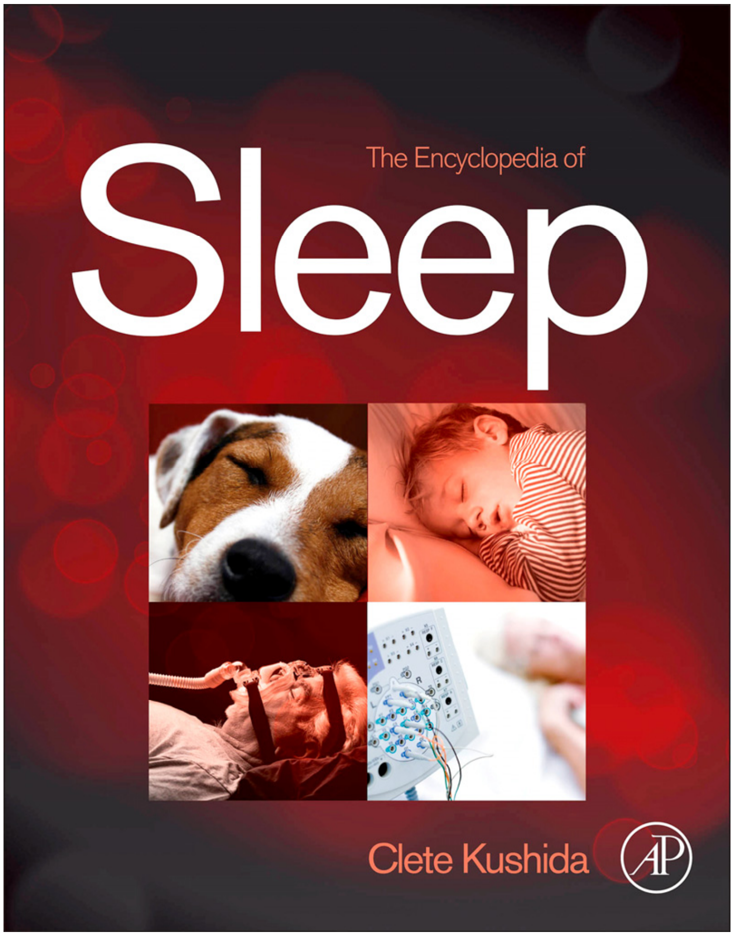

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Sleep in Aquatic Species

O I Lyamin, UCLA/VA GLAHS Sepulveda, CA, USA; Utrish Dolphinarium Ltd., Moscow, Russia; Severtsov Institute of Ecology and Evolution, Moscow, Russia
J L Lapierre, UCLA/VA GLAHS Sepulveda, CA, USA; University of Toronto, Toronto, ON, Canada
L M Mukhametov, Utrish Dolphinarium Ltd., Moscow, Russia; Severtsov Institute of Ecology and Evolution, Moscow, Russia

Glossary

Apnea: A temporary suspension of breathing.
Asymmetrical slow-wave sleep (ASWS): A sleep stage with greatly expressed interhemispheric electroencephalogram asymmetry both in the amplitude and frequency range of major rhythms.
Behavioral sleep: A state which includes sleep and quiet waking states; an estimate of the total sleep time based on behavior criteria.
Bilateral slow-wave sleep (BSWS): A sleep stage with EEG slow waves recorded synchronously in both brain hemispheres.
Cetaceans: Members of the order Cetacea, which includes the fully aquatic marine mammals commonly known as whales, dolphins, and porpoises.
Pinnipeds: Members of the order Pinnipedia, which includes a diverse group of semiaquatic marine mammals comprising the families Odobenidae (the walrus), Otariidae (eared seals – fur seals and sea lions), and Phocidae (earless seals or true seals).
Slow-wave activity (SWA): EEG slow waves in the range of 0.5–1.0 and 4.0 Hz.
Slow-wave sleep (SWS): A sleep stage with EEG slow waves recorded in cerebral hemispheres.
Total sleep time (TST): The time spent in SWS and rapid eye movement sleep combined.
Unihemispheric slow-wave sleep (USWS): A sleep stage with EEG slow waves recorded in one hemisphere simultaneously with low-voltage waking (desynchronized) EEG recorded in the other hemisphere.

Hallmarks of the Studies of Sleep in Aquatic Mammals

John Lilly pioneered early experimental studies of dolphins and proposed several theories regarding dolphin physiology and the nature of their sleep. Serafetinides and Sherley performed the first polygraphic recording (electroencephalogram (EEG), electromyogram, and electrooculogram) on an adult pilot whale (*Globicephala scammoni*), reporting frequency asynchrony and voltage discrepancies between the EEG in the two cerebral hemispheres. Lev Mukhametov and colleagues performed polygraphic recordings in four bottlenose dolphins (*Tursiops truncatus*) in 1973. They founded the Utrish Marine Station on the Black Sea in Russia and started an extensive research program investigating sleep in aquatic mammals. Ridgway et al. were the first to record sleep electrophysiologically in a pinniped species – the gray seal (*Halichoerus grypus*). To date, sleep (electrophysiologically or behaviorally) has been examined in more than 20 species of aquatic mammals, with the majority of experimental data collected at the Utrish Marine Station in Russia.

Sleep in Cetaceans

Sleep has been studied electrophysiologically in five cetacean species: the bottlenose dolphin (*Tursiops*), harbor porpoise (*Phocoena phocoena*), Amazon River dolphin (*Inia geoffrensis*), beluga (*Delphinapterus leucas*), and pilot whale (*Globicephala*). Several behavioral studies of cetaceans have described aspects of what was believed to be sleep. All the available descriptions of resting behavior of cetaceans in the wild are primarily anecdotal.

Unihemispheric Slow-Wave Sleep

Studies of cetacean sleep have led to one of the most unusual findings to date with respect to sleep in mammals – unihemispheric slow-wave sleep (USWS) (Figure 1), that is, cetaceans display EEG slow waves in one cerebral hemisphere, while the other hemisphere exhibits low-voltage EEG activity, indicative of waking. USWS is the major sleep state in all cetacean species studied to date. In the bottlenose dolphin, the most extensively studied cetacean species, USWS represents 70–90% of the total sleep time (TST) (mean of 88% for 6 animals), with the remaining time being occupied by episodes of asymmetrical slow-wave sleep (ASWS) or low-voltage bilateral slow-wave sleep (BSWS). Episodes of sleep in one hemisphere last between 4 and 132 min (mean of 42 ± 2 min) and the number of episodes range between 2 and 12 per day (mean of 5 ± 1). In an adult male beluga, USWS and ASWS accounted for 83% of the TST and the remaining sleep was scored as low-voltage BSWS. Twenty-six episodes of USWS were recorded over a period of 2 days, with episodes lasting between 10 and 81 min (mean of 44 ± 4 min). In all cetaceans, episodes of USWS alternated between the two hemispheres.

REM Sleep

Despite long periods of electrophysiological studies of sleep, no rapid eye movement (REM) sleep episodes, typical of terrestrial animals, have been observed in any of the studied cetacean species. Muscle jerks, body twitches, and REMs (all features of REM sleep) have been documented in behaviorally resting cetaceans. The number and expression of jerks vary significantly between individuals of the same species and among different

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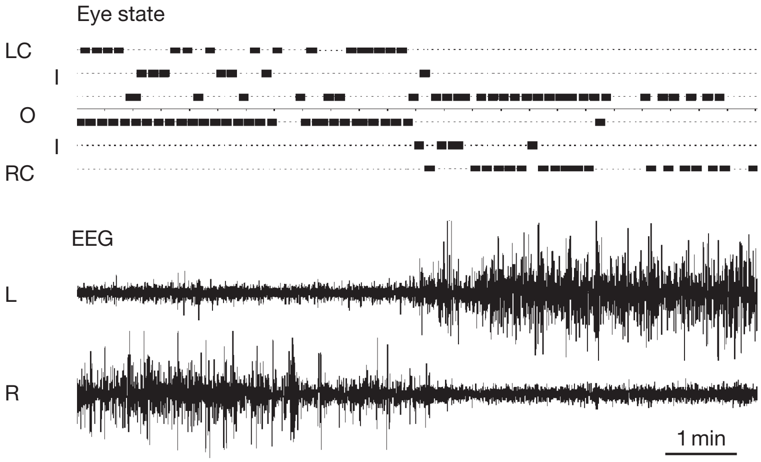

Figure 1 A representative example of recording showing the association between the EEG in the two hemispheres (L, left; R, right, lower panel) and eye state in a beluga. The state of each eye (L, left and R, right) is marked as open (O), closed (C), or intermediate (I). Reproduced with permission from Lyamin OI, Mukhametov LM, and Siegel JM (2004) Relationship between sleep and eye state in cetaceans. *Archives Italiennes de Biologie* 142: 557–568.

species (for instance, 6 jerks per day in a 1-year-old gray whale and 220 jerks per night in an adult beluga). In spite of the variability within and between species, there are several similarities regarding the phasic events recorded in cetaceans: jerks are frequently related to resting behavior (floating or slow swimming), some jerks follow each other creating a series of jerks and twitches, and serial jerks are often followed by arousal. Based on these characteristics, muscle jerks in cetaceans fit the behavioral features of REM sleep in terrestrial mammals. However, a significant portion of jerks occur at the beginning of the sleep periods and during quiet waking. Based on the available data, REM sleep is either absent in cetaceans or is present but has taken on a modified form that has escaped detection.

Sleep and Mobility

All cetaceans can sleep while slowly swimming, that is, motion in cetaceans is compatible with EEG slow-wave activity. Almost continuous swimming appears to be a characteristic of all small adult cetaceans (e.g., on average 97% of 24 h in the Commerson's dolphin, *Cephalorhynchus commersonii*) and cetacean calves (on average 96–100% of 24 h depending on the age of the bottlenose dolphin and killer whale, *Orcinus orca*, calves), indicating that newborn cetaceans must sleep during swimming. In contrast, long periods of immobility while floating on the surface or lying on the bottom of a pool were characteristic of all examined large cetaceans (on average 42–67% of the night-time in adult beluga and killer whales and 41% of 24 h in one gray whale calf). USWS has been recorded during each of these three sleep behaviors. When dolphins swim while displaying USWS, there is no asymmetry in their motor activity. Regardless of which hemisphere is exhibiting slow waves, captive dolphins tend to circle predominantly in only one direction – counterclockwise or clockwise.

Sleep and Unilateral Eye Closure

Lilly proposed that dolphins sleep with one eye closed and one eye open at a time to visually monitor the environment. Asymmetrical eye closure has been observed in different cetacean species (including large whales) while engaged in slow swimming or floating at the surface. For instance, pacific white-sided dolphins (*Lagenorhynchus obliquidens*) slowly swim in an echelon formation, usually with one eye open. When they switch positions, they also switch eye condition in such a way that the open eye is always directed toward their conspecifics. Bottlenose dolphin calves when continuously swimming next to their mothers are often seen with one eye open while the other eye remains closed. The eye directed toward the mother is open more often than the eye directed to the opposite direction, suggesting that calves continue to maintain visual contact with their mothers during sleep. Polygraphic recording while simultaneously documenting the state of both eyes in the bottlenose dolphin and beluga revealed a clear relationship between EEG and eye state (Figure 1). During USWS, the eye contralateral to the waking hemisphere was open or in an intermediate state (95–98% of the time), while the eye contralateral to the sleeping hemisphere was usually closed (40% and 52% of TST in the contralateral hemisphere in the beluga, respectively, for the left and right eye; 55% and 60% in the bottlenose dolphin) or in an intermediate state (46% and 31% in the beluga; 37% and 35% in the bottlenose dolphin). However, regardless of the general association (lasting minutes) between the sleeping hemisphere and the state of the two eyes in cetaceans, brief changes in the state of one eye (lasting seconds) were not necessarily accompanied by parallel changes in the EEG in the contralateral hemisphere. Further analysis indicated that the opening of both eyes in the dolphin and beluga was highly correlated with waking (on average 80% of the waking time in both species). The epochs with only one eye closed while the other eye was open indicated sleep in 80% of the cases in the bottlenose dolphin and 91% in the beluga.

Both eyes were rarely closed in the bottlenose dolphin and beluga (2.0% of the observation time in the dolphin and 1.6% in the beluga).

Sleep and Cardiorespiratory Pattern

Small-sized cetaceans (e.g., the harbor porpoise and Commerson's dolphin) maintain continuous swimming and regular breathing when asleep, with respiratory pauses that rarely exceed 60 s in duration. Dolphin and killer whale newborns swimming continuously with their mothers surface to breathe more frequently than their mothers (every 10–30 s). Larger adult cetaceans (e.g., beluga, killer whale, and larger whales) can experience long apneas during sleep while submerged. These apneas may last longer than 10 min and are usually followed by periods of frequent respiration. Respiratory acts in dolphins are fully compatible with uninterrupted USWS, that is, they do not necessarily cause arousal and behavioral awakening. Both during waking and sleep, the instantaneous heart rate (HR) of cetaceans is characterized by alternating periods of bradycardia (e.g., between 20 and 40 beats min^{-1} in a sleeping beluga), which coincide with apneas, and periods of tachycardia (between 60 and 90 beats min^{-1}), which correspond with breathing.

Pharmacological Studies

Dolphins were shown to be very sensitive to barbiturates. Changes in the EEG (low-voltage BSWS) were evident at a dose as low as 6 mg kg^{-1} (i.m.) and occurred simultaneously in all sites recorded across the cortex. At doses of 12 mg kg^{-1} or higher, high-voltage BSWS was seen. The increase in EEG amplitude in both hemispheres was accompanied by a cessation of breathing. Diazepam (or valium) administered i.m. at doses ranging from 0.5 to 2.0 mg kg^{-1} rapidly induced USWS. At higher doses (2–5 mg kg^{-1}), USWS turned to high-voltage BSWS. However, immediately prior to each breath, the EEG amplitude in one or both hemispheres decreased, such that the dolphin exhibited USWS, low-voltage BSWS, or waking. These observations indicate that high-voltage BSWS can be pharmacologically induced in dolphins. However, there is a large difference between BSWS elicited by barbiturates and benzodiazepines in terms of the inhibitory effect on respiratory acts.

Evolution of USWS in Cetaceans

It has been suggested that three possible factors may have been important in the evolution of USWS in cetaceans: (1) the need to come to the surface to breathe, (2) more efficient monitoring of the environment, and (3) thermogenesis. The need to come to the surface to breathe is an obvious life-sustaining requirement for any aquatic mammal. As a result, the act of breathing became incompatible with high-voltage BSWS and REM sleep. Alternation of SWS between the two brain hemispheres and keeping one half of the brain awake, as well as the disappearance, substantial reduction or modification of REM sleep, would have been a resolution to this contradiction. Monitoring the environment for predators and conspecifics to maintain group coherence may have also led to the form of sleep seen in extant cetaceans. The third factor is the need to maintain heat production in the face of the thermal challenge of living in water, which can be achieved through evolving of USWS, which allows (1) continuous motion and muscle thermogenesis and (2) continuous release of noradrenalin and heating of the brain.

Sleep in Eared Seals (Otariids)

Sleep has been studied electrophysiologically in four species of otariids: the northern fur seal (*Callorhinus ursinus*), Cape fur seal (*Arctocephalus pusillus*), Steller's sea lion (*Eumetopias jubatus*), and southern sea lion (*Otaria flavescens*). All the studied otariid species display all known forms of sleep: BSWS, USWS, and REM sleep. Among these species, sleep has been most extensively studied in the northern fur seal.

Sleep on Land

On land, fur seals sleep while lying on their sides, bellies or sitting. REM sleep is recorded only when animals are lying down and usually follows SWS. Juvenile (2–3-year-old) captive fur seals sleep on average 34% of 24 h while on land. The amount of REM sleep accounts for an average of 5% of 24 h, with single episodes lasting up to 12 min (mean of 3.6 min). The amount of time spent in all stages of sleep was maximal in 10–20-day-old pups (TST – on average 47%, SWS – 34%, REM sleep – 13% of 24 h) and minimal in adult females (TST – 20%, SWS – 17%, and REM sleep 3% of 24 h). When on land, fur seals display both BSWS, as seen in terrestrial mammals, and ASWS or USWS, as seen in cetaceans (Figure 2(a)). The proportion of BSWS depends on the age and sex of the animal. It was maximal in 10–20-day-old pups (on average 94% of the total SWS time) and minimal in juvenile males (55%).

Sleep in Water

When fur seals sleep in water, the expression of EEG asymmetry (i.e., the amount of ASWS and USWS) increases. Concomitantly, the amount of REM sleep substantially decreases and may even be absent for several days. REM sleep episodes in water do not last longer than 1 min. Sleep in water is characterized by striking motor asymmetry: fur seals sleep at the surface on their sides, paddling with one fore flipper, while holding the other three flippers above the surface to maintain their posture (Figure 2(b) and 2(c)). This posture prevents heat loss and optimizes thermoregulation while fur seals are asleep in water.

EEG Asymmetry, Eye State, and Movement

In fur seals, during USWS and ASWS, EEG asymmetry is strongly correlated with brief openings of one eye. The hemisphere contralateral to the open eye is awake or in a state of lower-voltage SWS, while the hemisphere contralateral to the closed eye is in a state of higher-voltage SWS. When in water, flipper movements and brief eye openings occur contralateral to the waking hemisphere or the hemisphere with lower-voltage EEG. The association between USWS, motion, and brief opening of one eye suggests that USWS in fur seals serves to maintain vigilance to detect predators and conspecifics while asleep.

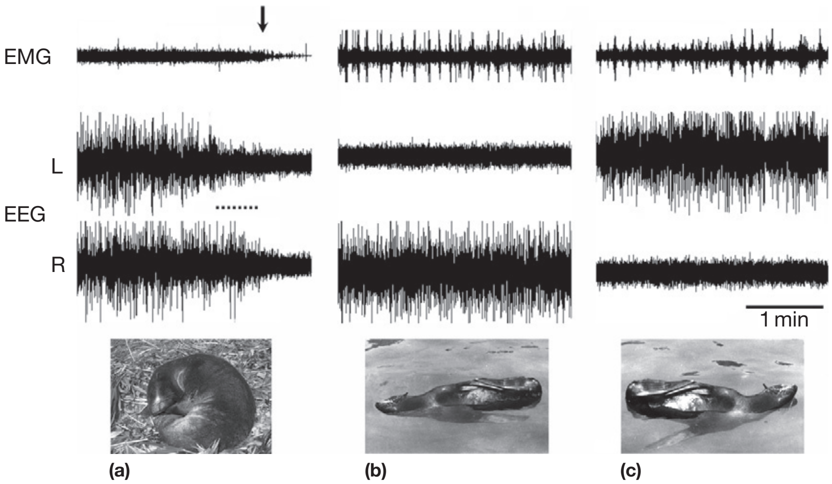

Figure 2 Representative examples of polygrams recorded in a fur seal while sleeping on land (a) and in water on the right (b) and left (c) side and characteristic sleep postures (photographs below the polygrams). EMG, electromyogram; EEG, electroencephalogram of the left (L) and right (R) hemispheres. (a) BSWS and ASWS, (b) right USWS, and (c) left USWS. The arrow on (a) marks the beginning of a REM sleep episode and the dotted line marks an episode of ASWS.

Cardiorespiratory Pattern

The breathing pattern of fur seals is regular during quiet waking and SWS both on land and in water; all respiratory pauses are shorter than 30 s, with the majority of them (80–94%) lasting 8–20 s. REM sleep on land is characterized by an increase in the irregularity of breathing, with apneas lasting between 30 and 62 s. During quiet waking and SWS, HR in fur seals varies between 60 and 150 beats min^{-1}. During eupnea (normal breathing), instantaneous HR is 90–150 beats min^{-1} and apneic HR is 60–90 beats min^{-1}, with higher rates during the postapneic periods. During REM sleep, HR is most variable, ranging between 35 and 160 beats min^{-1}.

Circadian Activity Under Controlled Light–Dark Conditions

Under a 12L/12D photoperiod, the majority of fur seals were found to be more active during the light period compared to the dark period. In continuous darkness, periods of rest in all seals were equally distributed between the day and night-time without features of a 'free-running' rhythm, suggesting a dampening of circadian control in fur seals as an adaptation to a more variable marine environment.

Sleep in True Seals (Phocids)

Sleep has been studied electrophysiologically in five phocid species: the gray seal (*Halichoerus grypus*), Caspian seal (*Phoca caspica*), harp seal (*Phoca groenlandica*), northern elephant seal (*Mirounga angustirostris*), and harbor seal (*Phoca vitulina*). Regardless of whether they sleep on land or in water, SWS in phocids is always bilateral. When on land, 3–5-month-old harp seals spent on average 22% and 3% of 24 h in SWS and REM sleep, respectively, and adult Caspian seals 13% and 2% of 24 h. Behavioral sleep has also been examined in several other species – in the smallest of the phocid species, the Baikal seal (*Phoca sibirica*) while in captivity, and in the northern elephant seal in the wild.

Sleep on Land

The true seals sleep lying on the ground (land, snow, ice) on their bellies or their side. Individual REM sleep episodes in phocids are shorter than in otariids (e.g., on average 2.0 min in 10–20-day-old harp seals compared to 5.6 min in 10–20-day-old fur seal pups) and they usually occur in series. Contrary to cetaceans and otariids, there are no reports of asymmetrical eye closure in true seals.

Sleep in Water

Phocids sleep in water while holding their breath, which allows them to sleep while floating motionlessly at the surface, at depth, or while lying on the bottom of the pool. They do not need to wake up to breathe when floating at the surface. However, they always wake up if they sleep at depth and need to initiate movement to emerge to the surface. Therefore, BSWS in true seals is incompatible with movement. The reported TST varies significantly between species, partly because of the difference between experimental conditions.

Cardiorespiratory Pattern

All studied phocids exhibit a similar respiratory pattern while sleeping: apneas alternating with periods of regular breathing. For instance, captive harp seal pups (<3 months old) sleeping on ice or land in SWS exhibit apneas ranging between 84 and 180 s alternating with periods of ventilation, with interbreath intervals of less than 4 s. Elephant seals experience even longer apneas, lasting up to 12 min in 4-month-old pups sleeping on land and up to 21 min in adults resting and apparently sleeping in the rookery. The majority of REM sleep episodes on land and all REM sleep episodes in water occur during a single apnea followed by ventilation and arousal. Instantaneous HR decreases during quiet waking and SWS apneas (on average 70 beats min^{-1} in 1-month-old harp seals and 44 beats min^{-1}

in 4-month-old elephant seals) and remains tachycardiac during the period of breathing (on average 110 beats min^{-1} in harp seals and 60 beat min^{-1} in elephant seals). During REM sleep, HR is most irregular. The hallmark of sleep in phocids is the ability to hold their breath, allowing them to sleep under the polar ice fields, and to minimize the time spent on the surface to avoid predation by sharks, killer whales, and polar bears.

Sleep in the Walrus (Odobenids)

Sleep has been examined in one freely swimming 2-year-old walrus. In another study, behavioral sleep was monitored visually in four juvenile walruses.

Sleep on Land and in Water

SWS and REM sleep in the examined walrus while on land averaged $21 \pm 3\%$ and $5 \pm 1\%$ of 24 h, respectively. REM sleep episodes on land lasted up to 18 min. When in water, sleep occurred while the walrus was floating motionless at the surface, standing in a shallow area with its head above water, or lying on the bottom of the pool. All REM episodes in water lasted less than 2 min and each occurred during a single apnea. The majority of SWS in the examined walrus was scored as BSWS (Figure 3). Episodes of ASWS were occasionally recorded both on land and in water. They accounted for <15% of SWS while on land and were nearly absent while in water (<4% of SWS).

Periods of Continuous Swimming

Walruses alternated periods of almost continuous swimming lasting 40–84 h, with extended periods of rest on land lasting 2–19 h. When in water, walruses were predominantly awake (88–99% of the time). On land, walruses slept on average 40–74% of the time.

Cardiorespiratory Pattern

While on land, the breathing pattern of the walruses was regular during quiet wakefulness and SWS. Most interbreath intervals (93% of all pauses) were less than 30 s. During REM sleep, the breathing was arrhythmic, with some apneas lasting up to 90 s. While in water, sleeping walruses alternated periods of ventilation with apneas. During ventilation on the surface, the instantaneous HR varied between 70 and 110 beats min^{-1}. At the time of diving, HR instantly decreased to 15 beats min^{-1} and then steadily increased to 45–50 beats min^{-1} over the course of the apnea (Figure 3). No significant differences were found between the corresponding parameters of HR during wakefulness, SWS, and REM sleep. Similar to phocids, the pattern of sleep in the walrus appears to be linked to the need to sleep while submerged.

Sleep in Other Aquatic and Semiaquatic Mammals

Manatee

Manatees sleep both at the surface and while submerged. Sleep has been studied electrophysiologically in one Amazonian manatee (order Sirenia, *Trichechus inunguis*). When asleep, the manatee woke up briefly for each respiratory act. Both BSWS and ASWS patterns were recorded, with BSWS accounting for 75% of TST. REM sleep occurred during a single apnea lasting up to 4 min. SWS and REM sleep occupied on average 27% and 1% of 24 h, respectively.

Sea Otter

Behavioral observations revealed that sea otters (order Carnivora, *Enhydra lutris*) sleep in water at the surface on their backs in a characteristic posture, holding their heads above the surface and balancing their bodies with their tails. When REM sleep occurs in water, the otter turns on its side or stomach and its head sinks under the surface. REM sleep

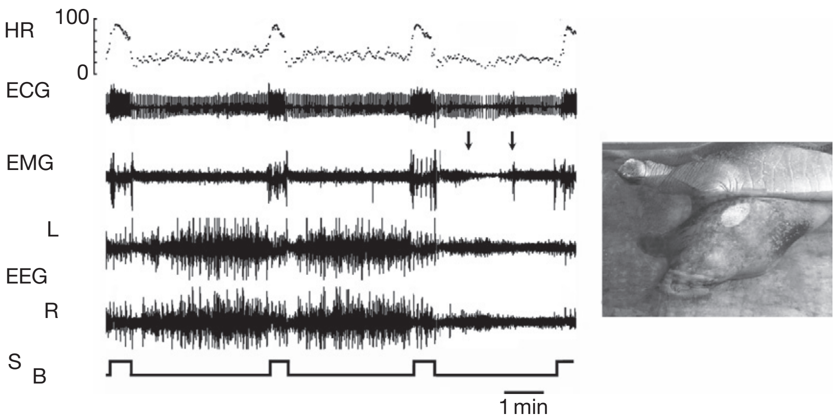

Figure 3 Representative examples of polygrams showing BSWS and REM sleep recorded in a walrus while in water and characteristic sleep postures (photograph). HR, instantaneous heart rate; ECG, electrocardiogram; EMG, electromyogram; EEG, electroencephalogram of the left (L) and right (R) hemispheres; HR, beats per min. Position of the animal (S, at the surface; B, lying on the bottom). The two arrows mark the beginning and end of the episode of REM sleep while resting at the bottom of the pool. The photo shows two sleeping walruses with their heads above and below the water surface.

episodes in sea otters lasted up to 6 min (mean of 95 s) and their durations did not differ while on land or in water. Behaviorally, TST and REM sleep in one adult animal averaged 29% and 2% of 24 h, respectively.

Hippopotamus

Behavioral sleep was examined in a group of three (mother, father, and their 2-month-old calf) hippopotamuses (order Artiodactyla, *Hippopotamus amphibius*) in a zoo. They slept both on land and in water. When in water the hippos slept while standing or lying on the bottom of pools in shallow places holding their heads above the surface and breathing regularly and only rarely lowering their heads below the surface. REM sleep occurred when the animals submerged their heads and laid on the bottom of the pool for up to 3 min. The total amount of behavioral sleep in the calf was greater than in its mother, who was very protective of her baby at all times, frequently opening both eyes while asleep.

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