

Chapter 4

Sea Otter Foraging Behavior



Randall W. Davis and James L. Bodkin

Abstract Sea otters are marine specialists but diet generalists, which feed primarily on benthic mega-invertebrates (i.e., body dimension >1 cm). They locate and capture epibenthic and infaunal prey with their forepaws by relying on vision and tactile sensitivity during short-duration dives (generally <2 min) in shallow waters (routine dives <30 m and maximum dive depth ~ 100 m) of the littoral zone. Sea otters have an elevated resting metabolic rate and small or no energy reserves in the form of blubber, so they feed every 3–4 h. Foraging dives often occur in bouts (i.e., two or more consecutive dives), which may last several hours with 1–2 min between dives, depending on the type of prey. Sea otters consume small or soft prey entirely or use their teeth or stone tools to access the flesh of mega-invertebrates with a shell, test, or exoskeleton. The daily percentage of time that sea otters devote to foraging depends on age, sex, presence of a pup, time of year, and prey abundance, which varies geographically, seasonally, and episodically. In areas occupied by sea otters for many years, epifaunal prey generally decline first followed by infaunal species, and this may result in greater foraging effort and diet specialization associated with density-dependent competition for food. Although prey availability strongly influences sea otter carrying capacity, both intrinsic and extrinsic factors influence population equilibrium density, resulting in spatiotemporal variations in foraging behavior.

Keywords Capture · Carrying capacity · Diet · Diving · Epibenthic · Foraging · Generalist · Infauna · Mega-invertebrate · Prey · Sea otter · Specialist · Tactile · Time budget · Tool · Vision

R. W. Davis (✉)

Department of Marine Biology, Texas A&M University, Galveston, TX, USA
e-mail: davisr@tamug.edu

J. L. Bodkin

U.S. Geological Survey, Alaska Science Center, Emeritus, Anchorage, AK, USA

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4.1 Sea Otters: Marine Specialists But Diet Generalists

An animal forages to remain in energy balance, grow, and reproduce. As a result, foraging is a prominent behavior, although the amount of time devoted to it will vary among species. Sea otters, which are marine specialists but diet generalists, feed primarily on benthic mega-invertebrates (i.e., body dimension >1 cm), such as mollusks, crustaceans, echinoderms, and cephalopod, although they also feed opportunistically on slow-moving demersal fishes, the egg cases of rays, and herring roe on kelp. They locate and capture epibenthic and infaunal prey with their forepaws by relying on vision and tactile sensitivity during short-duration dives (routine dives <2 min) in shallow water (routine dives <30 m and maximum dive depth ~100 m) in the littoral zone (see Sect. 3.2.3; Bodkin et al. 2004; Wolt et al. 2012; Thometz et al. 2016; Davis 2019). Because of their elevated basal metabolic rate (i.e., 2.9-fold higher than a terrestrial mammal of similar size) and food consumption (i.e., 25% of body mass daily; see Sect. 3.3.4), sea otters have a significant top-down effect on benthic mega-invertebrates, which affects littoral community structure (see Chap. 8; Estes and Palmisano 1974; Kenyon 1969; Estes and Duggins 1995; Estes 2015; Davis 2019).

4.2 Evolution of Sea Otter Foraging Behavior

The Lutrinae subfamily of otters exhibits two types of prey capture: hand-oriented and mouth-oriented. Hand-oriented otters (e.g., *Enhydra* and *Aonyx*) feed primarily on benthic invertebrates, which they capture and manipulate with their forepaws, sometimes using stones as tools for opening hard-shelled bivalves (Estes et al. 2009; Timm-Davis et al. 2015, 2017). Mouth-oriented otters (e.g., *Lutra*, *Lontra*, and *Pteronura*) feed primarily on fishes, which they capture (grasp) with their teeth. These two foraging behaviors are reflected in the morphology of the skull and teeth of sea otters and North American river otters (*Lontra canadensis*), respectively. Sea otters are durophagous (from Latin *durus* [hard] + *-phagy* [feeding on]) and feed primarily on mega-invertebrates with a shell (mollusks), exoskeleton (crustaceans), or test (sea urchins), although they feed opportunistically on other prey without an exoskeleton (e.g., octopuses). They have short, blunt skulls and postcanines with rounded or conical cusps (bunodont dentition) and large occlusal surfaces for crushing hard prey (Fig. 4.1a–d; see Sect. 3.1.1; Fisher 1941). In contrast, North American river otters are primarily piscivorous, and their teeth are adapted for grasping, piercing, tearing, and shearing soft prey, such as fish (Fig. 4.1e–h).

The ancestors of sea otters (*Enhydra*) diverged from other Eurasian otters in the early Pliocene (~5 Mya). One lineage was *Enhydritherium*, which dispersed from Europe around the northern rim of the North Atlantic Ocean and into the Gulf of Mexico ~2 Mya, where the first fossils of *Enhydritherium terraenovae* appeared in Florida (see Sect. 2.4). *E. terraenovae* and extant sea otters were similar in size, with a body mass of ~22 kg (Lambert 1997). However, according to the

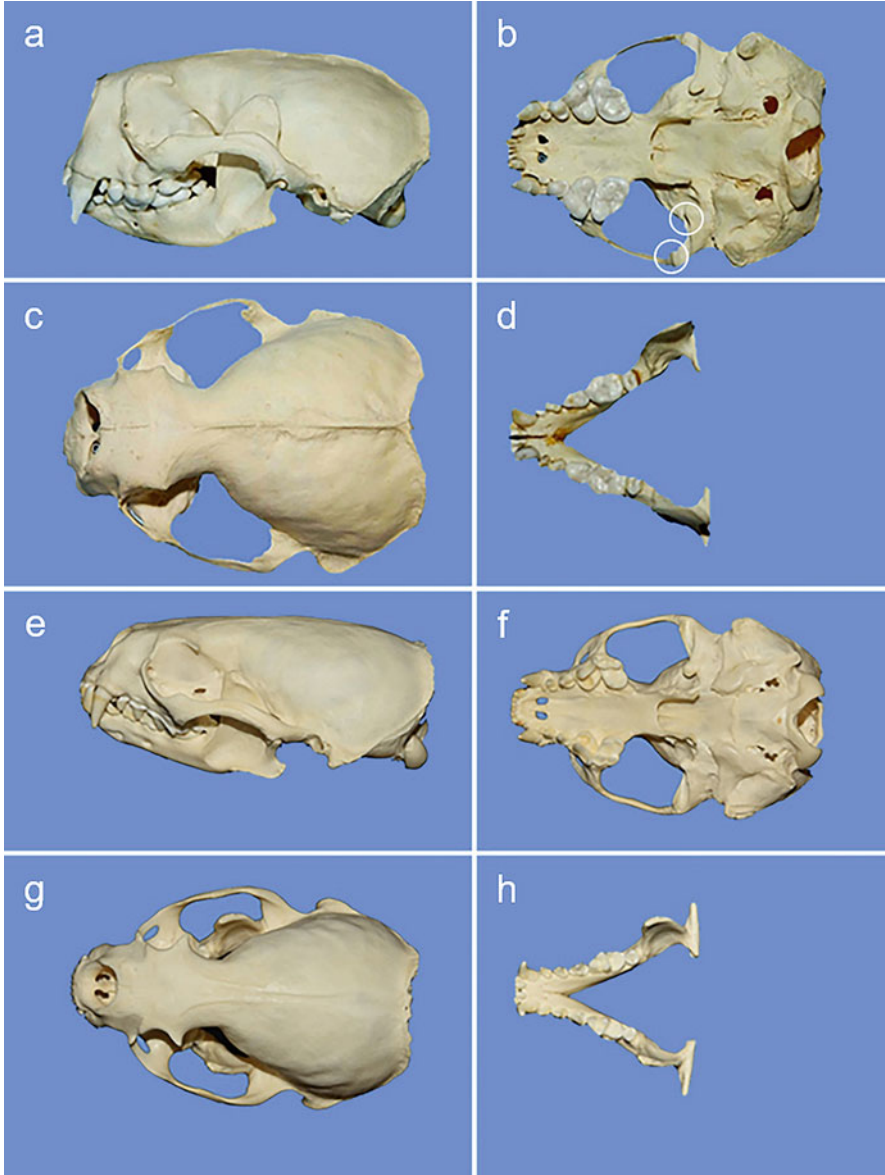


Fig. 4.1 Skull and jaw of a sea otter (a–d) and river otter (e–h). Circles in (b) identify the pre-articular and postglenoid processes, which partially surround the mandibular fossa and condyle that prevent transverse movement of the jaw

paleoenvironment of the fossil sites in Florida, *E. terraenovae* inhabited both nearshore marine and inland freshwater environments, whereas sea otters are restricted to marine habitats. Because it had morphological characteristics of both

river otters and modern sea otters, it is likely that *E. terraenovae* was transitional between mouth-oriented and hand-oriented prey capture. The diet of *E. terraenovae* likely consisted of hard prey, such as mollusks (similar to sea otters), because of the thick, heavily worn cusps on the carnassial teeth. However, their diet most likely included fish when in freshwater environments, indicating a habitat generalist rather than a marine specialist. The events leading to the dispersal of *Enhydritherium* into the Pacific Ocean through the Central American Seaway, where presumably it gave rise to *Enhydra* (3–1 Mya), remain uncertain and will require additional fossil evidence. We know that *Enhydritherium* became extinct in the Atlantic, and *Enhydra* dispersed around the North Pacific Rim, where it became adapted to a durophagus diet of marine invertebrates.

4.3 Foraging Dives

All otters feed primarily on aquatic prey, which they capture during short, shallow dives. Most otters are semi-aquatic and occupy a variety of habitats, including lakes, streams, rivers, marshes, swamp forests, estuaries, and coastal waters, where they feed primarily on fish and small invertebrates. In contrast, sea otters are marine specialists, which feed primarily on mega-invertebrates but occasionally sessile fish (Watt et al. 2000; Wolt et al. 2012). When swimming on the surface in a prone (belly down) position or while diving, sea otters use dorsoventral undulation with simultaneous pelvic paddling at speeds $<1.4 \text{ m s}^{-1}$ (Fig. 4.2; see Sect. 3.1.2.3; Williams 1989; Davis 2019). The forelimbs are held close to the body to reduce drag and are not used for locomotion. Sea otters are positively buoyant because of a lung volume that is substantially larger (3.3-fold) than in a terrestrial mammal of similar size (Kooyman 1973; see Sect. 3.2.1). Prior to a dive, sea otters hyperventilate to oxygenate blood hemoglobin and muscle myoglobin, which are the primary oxygen stores (Davis 2019). Unlike many marine mammals, the large lungs of sea otters also are a significant (40%) source of oxygen during a dive. Although diving lung volume has not been measured, sea otters inhale prior to a foraging dive, which causes them to float higher in the water, so they may dive on a full lung volume (see Sect. 3.2.1). To overcome positive buoyancy at the beginning of a foraging dive, a sea otter may leap out of the water with a powerful kick of the hind flippers, arch its back, and descend (Fig. 4.3).

Positive buoyancy means that sea otters must actively stroke with their hind flippers when descending during a dive. Assuming a full lung volume, sea otters reach neutral buoyancy at a depth of $\sim 35 \text{ m}$ (see Sect. 3.2.1). This is deeper than most foraging dives ($<30 \text{ m}$) made by sea otters in Alaska and California (Bodkin et al. 2004; Tinker et al. 2007; Wolt et al. 2012; Thometz et al. 2016). Hence, sea otters must actively stroke to remain submerged while capturing epibenthic and infaunal prey during routine dives less than $\sim 35 \text{ m}$ deep, although this analysis does not include changes in buoyancy resulting from the gradual loss of air (bubbles) from the fur (Fig. 4.4b). When they are ready to ascend, sea otters stop stroking and

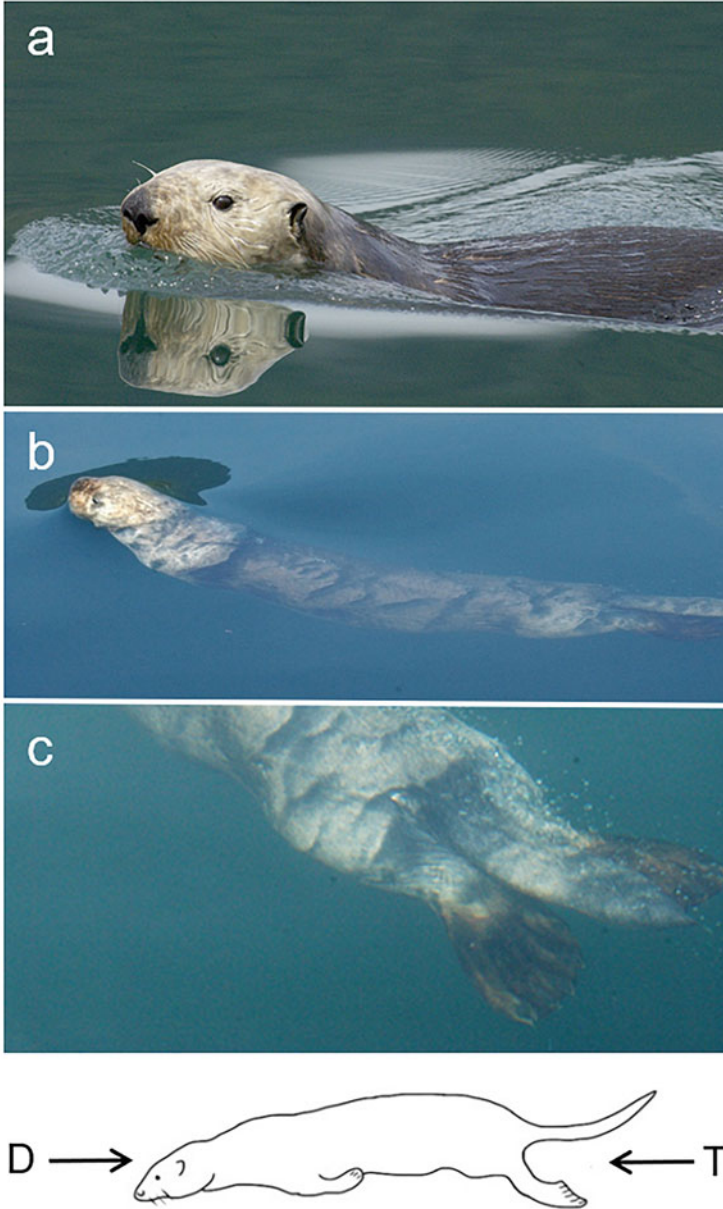


Fig. 4.2 Sea otters use their hind flippers when (a) swimming on the surface in a prone position and (b) swimming submerged. In both cases, sea otters use dorsoventral undulation and simultaneous pelvic paddling with their webbed hind feet (c), which generate thrust (T) to overcome drag (D) (d). The fore limbs are held close to the body to reduce drag and are not used for locomotion. Images (a–c) were obtained under USFWS Permit Nos. MA-043219 and MA-078744 to R. Davis

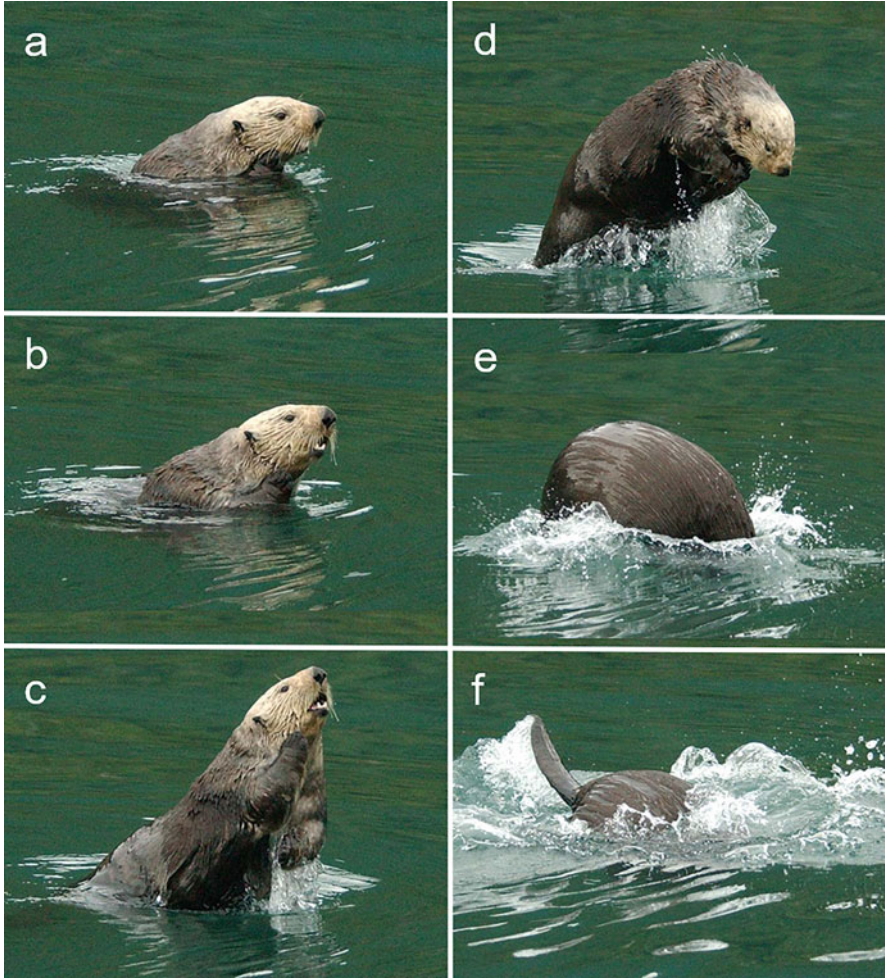
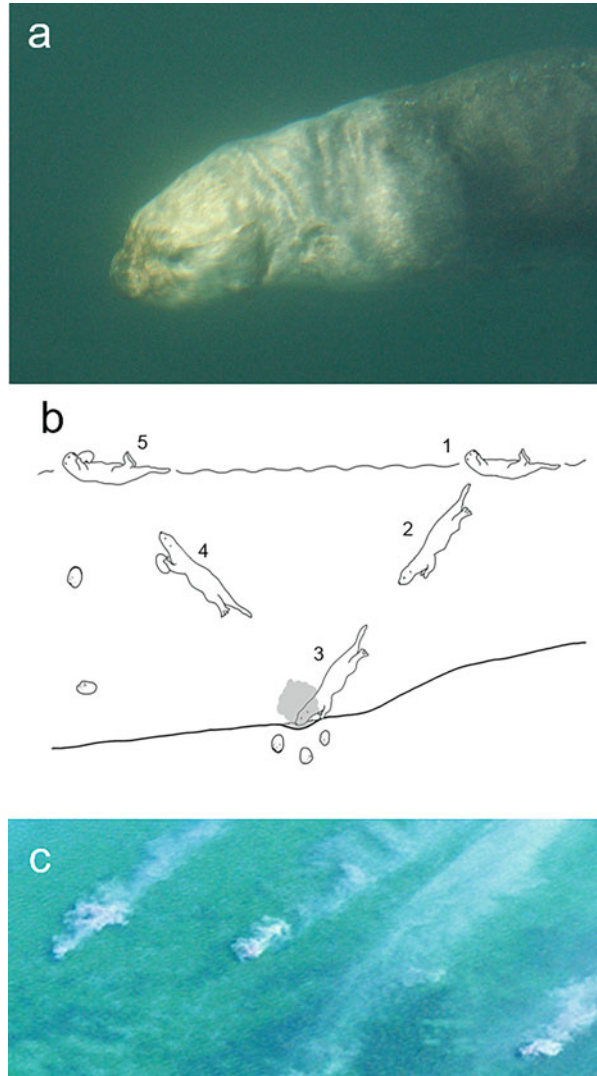


Fig. 4.3 Sea otter leaping out of the water at the beginning of a foraging dive. Images (a–f) were obtained under USFWS Permit No. MA84799B to R. Davis

rise passively to the surface, although ascent may be augmented with additional stroking to increase speed. At the maximum recorded dive depth of ~ 100 m, which is rare, a 25 kg sea otter is negatively buoyant, so stroking would be required during initial ascent until it becomes positively buoyant above a depth of ~ 35 m (Bodkin et al. 2004). Except for very deep dives, the mode of locomotion during a dive changes from active swimming during descent and benthic foraging to passive gliding during most of the ascent.

With a mean diving metabolic rate of $21.5 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$, a 25 kg sea otter has an aerobic dive limit (ADL) of ~ 3.7 min (see Sect. 3.2.3; Yeates et al. 2007; Cortez et al. 2016; Thometz et al. 2015; Davis 2019). This limits routine dive depth and available foraging habitat to nearshore, shallow (< 30 m) waters (Kenyon 1969;

Fig. 4.4 (a) Sea otter during a dive with open eyes. (b) Sequence of events during a foraging dive for clams in a soft-sediment benthic habitat: (1) hyperventilate at surface, (2) dive to the seafloor, (3) excavate soft sediments with forepaws using tactile sense (vision not possible because of turbidity) to distinguish clams from gravel, (4) return to the surface with a clam, (5) consume clam and discard shell. (c) Aerial image of sea otters digging in soft sediments in Prince William Sound, Alaska. Image (a) was obtained under USFWS Permit No. MA-043219 to R. Davis



Calkins 1978; Riedman and Estes 1990; Bodkin et al. 2004; Tinker et al. 2007; Wolt et al. 2012; Esslinger et al. 2014). Although deeper dives occur, they are rare (Newby 1975; Bodkin et al. 2004, 2012; Wolt et al. 2012). In Southeast Alaska, only 0.003% of dives were > 90 m, and in Prince William Sound, Alaska, 0.04% of foraging dives were > 50 m (Bodkin et al. 2004, 2007). The mean duration of foraging dives for all sea otters is about 2 min, with a maximum duration of ~8 min (Bodkin et al. 2004; Wolt et al. 2012; Thometz et al. 2016).

In Simpson Bay, Alaska, the average depth of foraging dives is 27 m with no significant difference between males and females (Fig. 4.5a; Osterrieder and Davis

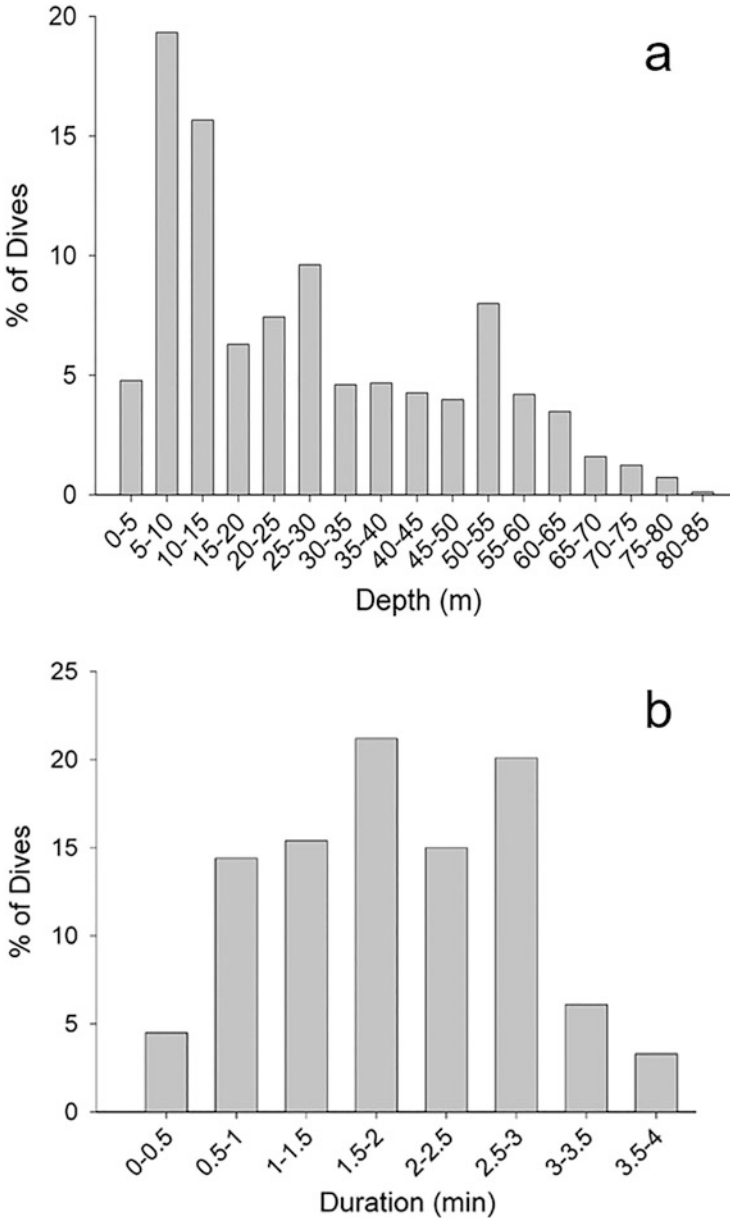


Fig. 4.5 Distribution of foraging dive (a) depths and (b) durations for adult male and female sea otters in Simpson Bay, Prince William Sound, Alaska (Wolt et al. 2012)

2009; Wolt et al. 2012). Nevertheless, sea otters exploit all of Simpson Bay proportional to the bathymetry (i.e., percentage of the bay within a depth range) down to a depth of 82 m, although there is a preference for shallower depths in the

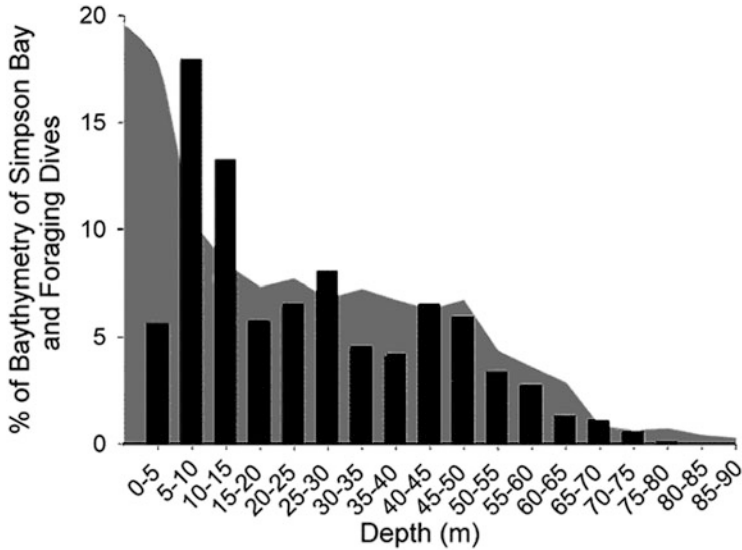


Fig. 4.6 Distribution of sea otter foraging dive depths (bars) and the percentage of the seafloor within each depth range (shaded area) for Simpson Bay, Alaska (Wolt et al. 2012)

range of 5–15 m (Fig. 4.6; Osterrieder and Davis 2009; Wolt et al. 2012). The mean foraging dive duration is 1.9 min with a normal distribution from 0 to 4 min and a peak at 1.5–2.0 min (Fig. 4.5b). There is a positive relationship between dive duration and depth because of the ADL, but shallow dives can be as long as deep dives (Fig. 4.7; Wolt et al. 2012; Thometz et al. 2016). In Western Prince William Sound, the mean duration of shallow foraging dives (<10 m in depth) is 0.7 min, while the mean duration of deeper dives (>15 m) is 1.6 min (Bodkin et al. 2007).

In Southeast Alaska, the mean depth and duration of foraging dives are 19 m and 1.4 min, respectively, with a preference for the depth range of 0–20 m relative to available benthic habitat (Kvitek et al. 1993; Bodkin et al. 2004). Males in Southeast Alaska and Western Prince William Sound exhibit this bimodal pattern, while females routinely forage at the shallower depths (Fig. 4.8). On average, males make more deep dives (>30 m) than females. In Washington State, mean foraging dive duration is 0.92 min, with a maximum of ~5 min (Laidre and Jameson 2006). In California, bimodal foraging behavior is not evident, although males generally forage at deeper depths than females (Thometz et al. 2016). Foraging in shallow water is associated with a large number (>200 day⁻¹) of short duration (~1 min) dives, with a high percentage (~70%) of each dive spent searching for prey on the seafloor (Bodkin et al. 2012). Foraging success is high among habitats, ranging from 70–90%, although the energy content of pre can vary (Kvitek et al. 1992, 1993; Doroff and Bodkin 1994; Dean et al. 2002; Wolt et al. 2012; Coletti et al. 2016).

Water depth is the defining characteristic of sea otter benthic habitat. Throughout their range, sea otters historically occupied littoral habitats from estuaries to exposed coastlines within their diving ability. For example, large numbers of sea otters occur more than 50 km offshore in the Bering Sea, where the bathymetry is within routine

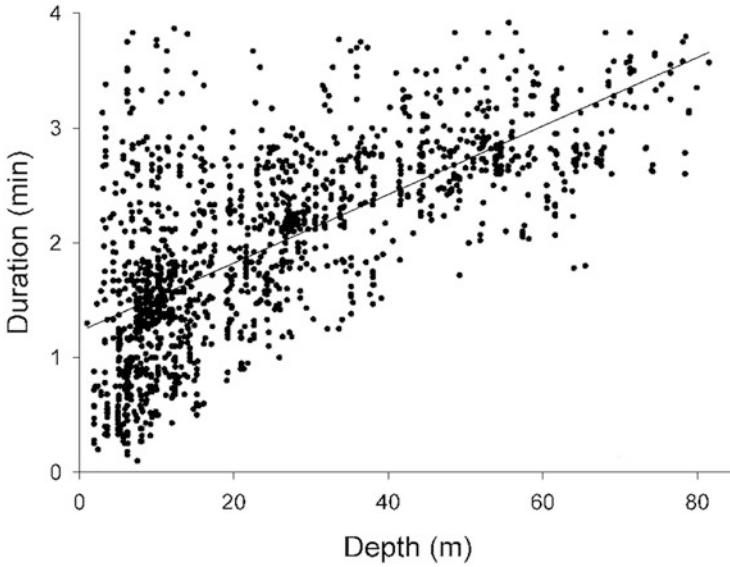


Fig. 4.7 Successful foraging dive depth as a function of dive duration (Wolt et al. 2012)

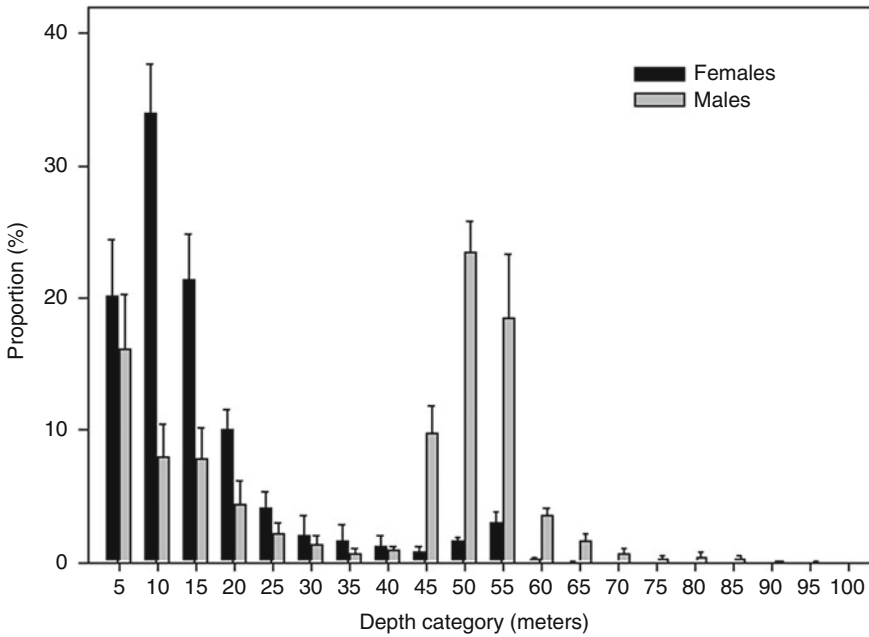


Fig. 4.8 Distribution of dive depths for sea otters in Southeast Alaska and Prince William Sound, Alaska

foraging depths (Bruggeman et al. 1988). In general, the depth and duration of foraging dives reflect the local variation in bathymetry and seafloor habitat.

4.4 Diet

Sea otters are diet generalists and feed primarily on mega-invertebrates, such as mollusks (e.g., clams, scallops, mussels, abalone, turban snails, and chitons), crustaceans (e.g., crabs, shrimp, and barnacles), echinoderms (e.g., sea urchins, sea cucumbers, and sea stars) and cephalopods (e.g., octopuses and squid) (Fig. 4.9; Williams 1938; Murie 1940; Barabash-Nikiforov 1947; Hall and Schallar 1964; Kenyon 1969; Estes et al. 1982; Kvitek and Oliver 1988; Kvitek et al. 1988, 1993;

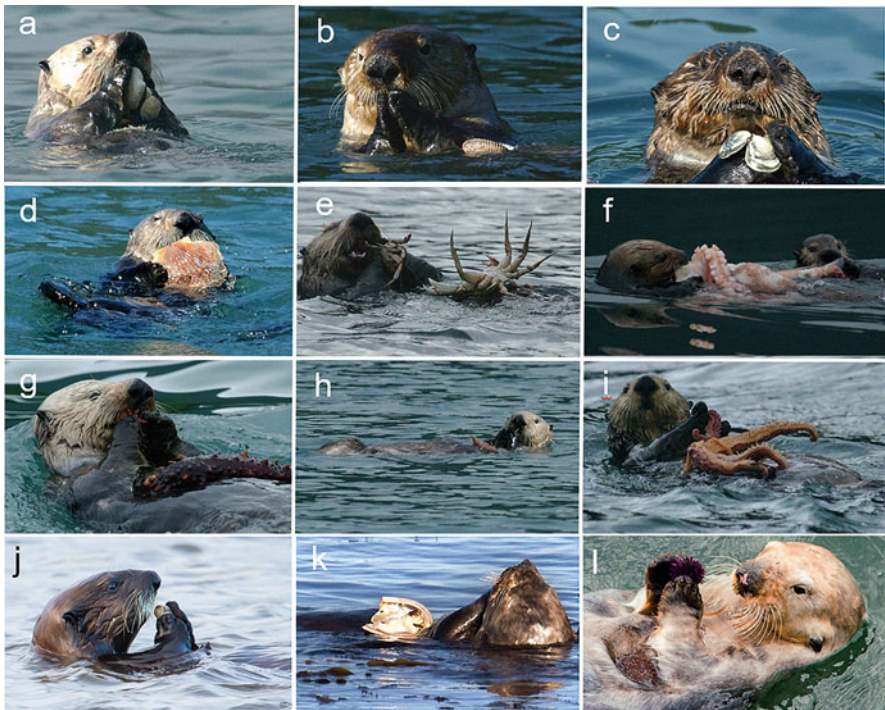
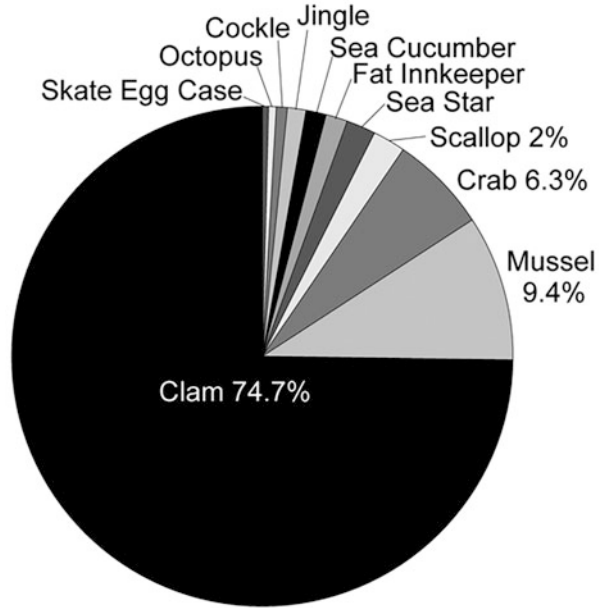


Fig. 4.9 Some prey species of sea otters in Alaska (a–i) and California (j–l): (a) butter clam (*Saxidomus gigantea*), (b) Nuttall’s cockle (*Clinocardium nuttallii*), (c) stained macoma (*Macoma inquinata*), (d) weathervane scallop (*Patinopecten caurinus*), (e) Dungeness crab (*Metacarcinus magister*), (f) giant Pacific octopus (*Enteroctopus dofleini*), (g) California sea cucumber (*Parastichopus californicus*), (h) Alaska spoonworm (*Echiurus echiurus alaskanus*), (i) sea star (probably *Evasterias echinosoma*), (j) Lewis’ moon snail (*Neverita lewisii*), (k) red abalone (*Haliotis rufescens*), and (l) Pacific purple sea urchin (*Strongylocentrotus purpuratus*). Images (a–i) were obtained under USFWS Permit No. MA84799B to R. Davis. Images (j) and (l) courtesy of J. Tomoleoni. Image (k) courtesy of N. La Roche

Fig. 4.10 Percent distribution of identified prey for sea otters in Simpson Bay, Alaska (Wolt et al. 2012)



Watt et al. 2000; Dean et al. 2002; Estes et al. 2009; Wolt et al. 2012; Tinker 2015; Coletti et al. 2016). However, they also feed opportunistically on slow-moving benthic fishes, the egg cases of rays, and herring roe on kelp (Kenyon 1969; Estes et al. 1982; Monson et al. 2000; Lee et al. 2009). Dietary analysis is based on stomach contents, fecal remains (spraint), and direct observations, and the method used can influence the results. Some prey, such as small mussels, are more commonly detected in spraint but are difficult to observe with binoculars or a spotting scope.

When sea otters have occupied an area for an extended period (i.e., >25 years), distinct diets are associated with two types of habitat. One diet, which is dominated by clams supplemented with mussels and crabs, is associated with unconsolidated or mixed sediments (e.g., mixed mud, sand, and gravel), often with a gently sloping bathymetry (Fig. 4.10; Barabash-Nikiforov 1947; Kenyon 1969; Calkins 1978; Kvitek et al. 1988, 1993; Dean et al. 2002; Laidre and Jameson 2006; Wolt et al. 2012; Hale et al. 2019). Sand lance (*Ammodytes hexapterus*) also may occur in the diet of sea otters in the Aleutian Islands and the Gulf of Alaska (Estes et al. 2009). The second diet, which is dominated by sea urchins (up to 90% *Strongylocentrotus* spp.) and various species of crabs, snails, and mussels, is associated with rocky-reef habitats, which often support both canopy and understory kelp forests (Barabash-Nikiforov 1947; Kenyon 1969; Estes et al. 1982; Estes and Duggins 1995; Watt et al. 2000; Tinker et al. 2007). In these rocky, kelp forest habitats, rock greenling (*Hexagrammos lagocephalus*) and Atka mackerel (*Pleurogrammus monopterygius*) may contribute significantly to the diet (Estes et al. 1982; Watt et al. 2000). The dichotomous diet associated with these two

habitats is apparent for sea otters in the Strait of Juan de Fuca (Washington State) (Laidre and Jameson 2006). In areas with a steep, rocky shoreline, the diet is dominated by red and purple sea urchins (up to >90%), whereas clams (63%) are the predominant prey in adjacent, soft-sediment habitats.

Foraging behavior and preferred prey can vary temporally in two contexts. One pertains specifically to sea otters recolonizing formerly occupied habitat in which prey species increased in abundance and size after the near extirpation of sea otters during the Maritime Fur Trade in the eighteenth and nineteenth centuries (see Chap. 10). As sea otters reoccupy historic habitat, large and easily captured prey (e.g., epibenthic abalone, sea urchins, and crabs) are consumed, resulting in reduced abundance and size (Lowery and Pearse 1973; Estes and Palmisano 1974; Kvitek et al. 1988). In some cases, this is followed by intraspecific dietary diversification (i.e., individual specialization) as foraging effort and prey become less energetically profitable because of their smaller size. As a result, some sea otters concentrate on certain prey using specialized foraging techniques, which may be transferred matrilineally (Tinker et al. 2007, 2008).

The other temporal context of sea otter prey preference, which may be independent of population density, is associated with seasonal, annual, decadal, or episodic changes in prey availability or energy content. For example, on Amchitka Island in the Aleutian Islands, Alaska, sea otters began to prey on the smooth lump sucker (*Aptocyclus ventricosus*), an oceanic fish that became a novel and significant part of the diet during winter and spring of a two-year study (Watt et al. 2000). In Prince William Sound, sea otters prey on small but numerous Pacific herring (*Clupea pallasii*) eggs, which are deposited as a thin layer on kelp during the spring spawn (Lee et al. 2009). Along the Katmai coast in Alaska, mussels are important (i.e., 34% occurrence in spraint) prey during winter and spring when they are gravid, but less important (5% occurrence) during summer (Coletti et al. 2016). Finally, there is a seasonal shift toward shallow water foraging in Prince William Sound, which is coincident with reproduction and increased energy density of intertidal bivalves (Bodkin et al. 2012).

4.5 Prey Capture

Sea otters are grouped with other raptorial predators even though they capture and manipulate prey with their forepaws (hand-oriented capture or prehension) rather than using their mouth (Werth 2000; Timm-Davis et al. 2015, 2017). This contrasts with the raptorial feeding behavior of mouth-oriented North American river otters, which feed primarily on fish. Unlike other carnivorous marine mammals, sea otters consume their prey at the surface rather than underwater (Figs. 4.4b and 4.9). As a result, they ingest and masticate food with rounded premolars and molars similar to those in terrestrial omnivores and carnivores (Fig. 4.1a–d; Reilly and Lauder 1990; Hiiemae and Crompton 1985; Markey and Marshall 2007; Timm-Davis et al. 2017). In contrast, Odontoceti (toothed whales) and Pinnipedia (seals, sea lions, fur seals,



Fig. 4.11 Sea otter using a stone as an anvil to open a butter clam. Image obtained under USFWS Permit No. MA-043219 to R. Davis

and walrus) capture and consume small prey underwater using either raptorial biting and/or suction without mastication, or slashing and tearing off pieces from larger prey that are small enough to swallow without further processing in the oral cavity (Kooymann and Davis 1986; Davis et al. 2013; Davis 2019).

Sea otters have foreshortened forelimbs, which they use to capture and manipulate prey and to grasp tools (e.g., rocks) to open hard-shelled prey, but not for locomotion (Figs. 4.9 and 4.11; see Sect. 3.1.2.2; Hall and Schallar 1964; Estes 1990; Fujii et al. 2015). Stones may be used as hammers to open hard prey at the surface or underwater. Because the phalanges are encased within the paws (i.e., the phalanges are not separate) and provide no independent movement or dexterity, rocks or prey must be held between the paws (Fig. 4.11; Pocock 1928; Howard 1975). Alternatively, a rock placed on the chest may serve as an anvil. A rock may be retained during foraging bouts and used multiple times by storing it beneath a flap of skin under the arm, which indicates anticipation and planning (Hall and Schallar 1964). The prevalence of tool use by sea otters varies geographically and may be passed culturally from females to offspring during the six-month dependency period (Mann and Patterson 2018; Estes et al. 2003). This behavior, which is more prevalent in sea otters along the coast of California and in Southeast Alaska than the Kuril Islands, Aleutian Islands, and Southcentral Alaska, may depend on diet specialization (e.g., turban snails) (Hall and Schallar 1964; Fujii et al. 2015, 2017). However, if sea otters from areas that normally do not use tools are given rocks or other hard objects while in captivity, they often pound the walls of their enclosure, sometimes causing significant damage (Kenyon 1969; R. Davis unpub. obs). This indicates that tool use may be an inherent behavior in sea otters, which manifests only when ecologically or behaviorally required.

To locate prey, sea otters use vision and the tactile sensitivity in their forepaws (Kenyon 1969). The eyes of sea otters are small and similar to those in diurnal terrestrial mammals, but with better accommodation underwater (Fig. 4.4a; see Sect.

3.3.1; Mass and Supin 2007). Underwater vision is emmetropic (focused), with a visual acuity similar to that in other marine mammals and the aerial acuity of many terrestrial mammals (see Sect. 3.3.1; Mass and Supin 2018). The eyes of sea otters differ from other marine mammals because the iris is attached to the frontal surface of the lens, so contraction and dilation of the iris significantly influences the curvature of the lens, allowing for emmetropic vision in air and underwater. However, there is no evidence for low-light adapted vision, which occurs in some Pinnipedia (Davis 2019). Hence, sea otters probably use vision to locate epibenthic prey under daylight conditions. However, tactile sensitivity may assist sea otters in locating epibenthic prey under low-light conditions, in rocky crevices, and under rocks (Shimek 1977; Kvitek and Oliver 1992). During the summer in Alaska, sea otters forage throughout the day because there is little change in diel light levels but transition to pronounced diurnal foraging during winter. This transition indicates the use of vision to locate epibenthic prey, although tactile sensitivity also may be important (Shimek 1977; Wolt et al. 2012; Esslinger et al. 2014).

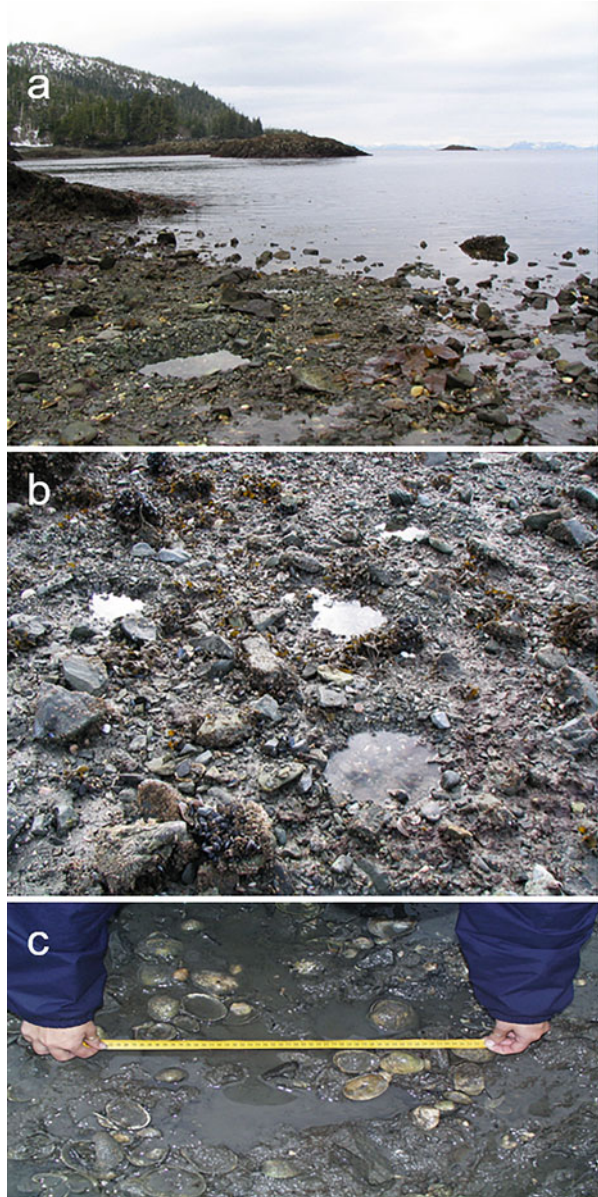
Sea otters use their teeth or stone tools to access the flesh of mega-invertebrates with a shell, exoskeleton, or test. When sea otters capture decapod crabs, they consume the limbs with the exoskeleton, while the body is consumed after removing the carapace (dorsal section of the exoskeleton) with the canine teeth (Fig. 4.9e). Abalone (*Haliotis* spp.), which are detached from rocks, are consumed by grasping and tearing pieces of the muscular foot and other organs with the upper and lower incisors and canine teeth. In some cases, sea otters may repeatedly strike an attached abalone with a rock, which facilitates capture by fracturing or jarring it loose (Hall and Schallar 1964; Houk and Geibel 1974; Hines and Loughlin 1980). Likewise, a stone tool may be used to crack the shells of moon snails (*Neverita lewisii*) and turban snails (*Tegula* spp.). To open sea urchins (i.e., *Mesocentrotus franciscanus*, *Strongylocentrotus droebachiensis*, *Strongylocentrotus purpuratus*), sea otters use their lower canine teeth to break the test from the ventral surface where the spines are shorter or use a stone to crack the test, then consume the yellow, fatty roe. When sea otters kill a Giant Pacific octopus (*Enteroctopus dofleini*), they consume the muscular legs and discard the head, but how they capture and handle these large (body mass ~15 kg with a radial arm span of up to four m) cephalopods underwater is a mystery (Fig. 4.9f; R. Davis, unpub. obs.). Small, epibenthic scallops (e.g., *Chlamys rubida*) and mussels (e.g., *Mytilus trossulus*) are eaten whole, while the shells of larger species (e.g., *Pecten caurinus*) are opened with the teeth (Fig. 4.9d). Sea cucumbers (e.g., *Parastichopus californicus*), Alaska spoonworms (e.g., *Echiurus echiurus alaskanus*), and sea stars (e.g., *Evasterias echinosoma*) are consumed whole (Fig. 4.9g, h, i). Sea otters consume fronds of kelp (e.g., *Saccharina latissima*) that are covered with the eggs of Pacific herring, which spawn during the spring in Alaska (Lee et al. 2009). Sessile benthic fish, such as kelp greenling (*Hexagrammos decagrammus*), Atka mackerel (*Pleurogrammus monopterygius*), Masked greenling (*Hexagrammos octogrammus*), and lumpfish (*Aptocyclus* sp.) also may be consumed (Kenyon 1969; Monson et al. 2000), but not moribund salmon after spawning (R. Davis unpub. obs.).

When searching for clams and other infaunal prey (e.g., *Saxidomus gigantea*, *Leukoma staminea*, *Macoma inquinata*, *Clinocardium ciliatum*, *Urechis caupo*), it is uncertain if sea otters search the seafloor for holes or siphons using vision (Hines and Loughlin 1980). Previous success may inform a sea otter on where to dig or to enlarge an existing hole. Once digging begins, sea otters excavate soft sediments (mud and mud-gravel) with their forepaws, creating foraging pits or trenches (i.e., 20–150 cm in diameter and 10–50 cm deep), although they may be enlarged during multiple dives (Figs. 4.4b and 4.12; Shimek 1977; Hines and Loughlin 1980; Kvitek et al. 1992, 1993; R. Davis unpub. obs.). This digging activity creates a plume of sediments and limits vision because of turbidity, so sea otters use the tactile sensitivity in their forepaws to locate clams and other infaunal prey (Fig. 4.4b, c; Shimek 1977; Hines and Loughlin 1980; R. Davis unpub. obs.). The threshold for tactile surface discrimination (i.e., alternating grooves) is ≤ 0.5 mm with a very rapid (< 1 s) response time, which is consistent with the enlarged somatosensory cortex representing the paws (see Sect. 3.3.3; Radinsky 1968; Strobel et al. 2018). This gives sea otters good tactile sensitivity to differentiate between clams and gravel, and their foraging dives are $\sim 87\%$ successful (Shimek 1977; Kvitek et al. 1993; Wolt et al. 2012). In some cases, sea otters may bring more than one prey item to the surface by placing them under a flap of skin (pouch) in the armpit (Mann and Patterson 2018). The role of vibrissae in prey detection is uncertain (see Sect. 3.3.3).

To extract the tissue from small bivalves (e.g., clams and mussels), prey is placed in the back of the mouth between the upper and lower premolars and molars, which requires a wide gape. In sea otters, gape angle ranges between $61\text{--}66^\circ$ with a maximum angle of 82° , which is greater than the maximum gape angle ($55\text{--}65^\circ$) for other carnivorans (Herring and Herring 1974; Timm-Davis et al. 2017). The jaws are closed and the shell is cracked or crushed with a bite force of up to 554 Newtons (125 pounds) (Timm 2013). The shells of otter-predated clams and other hard-shelled bivalves are commonly found along beaches and typically have one broken valve and one intact valve joined at the hinge (Fig. 4.13b, d). When a hard-shelled clam or cockle is cracked, the broken piece distal from the hinge is discarded, and the otter then opens the bivalve and scoops out the flesh with its lower incisors and canines (Fig. 4.9a). Soft-shelled clams (e.g., *Macomas*) are easily crushed into multiple pieces and discarded or partially consumed (Fig. 4.9c), while the broken shell and flesh of small mussels (e.g., *Mytilus* sp.) can be ingested entirely.

Because of their durophagous mode of feeding, the primary occlusal area provided by the enlarged, upper third premolars and lower first molars shows the greatest wear, breakage, and infection, which may limit longevity (Fig. 4.14; Fisher 1941; Kenyon 1969). In addition, significant malocclusion of the postcanine teeth may occur in recently weaned pups feeding on hard prey but whose deciduous teeth have not been replaced. When sea otters can no longer feed efficiently, they die rapidly of starvation because of their elevated basal metabolic rate (see Sect. 3.2.4).

Fig. 4.12 (a and b) Sea otter foraging pits, Prince William Sound, Alaska. (c) Sea otter foraging pit (~20 cm in diameter, 8 cm deep) in the intertidal



4.6 Daily Foraging Duration

Foraging dives often occur in bouts (i.e., two or more consecutive dives) with 1–2 min between dives depending on foraging success and prey handling (Bodkin et al. 2004; Wolt et al. 2012). Depending on the number of consecutive dives, bouts may be several hours in duration (Thometz et al. 2016). The amount of time that sea

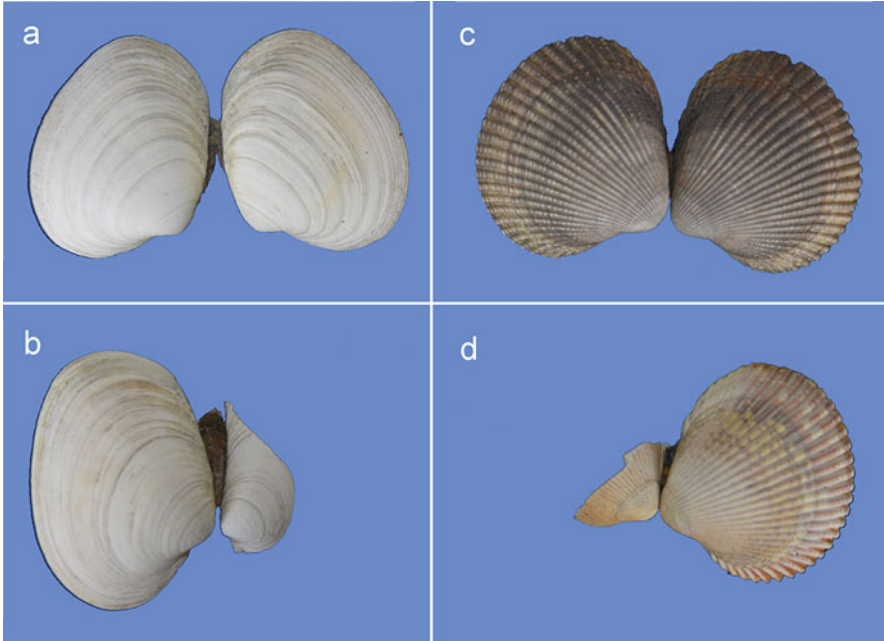


Fig. 4.13 Butter clams (*Saxidomus gigantea*) with (a) intact hinged valves and (b) one broken valve resulting from sea otter predation. Nuttall cockles (*Clinocardium nuttallii*) with (c) intact hinged valves and (d) one broken valve resulting from sea otter predation

otters devote to foraging depends on age, sex, reproductive status, presence of a pup, time of year, and prey availability (which varies geographically, seasonally, and episodically) (Shimek and Monk 1977; Monson et al. 2000; Dean et al. 2002; Esslinger et al. 2014; Tinker 2015; Coletti et al. 2016; Cortez et al. 2016). In addition, variation may result from the sampling method (direct observation vs. radio telemetry and time-depth recorders), diel period (daylight hours only vs. 24-h monitoring), and seasonality (summer vs. annual) (Loughlin 1980; Garshelis et al. 1986; Ralls and Siniff 1990; Gelatt et al. 2002; Bodkin et al. 2007; Tinker et al. 2007, 2008; Esslinger et al. 2014; Cortez et al. 2016). Unlike other marine mammals, sea otters have small or no energy reserves in the form of blubber, so they feed frequently (i.e., every 3–4 h). If feeding is interrupted, they enter a fasting state within 4–8 h and a state of starvation within 24 h. Hence, foraging is a daily activity that cannot be postponed, although it appears to be reduced in females with neonatal pups during the first 3 weeks postpartum (Gelatt et al. 2002; Esslinger et al. 2014; Thometz et al. 2014, 2016; Cortez et al. 2016).

Adult female sea otters demonstrate distinctive feeding behavior during pup rearing, which is independent of prey availability (Thometz et al. 2016). Female sea otters with pups <4 weeks of age (mean body mass = 1.8 kg) reduce (but do not eliminate) foraging effort to protect their altricial pups from predation by bald eagles (*Haliaeetus leucocephalus*) and other threats (Fig. 4.15; see also Sect. 7.4; Sherrod

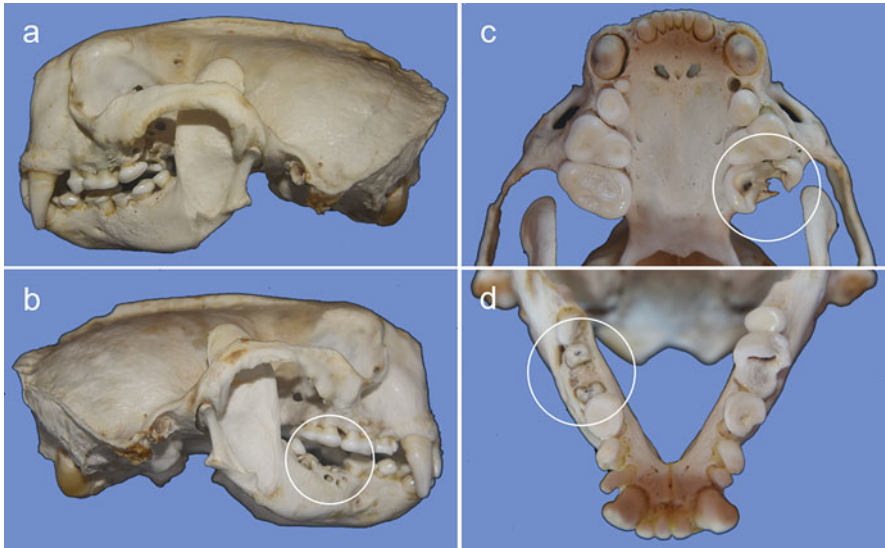


Fig. 4.14 The left (a) and right (b) side of the skull and the upper jaw (c) and lower jaw (d) from an adult sea otter skeleton that was found above the high tide line in Simpson Bay, Alaska. The teeth were heavily worn, and one upper and one lower molar (circles) were broken or missing. Bone necrosis was evident around the broken teeth and may have resulted from periapical abscesses (Kenyon 1969)

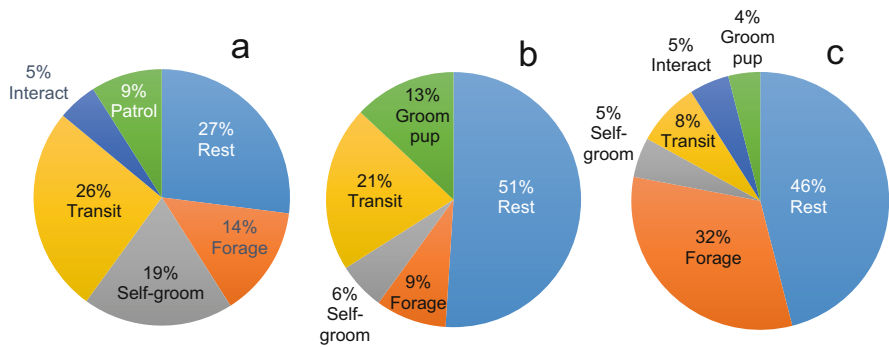


Fig. 4.15 Average 24-h activity budgets sea otters: (a) male, (b) female with pup <4 weeks old, and (c) female with pup 8–12 weeks old. Resting behavior includes sleeping on the water’s surface. Foraging behavior includes the time submerged and while handling prey at the surface between dives. Self-groom refers to felting the fur to maintain an air layer. Groomed refers to the pup being groomed by the female Transit refers to is directed swimming at the surface, usually in the supine position (belly up with head facing backward) using alternate or simultaneous pelvic paddling. Nursing refers to the percentage of time spent suckling. Interact refers to socializing with other otters and, in the female, occasional mating behavior. Data for females with pups were collected simultaneously in Simpson Bay, Alaska during the summer months of June to August (Cortez et al. 2016)

Table 4.1 Daily foraging effort (% of 24-h period) of sea otters in Alaska and California. Estimates were based on either direct observation, radio telemetry, time-depth recorders, or a combination of methods. Results are for adult and subadult males and females. Some of the females may have been pregnant or had pups. The Aleutian Islands and Prince William Sound are located in Alaska

Food Limited (%)	Non-Food Limited (%)	Location	References
40	29	Southeast Alaska	Bodkin et al. (2007)
55	17	Aleutian Islands	Estes et al. (1982)
50	37	Prince William Sound	Garshelis et al. (1986)
42	25	California	Tinker et al. (2008)
49	41	Prince William Sound	Dean et al. (2002)
44	37	California	Thometz et al. (2015)
<i>Mean</i>			
46.7	31.0		

et al. 1975; Esslinger et al. 2014; Gelatt et al. 2002; Thometz et al. 2016; Cortez et al. 2016). To remain in energy balance and lactate during this period, females rely on small fat deposits, which they acquire during gestation but deplete within 3 weeks (see Sect. 7.3). As the pup increases in size, so does the female's foraging effort. By the time a pup is 8–12 weeks of age (mean body mass = 5.8 kg), the female devotes 32–48% of the day to foraging to support her own metabolic needs and provide food (milk and prey) to the growing pup (Thometz et al. 2014, 2016; Cortez et al. 2016). As the pup approaches adult size (15–20 kg) at the weaning age of six months, the female may spend up to 50% of the day foraging (Estes et al. 1982). This leaves the remaining time for essential body maintenance behaviors, such as resting (~45%) and self-grooming (~5%), which may be a minimum for good health. At some point, the energetic demands may exceed the foraging ability of the female, reduce the time for body maintenance behaviors, and cause a decrease in body condition, which can lead to pup abandonment, early weaning, or mortality in severe cases (see Sect. 7.4; Chinn et al. 2016).

Although various factors influence the amount of time that sea otters forage, it generally increases as prey availability decreases and a population approaches carrying capacity (Table 4.1; Eberhardt and Siniff 1977; Estes et al. 1982; Garshelis et al. 1986; Dean et al. 2002; Bodkin et al. 2007; Tinker et al. 2008; Thometz et al. 2016). A comparison among seven studies showed that sea otters spent 46% (11.0 h) of each day foraging in areas that were food limited and 31% (7.4 h) in areas where it was not, although duration of reoccupation did not always correlate with food availability (Loughlin 1980; Estes et al. 1986; Bowlby et al. 1988; Ralls and Siniff 1990; Gelatt et al. 2002; Walker et al. 2008). In addition to the percentage of time spent foraging, the rate of energy intake has been used as a metric for prey availability (see Sect. 8.6). Along the Katmai coast of Southwest Alaska, sea otters had an energy intake rate of 12 kcal min⁻¹ (50 kJ min⁻¹) in 2006 when the population was growing (Coletti et al. 2016). By 2015, the energy intake rate had declined 62% after the sea otter population reached an equilibrium density (Fig. 8.5). As a result, sea otters spent more time foraging to remain in energy balance.

Sea otters in Prince William Sound show seasonal differences in foraging behavior (Esslinger et al. 2014). Females and males spend less time foraging during summer months compared to the remainder of the year. In addition, they spend more time foraging during daylight hours in the winter, which indicates that vision is important for prey detection.

4.7 Carrying Capacity and Foraging Behavior

As sea otters reoccupy an area from which they were extirpated, enhanced populations of epifaunal prey, such as sea urchins, crabs, and abalone, generally decline first, followed by infaunal species, such as bivalves, depending on the type of habitat (Kimker 1982; Ostfeld 1982; Kvitek and Oliver 1988, 1992; Kvitek et al. 1988, 1992, 1993; Coletti et al. 2016). In rocky habitats with thriving kelp forests where herbivorous mega-invertebrates have declined because of predation, sea otters may exhibit intraspecific diet diversity (i.e., diet specialization among individuals within a population) associated with density-dependent competition for food (Estes et al. 1982; Tinker et al. 2007). Sea otters in the Aleutian Archipelago increased consumption of demersal fish as sea urchin populations declined because of predation (Estes 1990; Watt et al. 2000). Similar to tool use, diet specialization as a response to competition for diminishing prey may be a learned behavior passed from females to their offspring, although it does not occur in all populations (Wolt et al. 2012; Thometz et al. 2016). For sea otters in soft-and mixed-sediment benthic habitats with low densities of epifaunal invertebrates, prey switching may not occur as bivalve densities decline. For example, in Prince William Sound, Alaska, foraging success rates remained high over many decades for a diet dominated by clams (Calkins 1978; Garshelis et al. 1986; Dean et al. 2002; Wolt et al. 2012; Cortez et al. 2016).

The exploitation of abundant mega-invertebrates by sea otters as they reoccupy historic habitat has increased our understanding of their role in the community structure of nearshore habitats (Estes and Palmisano 1974; Estes and Duggins 1995). As sea otter population density approaches carrying capacity, other extrinsic factors may influence population equilibrium. For example, killer whale predation on sea otters in the Aleutian Islands since the 1980s allowed sea urchin populations to recover and thrive as they did when sea otters were hunted to near-extinction during the Maritime Fur Trade (see Chap. 10; Estes et al. 1998). As sea otter abundance declined by ~90%, sea urchin populations increased and kelp forests disappeared, creating sea urchin barrens. Sea otters that remained were no longer food-limited and established a new equilibrium density regulated by killer whale predation (Tinker 2015).

Food availability is known to influence the equilibrium density of sea otter populations, and the amount of time that sea otters forage is an important indicator of the population status (Tinker 2015). However, each population has its own combination of intrinsic (territoriality, emigration) and extrinsic (food availability,

predators, disease, human-related mortality, weather, episodic environmental events) factors affecting equilibrium density. Hence, a single factor (e.g., food availability) regulating population density may not necessarily predominate or may vary over time to produce a complex interaction among the effects of various factors influencing foraging behavior (Fowler 1987; Davis et al. 2019; Watt et al. 2000; Smith et al. 2021).

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