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Short Note

Sea Otter (*Enhydra lutris*) Diet Diversity in Zoos and Aquariums

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Sea otters (*Enhydra lutris*) are marine mammals in the mustelid family listed as endangered by the International Union for Conservation of Nature (IUCN) (Koepfli & Wayne, 1998; Doroff & Burdin, 2015). Sea otters are the largest of the lutrinae (otter family), with adult males occasionally weighing up to 50 kg (averaging about 35 kg) and females (non-pregnant) weighing up to 35 kg (averaging about 25 kg) (Riedman & Estes, 1990). A unique feature of sea otters is that they are the only marine mammal without a blubber layer (Riedman & Estes, 1990). Thus, to keep warm in the cold North Pacific waters in which they live, sea otters rely on an extremely thick fur coat and a high metabolism to maintain body heat (Kenyon, 1969; Costa & Kooyman, 1984). Their extremely thick fur averages half a million hairs per square inch; and through the animals' frequent grooming, the fur traps an insulating layer of air against their skin keeping them warm and dry (Kenyon, 1969; Riedman & Estes, 1990). In addition to this thick fur, their body heat is maintained with a relatively high metabolic rate requiring sea otters to consume between 20 to 35% (averaging 25%) of their body weight per day just to maintain body condition (Costa & Kooyman, 1984).

Wild sea otters feed on a broad range of prey but prefer benthic macroinvertebrates such as clams, crab, sea urchins, and abalone (Riedman & Estes, 1990). In areas where macroinvertebrates are rare, sea otters will eat smaller invertebrates such as snails, occasionally fish, and sometimes even seabirds (Riedman & Estes, 1990). In 1938, Barabash-Nikiforov recognized the need to identify wild sea otter diets for the eventual successful husbandry of sea otters in human care. The analysis of sea otter scat, supplemented by direct observations of wild animals feeding, resulted in the first list of food items consumed by sea otters (Barabash-Nikiforov, 1947). At that time, it was noted that sea urchins were the primary food of the wild sea otters, followed by mollusks, crustaceans, and fishes (Barabash-Nikiforov, 1947).

Since the 1960s, biologists have been regularly and systematically observing what wild sea otters eat by recording the prey of foraging sea otters (Estes et al., 1981; Estes & Bodkin, 2002; Tinker et al., 2008; Maldini et al., 2010; Wolt et al., 2012; Newsome et al., 2015; Hale et al., in press). Sea otter foraging data provide information on prey composition and sizes, the approximate kilocalories consumed, and the effort required by foraging to meet energetic needs through dive times and surface intervals. Sea otters have been documented to consume more than 150 different prey species; however, habitat type influences the species available with only a few species predominant in the diet of most individuals (Estes & Bodkin, 2002; Maldini et al., 2010; Newsome et al., 2015; Hale et al., in press). In rocky reef habitats, most prey will be of slow-moving benthic invertebrates such as urchins and a variety of crabs and snails (Estes et al., 1981; Wolt et al., 2012). In habitats dominated by soft, unconsolidated sediments, such as mud and/or sand, the sea otter diet will be dominated by infaunal invertebrates, the majority being various species of clams, followed by worms, echinoderms, and crab (Estes et al., 1981; Maldini et al., 2010; Wolt et al., 2012; Weitzman, 2013). Diet diversity also tends to be driven at the individual level with clear prey species preferences found within individuals and among animals foraging in close proximity to one another (Tinker et al., 2008).

Sea otters are popular animals to exhibit in zoos and aquaria and have been displayed at an increasing number of facilities since the first sea otter was successfully kept in 1955 for 6 years at the Woodland Park Zoo in Seattle, Washington (Crandall, 1964). Husbandry techniques for sea otters in human care have changed considerably since Barabash-Nikiforov's study in 1938 as zoos and aquariums around the world continued to learn about and improve the welfare of these animals (Reed-Smith & Larson, 2017). When developing diet plans for sea otters in zoos and aquariums, a number of factors need to be considered, including the following: the

composition of a wild sea otter's diet, functional anatomy of their digestive tract, dental morphology, and an understanding of the effects that foraging and diet selection have for social behavior (Fidgett & Plowman, 2009).

To date, there has been no comprehensive documentation on a worldwide scale of the diets of sea otters living in zoological institutions. Thus, the following questions remain: (1) What do zoos and aquariums around the world feed their sea otters? and (2) Is the captive diet similar to what sea otters eat in the wild? Herein, we present results of a survey of institutions that house sea otters worldwide. The goal was to consolidate and share the composition of various captive sea otter diets in order to enhance the welfare of sea otters in human care.

Twenty-four institutions out of 26 worldwide participated in a voluntary survey of food items offered to the sea otters in their care. The geographic breakdown of responding institutions was as follows: United States (12), Canada (1), Europe (3), and Japan (8). The data included diets of 65 individual sea otters—40 females and 25 males. Eight questions were distributed to participating institutions:

1. What types of food were offered in the sea otters' regular diet?
2. What types of foods (if different from regular diet) were provided as enrichment?
3. What was their base diet offered per animal in kilograms?
4. What percentage of the diet is whole vs non-whole food (i.e., shells and bones included)?
5. Was live food offered and how often?
6. What percentage and type of roughage (e.g., shells and bones) was offered on a daily basis?
7. How many sea otters did they have?
8. What was the weight of their sea otters?

Diet items included in both the sea otter's regular diet and enrichment included 58 species of bony fish and macroinvertebrates (20 bony fish, 21 mollusks, 15 crustaceans, and 2 echinoderms; Table 1; see accompanying video, available on the *Aquatic Mammals* website: https://www.aquaticmammals-journal.org/index.php?option=com_content&view=article&id=10&Itemid=147). Diet items offered to the 65 sea otters represented in this survey were broken down as follows: 39 different types of bony fishes and invertebrates in the regular diet (41% bony fishes, 31% mollusks, 26% crustaceans, and 2% echinoderms; Figure 1). Items offered in the regular diet were dominated by squid, clam, shrimp/prawn, and fish (Table 1; Figure 1). The clam, fish, and crab food items were broken down further into specific species, with surf clam, capelin, and blue crab being the dominant species in each category, respectively.

Enrichment food items were provided in smaller quantities relative to the regular diet and were meant to stimulate an animal's natural behavior and provide variety in a sea otter's daily routine. For this survey, an enrichment food item was defined as a different species than what was offered in the regular daily diet or the same species as the regular diet but offered by a different delivery method (e.g., scattered, with an enrichment device, frozen, or alive). Enrichment food item general categories were as follows: 30% bony fishes, 30% mollusks, 25% crustaceans, 5% echinoderms, and 10% other (e.g., coconut water, bull kelp, nori, etc.; see Table 1 for list of enrichment items). Some of the more unique enrichment food items included Pacific hagfish (*Eptatretus stoutii*), American and spiny lobster (*Homarus americanus* and *Palinuridae* spp.), abalone (*Concholepas concholepas*), moon snails (*Euspira lewisii*), and even coconut water. One-third of the institutions gave food in the form of live invertebrates such as mussels and clams. In some cases, a particular enrichment item was only offered occasionally depending on supply availability and cost.

Eighty-seven percent of the institutions in this survey consistently provided roughage (e.g., fibrous indigestible material such as shells or bones) in the form of whole foods or partial whole foods to their animals on a daily basis as part of their regular diet or as enrichment, and the remaining 13% offered neither. The types of roughage offered consisted primarily of shrimp shells and tails, shells from mussels offered whole, thin-shelled clams, crab shells, and whole fish. Whole food items vs non-whole (e.g., shelled, cut, or fillet) items varied widely across institutions, ranging from a high of 90% whole foods to 0% whole foods.

The percentage of kilograms of food offered/kg of body weight for the 65 sea otters in the survey ranged from 12 to 26%, with an average of 18% offered daily. The sea otters' ages in the survey ranged from 1 to 21 years, and their weights varied from 17 to 35 kg. Caloric intake was provided by only one-third of the institutions (8 out of 24 reporting institutions). The percentage of food offered was significantly negatively correlated with body mass (-0.253, $p = 0.043$; linear regression; Realstats add-on in *Excel*), with larger animals being fed less than smaller animals.

Table 1. Food items offered to sea otters (*Enhydra lutris*) in human care in the regular diet and as enrichment items (identified to species by all institutions)

Sea otter regular diets		
Bony fish (41%)	Mollusks (31%)	Crustaceans (26%)
Argentine hake (*Merluccius hubbsi*)	Atlantic surf clam (*Spisula solidissima*)	Blue crab (*Callinectes sapidus*)
Atka mackerel (*Pleurogrammus* spp.)	Blue mussel (*Mytilus edulis*)	Blue swimmer crab (*Portunus pelagicus*)
Capelin (*Mallotus villosus*)	Butter clam (*Saxidomus gigantea*)	Dungeness crab (*Metacarcinus magister*)
Chum salmon (*Oncorhynchus keta*)	California market squid (*Loligo opalescens*)	Farmed white shrimp (*Penaeus vanemei*)
Coho salmon (*Oncorhynchus kisutch*)	Common octopus (*Octopus vulgaris*)	Farmed whiteleg shrimp (*Litopenaeus vannamei*)
Flounder	Cuttlefish (*Sepia* spp.)	Jonah crab (*Cancer borealis*)
Herring (*Clupea harengus* spp.)	Gaper clam (*Tresus* spp.)	Prawn (Canada) (*Pandalus* spp.)
Japanese horse mackerel (*Trachurus japonicas*)	Manila clam (*Venerupis philippinarum*)	Shrimp (Gulf of Mexico) (*Penaeidae* family)
Marlin spp. (*Istiophoridae*)	Purple butter clam (*Nuttalia obscurata*)	
Pacific cod (*Gadus macrocephalus*)	Quahog spp. (*Arcticae*)	
Pacific herring (*Clupea pallasii*)	Razor clams (*Siliqua patula*)	
Pacific mackerel (*Scomber japonicus*)	Scallop (*Argopecten irradians*)	
Pink cusk-eel (*Genypterus blacodes*)		
Pollock (*Gadus chalcogrammus*)		
Sand lance (*Ammodytidae* spp.)		
Enrichment items		
Bony fish (30%)	Mollusks (30%)	Crustaceans (25%)
Inland silverside (*Menidia beryllina*)	Chilean abalone – wild caught (*Concholepas concholepas*)	American lobster (*Homarus americanus*)
Meagre (*Argyrosomus regius*)	Cockles (*Clinocardium nuttallii*)	European green crab (*Carcinus maenas*)
Night smelt (*Spirinchus starksi*)	Green mussel (*Perna canaliculus*)	Irish brown crab (*Cancer pagurus*)
Northern anchovy (*Engraulis mordax*)	Horse clam (*Tresus* spp.)	Japanese spiny lobster (*Panulirus japonicus*)
Pacific hagfish (*Eptatretus stoutii*)	Japanese flying squid (*Todarodes pacificus*)	King crab (*Paralithodes camtschaticus*)
	Littleneck clam (*Leukoma staminea*)	Krill (*Euphausia superba*)
	Longfin squid (*Loligo pealeii*)	Snow crab (*Chionoecetes* spp.)
	Mediterranean mussel (*Mytilus galloprovincialis*)	
	Moon snail (*Euspira lewisii*)	

Note: Five percent of food that were echinoderms and 10% of food denoted "others" (e.g., coconut water, bull kelp, nori, etc.) not included in enrichment items.

This makes sense as smaller animals have a higher surface to area ratio and would theoretically lose heat faster than larger animals. The caloric intake values ranged from 96 to 215 kcal/kg/d, with an average of 143 kcal/kg/d. The total caloric intake measured in kilocalories in a 24-h period ranged from 1,910 to 5,814 kcal, with an average of 3,591 kcal ingested daily per sea otter.

The diets of wild sea otters have been well-documented over the past 50 to 60 years, with several thousands of foraging dives observed from Alaska to California (Estes et al., 1981, 2003; Kvitek et al., 1993; Hale et al., in press). Observations from foraging reveal that wild sea otters eat a diverse diet of primarily slow-moving benthic invertebrates, with only a few prey items tending to dominate their diet in populations that are not food limited, and which may vary over location and season (Estes et al., 1981, 2003; Kvitek et al., 1993; Hale et al., in press).

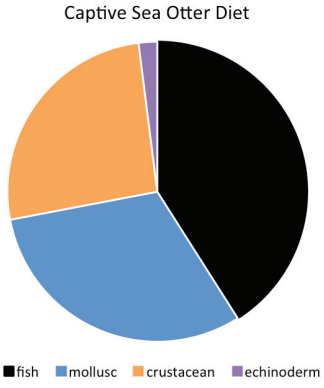

Figure 1. Percentages of different categories of food provided in the regular diet of sea otters (*Enhydra lutris*) over all institutions

One of the challenges for many zoological institutions is providing a diet for the animals in their care that closely replicates the wild diet (Fidgett & Plowman, 2009). Most zoos and aquariums can regularly acquire preferred food items in the wild sea otters' diets (e.g., crab, clams, and mussels). The types of food offered in zoological facilities tend to be commercially caught species readily available for purchase, which may or may not be part of the animal's typical diet in the wild (Worthy, 2001). Thus, the most common food types offered sea otters in human care were squid, capelin, surf clam, and shrimp, all commercially available species. However, over half of the institutions offered their sea otters a wide variety of food items that provides the institution a safety net in case the supply of one or more of the diet items becomes unavailable (Joseph & Antrim, 2012).

In many cases, the diet composition for each of the animals represented in this survey was similar to what their wild counterparts would consume—for example, crab (46% of facilities fed crab) and clam (92% of facilities fed clam). However, one major difference in the diet of sea otters housed in human care with those in the wild is that the dominant food fed to sea otters in human care was bony fish (Table 1; Figure 1). Wild sea otters do occasionally eat bony fish, but they tend to eat them seasonally; and it does not make up a large portion of their regular diet. Instead, most wild sea otters' diets were made up of predominantly mollusks (50%) and crustaceans (50%) (Estes et al., 1981; Riedman & Estes, 1990; Watt et al., 2000; Table 2). In addition, capelin made up a large percentage of fish fed to sea otters in human care, while wild sea otters have not been documented eating this particular species of fish (Estes et al., 1981; Watt et al., 2000). Most species of fish found in wild sea otter diets have been relatively slow-moving, schooling, or episodically abundant fishes such as lumpfishes or spawning sand lance (Estes et al., 1981; Watt et al., 2000). One reason why fish may be more common in a sea otter's diet in zoos and aquariums could be attributed to the relatively lower cost of fish vs the high cost of invertebrate items like crab, mussels, and clams. Finally, sea urchins were not part of the regular food items of most of the sea otter diets in human care but are often found in wild sea otter diets (Barabash-Nikiforov, 1947; Estes et al., 1981;

Table 2. Food items common in wild sea otter diets

Wild sea otter diets*		
Bony fish (0%)	Mollusks (*ca*. 50%)**	Crustaceans (*ca*. 50%)***
	Abalone (*Haliotis* spp.)	Cancer crabs (red rock, Dungeness, and graceful) (*Cancer* spp.)
	Bent-nosed clams (*Macoma nasuta*)	Kelp crab (*Pugettia producta*)
	Butter clams (*Saxidomus* spp.)	
	Horse clams (*Tresus* spp.)	
	Mussels (*Mytilus* spp.)	
	Octopus (*Octopus* spp.)	
	Razor clams (*Siliqua patula*)	
	Turban snails (*Tegula funebralis*)	

*Note that this is not an exhaustive list but those commonly found in sea otter diets where the populations have not reached carrying capacity or are not food limited (Riedman & Estes, 1990; Kvitek et al., 1993; Estes et al., 2003; Hale et al., in press).

**Dominant in soft sediment habitats

***Dominant in rocky and mixed habitat

Note: Others found in both captive and wild diets: Echinoderms: sea urchin (*Strongylocentrotus* spp.) and sea cucumber (*Holothuroidea* spp.)

Hale et al., in press). Instead, sea urchins were only offered intermittently for enrichment at 4% of the surveyed facilities. Availability and the cost associated with the amount of sea urchins necessary to sustain a substantial portion of a sea otter's diet are the most probable reasons for this exception. The wild sea otter diet most comparable to the diets fed to sea otters in human care are the diets of wild sea otters found occupying soft sediments, with clams predominating (Estes & Bodkin, 2002; Maldini et al., 2010; Weitzman, 2013; Newsome et al., 2015; Hale et al., in press).

A further notable difference in sea otter diets reported here compared to diets of wild sea otters is the amount of whole food vs non-whole food consumed. While wild sea otters do not always consume their prey whole (i.e., they often do not eat shells of larger clams and crabs), they arguably consume more roughage and whole foods than the majority of sea otters in human care. However, 90% of the institutions surveyed offered whole food types that included roughage (fibrous indigestible material such as shells and bones) on a daily basis. Ingesting daily roughage is thought to be healthy for sea otters' gastrointestinal tracts, more closely approximating the wild sea otter's diet. It is important to note that some institutions may limit offering whole foods because of concerns about exhibit aesthetics (e.g., too many discarded shells and bones), as well as water quality concerns with discarded debris blocking drains and fouling the overall quality of the water.

The amount of food fed to sea otters in this survey also differs from that consumed by wild sea otters. The 65 sea otters represented in this study were fed on average 18% of their body weight (12 to 26%). This is well below the 25% that has been considered necessary for wild sea otters to survive and thrive (Kenyon, 1969; Riedman & Estes, 1990). For example, it is thought that a 20-kg adult wild sea otter would need to be fed on average 5 kg of food equaling between 4,295 and 5,750 kcal in a 24-h period (215 and 288 kcal/kg/d, respectively) (Riedman & Estes, 1990). Only eight out of the 24 institutions reported kilocalories (reporting on 23 sea otters), but this subsample reports that zoos and aquariums offer their animals an average of 3,591 kcal/d, which is lower than that found consumed by wild sea otters.

It is probable that sea otters in human care do not need as much daily energy intake as wild sea otters to survive and thrive. Field studies on the energetic requirements of wild sea otters found that their largest energy expenditure was associated with foraging dives followed by swimming and grooming (Yeates et al., 2007). Caloric requirements have been shown to increase in the winter, possibly because of the cooler and windier weather conditions; while in calm, sunny weather, sea otters can conserve energy by resting more (Garshelis et al., 1986). Sea otters in zoos and aquariums do not typically expend energy foraging for their food and spend less energy swimming with dives of much shorter duration than wild sea otters (Yeates et al., 2007). Even the deepest sea otter enclosures are far shallower than the typical wild sea otter foraging dive averaging 25 m; therefore, it is understandable that sea otters in human care would expend less energy through swimming and diving activities (Riedman & Estes, 1990). Taking into account the lower energetic demands of sea otters in human care, the diet of an animal consuming on average 18% of their body weight daily is thought to be adequate for maintaining their energetic and thermoregulatory needs. In fact, most sea otters in zoos and aquariums do well with this amount of food in that they successfully complete all life stages, including sexual maturity and reproduction, and many reach ages that meet or exceed those typically found in wild populations (Casson, 2016). Maximum ages for sea otters in the wild, based on tooth annuli, are about 22 years for females and 15 years for males, while maximum ages for sea otters in human care are 25 years for females and 22 years for males (Riedman & Estes, 1990; Belting 2019).

Sea otters in human care have different dietary needs than their wild counterparts. They do not have to compete with conspecifics for food, are offered a reliable and stable diet, are provided with veterinary care when sick, and may be given additional food if needed to maintain body weight and body temperature. The diet variability and amount of kilocalories offered to sea otters in human care presented herein appears adequate for their growth, reproduction, and all life history milestones, as well as the ability to reach maximum life span. However, certain target nutritional values for sea otters in human care such as, but not limited to, the optimal amount of roughage in their diet needed per individual has not been formally investigated and is an area where more research is needed. In addition, more information is needed on the various environments to which sea otters in human care are exposed such as natural environmental conditions or artificial environments and variable water temperatures, as well as an attempt to quantify different activity levels of individuals to better account for calories expended and calories consumed.

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