in Thailand and in Sri Lanka. There has been active exploration for oil and gas in some parts of their documented range, including Western Australia, Timor Sea, and northwest Madagascar, involving seismic surveys that present the potential to disturb behavior and mask low-frequency vocalizations. With so little known about distribution and population sizes, it is not currently possible to fully assess conservation status or threats to this species.

See Also the Following Articles

Baleen Whales (Mysticeti) ■ Bryde's Whale

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OSMOREGULATION

Daniel P. Costa

Even though most marine mammals live in an aquatic medium, the animals' internal fluid composition differs from the ambient environment and therefore requires active processes to maintain it within a very narrow range. Osmoregulation describes the way in which the internal water and electrolyte concentration of this internal environment is maintained. When animals feed, they take in both water and electrolytes that must be excreted. While they gain water from metabolizing food, they lose water through evaporation when breathing to obtain the oxygen necessary for metabolism. Maintenance of a constant internal environment requires that whatever comes into the animal must equal what goes out. The ways water and electrolytes enter and leave the organism are shown in Fig. 1. For example, if a dolphin consumes a large volume of water and electrolytes, it must have the capability to excrete an equivalently large volume in the feces and urine, through breathing and in milk during lactation. Conversely, if a seal on the beach does not have access to food or water, it must be able to survive on water produced from metabolism, which requires mechanisms to reduce water loss.

I. Water and Electrolyte Ingestion

Water and electrolytes enter the animal through the ingestion of food and water. Water that is consumed in food or actively drunk is called preformed water. Compared to terrestrial mammals, marine mammals consume a water rich diet of fish and marine invertebrates (70%–80% water). Prey contains electrolytes and nitrogen

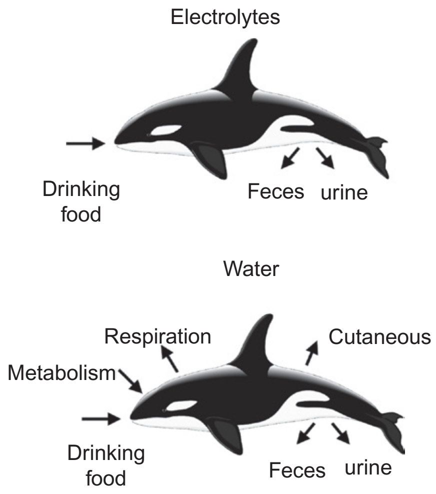

Figure 1 *Schematic of ways water and electrolytes enter and leave a marine mammal. Excretion of electrolyte and water as milk only occurs when females are lactating.*

that require water for excretion by the kidney. Ingestion of invertebrate prey (i.e., squid, krill, clams), results in the intake of more electrolytes than vertebrate prey (fish) (Table 2). While an animal like a manatee, *Trichechus* spp., with access to freshwater can drink freshwater to flush electrolytes, an oceanic dolphin can only drink seawater. Water is also produced by metabolism; this is called metabolic water production (MWP). The amount of MWP varies with the chemical composition of the diet. For example, 1.07 g of water is generated for every gram of fat oxidized, 0.56 g H_2O/g of carbohydrate, and only 0.39 g H_2O/g of protein.

II. Water and Electrolyte Output

Both water and electrolytes are excreted in the urine and feces, whereas only water is lost through evaporation. Water is lost via evaporation both across the skin, cutaneous water loss, and through the lungs, respiratory evaporative water loss. While pinnipeds have sweat glands, they do not produce much sweat so there is little loss of salt across the skin (Whittow et al., 1972). Unlike sea birds and marine reptiles, marine mammals lack specialized glands to concentrate and excrete salts and have developed a specialized kidney to handle the large volume of electrolytes and water they process (Ortiz, 2001).

III. Do Marine Mammals Drink Seawater?

In most cases, marine mammals can derive sufficient water from their diet so that they do not need to ingest seawater. Measurements of the water, electrolyte, and nitrogen intake, coupled with measurements of evaporative, urinary, and fecal water loss suggest that a feeding seal can get all of the water it needs from its prey (through both preformed and metabolic water) (Ortiz, 2001).

Can animals drink seawater when they become osmotically stressed? A marine mammal can gain freshwater by drinking seawater if they can produce urine that is more concentrated than seawater. The more concentrated the urine, the greater the amount of "freshwater" that can be derived. A simple calculation can show how much water is gained or lost relative to the concentrating ability of the kidney (Table 1). If a humpback whale, *Megaptera novaeangliae*, consumed 1000 mL of seawater and its kidney could excrete urine with a chloride concentration of 820 mmol/L, it could gain 350 mL

TABLE 1 Differences in the Urine Concentrating Ability of a Humpback Whale, *Megaptera novaeangliae*, and a Human Given to Show a Gain or Loss of Body Water After the Ingestion of a Liter of Seawater

	Seawater consumed volume (mL)	Cl^- concentration (mmol L^{-1})	Max urine concentration (mmol L^{-1})	Urine volume produced (mL)	Water balance gain or loss (mL)
Whale	1000	535	820	650	+350
Human	1000	535	400	1350	−350

TABLE 2 Upper Rows Show the Maximum Urine Chloride Concentration and Maximum Osmolarity Measured for Marine Mammals Compared to Values of Representative Terrestrial Mammals. The Lower Rows Show the Chloride Concentration and Osmolarity for Seawater and the Body Fluids of Representative Prey Items

Species	Cl concentration (mEq L^{-1})	Osmolarity (mOsm L^{-1})
MYSTICETES		
Blue whale, *Balaenoptera musculus*	450	1344
Fin whale, *Balaenoptera physalus*	850	1737
Sei whale, *Balaenoptera borealis*	370	1524
Humpback whale, *Megaptera novaeangliae*	820	1500
Minke whale, *Balaenoptera. acutorostrata*	291	1532
Bryde's whale, *Balaenoptera edeni*	266	1319
ODONTOCETES		
Long finned pilot whale, *Globicephala melas*		1081
Rough-toothed dolphin, *Steno bredanensis*		1700
Common bottlenose dolphin, *Tursiops truncatus*	2222	2658
Sperm whale, *Physeter macrocephalus*	476	1130
PINNIPEDS		
Baikal seal, *Phoca sibirica*	202	2374
Ringed seal, *Phoca hispida*	267	2400
Weddell seal, *Leptonychotes weddelli*		2034
Northern elephant seal, *Mirounga angustirostris*		1850
Harbor seal, *Phoca vitulina*	508	2050
South African fur seal, *Arctocephalus pusillus*	567	2364
California sea lion, *Zalophus californianus*	760	2223
Sea otter, *Enhydra lutris*	555	2130
TERRESTRIAL MAMMALS		
Human, *Homo sapiens*	400	1230
White rat, *Rattus norvegicus*	760	2900
Camel, *Camelus dromedarius*	1070	2800
Sand rat, *Psammonys obesus*	1920	6340
SOLUTE CONCENTRATIONS OF POTENTIAL PREY AND SEAWATER		
Market squid, *Loligo opalescens*	433	1032
Atlantic cod, *Gadus morhua*	150	308
Seawater	535	1000

of freshwater. Whereas humans, who cannot produce urine as concentrated as seawater, would lose 350 mL of freshwater for every liter of seawater consumed. The maximum urine concentrating ability of some marine and terrestrial mammals is presented in Table 2.

While many species of marine mammals have the capacity to drink seawater, they do not always do so. Studies using labeled water and/or electrolytes has documented that some marine mammals drink seawater (Table 3; Telfer et al., 1970). The difference between the total water and/or electrolyte influx and that measured from feeding or metabolism could only come from the ingestion of seawater. Specifically, sea otters (*Enhydra lutris*), common bottlenose dolphins (*Tursiops truncatus*), hooded seals (*Cystophora cristata*), and harp seals (*Phoca groenlandica*) that were feeding; and Galapagos fur seals (*Arctocephalus galapagoensis*), short-beaked common dolphins (*Delphinus delphis*), and short-finned pilot whales (*Globicephala macrorhynchus*), that were fasting, consumed seawater (Hui, 1981; Costa, 1982; Costa and Trillmich, 1988; Skalstad and Nordoy, 2000; Storeheier and Nordoy, 2001). In contrast, feeding and fasting harbor seals (*P. vitulina*), feeding northern fur seals (*Callorhinus ursinus*), and fasting Antarctic fur seals (*A. gazella*), all had negligible amounts of seawater ingestion (Depocas et al., 1971; Ortiz et al., 1978; Costa, 1987; Costa and Trillmich, 1988). Weaned northern elephant seal pups (*Mirounga angustirostris*) fasted for 3 months without measurable ingestion of seawater (Ortiz et al., 1978). However, fur seals in warm environments tended to drink seawater whereas those in colder climates did not (Costa and Trillmich, 1988).

IV. Relative Reductions in Water Loss

As described earlier, many marine mammals do not drink seawater. Amazingly, northern elephant seals can fast for months without access to food or water (Fig. 2). The only water available to fasting seals is MWP from the oxidation of fat and protein in their tissue (Ortiz et al., 1978). This requires that water lost in the urine, feces, and from cutaneous and respiratory evaporation water loss be less than MWP.

Given their aquatic lifestyle, marine mammals have low evaporative cutaneous (skin) water loss. In water, there would be no evaporative water loss, and on land, as pinnipeds apparently do not sweat, their cutaneous evaporative loss is quite low (Whittow et al., 1972). However, common dolphins (*Delphinus* spp.) and harbor porpoise (*Phocoena phocoena*) appear to lose a substantial amount of water across their skin surface (Hui, 1981; Andersen and Nielsen, 1983). Common dolphins lose as much as 4 L H_2O/day, or 70% of their total water intake. It may be that seawater ingestion is necessary to make up for the water lost across the skin.

Endotherms lose water through respiration (respiratory evaporative water loss) by the simple physics of warming and saturating the air they breathe. Ambient air is inhaled, warmed, and humidified to core body temperature. Air fully saturated (100% relative humidity) with water at 10°C contains 10 mL H_2O/L of air, whereas fully saturated air in the lungs at 37°C contains 40 mL H_2O/L of air. Unless there is a mechanism to recover water, a seal would lose 30 mL of H_2O for every liter of 10°C air it inhaled.

TABLE 3 The Rate of Seawater Ingestion Measured, Using Isotopic Tracers Techniques, in Marine Mammals

	Body mass (kg)	Rate of seawater consumption		
		mL kg^{-1} day^{-1}	mL day^{-1}	Proportion of total water influx (%)
Pilot whale, *Globicephala melaena*	605	4.5	2720	n.a.
Bottlenose dolphin, *Tursiops truncatus* feeding	198	37.5	7420	68.8
Common dolphin, *Delphinus delphis* fasting	57	12.5	700	17
Antarctic fur seal, *Arctocephalus gazella* fasting	39.4	1.0	39	15
Galapagos fur seal, *A. galapagoensis* fasting	37.4	18.3	684	84
Northern fur seal, *Callorhinus ursinus* feeding	23	1.8	41	2.0
Harbor seal, *Phoca vitulina* feeding	29.4	3.0	137	9.2
fasting	28.6	1.3	37	7.3
Harp seal, *Pagophilus groenlandicus* feeding	44.5	19	900	27
Hooded seal, *Cystophora cristata* feeding	29	9	300	14
Sea otter, *Enhydra lutris* feeding	24.3	62	1507	23

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Marine mammals employ a few tricks to reduce the water lost through respiration (Lester and Costa, 2006). The first is to breathe periodically (apneustic breathing); i.e., to inhale, hold their breath and then exhale. This increases the amount of oxygen extracted per liter of air inhaled. While terrestrial animals typically extract 4% oxygen per breath, marine mammals can extract as much as 8% per breath. Marine mammals thus breathe less frequently and thereby lose less water because they make fewer respirations to obtain an equivalent amount of oxygen.

Pinnipeds, sea otters, and polar bears (*Ursus maritimus*), further reduce their respiratory evaporative water loss by employing a nasal countercurrent heat exchanger. This structure is also present in rodents and desert ungulates. The nasal passages of these mammals are narrow and this allows them to recover water vapor and heat that was added to the air at inhalation (Huntley et al., 1984). The nasal turbinates are composed of very small passageways that allow intimate contact between the inhalant air and the nasal membranes (Fig. 3). As the cold air passes across the small nasal passage, it is warmed and water evaporates. Heat and moisture is transferred from the nasal passage to the air so that by the time it leaves the nasal turbinate it is warmed and humidified to body temperature. In the process of warming the inhaled air, the membranes lining the nasal passages have cooled. On the following exhalation the warm moisture laden air is cooled as it passes over the cool membranes. As the air temperature declines, water vapor condenses and is recovered in the nasal passage (Fig. 4).

Although there are no direct measurements, fecal water loss of feeding cetaceans is probably quite high. Fecal water loss in pinnipeds feeding on fish is comparable to that of terrestrial carnivores. However, it is not clear how marine mammals that ingest seawater avoid the laxative effect of $MgSO_4$. Fasting animals have negligible fecal water loss, as their fecal production is quite low.

The rate and amount of water lost in the urine is directly related to both the urine concentrating ability of the kidney and the hydration state of the animal. The kidney ultimately regulates the water and electrolyte state of the animal. When there is a surplus of water, the kidney produces dilute urine, whereas during periods of water stress, the kidney excretes concentrated urine. The kidney must be able to excrete metabolic end products in the form of urea and all excess electrolytes with the water that remains after cutaneous, respiratory, and fecal water loss. While at sea, marine mammals either get all of their water from their prey or they drink seawater. This requires the processing of large urine volumes at moderate-to-high urine concentrations, and most marine mammals

Figure 2 *A male northern elephant seal,* Mirounga angustirostris, *fasting on the beach without access to water. Elephant seals undergo fasts of up to 3 months without access to water (Photo by Dan Costa).*

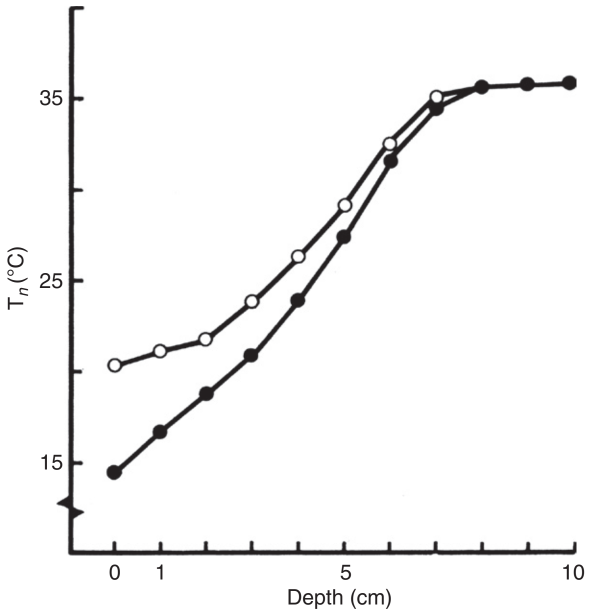

Figure 4 *Temperature at 1-cm intervals within the nasal passage of a weanling elephant seal where the ambient air temperature was 15°C (open symbols) and 5°C (closed symbols). With permission from the Company of Zoologists.*

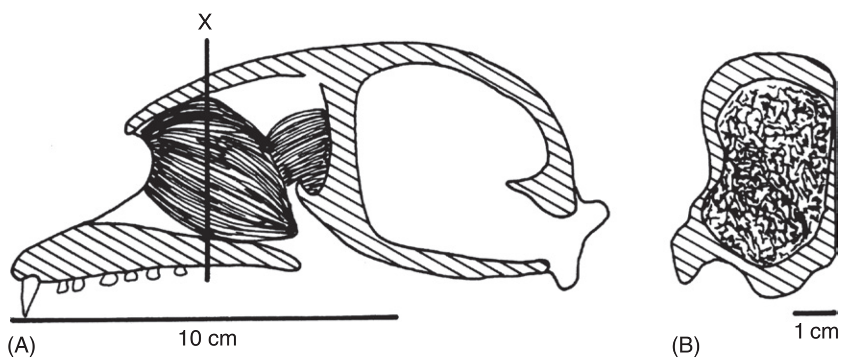

Figure 3 *(A) Sagittal section of a weanling elephant seal skull showing the nasal turbinates. (B) Cross section through one half of the skull at line "X" in A. With permission from the Company of Zoologists.*

(cetaceans, pinnipeds, sea otters) have a specialized lobulate or reniculate kidney that enables them to do this (Ortiz, 2001) (Fig. 5).

Marine mammals that live in freshwater, like the Baikal seal and river dolphins have the opposite problem in that they have to produce a very dilute urine that allows them to excrete the water that flows in and retain the electrolytes ingested with their food. Further, mammals that are strictly marine when held in freshwater require supplementation with electrolytes as their kidneys are not capable of producing a sufficiently hypo-osmotic urine (Geraci, 1972). Interestingly, Baikal seals not only have the ability to produce a hypo-osmotic urine and retain electrolytes, but also have retained the ability to produce a rather concentrated urine (Table 2).

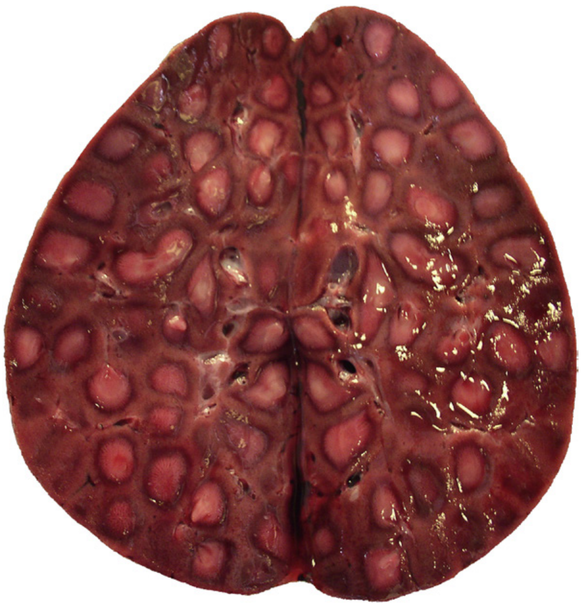

Figure 5 *A saggital section of a kidney from a California sea lion,* Zalophus californianus, *showing the two halves. Notice the individual lobules or reniculi that together make up the kidney. Each lobule acts like an individual kidney. Cetaceans, pinnipeds, and the sea otter have kidneys constructed this way (Photo by Dave Casper).*

Pinnipeds, such as the northern elephant seal, undergo prolonged fasts on land without access to water. These animals are able to stay in water balance by a combination of low rates of evaporative water loss, coupled with low rates of urine production (Lester and Costa, 2006). Elephant seals, *Mirounga* spp., utilize fat almost entirely (96%–98%) for their metabolism while fasting. Fat oxidation produces only CO_2 and H_2O, whereas oxidation of protein results in CO_2, H_2O, and urea. Urea is the end product of de-amination of amino acids and requires water to be excreted by the kidney. Therefore, fat is not only an efficient way to store energy, but also economical with respect to water balance.

V. Water Balance During Reproduction

Many female pinnipeds do not have access to water while they suckle their young, and thus could become dehydrated during lactation (Fig. 6). However, marine mammal milk is high in lipid and low in water compared to terrestrial mammals (Table 4). This has the advantage of providing the young with the maximum amount of energy with minimal loss of water from the mother. Pups also do not have access to water, and therefore must be capable of maintaining water balance entirely from the water provided in the milk.

VI. Evolutionary Implications

Modern tools including stable isotopes and molecular genetics are providing insight into the evolution of osmoregulation in marine mammals. As the stable isotope oxygen-18 is more abundant in seawater than freshwater it can be used to trace which ancient whales were completely marine (Thewissen et al., 1996). Surprisingly, fossils of *Ambulocetus*, a middle Eocene ancient whale, are found in marine sediments, but the isotopic signature of their teeth indicates that they ingested freshwater, implying that they either remained near sources of freshwater so they could drink or that their early development occurred in freshwater. In contrast, *Indocetus*, also a middle Eocene ancient whale, has O^{18} levels that are comparable to modern cetaceans who drink seawater indicating that this ancient cetacean was completely marine, completely independent of freshwater.

Finally, modern genomics has made it possible to examine whether osmoregulatory capacity has occurred at the molecular level. Gene sequences from 11 species of cetacean have shown that there has been positive selection for genes coding for angiotensin

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Figure 6 *A female northern elephant seal,* Mirounga angustirostris, *and her suckling pup. Over the entire 28 day lactation interval the mother does not eat or drink. All the water and energy contained in the milk provided to the pup must come from the mother. Milk is also the only source of water for the pup. After the pup is weaned it will fast on the beach between 2 and 3 months. During this fasting period the pups do not drink measureable amounts of seawater.*

TABLE 4 Water, Lipid, and Protein Content of Marine Mammal Milk Compared to Human and Cow Milk

	% Water	% Lipid	% Protein
Blue whale, *Balaenoptera musculus*	45.4	41.5	11.9
Minke whale, *B. acutorostrata*	60.4	24.4	13.6
Sperm whale, *P. macrocephalus*	64.5	24.4	9.1
Bottlenose dolphin, *T. truncatus*	69.6	15.3	11.5
Galapagos fur seal, *A. galapagoensis*	58.5	29.4	12.1
Northern fur seal, *C. ursinus*	44.3	41.5	14.2
Australian sea lion, *N. cinerea*	64.7	25.8	9.5
Northern elephant seal, *M. angustirostris*	36.6	54.4	9.0
Hooded seal, *C. cristata*	33.7	61.4	4.9
Grey seal, *H. grypus*	36.6	52.2	11.2
Human	87.6	3.8	1.2
Cow	87.3	3.7	3.3

converting enzyme (ACE), angiotensinogen (AGT), SLC14A2, and aquaporin 2 (AQP2) (Xu et al., 2013). AQP2 and SLC14A2 are associated with water and urea transport, while ACE and AGT are associated with water and salt transport. Positive selection in these gene are likely associated with the unique adaptations to retaining freshwater while eliminating and processing the additional salt load associated with life in the ocean.

See Also the Following Articles

Circulatory System ■ Diving Physiology ■ Thermoregulation

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OTTERS

Enhydra lutris and Lontra felina

M.T. Tinker, J.L. Bodkin, M. Ben-David and J.A. Estes

There are 13 extant otter species (Lutrinae, a subfamily of Mustelidae, Carnivora). At least six of these are fully or partially marine living. Of these, only sea otters (*Enhydra lutris*) are fully aquatic. The other species are semi-aquatic although chungungos (*Lontra felina*) feed exclusively in marine habitats (Fig. 1). Sea otters occupy a broad range of marine habitats, from protected bays and estuaries to exposed outer shores, while chungungos occur only along exposed shorelines.

I. Characteristics and Taxonomy

Otters are distributed over all continents except Australia and Antarctica; however, marine-living otter species and populations occur mainly at high latitudes (Fig. 2). At low latitudes, primary production in freshwater exceeds that of the coastal ocean, whereas at high latitudes the pattern is reversed. This production gradient may have drawn primitive water-living otters into the sea at high latitudes (Kruuk, 2006).

Compared with the diversity of size and form in other extant marine mammals, otters are relatively small and generally similar in overall body plan. Body mass ranges from <5 kg in chungungos to about 40 kg in sea otters. Their shortened limbs, lengthened and often stout tails, slim and elongated head, neck and body, and loosely articulated axial skeleton combine to create an almost serpentine appearance. The internal morphology of otters is generally unremarkable, except for the sea otter's comparative large lung and blood volumes (which facilitate floatation and oxygen storage), and