kvitek et al., 1993; Estes et al., 2003; Tinker et al., 2008). Sea otters in soft sediment environments optimize their foraging efficiency by feeding in patches containing smaller (but more abundant), less calorically rich prey that are buried at shallower depths (Kvitek et al., 1988; Kvitek et al., 1993). In soft-sediment habitat, sea otters will also forage over a greater geographical area than otters foraging in rocky substrate (Laidre & Jameson, 2006). When sea otters have the option, they will primarily choose prey with the highest caloric value (e.g., crabs, abalones, and sea urchins), then broaden their diet to less desirable prey (e.g., mussels, sea stars) when preferred prey are limited (Estes et al., 1978; Duggins, 1980; Ostfeld, 1982; Estes et al., 1981; Estes et al., 2003b; Laidre & Jameson, 2006). Sea otter males are also territorial and demonstrate optimal foraging patterns (Kvitek et al., 1988). Males set up territories in prey-rich areas and select the largest, most caloric prey first. Once desirable prey is depleted, they switch to less preferred prey within their territory (Ostfeld, 1982; Estes et al., 1982; Garshelis et al., 1986; Kvitek & Oliver, 1988; Kvitek et al., 1988; Estes et al., 2003). Sea otters are size selective predators and therefore generally choose prey (e.g., clams) within specific size classes (Kvitek et al., 1992; Tinker et al., 2008). For example, sea otters often select smaller, more abundant prey buried at shallower depths (Estes et al., 1978; Simenstad et al., 1978; Ostfeld, 1982; Kvitek & Oliver, 1988; VanBlaricom, 1988; Kvitek et al., 1992; Estes & Duggins, 1995; Dean et al., 2002; Tinker et al., 2008). In California it has been shown that sea otters forage for clams between 60 and 100 mm in length more frequently (Tinker et al., 2008). However, sea otters around the Kodiak archipelago were documented to consume bivalves greater than 30 mm (Kvitek et al., 1992). Larger prey may be more difficult to obtain because of the depth at which they are buried (30-50 cm), which increases dive time and excavation effort (e.g., foraging time) (Kvitek et al., 1992).

Biomechanical design of the shell of bivalves influences the cost of prey handling and therefore selection of prey (Blundon & Kennedy, 1982). The ability of prey to resist applied forces depends on the size, shape (Biewener, 1992) and for bivalves the material properties. In general, larger objects should resist greater forces and undergo greater deformations before breaking (Biewener, 1992). Larger clams may therefore not only increase excavation time for sea otters underwater, but may also require a greater breaking force to consume at the surface. Smaller, more easily accessible clams may require less force to break and thus decrease the otter's consumption time at the surface. However, if the object cannot absorb enough strain energy, regardless of a large size, shape, thickness, and material properties, it can still fail and fracture. Therefore, size selectivity of bivalves by sea otters are likely correlated with the force required to break open the prey and the time to crush prey. These traits in turn affect the consumption time and overall handling time of sea otters. By decreasing overall handling time (which is defined as dive and consumption time in this study), sea otters can consume more prey, which is required by the high metabolic rates (Riedman & Estes, 1990; Lairde & Jameson, 2006).

To understand the role of prey morphology on predator trophic ecology, the relationship between changing morphology and resultant diet should be investigated

(Hernandez & Motta, 1997). Morphological constraints (predator or prey) on feeding performance are the first determinants of ecological niche (Hernandez & Motta, 1997; Mara et al., 2010). Varying extrinsic ecological factors, such as competition and predation, can exclude an organism from its potential niche; however, morphological constraints limit the organism's prey choice (Wainwright, 1988; Hernandez & Motta, 1997). Increased bite capability allows organisms to exploit prey that is often unavailable to other species (Hernandez & Motta, 1997; Berumen & Pratchett, 2008; Marshall et al., 2012). While increased bite force capability allows for access to a wider range of prey, it is also associated with dietary specialization (Mara et al., 2010). Estimated bite force can be used to predict prey types consumed and determine diet, however few studies correlate bite force to characteristics (e.g., breaking force and size) of prey (Herrel et al., 2001; Aguirre et al.., 2003; Mara et al., 2010; Marshall et al., 2012). Shell strength, in the context of sea otter foraging ecology, can be measured by measuring the maximum force required to break the shell (e.g., Vasconcelos et al., 2011). Several studies have investigated the relationship between prey preference (size, breaking force) and durophagous predators (West et al., 1991; LaBarbera & Merz, 1992; Yamada & Boulding, 1998; Cotton et al., 2004; Korff & Wainwright, 2004; Fisher et al., 2011; Marshall et al., 2012). For example, predation by cownose rays (*Rhinoptera bonasus*) on shellfish is limited by shell size, gape and bite force capability of rays (Fisher et al., 2011). Loggerhead sea turtles (*Caretta caretta*) transition from an oceanic habitat to a neritic habitat and from soft prey to harder prey only when their feeding apparatus can generate forces great enough of break the smallest size classes of their hard prey (Marshall et al., 2012). Over time, increasing bite performance of loggerhead sea turtles decreases the amount of competition as bite capability increases as larger and harder prey are consumed. Sea otters are durophagous predators that generally forage for small, more abundant prey buried at shallower depths, which not only correlates to shorter dive time, but a predicted shorter consumption time at the surface. Therefore it is of interest to investigate the breaking force of bivalves consumed by sea otters at different size classes. In the current study, the breaking force of both butter and littleneck clams was measured and compared to the estimated bite force of otters (Chapter III), to determine the size range in which sea otters were capable of crushing. In general sea otters tend to forage on clams within a certain size range (between 60 and 100 mm) in length more frequently (Tinker et al., 2008). This is thought to decrease the amount of time foraging, and allow the otters to obtain more calories in a shorter amount of time. However, is the only advantage to choosing smaller, more abundant prey decreasing foraging time? It is hypothesized that by choosing smaller bivalves, otters may also be choosing prey with an intermediate or low breaking force, which would decrease the consumption time at the surface (see also Chapter VI). This would decrease the overall handling time of prey and be advantageous for a predator with such a high metabolic rate.

Time budgets of sea otters are correlated with prey availability and are thought to be a useful tool in monitoring sea otter populations (Shimek & Monk, 1977; Garshelis et al., 1986; Ralls & Siniff, 1990). The diversity of prey consumed is at its highest when sea otter populations are at high levels and primary prey are limited (Estes et al., 2003b).

Sea otters in a population that has reached its carrying capacity spend more time foraging for prey than in growing populations (Garshelis et al., 1986). This suggests that prey availability of sea otters in a region decrease with prolonged occupation of that region by otters, thus forcing the otters to spend more time foraging and less time resting or traveling (Estes et al., 1982; Garshelis et al., 1986). Prey is an important limiting resource to population size and prey availability varies with location (Ralls and Siniff, 1990).

Objectives and Hypotheses

The first objective of this chapter was to measure the breaking force (shell failure) of two sea otter bivalve prey at three size classes. Breaking forces of butter clams (*Saxidomus giganteus*) and littleneck clams (*Protothaca staminea*) at three size classes were measured and the resulting data was compared to the estimated bite force of sea otters and overall handling time in the wild. It was hypothesized that (1) large clams would require a greater breaking force than smaller clams and (2) breaking forces would correlate with theoretical bite force estimates of sea otters. An alternative hypothesis was that smaller bivalves require greater force to break due to the material properties, organization of the composite materials, and the geometry of the shell. The second objective was to quantify time budgets of foraging and feeding sea otters, identify their prey choice, and to record dive times, consumption times, and overall handling time per prey species of sea otters in Simpson Bay, Alaska. It was hypothesized that (1) sea otters not only choose intermediate sizes of bivalves due to the ease of foraging since they occur in shallower sediment but also due to the ease of breaking them at the surface (decrease surface/consumption time), and (2) the breaking force of prey types would incur additional costs of foraging, and would be positively correlated with high bite forces that sea otters are suspected to be able to generate (see Chapters II & III).

Material and Methods

Field Collection

Live littleneck clams (*Protothaca staminea*, n= 23) and butter clams (*Saxidomus gigantean*, n=59) from three size classes (small, medium, large) were collected from the south beach of the Alice cove base camp, Simpson Bay, Alaska, (Prince William Sound) in the littoral zone during low tides. Simpson Bay is composed of two arms (northwest and southeast) and is approximately 7.5 km in area and has an average depth of 30 m (Noll et al., 2008; Wolt et al., 2012). The benthos is primarily soft sediment with some rocky reefs (Noll et al., 2008). Feeding bouts of wild Alaskan sea otters were also recorded in Simpson Bay (ca. 60.4° N, 145.5° W).

Shell Morphometrics

Length (cm) and width (cm) were measured for each individual clam and species due to the prediction that shell strength is size-dependent (Vasconcels et al., 2011). Measurements were made with digital calipers (precision 0.01 mm). Since length is the best measure of size for bivalves (Weymouth et al., 1931), clam length was measured as the distance between the anterior and posterior margin (Figure 5-1). Clam width was measured as the distance between the umbo and opposing side (Figure 5-1). Size classes were established with a histogram of collected specimens and based on length of the shell. For butter clams, the small size category ranged from 42-54 mm, the medium size category ranged from 56-67 mm, and the large size category ranged from 67-75 mm. The size range for littleneck clams was much less than for butter clams. For littleneck clams, the small size category ranged from 38-40.9 mm, the medium size category ranged from 41-42.8 mm, and the large size category ranged from 42.9-48 mm. Mass was measured using a digital balance (±0.01 g). Mass varies widely among individuals since the mantle cavity and sinuses of the foot hold a variable amount of water as well as seasonal fluctuations in the size of the gonads, which compose 10-30% of the total mass (Weymouth et al., 1931).

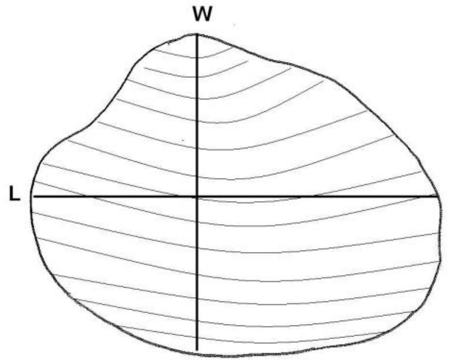

Figure 5-1. Morphometrics of clam. *W,* width; *L,* length.

Breaking Force of Clams

To test the maximum breaking force, all clams (small, medium, and large) were placed in the loading frame, between two flat steel platens, so that the force was applied at the highest point of the shell. These are the sites that sea otters have been observed to place between the occlusal surfaces of their molars (Chapter IV). Also, in previous studies, no significant differences were found between using flat steel platens and plates with teeth-like structures to test the breaking force required to crush hard prey (Wainwright, 1987; Kiltie, 1982; Hernandez, 1997). Bivalves were tested in compression until failure at a loading speed of 5 mm/s. The failure criteria was set to >25% drop in the force-extension curve.

Foraging Time Budgets

Feeding events were documented using a Sony TRV950 video camera (Sony Corp., New York, NY, USA) at 60 Hz from a small 6 meter aluminum skiff or 5 m fiberglass skiff. Feeding bouts began with the onset of a foraging dive and ended with the final consumption of prey at the surface. Foraging dive times and consumption times at the surface were recorded with a stopwatch for each feeding event (n=160). The type of prey and number of individual prey items was identified for each feeding event. The dive time plus the consumption time was calculated as the overall handling time for each event.

Results

Shell Morphometrics

A total of 57 butter clams and 23 littleneck clams were measured (Table 5-1). The mean width, length, and mass of large butter clams was 54.81±1.73 mm, 71.20±2.08 mm, and 72.74±7.43 mm (Table 5-1). The mean width, length, and mass of small butter clams was 36.38±3.22 mm, 48.80±3.67 mm, and 23.24±5.24 mm (Table 5-1). The mean width, length, and mass of large littleneck clams was 36.79±1.66 mm, 45.30±1.87 mm, and 19.89±2.33 (Table 5-1). For littleneck clams, the mean width, length, and mass for small clams were 33.82±1.15 mm, 39.83±0.81 mm, and 15.82±2.03 mm.

Table 5-1. Shell morphometrics for butter clams and littleneck clams. Mean mass includes the shell.

	Mean Width (mm)	**Mean Length(mm)**	**Mean Mass (g)**
Butter Clams			
Large (n=18)	54.81±1.73	71.20±2.08	72.74±7.43
Medium (n=22)	47.17±3.29	60.7±3.70	45.88±9.72
Small (n=17)	36.38±3.22	48.80±3.67	23.24±5.24
Littleneck Clams			
Large (n=10)	36.79±1.66	45.31±1.87	19.89±2.33
Medium (n=7)	34.20±0.97	42.16±0.50	17.12±1.34
Small (n=6)	33.82±1.15	39.83±0.81	15.82±2.03

Breaking Pattern

Typically clams tested in compression exhibited catastrophic failure. That is, the maximum breaking force was always followed by a significant drop in force that clearly indicated one or more major breaks in the shell. Initial breaks were formed at the highest point of the clam, followed by a fracture of the shell directly to the umbo, or hinge, where breaking point is predicted to be the weakest point of the clam (Currey, 1977; Bourdeau and O'Connor, 2003). The breaking patterns observed during testing (Figure 5-2) were consistent with the breaking patterns of clams found on the beach in Simpson Bay, AK that were consumed by sea otters and with observations of free-ranging otters consuming bivalves (Figure 5-2).

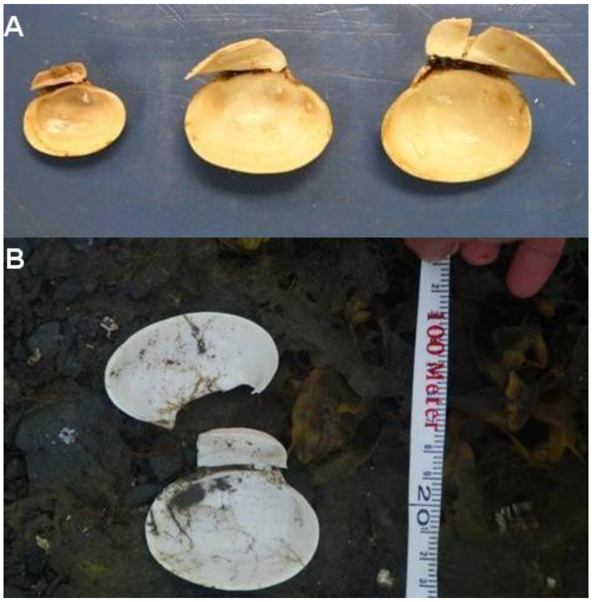

Figure 5-2. (A) Breaking pattern of small, medium, and large butter clams broken with the MTS (left-to-right). The breaking pattern was consistent with the pattern found on (B) butter clams in Simpson Bay, AK (image courtesy of Ryan Wolt), where sea otters commonly prey on bivalves.

Breaking Force

Overall, for each size class, butter clams were larger in width, length, and weight than littleneck clams (Table 5-1). The breaking force of butter clams increased with increasing size, whereas the breaking force of littleneck clams decreased with increasing size (Figure 5-3).

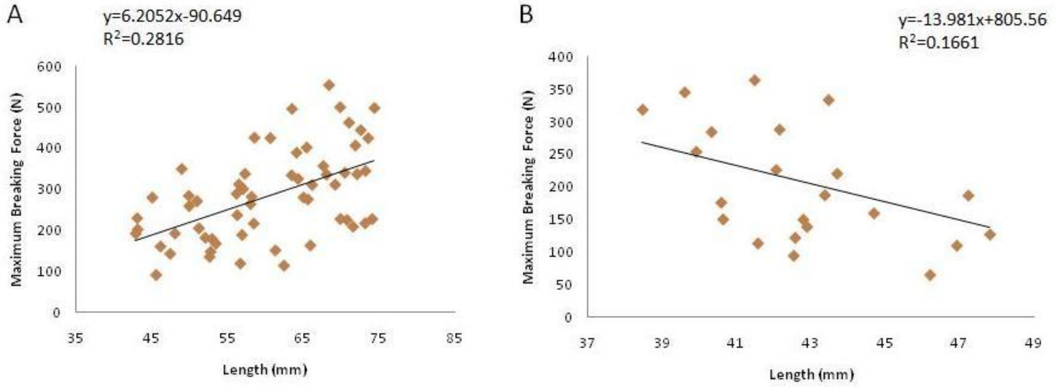

Figure 5-3. Maximum breaking force of (A) butter clams and (B) littleneck clams at varying lengths.

Large butter clams had the greatest mean breaking force of 356.4±108.8 N (Table 5-2), and breaking forces ranged from 208.2 N-553.9 N. Medium sized butter clams had a mean breaking for of 288.0±100.8 N, with a range of 112.9 N-495.9 N. Small butter clams had a mean breaking force of 209.8±59.8 N, with a range of 134.3-349.2 N (Table 5-2).

For littleneck clams, the greatest mean breaking force was observed in smaller clams (254.2±77.6 N) (Table 5-2). The range for small littleneck clams was 149.9-344.5 N. The mean breaking force for medium sized littleneck clams was 193.5±101.6 N, with a range of 94.2-363.1 N. The mean breaking force for large littleneck clams was 183.9±85.6 N, with a range of 64.8-332.7 N.

Table 5-2. Breaking force (N) of butter clams and littleneck clams.

	Length (mm)		Breaking Force (N)	
	Range	**Mean**	**Range**	**Mean**
Butter Clams				
Large (n=18)	67.6-74.3	71.20±2.08	208.2-553.9	356.4±108.8
Medium (n=22)	56.1-66.1	60.7±3.70	112.9-495.9	288.0±100.8
Small (n=17)	42.8-53.4	48.80±3.67	134.3-349.2	209.8±59.8
Littleneck Clams				
Large (n=10)	42.9-47.8	45.31±1.87	64.8-332.7	183.9±85.6
Medium (n=7)	41.5-42.8	42.16±0.50	94.2-363.1	193.5±101.6
Small (n=6)	38.5-40.6	39.83±0.78	149.9-344.5	254.2±77.6

Mean estimated bite forces at the carnassials of Alaskan sea otters (836.8±140.8 N), California sea otters (966.2±204.3 N), and Russian sea otters (920.5±122.8 N) were greater than the maximum breaking force of butter clams (553.9 N) and littleneck clams (344.5 N) (Table 5-2 and 5-3). These data show that sea otters are capable of crushing all size classes of bivalves investigated at the carnassials.

Table 5-3. Estimated bite forces (N) at the incisors, canines, and carnassials for sea otters. Measurements were obtained by the dry skull method (See Chapter III).

Species	Mean BF (N) at Incisors	Mean BF (N) at Canines	Mean BF (N) at Carnassials
Alaska Sea Otters	376.1±68.9	423.6±72.9	836.8±140.8
California Sea Otters	440.6±89.7	487.2±106.4	966.2±204.3
Russian Sea Otters	404.9±62.7	456.4±71.7	920.5±122.8

Frequency of Prey

Data were collected from 58 individuals (20 in June 2009 and 38 in July 2010) with a total of 160 feeding events (63 in June 2009 and 97 in July 2010). Alaskan sea otters were observed feeding on a wide spectrum of prey (N=15; Table 5-4). The main prey consumed in Simpson Bay were butter clams and littleneck clams (55%), mussels (21%), crabs (7.5%), and sea stars (5%) (Figure 5-4). In several feeding bouts, mussels were attached to the kelp, and the sea otters would feed on both kelp and mussels simultaneously. However, due to the low nutritional value, it was suspected that sea otters were consuming the kelp because of the mussels attached (Tinker et al., 2006). During the early month of June, sea otters were regularly observed feeding on herring roe and kelp. Herring roe was always consumed in the same general location, near the transition point between the left and right arm of Simpson Bay, where the water was shallow (10 m or less). This was consistent with observations from Lee et al., (2009). To identify the species of fish eggs, samples were collected at this location, hatched at the research field camp, and identified under a microscope. Again, because kelp has little or no nutritional value (Kenyon, 1969; Estes et al., 1982), it was predicted that otters were eating the kelp and roe, specifically for the high protein roe. On two occassions, a female was observed feeding on a giant octopus with her pup. Both of these feeding events lasted more than one hour, with several foraging dives until the octopus was killed and brought to the surface for consumption.

Table 5-4. Prey of Alaskan sea otters (*Enhydra lutris kenyoni*) in Simpson Bay, Alaska in June 2009 and July 2010 (N=15).

Common Name	**Scientific Name**
Dungeness crab	*Cancer magister*
Butter clam	*Saxidomus gigantean*
Littleneck clam	*Protothaca staminea*
Mussels	*Mytilus spp.*
Sea cucumber	*Unknown species*
Tanner crab	*Chionoecetes bairdi*
Sea star	*Unknown species*
Kelp	*Laminaria saccharina*
Herring eggs	*Clupea pallasii*
Scallops	*Unknown species*
Skate egg case	*Unknown species*
Fat innkeeper worm	*Urechis caupo*
Sea urchin	*Unknown species*
Shrimp	*Unknown species*
Giant Pacific Octopus	*Enteroctopus dofleini*

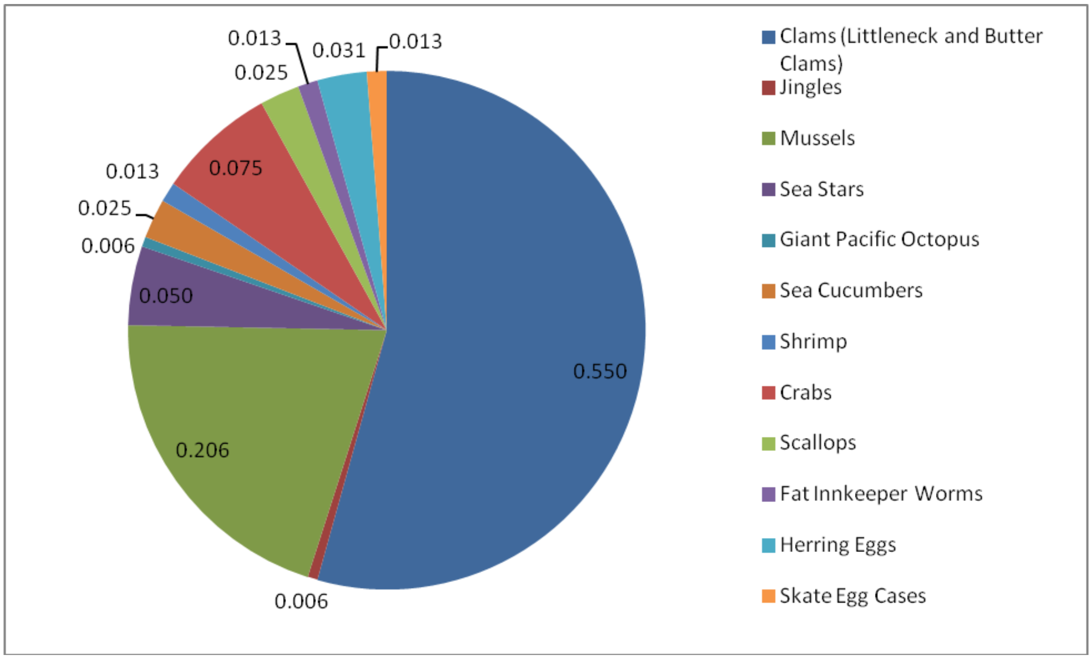

Figure 5-4. Frequency of prey choice per feeding event in Simpson Bay, Alaska (total feeding events=160) for June 2009 and July 2010.

Foraging and Feeding Behaviors

Sea otters handled each prey type (e.g., hard vs. soft, or 1 vs. multiple prey items) at the surface differently, which ultimately affected the consumption time. When feeding on hard prey, sea otters would open the jaws wide to place larger items (such as large bivalves) in the back of the jaws. Both small and large clams were placed in the back of the jaws; however, larger clams required a greater gape angle (see Chapter IV). Once clams were broken by the molars, the flesh was removed by using the incisors or canines. Although smaller clams did not require multiple bites to break the shell, larger clams often did, which increased handling time at the surface. While consuming crabs, sea otters brought the entire, live crabs to the surface at which time each was dismembered and consumed. Legs were consumed first by biting down on the leg and crushing it, then the carapace was cracked with the molars and incisors were used to scrape out the contents. While feeding on soft-bodied prey (e.g., octopus, sea cucumbers), sea otters did not need to open the jaws very wide to consume (see Chapter IV). When foraging for a giant Pacific octopus (soft-bodied prey), the females conducted several short dives and surfaced with only pieces of flesh. These pieces of flesh were consumed rapidly at the surface with minimal chewing. However, once the octopus was dead (underwater dispatching of prey), the otters brought the octopus to the surface and draped it over their body. Once at the surface, the consumption time increased dramatically as the otter picked pieces of flesh off with their incisors and canines. Total consumption time was more than 1 hour for the entire octopus. When other soft-bodied prey was brought to the surface, such as innkeeper worms and sea cucumbers, sea otters would place the in the posterior part of the jaws and quickly dismember it. When foraging for shrimp, sea otters would bring several to the surface at one time. Multiple shrimp were placed on the belly and individual shrimp were consumed separately. Shrimp were individually placed in the back of the jaws (over the molars) and pieces were chewed off; shrimp were not consumed whole.

Handling Time

Differences in overall handling time were also observed between hard prey species. Both butter and littleneck clams required intermediate dive times (82 s) and consumption times (46 s) (Figure 5-5). For most feeding bouts, sea otters brought only one or two clams to the surface for consumption at one time. Dive or foraging time was greater than consumption time at the surface. Overall handling time was intermediate (149 s) when compared to other prey (Figure 5-7). While foraging for crabs, the average dive time was 138.5 s (Figure 5-5) and the consumption time was 107 s (Figure 5-6). The increased dive/foraging time and consumption time increased the overall handling time (261 s) (Figure 5-7).

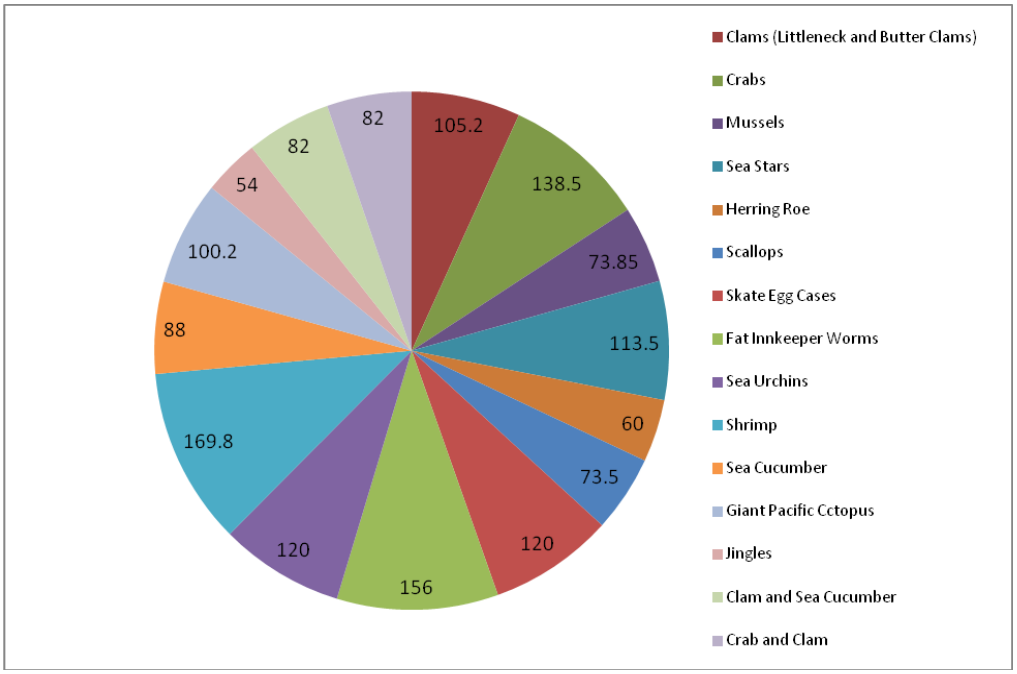

Figure 5-5. Mean dive times (s) for each prey type in Simpson Bay, Alaska for June 2009 and July 2010.

Dive time was short when foraging for giant Pacific octopus (Figure 5-5). The two feeding bouts occurred close to shore where water depth was minimal. However, when considering the entire feeding event, both above and below water, giant Pacific octopus had the longest consumption and overall handling time. The entire feeding event, on both occasions, was over an hour long. However, before the entire octopus was brought to the surface, consumption time was short; only lasting 27 s on average (Figure 5-6). This is because the sea otter was still killing the octopus below water and only bringing up pieces of flesh to consume at the surface. Pieces of flesh were small and consumed rapidly. During both feeding bouts, the sea otter was a female with a pup. Once the octopus was brought to the surface, pieces of flesh were taken off and given to the pup for consumption.

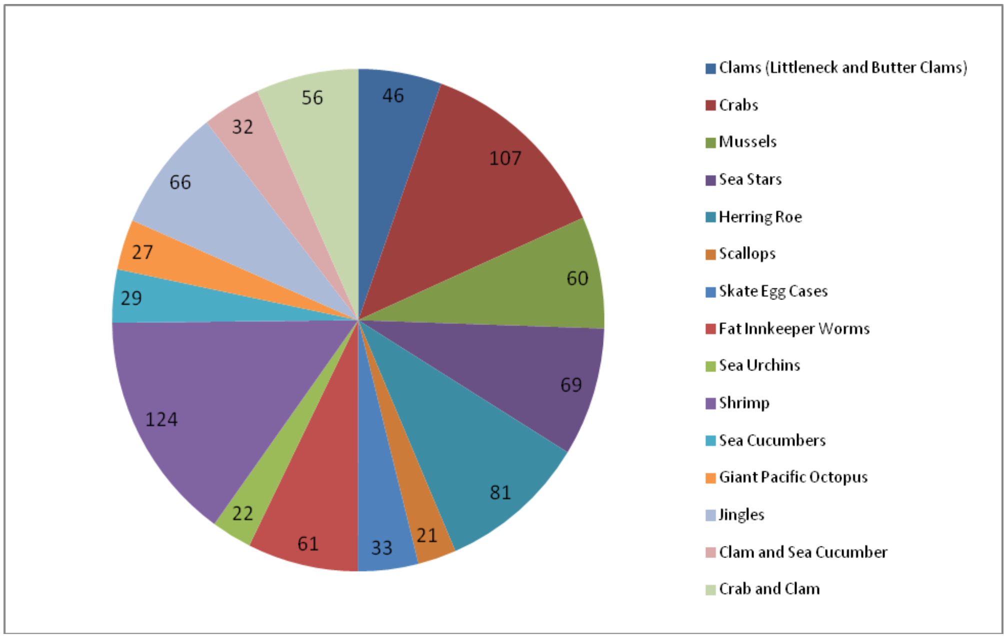

Figure 5-6. Mean consumption times (s) for each prey type in Simpson Bay, Alaska for June 2009 and July 2010.

Overall handling time differed between observed soft prey. When foraging for fat innkeeper worms, sea otters had a much greater dive and foraging time (156 s) than when feeding on sea cucumbers (88 s) (Figure 5-5). Consumption time at the surface was also greater when consuming fat innkeeper worms (61 s) than sea cucumbers (29 s) (Figure 5-6). Thus overall handling time of fat innkeeper worms (217 s) was much greater than sea cucumbers (117 s) (Figure 5-7).

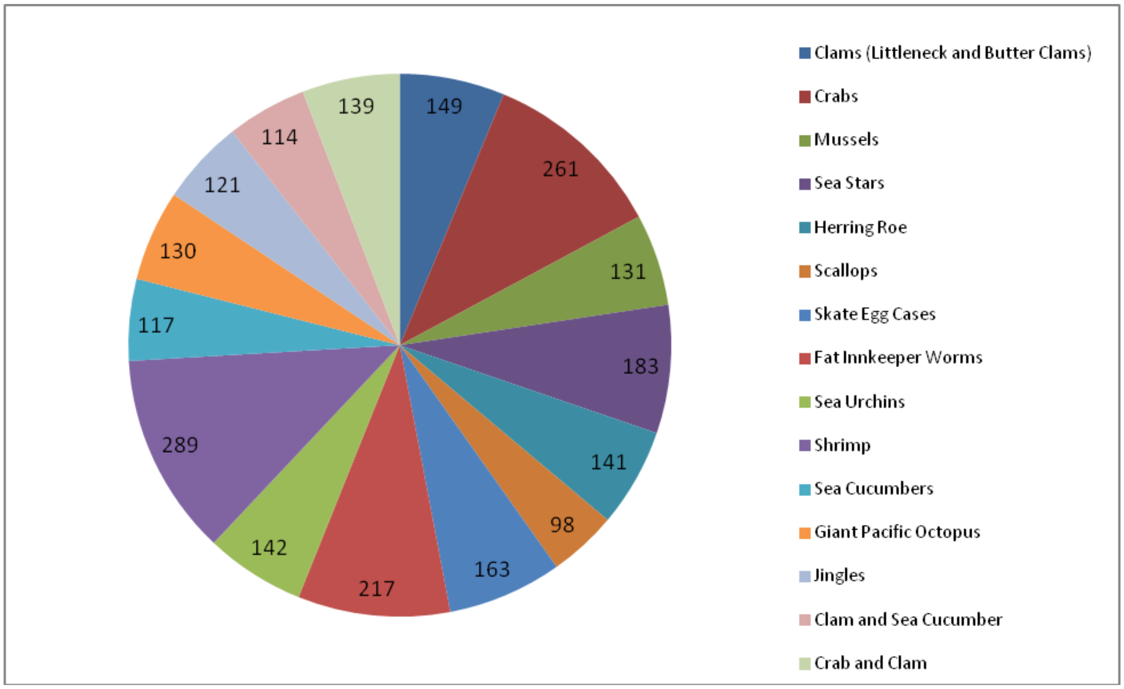

Figure 5-7. Mean overall handling time (s) for each prey type in Simpson Bay, Alaska for June 2009 and July 2010. Overall handling time includes dive time and consumption time at the surface.

While foraging for herring roe on kelp, dive time was very minimal, only 60 s on average (Figure 5-5). Water depth was shallow in the foraging area (<10 m) and kelp was easily accessible. Consumption time (81 s) was much longer than dive time (Figure 5-6). Once kelp was brought to the surface, sea otters would both scoop herring roe off the kelp with incisors and canines as well as eat pieces of kelp with the roe attached. Large pieces of kelp were also brought to the surface at one time, increasing the consumption time and thus overall handling time (Figure 5-7).

Dive time, consumption time, and overall handling time was greatest when foraging for shrimp. On average, dive time was 169.8 s (Figure 5-5), consumption time was 124 s (Figure 5-6), and overall handling time was 289 s (Figure 6-4). Sea otters brought multiple shrimp to the surface at one time, which increased dive and foraging time. Once at the surface, shrimp were not consumed whole. Shrimp were individually placed in the back of the jaws and pieces were chewed off using the molars. The large quantity they brought to the surface at one time and the fact that they did not consume the prey whole (or multiples at one time) greatly increased the overall handling time.

Discussion

Sea otters have morphological, biomechanical, physiological and kinematic adaptations to durophagy (see Chapters II-IV). Breaking force of prey is an important and interesting part of the energetics of foraging that has not received much attention previously. By comparing breaking force of bivalves and bite force of sea otters, it is evident that sea otter crushing capability is more than adequate to consume the bivalves tested at all size ranges. However, it appears that the integration of durophagy and prey choice combine for optimal foraging by sea otters. Sea otters in Simpson Bay, Alaska, were observed feeding on a wide variety of prey (N=15) that included both hard and soft-bodied prey (e.g., clams, mussels, scallops, sea stars crabs, fat innkeeper worms, sea stars, shrimp). This was consistent with other reports from Simpson Bay over several decades (Calkins, 1978; Garshelis, 1983; Doroff & Bodkin, 1994; Garshelis et al., 1986; Wolt et al., 2012). The results are also consistent with many otter populations across Alaska, Washington, and Oregon, in that the majority of the diet consisting of clams (Garshelis et al., 1986; Green & Brueggeman, 1991; Kvitek et al., 1993; Estes & Bodkin 2002; Lairde & Jameson, 2006; Wolt et al., 2012). No specialization of prey, other than clams, was observed in Simpson Bay, which is consistent with a more comprehensive study of sea otter foraging in soft sediments (Wolt et al., 2012). In contrast, individual specialization has been documented in California populations, where a greater number of prey species was observed in contrast to Prince William Sound (Tinker et al., 2007). According to optimal foraging theory, sea otters should consume the largest, more caloric rich prey first, and then generalize to less preferred prey once desired prey becomes depleted (Pyke, 1984; Ostfeld, 1982; Kvitek et al., 1988). Dungeness crabs should be the highest caloric prey in Simpson Bay (Ensminger et al., 1994; Wolt et al., 2012), however after sea otters moved into the area in 1977, large Dungeness crabs were depleted (Wolt et al., 2012). Therefore, the majority of crabs in the diet of sea otters now consist of smaller (<100 g) species (Wolt et al., 2012). Although crabs are more calorically rich prey than clams (Cortez, unpublished data), clams are the most frequently preyed upon in the area. Simpson Bay is primarily composed of soft or mixed sediment (some rocky reefs) where bivalves are dominant (Garshelis et al., 1986; Estes & Bodkin, 2002; Finerty et al., 2009; Wolt et al., 2012). There are no large bodied kelp canopies (e.g., *Macrocystis sp.*), but rather smaller marine algae such as sugar kelp (*Laminaria saccharina*), a brown alga that covers the shallow bottoms of the bay in many areas (Finerty et al., 2009). The diversity of prey consumed is at its highest when sea otter populations are at high levels and primary prey are limited (Estes et al., 2003b). However, recently otters have been observed feeding on Pacific herring eggs (*Clupea pallasi*) and kelp, which are energy-poor sources of food (Lee et al., 2009). This suggests a dietary shift towards less calorically rich prey in this area (Lee et al., 2009). Although sea otters feeding on kelp and herring roe are not uncommon in Prince William Sound (Garshelis et al., 1984) it does appear that an increase in the number of otters feeding on herring roe may be increasing (Garshelis, 1983; Lee, 2009). It is possible that nutritional stress is affecting prey selection in this population and thus causing a dietary shift that includes energy-poor prey (Ostfeld, 1982). Sea otters are experiencing developmental instability as shown in the increase of fluctuating asymmetry within the skull (see Chapter II). The decrease in abundance of energy rich prey (e.g., Dungeness crabs and large clams) in Simpson Bay, may be the cause for this dietary shift (Garshelis, 1983; Lee, 2009) and may be showing in the development of sea otters.

In wild Alaskan sea otters, placement of medium sized clams were positioned further back in the jaws towards the location of the carnassials (see Chapter VI). This is likely due to prevent damage to the anterior teeth and to use the broad and flat surface of the carnassial teeth to crush a hard surface. The breaking pattern of bivalves was consistent with not only shells crushed in the lab but also with shells cast up on the shores of Simpson Bay, presumably consumed by sea otters, with observations of feeding in wild sea otter populations, and with the pattern observed in the fossil record involving predation by sea otters (Walker & Brett, 2002). Within the fossil record, fractures were observed on the dorsal, middle section of fossil clams that were predicted to be preyed upon by sea otters (Walker & Brett, 2002). The data presented here on clam break patterns support the paleoecological evidence.

In general, larger clams are usually more difficult to break and are buried at a greater depth (Vasconcelos et al., 2011). In Simpson Bay, sea otters were observed feeding on small to medium sized butter clams more frequently than large clams (personal observation; see Chapter VI). Large clams would presumably require a lot of energy to excavate from their deep burrows. Small-to-medium size clams are much more accessible due to shallower location. In addition, it is thought that small-to-medium sized butter clams should require less force to break than larger clams (Kvitek et al., 1992; Tinker et al., 2008 time (e.g., foraging for clams at shallower depths) and decreased handling time at the surface (less effort to break clam).   However, littleneck clams demonstrated an inverse relationship between breaking force and size; smaller littleneck clams required more force to break than larger clams. Upon inspection of clam morphology it was concluded that the increased breaking force was likely related to distribution of material and geometry of this species. Unlike butter clams, which possess a smooth surface, littleneck clams have a striated pattern across the shell. Littleneck clams were also more concave in the middle of the shell, increasing the height and thickness of the shells. Although more detailed studies need to be conducted it appears that the increased height or concavity as well as the striations across the shell functions as buttresses that distribute the force over a larger surface area and allow the smaller size classes to absorb additional strain energy, therefore requiring a greater force to break the shell.

These data demonstrate that generalizing breaking force-size relationships, while intuitive, may not hold for all species of prey. In situations where the bivalves are exposed to dynamic loading (high rate loading), the ability of the material to store strain energy determines its ability to resist breaking (Biewener, 1992). A bivalve will break, or have a high failure stress rate, if it cannot absorb enough strain energy, even if the shell is large and strong (Biewener, 1992). These factors depend highly on the shape and design of the shell. Although shell strength is usually correlated with size, shell thickness can be a better predictor of shell strength (Zuschin & Stanton, 2001; Zuschin et al., 2003; Vasconcelos et al., 2011). Increased thickness may be a defense mechanism against predation (Zuschin & Stanton, 2001; Zuschin et al., 2003; Vasconcelos et al., 2011). The breaking force data supports both the original and the alternative hypotheses. Breaking force of bivalves is likely to be species specific with numerous variables that influence the strength. Although the breaking force was greater for smaller littleneck clams, sea otters in Simpson Bay were more commonly observed feeding on medium to small littleneck clams. It is most likely that sea otters consumed larger littleneck clams first when they reoccupied Simpson Bay. Although sea otters optimize their foraging by excavating shallower buried prey, the maximum breaking force of littleneck clams was much less than the maximum breaking force of large butter clams.

The size class of prey consumed by sea otters in Simpson Bay is supported by similar data in other sea otter populations (e.g., California and Kodiak archipelago). In these populations sea otters were observed to be size selective in prey choice (60-100 mm; $\geq$ 30 mm) (Tinker et al., 2008; Kvitek et al., 1992). Medium sized butter clams in this study had a mean length of 60.7$\pm$3.70 mm, which overlapped the size classes more frequently preyed on by sea otters in other populations (60-100 mm, Tinker et al., 2008; Kvitek et al., 1992). By selecting medium to small butter clams sea otters are likely reducing their energetic costs through decreasing dive and consumption times, thus overall handling time.

Dive time (a proxy for foraging time) varied with prey choice and location within the bay (i.e., close to shore and shallow vs. middle of the bay and deeper water) and is linked to the number of individual prey brought to the surface, bivalve size class, and the breaking force of the prey. Dive time was longest when foraging for crabs and shrimp. This is most likely due to the amount of shrimp the otter was observed to bring up on a single dive, thus capturing multiple individuals mitigates this increased dive time. Sea otters were also observed feeding on mussels on reefs at both low and high tide. At low tide, sea otters didn't have to dive for mussels and therefore consumed many mussels at the surface with presumably lower energy expenditure on diving and foraging. Although mussels are hard shelled bivalves, the breaking force of their shells is very low; even humans can easily crush their shells (pers. observation).

Consumption time also varied depending on the breaking force of prey. In general, harder prey required more surface time. Crabs had to be dismembered on the surface in order to consume the meat which increased the surface time. Crabs are also mobile, which may require more foraging time underwater. There were differences in dive and consumption times between soft bodied prey as well. Dive and consumption times were greater when foraging for fat innkeeper worms than sea cucumbers. Greater dive time could be explained by the depth within the sediment at which fat innkeeper worms are found. Fat innkeeper worms get their name by the U-shaped burrows it forms in sand, which can reach an interstitual depth of 50 cm (Anker et al., 2005). However, sea cucumbers tend to spend half of the day buried (partially or fully) and the other half on the surface of the sea floor (Hamel et al., 2001), readily accessible for sea otter predation.

Overall handling time of prey depended on dive time and consumption time, which are influenced by the number of prey and size of prey brought to the surface. Shrimp and crabs accounted for the greatest overall handling costs, but provide a greater caloric content (Ensminger et al., 1994). Dive time and consumption times were high when searching for and consuming shrimp and crabs (more caloric rich prey) than for mussels (less caloric rich prey) (Garshelis et al., 1986). Otters were also found to consume multiple mussels at a time when reefs were exposed at low tide. Mussels require little to no dive time and short consumption times, since they would often ingest the entire mussel. Clams did not require a large amount of foraging time or consumption time at the surface and were the most commonly consumed prey. Clam density is assumed to be much greater than other prey consumed by sea otters in the area due to the large amount of empty shells observed in the littoral zone (consumed by sea otters) and by the large frequency of feeding bout in which clams were observed to be consumed within this study. Consumption time also varied depending upon clam size and species. Larger clams required a larger gape angle, which could result in a decrease in muscle tension produced. However, sea otters may possess a high bite force, while maintaining a relatively wide gape (see Chapter III), as demonstrated in felids (Türker & Mackenna, 1978). Certain clam species may require additional force compared to other bivalve species of the same size. Observations of sea otters feeding on larger size classes of clams were observed to make numerous attempts to break the prey before consumption could occur. Species capable of generating a greater bite force to consume harder prey can benefit from reduced competition (Anderson et al., 2008; Kolmann & Huber, 2009; Marshall et al., 2012). For example, it has been suggested that otters select different macro- and micro-habitats and select different prey choices in order to minimize interspecific competition (Kruuk et al., 1994). Sea otters in Simpson Bay share a habitat with North American river otters (*Lontra canadensis*). However, due to variations in cranial morphology (see Chapter II) and bite force capability (see Chapter III), sea otters are able to exploit a new niche with hard, benthic prey unsuitable for North American river otters (piscivores). It is predicted that sea otters will optimize their foraging success by feeding in patches containing smaller, more abundant prey (e.g., clams) buried at shallower depths as shown in other otter populations (Kvitek et al., 1988; Kvitek et al., 1993). However, when the opportunity to consume more energy efficient prey (e.g., calorically rich octopi or crabs) was present, otters appeared to invest in the longer foraging and/or consumption times for the greater benefit of more caloric rich prey.

In conclusion, cranial morphometrics of sea otters correlate to a durophagous diet. A modification of the feeding apparatus to allow for a durophagous behavior (e.g., increased bite force) opens up new trophic niches for this marine mammal (McCormick, 1998; Verwaijen et al., 2002; Nogueira et al., 2005) and reduces interspecific competition with other otter species. An increase in bite force and the ability to reduce consumption time allows durophagous predators to increase their overall energy intake while foraging (MacArthur & Pianka,, 1966; Pfaller et al., 2011). Adaptations for a high bite force and an extreme large gape angle (see Chapter III) also provide the advantage for sea otters to consume larger clams when available. Therefore, in addition to foraging for specific size classes of clams at specific depths, sea otters may be choosing species with minimal to intermediate breaking forces. Thus less energy is required to break the prey, reducing surface handling time and overall foraging cost.

CHAPTER VI

CONCLUSION

Overall Discussion

Otters display a vast diversity of feeding behaviors that have been predicted to correlate with craniodental morphology and bite performance (Wilson et al., 1991; Pardini, 1998; Villegas et al., 2007; Sepulveda et al., 2007). This study provides further data that supports the two feeding specializations documented in otter evolution: mouth-oriented piscivory vs. hand-oriented invertebrate feeding. The North American river otter (*Lontra canadensis*), Neotropical river otter (*Lontra longicaudis*), giant river otter (*Pteronura brasilliensis*), smooth coated otters (*Lutrogale perspicillata*), Eurasian river otters (*Lutra lutra*), and hairy-nosed otters (*Lutra sumatrana*) are piscivores, which is considered to be the basal mode of feeding (Toweill, 1974; Berta & Morgan, 1986; Sivasothi and Nor, 1994; Pardini, 1998; Lariviere & Walton, 1998) and are mouth-oriented predators. Sea otters (*Enhydra lutris*), Asian small-clawed (*Aonyx cinerea*), African clawless (*Aonyx capensis*) primarily feed on benthic invertebrate prey (Wade, 1975; Ostfeld, 1982; Sivasothi & Nor, 1994; Carss, 1995; Estes & Duggins, 1995; Somers, 2000; Tinker et al., 2007) and are hand-oriented predators.

There is a basic cranial pattern observed in the two trophic specializations (mouth vs. hand-oriented) in otters that correlates with diet (fish, combination of fish, amphibians, crustaceans, or benthic invertebrates). Although both groups are biters, otters specialization on fish possess high velocity jaws and otters specializing on hard prey possess a more powerful bite for crushing prey. Giant river otters and North American river otters are mouth-oriented predators that possess long mandibles, rostrums, and long gracil pterygoid hamuli. Longer, narrower skulls, and long mandibles position the resulting bite force further from the temporal-mandibular joint (TMJ), providing jaws with greater velocity at the expense of bite force capability. High velocity jaws are an important adaptation for mouth-oriented species that catch fast moving prey, such as fish. In giant river otters, larger temporal mechanical advantage contributes to the mouth-oriented strategy, which is more dependent on fast closing jaws than increased bite force. Although giant river otters possessed low mechanical advantages, they still possessed a slightly higher bite force than other otters. The greater bite force could be explained by body size, a greater muscle mass of the temporalis (i.e. greater in-force contribution to the lever system), rather than mechanical advantage. Giant river otters also lack crushing bunodont molars/carnassials. Therefore, the skulls of the giant river otters appear to be designed for increased velocity and increased force at the anterior of the jaws, since the temporalis provides power to the anterior jaws. Feeding performance studies of giant river otters are likely to support these statements.

North American river otters possessed the largest temporalis mechanical advantage compared to other otter species investigated, but an intermediate masseteric mechanical advantage and an intermediate estimated bite force. This would suggest that the temporalis provides the greatest amount of force at the anterior of the jaws, during jaw closure and is likely the result of an increased moment arm of the temporalis. North American river otters primarily feed on fish, but also incorporate crustaceans (e.g., crayfish), amphibians, birds, and mollusks (Toweill, 1974). Similar to the giant river otter, North American river otters possess longer and narrower cranial morphology, which places resulting bite force points further from the jaw joint. This provides the advantage of high velocity jaws. North American river otters also possessed the greatest coronoid length, which is an insertion of the temporalis muscle and allows for an increase in leverage (e.g., increase in moment arm for temporalis) and jaw muscle area and volume (Freeman, 1979; Sacco & Van Valkenburgh, 2004; Figueirido et al., 2009). Therefore, as in the giant river otter, the temporalis muscle of North American river otters appears to most important, during the biting behavior. This is an advantageous trait for a mouth-oriented predator.

Sea otters and Asian small-clawed otters are hand-oriented predators with further modified dentition and shorter skull and mandibles (relative to size) compared to giant river otters and North American river otters. Shorter mandibles position the resulting bite force closer to the TMJ, providing a more forceful bite at the expense of velocity. This suite of morphological and biomechanical traits is an important adaptation for crushing hard, benthic prey at the posterior of the jaws. Asian small-clawed otters primarily prey upon invertebrates; however, they will occasionally incorporate fish into their diet. Therefore, the postcanine teeth are not as broad and flat as observed in sea otters, reflecting dietary differences of these hand-oriented predators. Asian small-clawed otters also possess a more narrow interorbital distance compared to sea otters. Asian small-clawed otters had one of the highest mechanical advantage at the temporalis muscle.

Unlike piscivore specialists (mouth-oriented predators), sea otters possessed greater mechanical advantages at the masseter, providing more force at the posterior of the jaw for crushing. Sea otters also had a suite of morphological traits that were likely related to their extremely blunt mandible; these traits include: well-developed zygomatic arches, deep masseteric fossa, large mandibular ramus height, and tall rostrum, all of which are indicative of a biting feeding mode. Sea otters demonstrated high fluctuating asymmetry of the skull, compared to other otters investigated. Low population size, disease, fishing techniques, and predation are the most likely causes of population declines in sea otter populations, possibly causing females (due to stress) to produce offspring with asymmetrical skulls. This is a sign that sea otters are under great stress and should be monitored more closely.

Further evidence for durophagous or biting behavior in sea otters was observed in the feeding kinematics. Sea otters employed large gape angles and gapes, consistent with a biting feeding mode. Shorter, blunter skulls and mandibles in sea otters, along with increased mechanical advantages at the masseter muscles, and increased bite force capability also correlate to the biting mode of sea otters.

In general, breaking force of bivalves is thought to be size dependent, and larger clams are usually more difficult to break. This is true of butter clams; however, the breaking force of littleneck clams was inversely related with size. That is smaller sized clams required more force to break, likely due to a greater shell thickness shell striations that resist cracking. Estimated bite forces of sea otters were large enough to crush all size classes of butter and littleneck clams; however, sea otters are size selective predators and generally choose bivalves of small to medium size. Medium sized butter and littleneck clams required an intermediate breaking force, and are buried at a shallower depth than larger clams. By reducing dive time (choosing smaller, but more abundant clams buried less deep) and consumption time at the surface (intermediate breaking force), sea otters may be decreasing their overall handling time, allowing them to consume a greater quantity of prey in a shorter amount of time.

Overall handling time of prey depended on dive time and consumption time, which are influenced by the number of prey and size of prey brought to the surface. Shrimp and crabs accounted for the greatest overall handling costs, but provide a greater caloric content (Ensminger et al., 1994). Dive time and consumption times were high when searching for and consuming shrimp and crabs (more caloric rich prey) than for mussels (less caloric rich prey) (Garshelis et al., 1986). While foraging for shrimp, sea otters would bring multiple shrimp to the surface, which would account for an increase in dive time and consumption time. Clams did not require a large amount of foraging time or consumption time at the surface and were the most commonly consumed prey. Clam density is assumed to be much greater than other prey consumed by sea otters in the area due to the large amount of empty shells observed in the littoral zone (consumed by sea otters) and by the large frequency of feeding bouts involving clam consumption observed within this study. The study area is mostly soft sediment, and it is predicted that sea otters will optimize their foraging success by feeding in patches containing smaller, more abundant prey, such as clams, buried at shallower depths as shown in other otter populations (Kvitek et al., 1988; Kvitek et al., 1993).

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