CHAPTER

25

C0125

Sleep in Aquatic Mammals

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s0010

I INTRODUCTION

p0010 Sleep in terrestrial mammals is described as (1) a state of behavioral quiescence in (2) a specific posture (3) with a reduced ability to respond to external stimuli. All terrestrial mammals display two distinctive sleep stages—slow-wave sleep (SWS) and rapid eye movement (REM) sleep, which are usually scored based on the electroencephalogram (EEG), electromyogram (EMG), electrooculogram (EOG), and the pattern of heart and breathing rate. Air-breathing animals sleeping in water face many challenges, which are determined by physical properties of the aquatic environment. They have to surface regularly for breathing and to prevent inhaling water into the lungs during respiration, factors that exclude immobility, which is a key feature of sleep in terrestrial mammals. At the same time, staying at the water surface exposes aquatic mammals to predators. Thermal conductivity of water is also many times greater than that of air. This requires that aquatic mammals have some behavioral and physiological adaptations preventing excessive heat loss or overheating by maintaining postures or motion and excluding prolonged periods of immobility when sleeping in water. The aim of this review is to summarize the information on the adaptive features of sleep in aquatic and semiaquatic mammals, allowing them to sleep in water or both on land and in a water environment.

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II SLEEP IN CETACEANS

p0015 Cetaceans (order Cetacea) are fully aquatic marine mammals that have evolved about 50 million years ago (mya). They share a common terrestrial ancestor with hippopotamuses. The two modern groups of cetaceans—Mysticeti (baleen whales) and Odontoceti (toothed whales)—are thought to have separated from each other around 30 mya (Thewissen, Cooper, George, & Bajpai, 2009). To date, sleep has been studied electrophysiologically in five cetacean species: the bottlenose dolphin (*Tursiops truncatus*), harbor porpoise (*Phocoena phocoena*), Amazon river dolphin (*Inia geoffrensis*), beluga (*Delphinapterus leucas*), and pilot whale (*Globicephala* sp.). The bottlenose dolphin is the most extensively studied species, with more than 30 individuals studied. In the other species, the experimental data were collected in only a few (two Amazon river dolphins and three harbor porpoises) or in single (in the beluga and pilot whale) individuals.

A Unihemispheric Sleep (USWS) s0020

p0020 All cetaceans studied during sleep displayed slow waves in the EEG of one cerebral hemisphere, while the other hemisphere exhibited low-voltage activity, resembling the waking state (Mukhametov, Supin, & Polyakova, 1977, Mukhametov & Polyakova, 1981; Lyamin, Mukhametov, Siegel, et al., 2002; Ridgway, 2002; Serafetinides, Shurley, & Brooks, 1972; Fig. 25.1). Consequently, sleep in cetaceans is called unihemispheric SWS (USWS). This state also represents unihemispheric waking. Parallel recordings from symmetrical areas of the two cerebral hemispheres revealed that, regardless of regional differences between EEG signals within one hemisphere, the differences between the two hemispheres were always more pronounced. When the EEG was recorded simultaneously from the cortex and thalamus, EEG changes in the cortex were parallel with those in the ipsilateral thalamus, suggesting that USWS not only is a cortical phenomenon but also appears to involve, at a minimum, the entire cortical-thalamic system (Lyamin, Manger, Ridgway, Mukhametov, & Siegel, 2008; Mukhametov, Oleksenko, & Polyakova, 1997). The transition from waking to USWS in dolphins is associated with a temperature decrease in the

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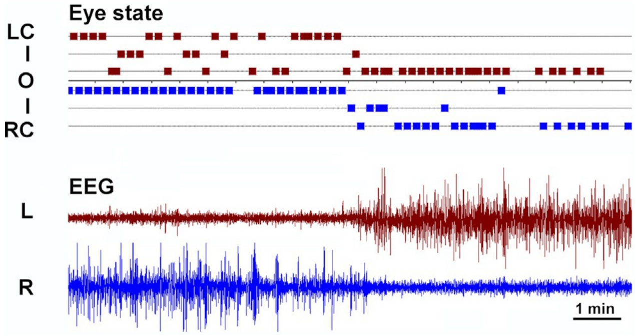


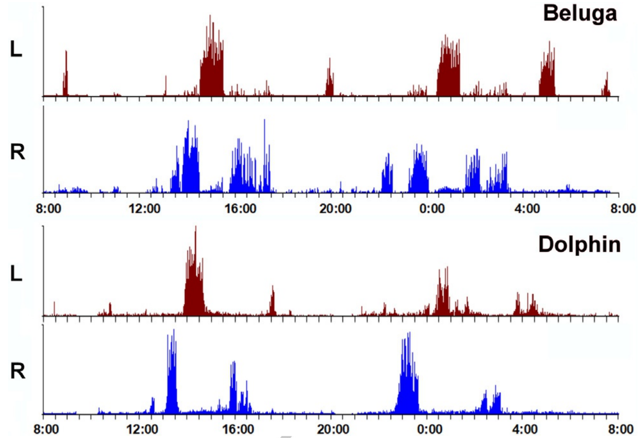
f0010 **FIG. 25.1** Association between unihemispheric sleep and EEG in the two hemispheres (*L*, left; *R*, right) and eye state in a beluga. The state of each eye (*L*, left; *R*, right) is marked as open (*O*), closed (*C*), or intermediate (*I*). *Reproduced from Lyamin, O. I., Mukhametov, L. M., & Siegel, J. M. (2004). Association between EEG asymmetry and eye state in Cetaceans and Pinnipeds.* Archives Italiennes de Biologie, 142*, 557–568.*

“sleeping” hemisphere, while the temperature of the “waking” hemisphere remains unchanged. Awakening is accompanied by a gradual increase in the temperature of only the “sleeping” hemisphere (Kovalzon & Mukhametov, 1983).

p0025 USWS is a core feature of cetaceans sleep. It is present in both males and females of varying ages. Further, cetaceans displayed USWS regardless of the specific experimental conditions, including when the animals were lying in stretchers, swimming in shallow pools while connected to recording equipment with low-noise cables, or freely swimming in spacious pools or enclosures when the EEG was recoded via portable data loggers attached to the animals (Lyamin, Manger, et al., 2008; Mukhametov et al., 1997).

p0030 USWS in cetaceans represents the most extreme case of interhemispheric EEG asymmetry recorded in mammals and birds. In different cetaceans, USWS represented 70%–90% of the total sleep time (TST), making USWS the major sleep state. The remaining time was occupied by episodes of both hemispheres displaying either (1) different forms of EEG synchronization (high-voltage EEG of maximal amplitude in one hemisphere and low-voltage EEG in the other) or (2) low-voltage EEG in both hemispheres; these states represent asymmetrical SWS (ASWS, 4%–15% of the total SWS time in different animals) or low-voltage bilateral SWS (BSWS, 7%–22%), respectively. High-voltage BSWS was never recorded in studied cetaceans under normal conditions (Lyamin, Manger, et al., 2008; Mukhametov, 1987; Mukhametov et al., 1997; Mukhametov & Polyakova, 1981), except for instances of several seconds of BSWS in a beluga (<0.2% of TST; Lyamin, Mukhametov, Siegel, et al., 2002).

p0035 In bottlenose dolphins, uninterrupted episodes of USWS lasted 4–132 min (on average 42 ± 2 min), and the number of episodes ranged between 2 and 12 per day (5 ± 1; Mukhametov et al., 1997, Lyamin, Mukhametov, & Siegel, 2004). In the beluga, episodes of USWS lasted 10–81 min (44 ± 4 min; Lyamin, Mukhametov, Siegel, et al., 2002). In Amazon river dolphins and harbor porpoises, USWS episodes could be longer than 2 h (Mukhametov, 1987; Mukhametov & Polyakova, 1981). In all cetaceans, USWS tended to alternate between the two hemispheres (Fig. 25.2). During any single recording day, the amount of sleep in either the right or left hemisphere in most studied individuals was greater than in the other hemisphere. However, whenever recordings were conducted for several continuous days, the average amount of USWS did not differ significantly between the two hemispheres.



f0015 **FIG. 25.2** EEG slow-wave power in the range of 1.2–4 Hz in the right (*R*) and left (*L*) hemispheres in a bottlenose dolphin and beluga recorded over 24 h. *Reproduced from Lyamin, O. I., Manger, P. R., Ridgway, S. H., Mukhametov, L. M., & Siegel, J. M. (2008). Cetacean sleep: an unusual form of mammalian sleep.* Neuroscience & Biobehavioral Reviews, 32*, 1451–1484.*

B Absence of REM Sleep s0025

p0040 REM sleep has been recorded in all land mammals. It is characterized by cortical arousal, rapid eye movements, muscle jerks, muscle tone suppression, and increased heart and breathing rate variability, among others (Siegel, 2017). Shurley, Serafetinides, Brooks, Elsner, and Kenney (1969) reported recording one REM sleep episode lasting 6 min in a pilot whale. This episode was characterized by a loss of tonus of trunk muscle and eye movements. This study is the only report of REM sleep in cetaceans. For instance, the list of parameters used to detect features of REM sleep in bottlenose dolphins included the EEG of the cortical hemispheres, lateral geniculate bodies, and the hippocampi, as well the EMG, eye movements, electrocardiogram (ECG), respiration rate, and brain temperature (Mukhametov et al., 1997). None of these physiological parameters unequivocally indicated the presence of REM sleep (reviewed in Lyamin, Manger, et al., 2008). However, it is noteworthy that the criteria used to identify and score REM sleep in land mammals are not designed to detect short REM sleep episodes lasting for only several seconds.

p0045 Some features of REM sleep in land mammals, such as muscle jerks, body twitches, and rapid eye movements, have been recorded in cetaceans. They were documented in resting (and apparently sleeping) cetaceans of six different species (Lyamin, Manger, et al., 2008). These jerks and twitches often followed each other creating series, and the serial jerks were then followed by arousal. Jerks often occurred periodically and more often during the night/rest period. At the same time, jerks in cetaceans also occurred at the beginning of the rest periods. Their number and intensity varied substantially between individuals of the same species (e.g., between 15 and 98 per day in bottlenose dolphins; Mukhametov & Lyamin, 1997). Among the species, the greatest number of jerks was recorded in an adult beluga (220/night; Lyamin, Shpak, Nazarenko, & Mukhametov, 2002) and the smallest in a 1-year-old gray whale (6/day; Lyamin, Mukhametov, Siegel, Manger, & Shpak, 2001). There are also other features of REM sleep in some land mammals, for example, penile erections, that were recorded in at least three species of behaviorally sleeping cetaceans. In some cases, the erections were associated with muscle jerks. However, the number and duration of erections also varied among individuals of the same species (e.g., between 2 and 31 per day and 4 and 102 s in the bottlenose dolphin). Since erections and muscle jerks were also recorded during active behavior (Mukhametov & Lyamin, 1997; Shpak, Liamin, Manger, Siegel, & Mukhametov, 2009), they cannot be considered a reliable feature of REM sleep.

p0050 The presence of behavioral correlates of REM sleep in cetaceans should not be ignored. However, those features are obviously not sufficient to make a conclusion on the presence of REM sleep before an association between electrophysiological and behavioral features is established. Parallel recording of the EEG and video recording of muscle jerks in three freely swimming bottlenose dolphins revealed that jerks occurred both during quiet wakefulness and USWS. For instance, in the dolphin showing the greatest number of jerks and twitches (12/day), 26% of those events occurred during quiet wakefulness, 26% during USWS, and 52% during episodes of quiet wakefulness that followed episodes of USWS. The last group of jerks is the most interesting, because they were recorded during a period similar to that when REM sleep was recorded in land mammals. To conclude, muscle jerks and twitches (behavioral features of REM sleep) were not unequivocally associated with a particular EEG or behavioral state in the studied dolphins. Thus, they cannot be used as a criteria of the presence or absence of REM sleep in cetaceans.

p0055 Based on the available data, we currently cannot exclude that either (1) REM sleep is absent in cetaceans or (2) REM sleep in cetaceans may take a modified form that has escaped detection (Lyamin, Manger, et al., 2008). REM sleep in land mammals features elevated arousal thresholds, impaired thermoregulation, and muscle tone suppression (Siegel, 2017). Long episodes of REM sleep at the surface would be an obviously maladaptive or dangerous behavior for cetaceans. On the other hand, REM sleep is compatible with the aquatic mode of life because it is seen in water in some seals and walruses. The absence of REM sleep in dolphins may be related to the unihemispheric pattern of their sleep (this will be discussed later in this review).

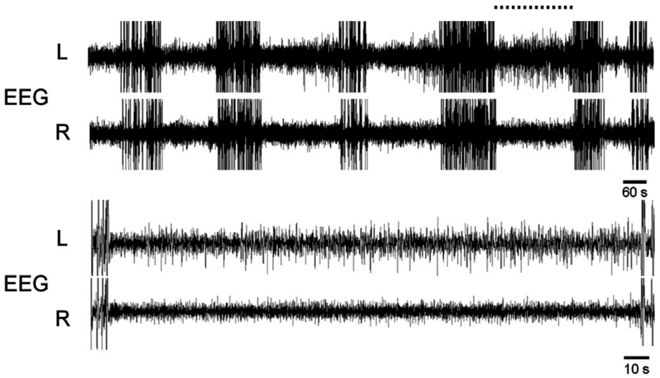
C Sleep and Motion s0030

p0060 In all studied cetaceans, EEG slow waves were associated with motion. When sleeping, they were slowly swimming around the pool (bottlenose dolphin, Mukhametov et al., 1977; harbor porpoise, Mukhametov & Polyakova, 1981; and Amazon river dolphin, Mukhametov, 1987) or repeatedly submerged and surfaced in place (the beluga, Lyamin, Mukhametov, Siegel, et al., 2002). Regardless of which hemisphere exhibited EEG slow waves, sleeping dolphins and porpoises tended to circle in one direction. No visually detectable asymmetry in motor activity was observed at this time.

p0065 All bottlenose dolphins and the beluga studied also displayed EEG slow waves while resting/floating at the surface (Lyamin, Mukhametov, Siegel, et al., 2002; Mukhametov et al., 1977). They were never fully motionless at this time, as they moved their tail fluke and flippers to stabilize their postures. Some bottlenose dolphins slept predominantly while floating at the surface (up to 85% of TST), while others during swimming around the pools (up to 90% of TST). In both cases, sleep cannot be reliably discriminated from wakefulness based on the pattern of motion. Smaller harbor porpoises and Amazon river dolphins never stopped at the surface for a period longer than several seconds (Mukhametov, 1987; Mukhametov & Polyakova, 1981).

p0070 During these studies, only one bottlenose dolphin displayed episodes of USWS while submerging and resting motionless on the bottom of the pool. Usually, several such episodes followed each other lasting between 150 and 212 s. USWS was interrupted by brief arousals when the dolphin surfaced to breathe. Sleep on the bottom comprised only 4% of TST over the 4 recording days (Lyamin, Manger, et al., 2008; Fig. 25.3).

p0075 To conclude, based on the EEG studies, USWS may occur in cetaceans during slow swimming, floating at the surface, or resting on the bottom of pools. These three behaviors represent behavioral sleep in cetaceans. It is



f0020 **FIG. 25.3** *Top*: several consecutive episodes of unihemispheric sleep in the left hemisphere in a bottlenose dolphin lying on the pool floor. High-voltage artifacts are periods of surfacing and respirations. *Bottom*: episode on the bottom is a fragment of the top recording at the time marked by the dotted line. *EEG*, electroencephalogram; *L* and *R*, left and right hemisphere, respectively.

important that all cetaceans must be capable of swimming during sleep, as swimming is life sustaining for this group of animals. Thus, the key role of USWS is viewed as enabling continuous motion through maintaining activation of certain brain centers involved in controlling coordinated movement.

s0035 D Sleep and Unilateral Eye Closure

p0080 Parallel recordings of the EEG of both cortical hemispheres and of the state of both eyes in a beluga and bottlenose dolphin revealed that during USWS, the eye contralateral to the waking hemisphere was predominantly open or in an intermediate state (95%–98% of the time). At the same time, the eye contralateral to the sleeping hemisphere was usually closed or in an intermediate state (81%–95% of the time; Fig. 25.1). The opening of both eyes was highly correlated with waking (on average 80% of the waking time in both species), while the asymmetrical eye state was correlated with sleep (80% of time in the dolphin and 91% in the beluga). Both eyes were rarely closed at the same time (<2.0% of the time; Lyamin et al., 2004; Lyamin, Mukhametov, Siegel, et al., 2002). While unilateral eye opening or closure is not always strictly associated with changes in the EEG of the contralateral hemisphere on a second by second basis, a clear relationship between these two phenomena occurs over longer time intervals. This should not be considered a contradiction to the association between the pattern of EEG and the state of the eyes in cetaceans, but rather provides a clue regarding the mechanisms underlying this association and to the "active" role of the cortex in these events. In other words, USWS is not a consequence of the asymmetrical eye closure and opening, but rather unihemispheric waking facilitates one eye opening and the analysis of visual information. Unilateral eye closure also appears to be a behavioral criterion of sleep in resting cetaceans.

E Sleep and Cardio-Respiratory Patterns s0040

The breathing pattern in all cetaceans features an alternation of periods of fast respiration and breath holdings (or apneas, which usually exceed 60 s). This pattern persists regardless of whether the animals are swimming or floating at the surface. In captivity, apneas in cetaceans during resting, swimming, and floating at the surface rarely exceed 4 min (e.g., in Commerson's dolphins, Shpak et al., 2009; bottlenose dolphins, Mukhametov & Lyamin, 1997; Lyamin, Manger, et al., 2008). When they rest on the bottom, the apneas are longer: up to 5 min in bottlenose dolphins, 8 min in a gray whale calf, 9 min in killer whales, and 12 min in belugas. USWS in cetaceans is fully compatible with breathing, just as bilateral SWS is compatible with breathing in land mammals. However, the amplitude of EEG slow waves in the sleeping hemisphere can briefly decrease at the time of the respiratory act. p0085

The instantaneous heart rate (HR) in a beluga, both during wakefulness and USWS, was characterized by alternating periods of bradycardia (16–40 beats/min), which coincided with breath holding, and periods of tachycardia (60–90 beats/min), which corresponded to periods of fast breathing. Histograms of the distribution of cardiac intervals or breathing pauses did not differ significantly between wakefulness and USWS (Lyamin, Siegal, & Mukhametov, 2010). p0090

Pharmacological studies showed that low doses of sodium pentobarbital or valium induce high-voltage BSWS in dolphins. The valium-induced episodes of BSWS were reversible; interestingly, they always converted to USWS before the respiration. At the same time, pentobarbital-induced high-voltage BSWS was not reversible. It always caused the cessation of breathing, and dolphins would have died if they had not been on mechanical ventilation. These findings led to the conclusion that autonomous breathing in dolphins is not compatible with high-voltage BSWS and that the "active state of at least one hemisphere" is required to maintain respiration (Mukhametov et al., 1997; Mukhametov & Polyakova, 1981). p0095

Lilly (1964) proposed that respiration in dolphins is controlled at the thalamocortical level of the CNS, rather than the respiratory centers located in the medulla and at the pontomedullary junction as in land mammals, speculating that dolphins and porpoises have respiration that is "almost, if not fully, voluntary." However, McCormick (1969) presented controlled mixtures of CO_2, O_2, and NO_2 and discovered that respiration in dolphins can be p0100 driven by peripheral and central chemoreceptors in a manner not dissimilar to other mammals. He suggested that the loss of respiration in dolphins prior to the loss of consciousness during induction of an anesthetic state may be due to certain neuromuscular problems, rather than a shift of a brain stem function to the thalamocortical level.

p0105 To summarize, the available data suggest an important (and likely critical) association between USWS and the maintenance of normal breathing in dolphins and porpoises. These observations led the formulation of the clear and logical hypothesis that USWS primarily supports breathing during quiescence. However, the exact mechanisms underlying the relationships between breathing and sleep are unknown. In spite of a widely held notion that dolphins must be conscious and alert to be able to breathe, there is absolutely no evidence at this time that during USWS, the waking hemisphere in dolphins is involved in controlling brain stem respiration circuits. As we have mentioned earlier in this review, several species of cetaceans were shown to be able to sleep in water while resting motionless at a depth or on the bottom of pool. This is the same behavior displayed by phocidae seals, which have terrestrial-type BSWS while sleeping in water and do not exhibit USWS. At the same time, USWS is clearly critical for supporting uninterrupted breathing in cetaceans because it allows motion and surfacing without full awakening.

s0045 F Sleep Deprivation

p0110 Total and USWS deprivation was performed in dolphins for 35–119 h (Oleksenko, Mukhametov, Polyakova, Supin, & Kovalzon, 1992), which induced an increase in the amount of USWS in both cortical hemispheres or in the deprived hemisphere, respectively. Both types of deprivation increased the tendency for USWS to alternate between the two hemispheres (87% and 80% after bilateral and unilateral sleep deprivation compared with 67% under baseline conditions). Although the increase in the amount of SWS on the first recovery day was present, the effect was highly variable. There was also no correlation between the amount of sleep lost during deprivation and the amount of sleep in each hemisphere during recovery sleep.

s0050 G Anatomical Features of the Cetacean Brain

p0115 All neural elements involved in sleep regulation found in terrestrial mammals are present in cetaceans, including toothed and baleen whales. However, the number of pontine cholinergic and noradrenergic neurons in cetaceans is higher than in other large terrestrial mammals in proportion to total brain size. Other major features of the cetacean brain that may be related to USWS include smaller telencephalon commissures, the larger posterior commissure and the complete crossing of the optic nerve fibers at the chiasm level (Dell et al., 2016; Dell, Patzke, Spocter, Siegel, & Manger, 2016; Wright, A., et al., 2017). Thus, USWS in cetaceans is associated with altered interhemispheric communication, which does not exclude other mechanisms. For instance, in a single bottlenose dolphin implanted with electrodes in the pontine tegmentum, the intensity of stimuli required to induce bilateral EEG arousal by electric stimulation was measured to be 1.4–1.7 times smaller when USWS was present in the hemisphere ipsilateral to the stimulation electrode compared with USWS in the contralateral hemisphere. These findings may indicate asymmetrical (ipsilateral) ascending activation signals from the brain stem in cetaceans, which could lead the EEG asymmetry (Lyamin, Manger, et al., 2008).

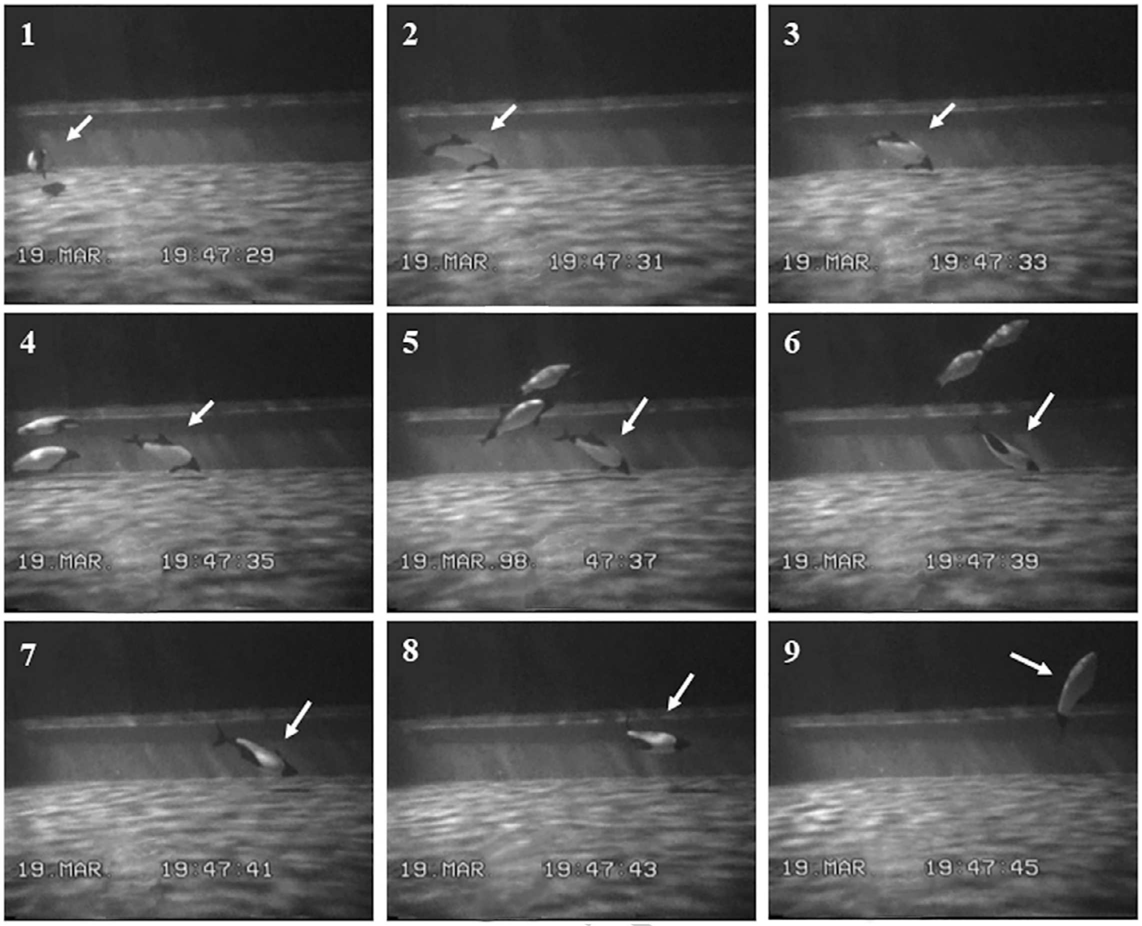
H Behavioral Studies s0055

1 *Resting While Swimming* s0060

In aquaria, stereotypic slow swimming (or "resting swimming") of variable speed along the enclosure perimeter may occupy a significant portion of time in cetaceans (e.g., Goley, 1999; Lilly, 1964; Mukhametov & Lyamin, 1997; Shpak et al., 2009). Commerson's dolphins display periods of slow swimming and even stopped paddling their fluke tails for several seconds while circling at the bottom of the pool (Fig. 25.4). It is likely that the described episodes of slow swimming represent the deepest form of sleep in this species. A similar behavior (alternation of short and long dives) is observed in harbor porpoises at sea (Watson & Gaskin, 1983). p0120

Based on data collected using sound and movement archival tags (DTAGs), several cetacean species engage in repeated slow-speed dives. No features of foraging or travel behaviors are recorded at this time (Izadi, Constantine, Johnson, & Aguilar de Soto, 2018; Wright, A.J., et al., 2017). In harbor porpoises, nearly half of these dives contained no echolocation clicks. They were identified as potential sleeping periods (Wright, A.J., et al., 2017). However, those episodes made up on average only 4.0% (0.1%–8.8% between animals) of the total recording time, which would be the least TST in any mammal studied. Harbor porpoises, as other cetaceans, are likely to sleep during other diving and surface behaviors, including those when vocalization was recorded. p0125

Some cetaceans, all of them relatively small, swim virtually continuously, only surfacing briefly to breathe (e.g., Goley, 1999; Mukhametov & Polyakova, 1981; Pilleri, 1979; Shpak et al., 2009). Almost continuous swimming also appears to be characteristic of cetacean calves and their mothers, who initiate this behavior (Lyamin, Pryaslova, Kosenko, & Siegel, 2007; Lyamin, Pryaslova, p0130



f0025 **FIG. 25.4** Slow swimming in Commerson's dolphins. The photos were taken in 2 s intervals. Note the difference in speed between the dolphin marked by a *white arrow* and the two other dolphins. The marked dolphin virtually stopped moving for about 10–12 s (*frames* 4–8) and then accelerated and emerged to the surface (*frame* 9).

Lance, & Siegel, 2005). During pregnancy, mothers rest and appear to sleep largely while floating at the surface. However, rest and sleep at the surface disappear for several weeks or even months postpartum. At this time, calves continuously follow their mothers, and they rest and sleep while in motion. Continuous activity in small cetaceans and newborn calves may help to maintain body temperature. Further, motor activity in close contact with mothers should reduce predation in calves. As the calves grow, their body mass increases, and insulating blubber develops. In parallel, the time of rest floating at the surface gradually increases both in calves and their mothers. Resting while swimming in tight echelon formations has also been recorded in cetaceans in the wild. When swimming in one direction, they dive and surface while synchronizing their breathing (e.g., Ford, 2009; Würsig & Würsig, 1979).

s0065 2 *Rest While Floating at the Surface*

p0135 In aquaria, rest at the surface (also floating or logging) is a common behavior not only in bottlenose dolphins (e.g., McCormick, 1969; Mukhametov & Lyamin, 1997) but also in other species. Killer whales can be completely immobile for about 1 h and a captive gray whale calf even longer—up to 98 min (Lyamin et al., 2001; Lyamin, Manger, et al., 2008). In the wild, rest while floating at the surface is rarely recorded in small cetaceans (e.g., less than 7.5% of the recording time in the harbor porpoise, the smallest among cetaceans; Watson & Gaskin, 1983). This could be due to both objective (e.g., storms, waves, current, and tides exposure to predators) and methodological (e.g., daytime observations restricted to good weather conditions) factors. At the same time, rest while floating (also called "logging") at the surface was often reported in the Baleen whales. Thus, several species, including Greenland whales (Gray, 1927), pygmy and dwarf sperm whales (Reeves, Stewart, Clapham, & Powell, 2002), and mink whales (Christiansen, Lynas, Lusseau, & Tscherter, 2015), were described resting motionlessly at the surface with a low rate of respiration. Obviously, large baleen whales are less disturbed by ocean waves and currents when resting at the surface.

However, this behavior is believed to make them more vulnerable not only to predation but also to vessel strikes (e.g., Izadi et al., 2018).

s0070 3 *Rest at Depth*

p0140 Rest on the bottom of pools has been described in captivity in several species of cetaceans. In adult bottlenose dolphins, this behavior occupied between 0.2% and 5.4% of 24 h and in an adult killer whale female on average 21% of the nighttime. Rest on the bottom has been recorded even in calves. It occupied on average 5% of the nighttime in a killer whales calf (one-fourth of that in its mother) and 13% of 24 h in a gray whale calf (Lyamin et al., 2001; Lyamin, Manger, et al., 2008; Sekiguchi & Kohshima, 2003). Rest on the bottom is even more common in belugas. Thus, one was observed to rest at the bottom for an average of 67% of the nighttime, and it was the major resting behavior in this beluga for years (Lyamin, Shpak, et al., 2002). Together, these data indicate that rest on the bottom (and most likely sleep) during breath holding is a common behavior in some cetaceans in aquaria.

p0145 Some cetaceans not only perform repeated shallow dives swimming at a slow speed without acceleration but also often drift motionless at this time. For instance, sperm whales were seen to be motionless for up to 32 min in a vertical head-up or head-down positions at a depth of 10–20 m. They do not echolocate at this time and do not consistently respond to approaching vessels (Miller, Aoki, Rendell, & Amano, 2008). The nonresponsiveness and immobility of whales suggest that they were in a deep sleep during some portion of this time. The total duration of drift dives accounted for only about 7% of the recording time, suggesting that sperm whales also obtained sleep during other behaviors, including diving and floating at the surface. Thus, the rest behavior pattern in the sperm whale is generally similar to that shown by larger cetaceans in aquaria. Since electrophysiologically studied cetaceans displayed USWS when motionless, it is incorrect to assume that inactive sperm whales have BSWS, as hypothesized by Miller et al. (2008).

s0075 4 *Asymmetrical Eye State*

p0150 Following Lilly's hypotheses (1964) that dolphins sleep with one eye closed and one eye open at a time, visual observations revealed that resting behavior is often associated with an asymmetrical eye state not only in bottlenose dolphins (e.g., Sekiguchi & Kohshima, 2003) but also in several other cetacean species, including the white-sided dolphin (Goley, 1999) and even in the gray whale (Lyamin et al., 2001). Thus, white-sided dolphins resting while slowly swimming in echelon formation directed the open eye toward their schoolmates (Goley, 1999). Similarly, bottlenose dolphin mothers and their calves were shown to maintain constant visual contact, surfacing either with both eyes open or with their open eye facing each other (Lyamin et al., 2007). Whenever a visual stimulus was presented to a unilaterally opened eye, the behavioral response (such as startling or bursting swimming) was always rapid (Mukhametov & Lyamin, 1997). These data indicate that during resting swimming, dolphins are able to analyze visual information via the open eye. Thus, the open eye appears to serve a sentinel function, allowing them to maintain visual contact with conspecifics or detect predators (Lilly et al., 1964; Goley, 1999; Lyamin et al., 2007). USWS is seen as the neurophysiological mechanism, which allows cetaceans to monitor the environment while obtaining sleep at the same (Lyamin, Manger, et al., 2008).

5 *USWS and Continuous Vigilance* s0080

Because of the relatively poor visibility in the ocean, dolphins use echolocation to gain information about their environment. Although cetaceans are usually silent during resting swimming, Gangetic dolphins (*Platanista gangetica*), which have poor vision, generated echolocation clicks during the entire day with interruptions lasting between 4 and 60 s (Pilleri, 1979). It was also reported that two bottlenose dolphins were able to continuously echolocate (producing 10–120 clicks/min) and accurately report the presence of targets for 5–15 days without interruption (Branstetter, Finneran, Fletcher, Weisman, & Ridgway, 2012). USWS in dolphins may be compatible with echolocation events, which are controlled by the waking hemisphere (Ridgway, 2002). However, measurement of underwater activity in tagged cetaceans revealed that they continuously produce echolocation clicks only during deep "foraging" dives and do not echolocate during nonforaging, near-surface dives when they may rest (Miller, Johnson, Tyack, & Terray, 2004; Wright, A.J., et al., 2017). Another possibility is that USWS during echolocation is interrupted by echolocation clicks. None of these hypotheses have been tested with parallel EEG and echolocation click recording studies. p0155

III SLEEP IN PINNIPEDS: OTARIIDS OR EARED SEALS s0085

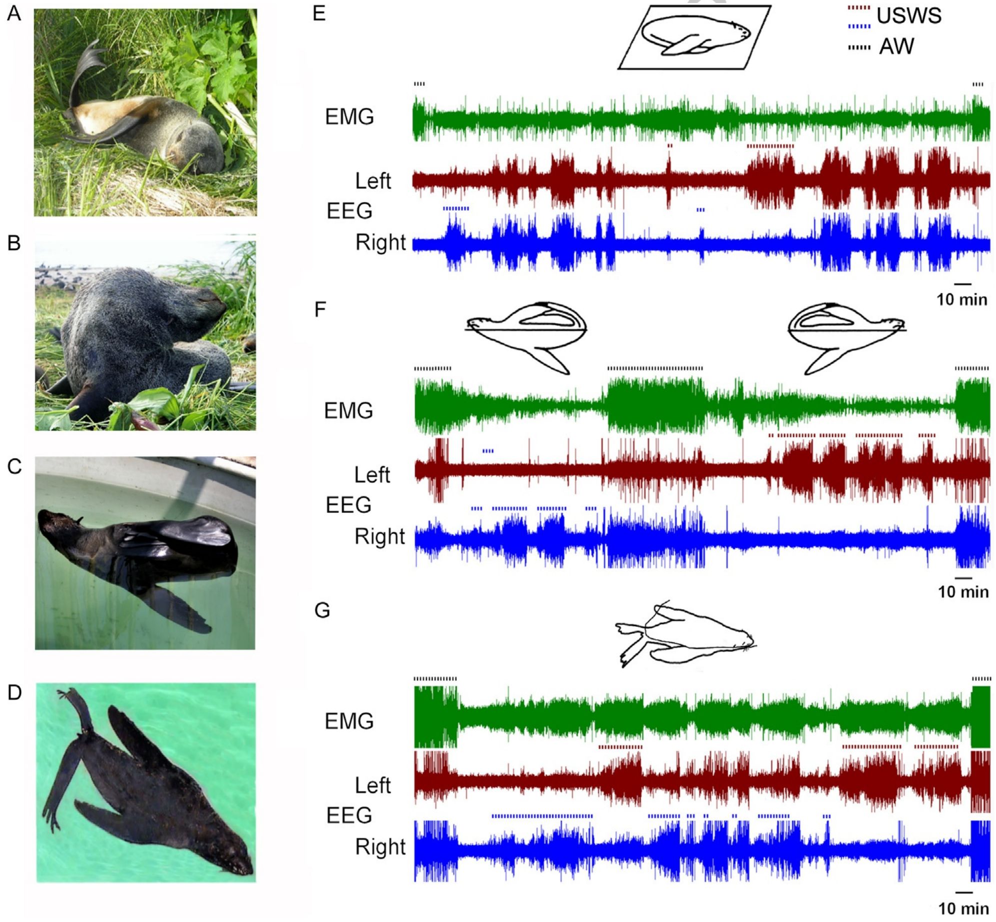
Pinnipeds are semiaquatic mammals and include three families: the Otariidae (15 species), Phocidae (19 species), and Odobenidae (1 species). Pinnipeds differ substantially not only in their regional distributions but also in their anatomy, ecology, and behavior. The earliest pinnipeds were aquatic carnivores with well-developed paddle-shaped feet with a fossil record from the North Pacific extending back to approximately 25 mya (Berta, 2017). p0160

The family Otariidae (eared seals) is composed of fur seals and sea lions. Most species inhabit temperate latitudes, while several species inhabit subpolar and p0165 equatorial regions. They breed on land. Fur seals are smaller than sea lions, have longer fur, travel further and longer for foraging trips, and exhibit greater sexual dimorphism.

p0170 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 otariids can sleep on land and in water. Among these species, sleep has been most extensively examined in the northern fur seal, one of the smallest and most pelagic fur seals. During the winter migratory season, seals migrate more than 2000 km to the wintering grounds and remain in the ocean for up to 10 months. During the summer breeding/molting season, they alternate between staying on land and going for foraging trips to the ocean, which can last up to 2 weeks (Gelatt & Gentry, 2017).

A USWS and BSWS s0090

p0175 Fur seals display both BSWS, as seen in terrestrial mammals, and SWS with interhemispheric EEG asymmetry (ASWS and USWS), as seen in cetaceans (Fig. 25.5). Similar to dolphins, the EEG asymmetry in the fur seal is recorded across the entire dorsal cerebral cortex (including sensory, motor, and associative cortical areas), and the EEG changes in the ipsilateral cortex and thalamus occur synchronously. The EEG asymmetry is expressed in the range of 1.2–16 Hz, including the band of 1.2–4 and 12–16 Hz (Lyamin, Kosenko, Lapierre, Mukhametov, & Siegel, 2008; Lyamin, Mukhametov, & Siegel, 2017; Lyamin, Pavlova, Kosenko, Mukhametov, & Siegel, 2012). The EEG asymmetry in the cerebral cortex in fur seals occurs together with a greater release of acetylcholine in the waking hemisphere (Lapierre et al., 2007), suggesting of a functional asymmetry between subcortical



f0030 **FIG. 25.5** The pattern of sleep in the fur seal on land and in water. *Left column*: postures of sleep in the fur seals on land (A, B) and in water (C, D). *Right column*: Representative polygrams of recordings from fur seals sleeping on land (E) and at the water surface in the lateral (F) and in a prone position (G). The duration of each polygram is approximately 6 h. *EMG*, neck electromyogram; *EEG*, electroencephalogram in symmetrical left (L) and (R) fronto-occipital derivations. Episodes of unihemispheric sleep (*USWS*) in the left and right hemispheres and active wakefulness (*AW*) are marked by *brown*, *blue*, and *black* dotted lines, respectively. Postures of fur seals are shown on the diagrams. *Reproduced from Lyamin, O. I., Kosenko, P. O., Korneva, S. M., Vyssotski, A. L., Mukhametov, L. M., & Siegel, J. M. (2018). Fur seals suppress REM sleep for very long periods without subsequent rebound.* Current Biology, *28, 2000–2005.*

structures (e.g., basal forebrain and brain stem, which send the major ascending cholinergic projections to the cortex and thalamus).

p0180 The studies of sleep in Steller's sea lion pups and yearlings of southern sea lions and in one adult Cape fur seal female have confirmed that all of them display both BSWS and ASWS/USWS (Lyamin & Chetyrbok, 1992; Lyamin, Mukhametov, Chetyrbok, & Vassiliev, 2002), as described in the northern fur seal. The extent of EEG asymmetry in fur seals and sea lions is generally smaller than in dolphins, and the duration of asymmetrical episodes is shorter.

s0095 B Sleep on Land

s0100 1 Postures, Sleep Composition

p0185 SWS (BSWS and USWS) occurs in fur seals and sea lions in lying or sitting positions. During SWS on land, they are as motionless as land mammals. REM sleep is usually recorded when seals and sea lions are lying with the head resting on the ground. This state has all behavioral and electrophysiological features of REM sleep recorded in terrestrial mammals (Siegel, 2017). REM sleep in fur seals usually occurs after high-voltage BSWS, but it can be recorded after ASWS/USWS. In all studied fur seals and sea lions, regardless of the recording condition (indoor or outdoor pools, 12L/12D or natural illumination), most ASWS was recorded during the light hours, while high-voltage BSWS and REM sleep occurred mostly during the night hours (Lyamin & Mukhametov, 1997; Lyamin et al., 2017).

p0190 When northern fur seals sleep on land, EEG asymmetry is 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 (Lyamin et al., 2004, 2017). A similar correlation was observed in an adult female southern African fur seal (Lyamin & Chetyrbok, 1992). Unilateral eye opening was also observed in sleeping Steller's sea lion pups, but not in 1-year-old southern sea lions. They always slept with both eyes closed and the amount of USWS/ASWS was much lower (<5% of the total SWS time) than in juvenile and adult fur seals (Lyamin et al., 2017; Lyamin, Mukhametov, Chetyrbok, et al., 2002).

s0105 2 Amount of Sleep Stages

p0195 The amount of sleep stages in fur seals depends on the animal's age and experimental conditions. When on land, juvenile fur seals (2–3 year old) stayed asleep on average 34% of 24 h (n = 4). The total SWS time represented on average 85% of sleep time, and the rest (15%) represented REM sleep. The amount of REM sleep accounted for an average of 5% of 24 h, with single episodes lasting up to 12 min (mean of 3.6 min; Lyamin & Mukhametov, 1998). Ten- to twenty-day-old pups recorded under similar experimental conditions stayed asleep longer, with SWS and REM sleep comprising on average 34% and 13% of 24 h, respectively (a 30% and 250% increase compared with juveniles). The average duration of REM sleep episode was 5.5 min. The smallest amount of sleep on land was recorded in a group of 3- to 10-year-old females (16% and 3%, respectively). Therefore, the duration of both sleep stages in the fur seal drops substantially with age, as generally described in land mammals.

Not only the amount of SWS and REM sleep but also the proportion of ASWS/USWS change with age in fur seals. In 10- to 20-day-old pups, SWS with EEG asymmetry represented on average only 5.5% of the total SWS time. At the age of 2–3 month, USWS on land increased by almost fivefold and averaged 24.7% of the total SWS. However, in general, it was still less than in juveniles: 35%–60% of SWS in different studies (Lyamin et al., 2017; Lyamin & Mukhametov, 1998). Ten- to twenty-day-old pups nurse from their mothers and spend most of their time on land, while 2- to 3-month-old pups still nurse but can already swim and sleep in water. Thus, the proportion of ASWS/ USWS in fur seal pups increases almost to juvenile levels by the time pups are able to sleep in water. p0200

The total duration ASWS in 1-year-old southern sea lions sleeping on land varied from 1.1% to 10.6% of the total SWS and is among the shortest recorded in otariids. It averaged 5% of SWS, which is comparable with that in 10- to 20-day-old fur seal pups. Another feature the sleep of sea lions is a high proportion of REM, on average 40% of TST (Lyamin et al., 2017; Lyamin, Mukhametov, Chetyrbok, et al., 2002). Although 1-year-old southern sea lions can swim, they continue to nurse from their mothers, as do 10- to 20-day-old fur seal pups. Thus, the amounts of ASWS/USWS in fur seals and sea lions appear to be low at earlier stage of postnatal ontogenesis. p0205

C Sleep in Water s0110

1 Sleep Postures, Movement, Asymmetrical Eye State and USWS s0115

When in water, fur seals predominantly display USWS. They sleep more often in the lateral posture, which is characterized by striking motor asymmetry: seals sleep at the surface on their sides, paddling with one fore flipper to stabilize the posture, while holding the other three flippers above the surface. During sleep in this position, the waking hemisphere (displaying low-voltage EEG) is contralateral to the moving flipper, while the sleeping hemisphere (displaying high-voltage EEG) is always ipsilateral to the moving flipper (Fig. 25.5). Other species of fur seals have also been p0210 observed in water sleeping in the same position, suggesting that this posture is may be characteristic of all fur seals. This posture was also observed in pups between 2 and 3 months of age. The correlation between the patterns of EEG in the two hemispheres and movement in the fur seal provides strong evidence that USWS enables motion in seawater. Fur seals lose heat through their naked rear flippers, which are the longest and thinnest of any pinniped. Therefore, the lateral sleep posture prevents heat loss and optimizes thermoregulation. Also, this posture, with the nostrils held above the surface, facilitates breathing (Lyamin et al., 2017, 2018; Lyamin & Mukhametov, 1998).

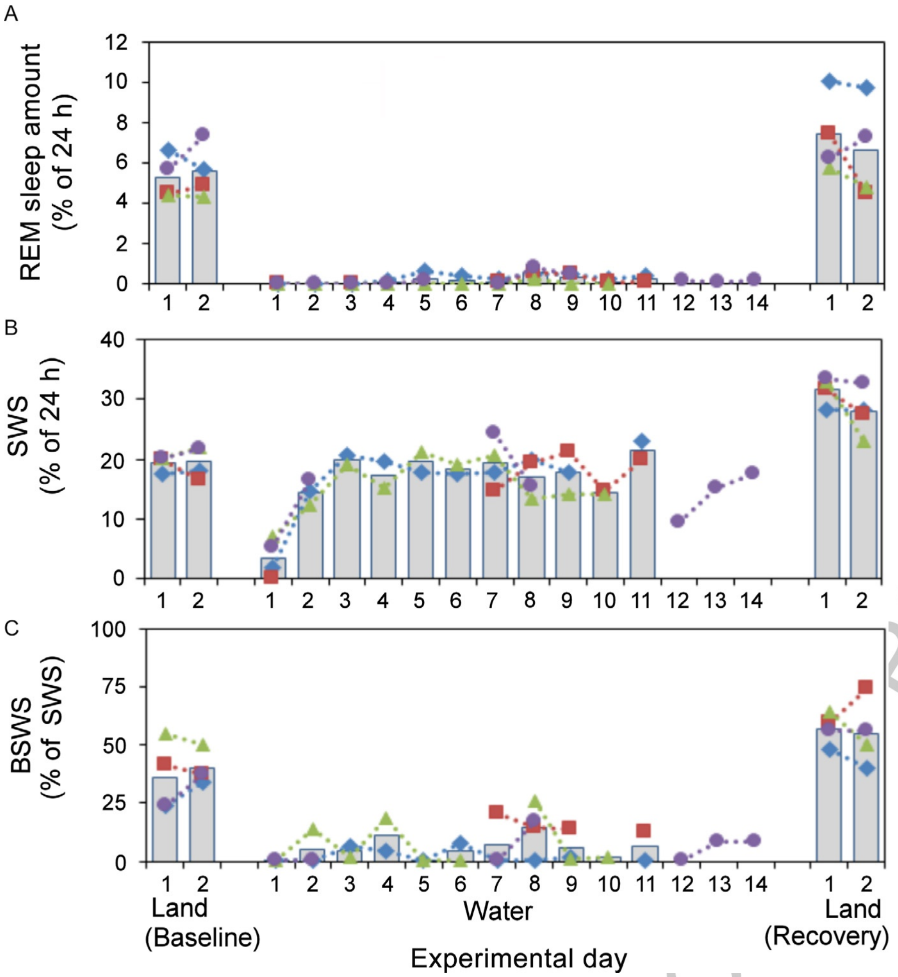
p0215 Fur seals can also sleep in a prone position (Fig. 25.5). USWS represents the majority of sleep in this position as well, but the bouts of USWS in resting seals may occur in both hemispheres. Movements are minimal in this posture and no noticeable correlation is apparent between the pattern of EEG asymmetry and motion. Thus, the maintenance of movement is not the only function of USWS in the fur seal.

p0220 Another interesting feature of sleep in the fur seal in the lateral position is the asymmetrical state of the eyes. In this posture, one eye is directed upward and away from the water. This eye is often closed and contralateral to the sleeping hemisphere during USWS. The other eye is directed to, and often immersed in, the water. Although it is difficult to monitor, infrequent observations suggest that during rest and sleep, this eye periodically opens. This eye is contralateral to the waking hemisphere during USWS. Having the open eye directed to the water facilitates monitoring predators such as killer whales and sharks. In addition, in this posture, the vibrissae from only one side of the fur seal head are directed to the water. They are contralateral to the waking hemisphere, as is the case for the open eye and moving foreflipper. It is reasonable to assume that the vibrissae supply the brain with information crucial for controlling the position of the head. It is noteworthy that the representation of vibrissae in the contralateral somatosensory cortex of the fur seal is magnified disproportionally compared with other parts of the body (Supin, Popov, & Mass, 2001). To summarize, in addition to the facilitation of movement, USWS in the lateral position appears to serve the function of processing sensory information (visual from the open eye and somatosensory from the vibrissae at the minimum) to maintain vigilance (minimize the risk of predation) and to stabilize the sleep posture (to secure safe breathing and thermoregulation).

p0225 Among the other otariids, sleep in water was examined only in 3- to 5-month-old Steller's sea lion pups briefly placed in water for 12–24 h (Lyamin, 2004). Three of four pups exhibited SWS in water, while all looked exhausted by the end of the recoding. The pups were sleeping in water while slowly moving around the pool at the surface, periodically submerging the head for up to 110 s, and then raising the head above the surface and taking several breathes with shorter intervals (>30 s). USWS represented the majority of SWS (68%–98%) while in water. USWS was not always interrupted during breathing, but the amplitude of EEG activity occasionally becomes smaller. Based on visual observations, sea lions in captivity often rest at the surface while floating in proximity to each other. They may raise flippers out of the water at this time. However, we are not aware of any reports of sea lions sleeping in the lateral positions, as do fur seals. Thus, the similarity between fur seals and sea lions is in maintaining motion during sleep and extending flippers out of the water to reduce heat loss. Having long flippers allows fur seals and sea lions to move on the ground and effectively regulate body temperature on land (including at warm temperatures) but requires taking some measures to minimize the exposed area of body surface when in water. It is not known whether sea lions can sleep with one eye closed and another one open.

2 *REM Sleep in Water* s0120

p0230 REM sleep in water was examined only in fur seals when animals were kept without access to land for several weeks (Lyamin et al., 2018; Lyamin & Mukhametov, 1998). No REM sleep was recorded in water during the first 3–11 days. When REM sleep was recorded, it was characterized by head jerks and drops, submergence of the head, HR deceleration, arrhythmia, apneas, and cortical arousal. In the most recent study conducted in freely moving seals instrumented with portable data loggers and housed in water for 10–14 days, the average daily amount of REM sleep was reduced by 96.4% ± 1.0% of the values when they slept on land (3 vs 80 min/day). The number of REM sleep episodes decreased to 20% ± 3%, and the duration of REM sleep episodes decreased to 13% ± 1% of that on land. The estimated cumulative loss of REM sleep in the seal, which stayed in seawater for 14 days, the longest period studied, was 21.5 h, corresponding to 1369% of the daily baseline. In contrast to the near-elimination of REM sleep in water, the amount of SWS ranged between 45% and 130% of the baseline values on land. On the first 2 days after the seals were returned to land, the amounts of REM sleep, the number of sleep episodes, and their duration were not significantly greater than the typical values seen on land, suggesting no apparent rebound. At the same time, the amount of BSWS is more than doubled during both recovery days with respect to the amounts on land (Fig. 25.6). These experiments simulated the period of summer foraging trips when fur seals stay in water for no longer than 2–3 weeks. However, there is some evidence that fur seals can experience a



f0035 **FIG. 25.6** REM sleep is suppressed when fur seals are in seawater with little or no rebound when returned to baseline (land) conditions. (A) The amount of REM sleep substantially decreased in fur seals during the entire period in seawater. There was no apparent rebound when the seal returned to land. (B) The total amount of SWS (BSWS plus USWS) was reduced only on the first day after seals were placed in water. The amounts of SWS increased in all seals after they were returned to land. (C) The proportion of bilateral SWS (BSWS) was significantly reduced during all periods the seals stayed in water and increased in all seals on the first recovery day on land. The *colored lines* and *symbols* mark individual seals, and the *gray bars* indicate the average values. *This figure is an abbreviated version of fig. 25.3 from Lyamin, O. I., Kosenko, P. O., Korneva, S. M., Vyssotski, A. L., Mukhametov, L. M., & Siegel, J. M. (2018). Fur seals suppress REM sleep for very long periods without subsequent rebound.* Current Biology, 28*, 2000–2005.*

reduced amount of REM sleep in water for durations of up to 1–2 months; it is not known what happens to REM sleep when they are aquatic for even longer (6–10 months) time periods.

p0235 The findings summarized above have several important implications for our understanding of the functions and biological role of REM sleep. First, fur seals “naturally” eliminated or substantially reduced the amount of REM sleep for days or weeks in water, which appears to be more beneficial for the fur seal than having REM sleep. Second, REM sleep in the fur seal is eliminated at a time when the animal requires high levels of alertness, performance, learning, and motor activity to navigate, locate prey, and avoid predators, compared with when the seal is resting on land. These observations cannot easily be reconciled with the idea that REM sleep is essential for maintaining cognitive functions. Third, the absence of a REM sleep rebound in fur seals after accumulating a profound REM sleep deficit in seawater challenges the idea that REM sleep is homeostatically regulated. Fourth, there are obvious similarities between fur seals and dolphins, as dolphins exhibit only USWS and no clear evidence of REM sleep, while fur seals have REM sleep and high-voltage BSWS when sleeping on land but eliminate both stages when they switch to USWS in water. These data support the idea that REM sleep may serve to reverse some adverse, yet unknown consequences of deep SWS, such as a reduced brain temperature, hypometabolism, or some other unidentified factor.

D Cardio-Respiratory Pattern s0125

p0240 The breathing pattern of juvenile fur seals and sea lions is regular (as in land mammals) during quiet waking and SWS both on land and in water. The majority of all respiratory pauses were shorter than 30 s (Lyamin, Kibalnikov, Kosenko, Mukhametov, & Siegel, 2010; Lyamin, Mukhametov, Chetyrbok, et al., 2002). REM sleep on land and in fur seals in water is characterized by an increase in the irregularity of breathing, with occasional apneas lasting longer than 1 min when the head submerged (Lyamin et al., 2018). Unlike the cetaceans, high-voltage BSWS is compatible with normal breathing in otariids.

p0245 The instantaneous HR of the fur seal features expressed respiratory sinus arrhythmia. During quite waking and especially SWS, instantaneous HR is stereotypic, ranging between 60 beats/min during the phase of breath holding and 150 beats/min concurrent with inhalations. During REM sleep, this stereotypic pattern is disrupted. The variability of HR greatly increases during the most intense muscle jerks and body twitches, when instantaneous HR may decrease to as low as 35 beats/min (Lyamin et al., 2010, 2018; Lyamin & Mukhametov, 1998). In Californian sea lions resting on the beach, the mean minimum and maximum instantaneous HR averaged 42 and 87 beats/min, respectively (McDonald & Ponganis, 2014).

s0130 E Microdialysys Studies

p0250 In land mammals, the cortical and subcortical release of monoamines (histamine, serotonin, and noradrenaline) progressively decreases at the transition from active wakefulness (the state with the greatest levels of both muscle tone and activity), to quiet wakefulness, to bilateral SWS and even further in REM sleep (the state of immobility with the most substantial reduction in muscle tone). The release of four neurotransmitters was examined during sleep and waking states in the fur seal, and the pattern was generally similar to that in land mammals (Lapierre et al., 2007; Lyamin, Korneva, Obukhova, Mukhametov, & Siegel, 2015). Further, subcortical levels of norepinephrine and serotonin in the fur seal showed a pattern similar to that seen in the cortex. Also similar to land mammals, the cortical release of acetylcholine in the seal during waking and REM sleep was greater than in BSWS. Noradrenaline and serotonin release in the cortex and diencephalon was bilaterally symmetrical, and the release of histamine was symmetrical in the cortex. Of the transmitters examined, only acetylcholine release was asymmetrical in USWS, with significantly greater release in the activated hemisphere.

p0255 Different arousal systems do not contribute equally to EEG control, with activity of the cholinergic system known to be more closely related to EEG arousal than the other (monoaminergic) arousal systems. In the fur seal, the activity of the acetylcholine system on both sides of the cortex can be controlled independently, either by mechanisms within the cerebral cortex or unilaterally from subcortical structures (e.g., basal forebrain or reticular formation). In contrast, monoamine release is closely associated with level of behavioral arousal and motor activity within the waking state, but not with EEG arousal. Other systems may also be involved in controlling the cortical asymmetry of the EEG. These speculations may also be applicable to dolphins, since phenotypically, behavioral features of USWS in cetaceans and fur seals appear to be very similar.

s0135 F BSWS Deprivation

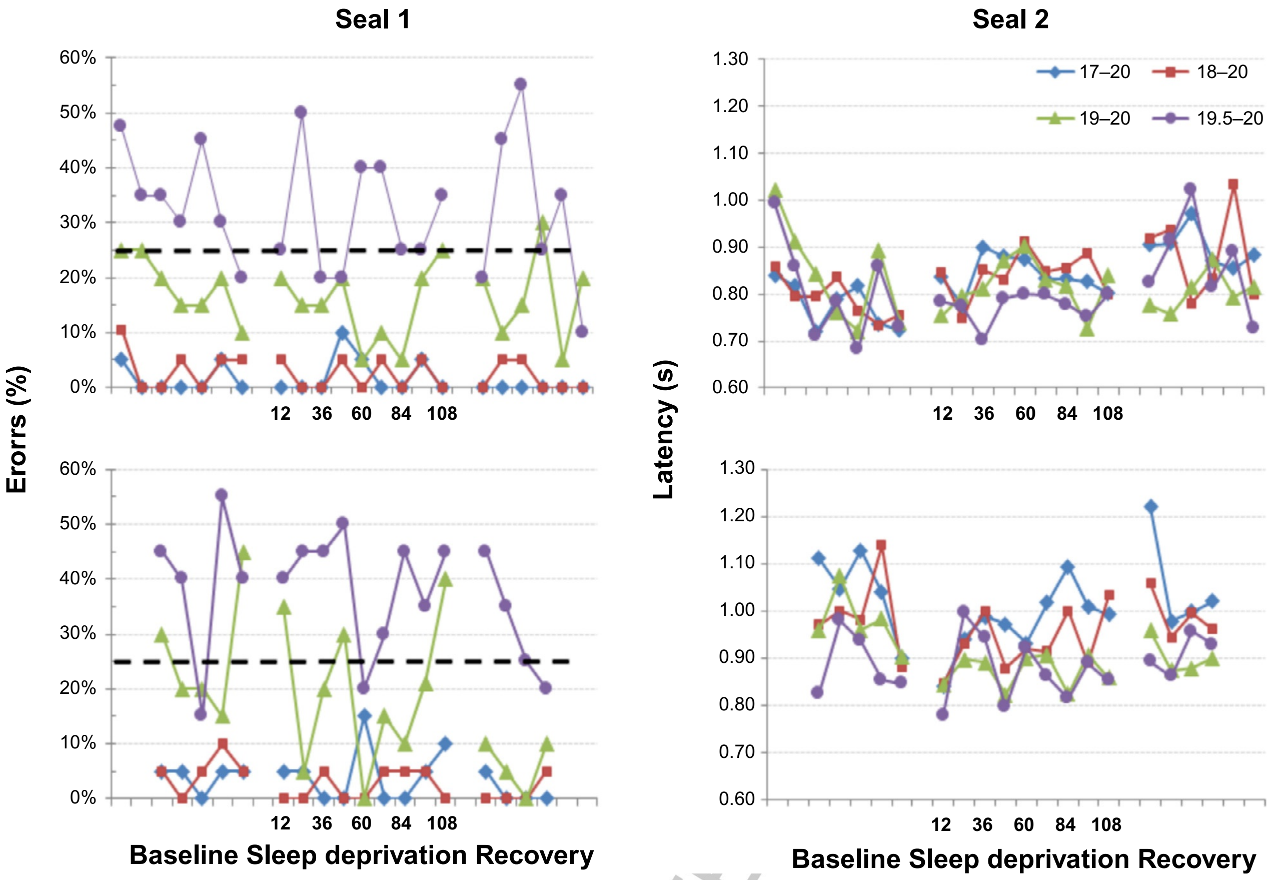
p0260 As discussed, fur seals virtually eliminate REM sleep in water for at least 2 weeks. Surprisingly, on land, seals repeatedly enter BSWS when deprived even for 3 days (Lyamin, Lapierre, Kosenko, Mukhametov, & Siegel, 2008). BSWS sleep deprivation was shown to reduce the percentage of high-voltage BSWS on average to 14% of baseline levels, which was comparable with the reduction of BSWS when in water. Deprivation also significantly increased the amount of ASWS during recovery in all seals to 235% of the baseline values. On the first recovery day, both high-voltage BSWS and the amounts of SWS in each hemisphere were significantly elevated during the first 4 h of recovery in all seals. Thus, fur seals appeared to display a rebound of SWS. However, the increase was not proportional to the amount of sleep lost. Sleep deprivation also reduced the amount of REM sleep to 60% of baseline levels. The primary cause for the decrease of REM sleep during SD appears to be the disruption of the "normal sleep" pattern, specifically the decreased amount of high-voltage BSWS, which usually precedes REM sleep when on land. Therefore, fur seals are capable of almost completely eliminating REM sleep when in water, but they appear to be unable to do this when on land, where they repeatedly initiating this state.

s0140 G Cognitive Functions Under the Conditions of Sleep Deficit

p0265 It is widely acknowledged that sleep is crucial to maintaining cognitive functions, such as attention, sensory perception, decision-making, learning, and memory. However, most of the conclusions were made based on the data collected in humans and other land mammals (predominantly rodents). We found that the ability of seals to visually discriminate objects depended only on the difficulty of the task and did not deteriorate under conditions of a sleep caused by 108 h of total sleep deprivation when compared with baseline conditions (Fig. 25.7; Lyamin et al., 2015). Thus, unlike humans and other land animals, fur seals (and apparently other marine mammals) appear to be capable of preserving a high level of cognitive functioning and performance when undergoing profound sleep deprivation over a period of several days.

s0145 IV SLEEP IN PINNIPEDS: PHOCIDS OR TRUE SEALS

p0270 With the exception of two species of tropical monk seals, all Phocidae species inhabit polar, subpolar, and temperate latitudes; they breed on pack ice and on land.



f0040 **FIG. 25.7** Percent of errors and response latency in two northern fur seals when discriminating the larger of two circles under baseline conditions, during 108 h total sleep deprivation and during recovery. During sleep deprivation, the average amount of rest was decreased to 1/80 of the baseline value in seal 1 and to 1/68 in seal 2. The performance of the seals depended only on the difficulty of the task (the difference between the diameters of two circles) and did not depend on the experimental conditions. Different markers signify averages for different pairs of circles (20 vs 17, 20 vs 18, 20 vs 19, and 20 vs 19.5 cm) in consecutive tests. The duration of sleep deprivation is shown in hours. The *broken lines* indicate the error rates of random responses (25%, 5 errors out of 20 trails, binomial test, $P = .05$).

True seals are more streamlined than fur seals and sea lions, with a respiratory system that is better adapted to prolonged dives (Berra, 2017). Sleep has been studied electrophysiologically in five phocid species: the gray seal (*Halichoerus grypus*), Caspian seal (*Phoca caspica*), harp seal (*P. groenlandica*), northern elephant seal (*Mirounga angustirostris*), and harbor seal (*P. vitulina*).

s0150 A Sleep on Land

p0275 In three species studied to date (the Caspian seal, harp seal, and northern elephant seal), the EEG was recorded form both cortical hemispheres (Lyamin et al., 1983; Mukhametov, Supin, & Polyakova, 1984; Castellini et al., 1994). In all records, EEG slow waves occurred synchronously in both cerebral hemispheres regardless of whether the seals were sleeping on land (snow) or in water. True seals usually hold their head withdrawn into the body when in SWS and rest the head on the ground at the onset of REM. In contrast to cetaceans and otariids, there are no reports of asymmetrical eye closure in phocids during SWS.

REM sleep episodes in phocids are generally shorter than in otariids (e.g., on average 2.0 min in 10- to 30-day-old harp seals compared with 5.5 min in 10- to 20-day-old fur seal pups (Lyamin, 1993); on average 1.8 min in adult Caspian seals and 3.6 min in juvenile fur seals (Lyamin & Mukhametov, 1998; Mukhametov et al., 1984)). Episodes of REM sleep usually occur in series after bouts of SWS (e.g., 2–9 episodes per series in harp seals). The amount of REM sleep did not change during the first month of the harp seal pup's life (8.0% and 7.5% of 24 h in 10- and 30-day-old pups, respectively), while total SWS time decreased slightly during this period (from 36.2% to 26.8% of 24 h, respectively). p0280

Compared with otariids, the amount of REM sleep in 10- to 30-day-old harp seal pups (8% of 24 h) was substantially smaller than in fur seal pups of the same age (13.1% of 24 h), but it was close to that in 2- to 3-month-old pups (7.1%) and 1-year-old southern sea lions (9.1%). At the same time, the amounts of SWS in harp seals were greater p0285 than in all studied pinnipeds. Since REM sleep (but not SWS) impairs thermoregulation in land mammals, the relatively low amount of REM sleep (60% of that in the fur seal of same age) and large amount of SWS in newborn harp seals are likely related to the cold environment that they inhabit during the first month of their lives. The amounts of SWS and REM sleep in 4-month-old northern elephant seals were reported to average 40% and 5%, respectively, of the recording time (Castellini et al., 1994), values that were greater and smaller than corresponding average values in other pinnipeds. However, differences between experimental conditions and the short duration of recording do not allow for a reliable comparison between these species.

s0155 B Sleep in Water

p0290 Sleep in three species was examined when the animals were kept in water without access to dry platforms. In adult Caspian and 3- to 5-month-old harp seals, both SWS and REM sleep occurred when the seals were floating motionless at the surface, at depth, or while lying on the bottom of the pool (Lyamin, 1993; Mukhametov et al., 1984). Seals did not always wake up for breathing when they had SWS at the surface. However, they did always wake up if they were sleeping at a depth and needed to initiate movement to emerge to the surface. Therefore, BSWS in true seals is compatible with breathing but incompatible with movement. It was reported that in water, REM sleep in gray seal yearlings started in quiet waking and preceded SWS; it was characterized by regular breathing (Ridgway, Harrison, & Joyce, 1975). Thus, gray seals stayed at the surface to have uninterrupted REM sleep episodes. It was also unusual that periods of REM were as long as 63 min. It is likely that those "periods of REM" included different behavioral states, rather than uninterrupted REM sleep episodes.

p0295 The amount of sleep in water in the studied phocids varied substantially, due to individual differences (age and sex) and varying experimental conditions (telemetry and cable recordings, temperature, duration of recordings, etc.), which does not allow comparisons among species. In the same Caspian and harp seals, the amounts of REM sleep in water were generally smaller than on land. However, in contrast to fur seals, some Caspian and harp seals displayed REM sleep even on the first day they were placed in water.

s0160 C Cardio-Respiratory Pattern

p0300 In all five species of phocids studied to date, breathing was irregular during wakefulness. During SWS, all seals show a similar respiratory pattern: alternation of apneas with periods of regular breathing. For instance, captive harp seal pups (<1 month old) during SWS on ice exhibited apneas lasting up to 140 s, interrupted by periods of regular breathing ranging between 20 and 190 s, with interbreath intervals of less than 4 s (Lyamin, Oleksenko, & Polyakova, 1993). Four-month-old northern elephant seal pups resting on land displayed apneas lasting up to 12 min when in SWS on land (Castellini et al., 1994), while adult animals resting (apparently sleeping some of the time) exhibited apneas lasting up to 21 min (Blackwell & LeBoef, 1993). In all true seals except for the gray seals, the majority of REM sleep episodes occur during single apneas, which were interrupted by periods of sporadic and fast respirations and brief arousals (Castellini et al., 1994; Lyamin et al., 1993). After a long period of SWS without REM sleep, seals often experienced a complete sleep cycle (wakefulness, SWS and REM sleep) within one apnea. This interrupted pattern of breathing with apneas, which becomes longer with age, allows phocids to sleep in water in virtually any posture, for example, floating horizontally or in vertical position or resting on the pool floor. Only in gray seals was breathing reported to become regular (12–16 per min) during REM sleep (Ridgway et al., 1975; see above).

p0305 HR in phocids was characterized by pronounced sinus arrhythmia. During quiet waking and SWS, HR decreases during apneas (on average to 70 beats/min in 1-month-old harp seals and 41–44 beats/min in 4-month-old elephant seals) and then increases during the period of regular breathing (on average to 110 beats/min and to 54–60 beat/min in these two species, respectively). During REM sleep, HR is irregular, but the range is about the same as during SWS, except as described in the gray seal (Castellini et al., 1994; Lyamin et al., 1993; Mukhametov et al., 1984; Ridgway et al., 1975).

D Behavioral Data s0165

p0310 Behavioral sleep has also been examined in 2- to 6-month-old pups of the Baikal seal (*Pusa sibirica*), which is the smallest of the phocid species. At the age of 2–4 months, the amounts of quiet sleep and REM sleep on land averaged 22.7% and 2.5% of 24 h, respectively. The behavioral and breathing pattern was the same as described in other true seals. During sleep, both eyes were closed, and when in water, animals rested at the surface. REM sleep was characterized by distinct muscle jerks, rapid eye movements, muscle relaxation, and apneas lasting on average 90–140 s on land and up to 6 min in water. Between 50% and 60% of REM sleep episodes on land and all episodes in water occurred within one apnea (Nazarenko, Lyamin, Shpak, & Mukhametov, 2001). The Baikal seal pups were not seen sleeping on the bottom of the pool. However, adult seals of other species of the Phocidae family have been often observed and videotaped while resting motionless on the bottom of pools in different aquaria.

p0315 Phocids engage in long-distance migrations lasting for several months during which they spend most of this time underwater traveling and feeding (e.g., elephant seals 83%–90% of their time at sea (Le Boeuf, Naito, Huntley, & Asaga, 1989) and harbor seals 76%–93% (Ries, Paffen, Traut, & Goedhart, 1997)). For instance, elephant seals stay at the surface for breathing only several minutes and then dive to a depth of 350–800 m, with the longest recorded dive to a depth of 1523 m. The duration of dives averaged 21–24 min; the longest was 77 min (DeLong & Stewart, 1991). It was suggested that they sleep during deep dives. A recent study in tagged northern elephant seals revealed that, during some dives, they switch from fast vertical to a low-speed drift descending phase. While descending to a depth of more than 370 m, they might even hit the sea bottom but often continue to remain immobile for over 5 min (Mitani et al., 2010). Based on 3-D accelerometer data, elephant seals showed inactivity with no flipper strokes, a stereotypical belly-up posture in drift dives and reduced responsiveness to stimulation when they hit the sea floor. All of these behaviors meet the necessary criteria for sleep. Sleeping at a depth would provide security from near-surface predators (killer whales and sharks, Le Boeuf et al., 1989). Interestingly, elephant seal did not switch from the fast speed vertical to the low-speed belly-up drift dive phase until they reached a depth of at least 135 m, which is close to the lowest level of the zone (150 m) where killer whales spend most of their time (Baird, Hanson, & Dill, 2005). To reduce the risk of predation by polar bears, some arctic seals also remain in the water most of the time. For instance, females of the bearded seals spend an average of 92% of the time in water, diving approximately half of this time, and go to the ice only to feed their pups (Kraf, Lydersen, Kovacs, Gjertz, & Haug, 2000). Episodes of behavioral sleep were video recorded in Mediterranean monk seals in the sea (Karamanlidis, Lyamin, Adamantopoulou, & Dendrinos, 2017). The animals were lying motionless with both eye closed at the sea bottom at a depth of 5–10 m. They woke up and swam away when speargun fisherman approached too close. Thus, monk seals appeared to be secure enough to sleep on the sea floor even if they were close enough to land. All of these behavioral data indicate that Phocids can sleep while diving at depth including while resting on the sea bottom.

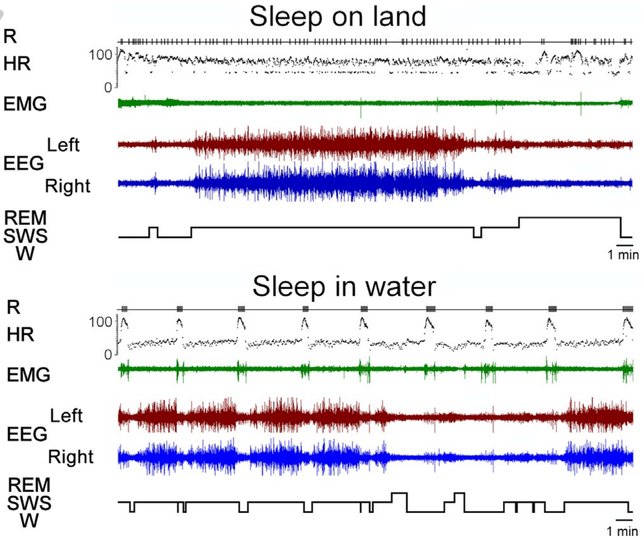
s0170 V SLEEP IN PINNIPED: ODOBENIDS (THE WALRUS)

p0320 The walrus is the only living species (*Odobenus rosmarus*) in the family Odobenidae, which is the third family of the clade of pinnipeds. The walrus inhabits the seas of the Arctic Ocean (Berta, 2017). Behavioral sleep was monitored in four juvenile walruses (Pryaslova, Lyamin, Siegel, & Mukhametov, 2009). In a subsequent study, sleep on land and in water was examined electrophysiologically in one of these animals (Lyamin, Kosenko, et al., 2012).

A Sleep on Land and in Water s0175

Sleep on land in the walrus occurred in a recumbent position. Most sleep in water (89% of the TST) occurred during repeated submergings to the bottom (on average 200 ± 6 s) and surfacings for breathing (63 ± 4 s). The walrus always woke up several seconds before the surfacing. The remaining sleep was recorded while floating at the surface. REM sleep in water occurred only when the walrus lay on the bottom. Usually, 2–3 REM episodes followed a series of episodes of SWS (Fig. 25.8). p0325

The amount of SWS on land and in water was similar and averaged 20% of 24 h (based on 5- and 3-day continuous recordings). However, the amount of REM sleep in water was only one-seventh of that on land (on average 1% and 7%, respectively). Episodes of REM sleep on land lasted between 0.3 and 23 min, while all episodes in water were shorter than 2.1 min. The majority of SWS was scored as BSWS. Episodes of ASWS were occasionally recorded on land and accounted for less than 15% of SWS. Those episodes were associated with brief opening of the eye, which was contralateral to the hemisphere with low-voltage EEG, as in cetaceans and fur seals. ASWS was nearly absent when in water (<4% of SWS). p0330



f0045 FIG. 25.8 Polygrams of wakefulness, slow-wave sleep, and REM sleep in a walrus on land (*left*) and in water (*right*). *HR*, instantaneous heart rate (beats/min); *EEG*, electroencephalogram of the left and right hemispheres; *EMG*, electromyogram of neck muscles; *R*, respiratory acts (breaths); *W*, wakefulness; *SWS*, slow-wave sleep; *REM*, rapid eye movement sleep. During breath holdings (apneas) in water, the walrus submerged and lay on the bottom of pool.

To summarize, the pattern of sleep and breathing in the studied walruses is similar to that of the Otariidae seals while on land and the Phocidae seals.

s0180 B Cardio-Respiratory Pattern

p0335 While on land, the breathing pattern of the walruses was regular during quiet wakefulness and SWS. Most interbreath intervals (95% of all pauses) ranged between 10 and 30 s. During REM sleep, breathing was sporadic, with apneas lasting up to 91 s and alternating with periods of regular breathing. When the walrus slept at the surface of water, breathing could be regular or interrupted at times, but apneas were shorter (111–150 s, on average 131 ± 6, $n = 6$) than when submerged to the bottom (up to 220 s). HR became stereotypic when quiet waking progressed to SWS and ranged between 50 beat/min (during breath holding) and 90 beat/min (during inhalation). HR was irregular during REM sleep, and its range was wider—between 45 and 105 beat/min.

s0185 C Behavioral Data

p0340 Behavioral data collected in captivity showed that 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). When on land, walruses slept on average 40%–74% of the time (Pryaslova et al., 2009). This behavioral pattern may be related to seasonal migratory behavior. The data collected in captivity are also consistent with those obtained in the wild. For instance, one of the tagged walruses dove continuously over several days and then stayed at the surface for a prolonged period (Wiig, Gjertz, Griffiths, & Lydersen, 1993). The ability to reduce or even eliminate sleep for a few days may be an adaptation of marine mammals to the aquatic environment they inhabit, specifically the movement of the water (tides, waves, currents, and storms), the absence of sleeping sites, and the need to migrate to and from feeding grounds.

s0190 VI SLEEP IN OTHER AQUATIC MAMMALS

s0195 A Manatee

p0345 Rest and sleep behavior was examined in a 2-year-old Amazonian manatee female (order Sirenia, *Trichechus inunguis*). In the first study, the behavior of this animal was monitored in a spacious fresh water pod for 3 continuous days. In the following electrophysiological study, EEG, EMG, and ECG were continuously recorded during 5 consecutive days when the animal was placed in a shallow pool (Mukhametov, Lyamin, Chetyrbok, Vassilyev, & Diaz, 1992).

When residing in the pod, the manatee rested while motionless at the water column or lying on the pod floor as described in captivity (e.g., Horikoshi-Beckett & Schulte, 2006). In our study, the majority of rest in the manatee occurred between 1800 and 0300. The average dive (breath holding) duration during rest period was 248 and 170 s during active periods. SWS in the manatee was composed of both BSWS and ASWS, with BSWS accounting for 75% of TST. SWS and REM sleep occupied, on average, 27% and 1% of 24 h, respectively. REM sleep episodes occurred during apneas lasting between 20 and 253 s. Both sleep stages occurred while the manatee was resting motionless on the pool floor and waking up to surface for each respiratory act. Consistent with the behavioral study, most sleep was recorded between 2000 and 0300. Thus, the pattern of sleep in the studied manatee shared the features of sleep both the Otariidae seal (ASWS and BSWS) and Phocidae seals (sleep during immobility and breath holding). It remains unclear which mechanisms might cause interhemispheric EEG asymmetry in the manatee, because neither motion nor eye state asymmetry was recorded during SWS in this animal. p0350

B Sea Otter s0200

Behavioral observations in two 6- to 8-month-old captive sea otters (order Carnivora, *Enhydra lutris*) revealed that they sleep both on land and in water. When in water, quiet sleep occurred in a characteristic posture while swimming on their backs, holding their heads above the surface, and balancing their bodies and tails to stabilize this position. In parallel with muscle jerks and body twitches (features of REM sleep), the otter overturned on the side or in the belly-down position, with the paws extended and the head submerged. The average duration of REM sleep episode was about 90 s and did not differ between land and water. The average breathing pauses during quiet wakefulness and quiet sleep were about 6 s, which also did not differ between land and water. Breath holding longer than 30 s occurred only during REM sleep in water when the head dropped into water, with the longest instance lasting 70 s. The total amounts of quiet sleep and REM sleep accounted for 20%–32% and 0.7%–1.8% of 24 h, respectively (Lyamin, Oleksenko, Sevostiyanov, Nazarenko, & Mukhametov, 2000). These values were smaller than those reported for an adult female with a pup in an aquarium (on average 38%), while the postures of resting animals on land and in water were similar in both studies (Hanson, Bledsoe, Kirkevold, Casson, & Nightingale, 1993). Therefore, similar to cetaceans and fur seals, sea otters appear to be able to sleep during motion. These data suggest that sea otters likely have USWS. p0355

s0205
C Hippopotamus

p0360 Behavioral sleep has been studied in a group of three (female, male, and their 2-month-old calf) hippopotamuses (*Hippopotamus amphibius*, order Artiodactyla) in a zoo (Lyamin & Siegel, 2005). All hippos rested both on land and in water. When in water, they were sleeping motionless while standing or lying on the bottom of pools in shallow places. They positioned their heads above the surface and breathed regularly, rarely lowering their heads below the surface. Occasionally, they rested on the bottom, and apneas lasted up to 3 min. Some of these episodes might represent REM sleep, even though muscle jerks and body twitches were rare. The total amount of behavioral sleep was similar in all three animals and comprised 57%–60% 24 h. However, the female was more vigilant, likely to protect her calf. When sleeping, she briefly opened the eyes, particularly when on land during the light hours. In contrast to the numerous field observations reporting that hippopotamuses feed on the grazelands at night and rest and socialize in water during the day (Gates, 2017), the majority of sleep (83%–90%) in the zoo animals occurred in water during the nighttime. As in phocids, whenever both eyes in the hippopotamuses were visible, they opened and closed simultaneously. This suggests that SWS occurs in the hippopotamus symmetrically in both cortical hemispheres.

s0210
VII CONCLUSIONS

p0365 In summary, it is likely that three life-sustaining factors have exerted important influences on the evolution of the patterns of sleep seen in present-day aquatic mammals: (1) the need to come to the water surface to breathe, (2) more efficient monitoring of the environment, and (3) thermogenesis.

p0370 Unihemispheric sleep allows cetaceans to surface without awakening and for Otariidae seals to maintain a characteristic posture at the surface. Movement during unihemispheric sleep also facilitates muscle thermogenesis and postural thermoregulation. This pattern can be achieved only in open (ice-free) waters, which is the typical habitat for the majority of cetaceans and all otariids. Sleeping at the surface requires maintaining continuous vigilance to minimize the risk of near-surface predators. Thus, USWS has evolved as a neurophysiological mechanism, which allows cetaceans and otariids to maintain movement and continuous vigilance, while allowing slow waves to be present in at least half of their brain at a time. The absence/reduction of REM sleep when sleeping at the surface is adaptive primarily because it minimizes the time when the animal is less responsive and most vulnerable to predation. The suppression of REM sleep also minimizes the time when the animal is unable to effectively regulate its body temperature. Semiaquatic otariids have preserved the typical terrestrial type of sleep (BSWS, immobility, regular breathing, and REM sleep) when on land but are capable of switching to a more aquatic cetaceans mode of sleep (USWS, sleep in motion, and reduction of REM sleep) when in water.

Most of the phocids and the walrus inhabit cold waters of the subpolar and polar regions. Anatomical and physiological adaptations allow them to manage their body temperature in cold habitats. The ability to hold their breath and to endure long apneas is the hallmark of their sleep. While holding their breath, seals can minimize the time at the surface by sleeping at a depth that is below the level where near-surface predators are active. This strategy reduces predation and exposure to harsh environmental conditions when seawater freezes and forms pack ice. This pattern of sleep does not require motion, and consequently, SWS in phocids is bilateral, as in terrestrial mammals. Phocids need to awaken to surface for breathing. Effective protection against hypothermia and sleep where predators are not present does not prevent REM sleep from occurring at depth. p0375

Finally, the pattern of sleep in other aquatic (manatee) and semiaquatic mammals (sea otters and hippopotamus) shares the features of sleep in cetaceans and pinnipeds. p0380

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