



Research report

Behavioral sleep in the walrus

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ABSTRACT

In this study we examined behavioral sleep in the walrus, the only living species of the family Odobenidae. The behavior of four 1.5–2-year-old captive walruses was videotaped continuously for 7–17 days and scored in 1-min epochs. When walruses had access to water and land, behavioral sleep, the combined amount of quiet and rapid eye movement (REM) sleep, occupied on average $17 \pm 4\%$ of 24 h ($n = 4$) with the majority of sleep occurring on land. All walruses alternated periods of almost continuous swimming lasting for 40–84 h with periods of rest on land lasting for 2–19 h. When in water they were predominantly awake (88–99% of the time). On land walruses were asleep on average 40–74% of the time. The total sleep time varied between 0 and 60% of 24 h with the daily amount of REM sleep ranging from 0 to 5% of 24 h. In water, walruses slept while floating at the surface, lying on the bottom or standing and leaning against the pool wall. REM sleep in water occurred in all positions. On land the breathing pattern was regular during quiet sleep (most pauses were <30 s) and arrhythmic in REM sleep (apneas lasted up to 160 s). While in water the irregularity of breathing further increased (apneas were >4 min) and all REM sleep episodes occurred during a single apnea. Data indicate that the pattern of sleep and breathing in walruses is similar to the Otariidae seals while on land and the Phocidae seals while in water.

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1. Introduction

Members of the three Pinnipedia families (Otariidae, Phocidae and Odobenidae) differ substantially not only in their distributions, but also in their anatomy, ecology and behavior [5]. The earliest pinnipeds were aquatic carnivores with well-developed paddle-shaped feet with a fossil record from the North Pacific extending back to 25–27 Mya. The current view supported by both morphological and molecular data analysis suggests a monophyletic (having one ancestor) origin for the three pinniped families [3].

Sleep has been studied electrophysiologically in four species of otariids: the northern fur seal (*Callorhinus ursinus*; [16,17,21,25]), Cape fur seal (*Arctocephalus pusillus*; [15]), Steller's sea lion (*Eumetopias jubatus*; [14]) and southern sea lion (*Otaria flavescens*; [19]). Among these species, sleep has been most extensively examined in the northern fur seal. When on land fur seals predominately display bilaterally symmetrical slow wave sleep (SWS) and rapid eye movement (REM) sleep, which is typical for all terrestrial mammals. Fur seals also exhibit SWS with greatly expressed interhemispheric electroencephalogram (EEG) asymmetry (both in the amplitude

and frequency range of major rhythms), which resembles the uni-hemispheric sleep observed in cetaceans [22,26]. The proportion of asymmetrical SWS greatly increases when fur seals sleep in water, while the amount of REM sleep substantially decreases [16,20]. In water, the sleep of fur seals is also characterized by striking motor asymmetry: they sleep at the surface on their sides, paddling with one foreflipper, while holding the other three flippers above the surface. As in terrestrial mammals, the breathing pattern of fur seals during SWS is regular. In REM sleep, breathing becomes irregular but apneas rarely last longer than 30 s [16]. The studies of sleep in pups and yearlings of Steller's and southern sea lions as well as in one adult Cape fur seal have confirmed that these otariid species also display both bilaterally symmetrical and asymmetrical SWS [13–15,19] as described for the northern fur seal. Therefore, when on land the pattern of sleep in otariids is similar to that of terrestrial mammals but when in water it resembles the sleep of cetaceans.

To date, sleep has been also examined in five species of phocids: the gray seal (*Halichoerus grypus*; [32]), Caspian seal (*Pusa caspica*; [24]), harp seal (*Phoca groenlandica*; [12,18]), northern elephant seal (*Mirounga angustirostris*; [6]) and harbor seal (*Phoca vitulina*; [35]). As in terrestrial mammals, SWS in the Phocidae seals is always bilateral [6,12,18,24]. Unlike otariids, phocids can hold their breath for several minutes while asleep on land or in water. During SWS, such apneas alternate with periods of fast regular breathing. During REM sleep, breathing becomes irregular and many episodes occur within a single apnea [6,18]. The ability of phocids to hold their breath

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when asleep allows sleeping below the water surface. The sleep of phocids in water is also accompanied by complete immobility. However, they usually wake up while surfacing to breathe [12,24]. Therefore, the pattern of breathing is the only essential difference observed between the sleep of phocids and terrestrial mammals.

The Odobenidae family includes only one species (*Odobenus rosmarus*) with two subspecies (the Pacific walrus and Atlantic walrus). Found in the Arctic, the walrus is among the largest pinnipeds. They are migratory animals: every winter they move south to breeding areas and then in spring return north where females give birth to pups on drifting ice floes. Walrus feed on the ocean floor, mostly on clams while other pinnipeds usually feed on fish [11].

Sleep has recently been examined in one 2-year-old young walrus implanted with EEG, electromyogram, and electrooculogram electrodes for polygraphic recording [23]. SWS and REM sleep averaged $21.1 \pm 3.1\%$ and $4.6 \pm 1.0\%$ of 24 h, respectively, during 3 continuous days on land. 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. Occasionally, episodes of interhemispheric EEG asymmetry were recorded while the walrus slept on land. The detailed results of the EEG study will be presented elsewhere. This study focused on the behavioral aspects of sleep in freely swimming captive walrus.

2. Materials and methods

2.1. Animals

The behavior of four young Pacific female walrus was investigated. The animals were caught in the Chukotka Sea, Russia. Observations were conducted in March–July at the Utrish Marine Station (Black Sea, Russia) of the Russian Academy of Sciences. During the time of observation, the animals were approximately 1.5–2 years old and weighed 130–220 kg. They were healthy and well adapted to captivity.

2.2. Experimental conditions

All walrus were housed individually in outdoor pools with seawater and undisturbed except for the times they were fed and the pools were cleaned. Walrus 1 and 2 (W1 and W2) were housed in rectangular pools with dimensions of $4 \text{ m} \times 2 \text{ m} \times 1.3 \text{ m}$. W3 and W4 were kept in larger pools— $4 \text{ m} \times 4 \text{ m} \times 1.3 \text{ m}$. All pools were equipped with wooden platforms above the water, either located next to the pools (W1 and W2) or in the center of the pools (W3 and W4). W1–W3 lived in the pools for a minimum of 2 months before the observations whereas W4 was moved to the experimental pool 1 week prior to the start of the observations.

During the period of observation sunrise began approximately between 06:00 (June) and 07:00 (March). Sundown started between 18:00 (March) and 20:30 (June). During the nighttime, the pool area was illuminated by a 100-W electrical lamp positioned 3 m above the platform, providing approximately 30 lx at the level of the platform. Air and water temperature were measured 3 times per day (between 05:30 and 07:00 before cleaning the pool and at 12:00 and 20:00). For all observation periods combined, air temperature ranged between -2 and $+25^\circ\text{C}$ and water temperature between $+5$ and $+22^\circ\text{C}$. The mean air and water temperatures during the entire period of observation were: $+12.8$ and $+12.5^\circ\text{C}$ in walrus 1, $+16.7$ and $+17.1^\circ\text{C}$ in walrus 2, $+6.7$ and $+4.7^\circ\text{C}$ in walrus 3, and $+20.4$ and $+20.8^\circ\text{C}$ in walrus 4, respectively. However, for any single day the daily variation of air and water temperatures did not exceed 10 and 3°C , respectively.

Pools were cleaned and the water was changed daily between 07:00 and 09:00. W1–W3 were fed fish and squid three times per day between 08:00 and 09:00, 13:00–14:00 and 17:00–18:00. Each feeding lasted between 10 and 30 min and was accompanied by a short training session. At the time of observations, W4 was bottle fed a liquid soymilk and fish formula four times a day at 08:00, 12:00–12:30, 16:00 and 20:00.

2.3. Video recording and visual observations

Walrus were continuously videotaped via several TV-cameras (380–450 lines, 0–0.02 lx) located above the pool and continuously observed by an experimenter for 24 h. One of the cameras provided a panoramic view of the entire enclosure. Three (W1 and W2) and four (W3 and W4) additional aerial cameras were directed to the different parts of the platform and the pool to record enlarged views. When the animals were active (swimming or walking on the pool bottom or platform), the video image from the panoramic camera or the images of the different pool areas were recorded in quad-mode. When the walrus were resting on the platform or in water, the camera which provided the best view of the animal (the head and the upper part of the trunk) was connected to the recorder by the experimenter. Usually

one or two eyes were visible in W3 and W4 when the animals slept on the platform located in the center of the pool. In W1 and W2 the eyes were rarely seen because these animals preferred sleeping on their side on the platform close to the enclosure wall, so one eye was usually directed to the nontransparent wall and the other eye was directed to the platform. When W3 and W4 were asleep they were also directly observed by an experimenter from above the water from a position located 3–4 m far from the pool to visually document muscle jerks and the state of eyes.

All walrus were free to swim in water or stay on the platform. The observations continued for 9 days in W1, 7 days in W2, 12 days in W3 and 6 days in W4. One walrus (W3) was also kept afloat (i.e., the platform was removed) for three continuous days to further examine sleep in water.

2.4. Scoring of vigilance states and data analysis

Videos were scored visually in 1-min epochs. Each epoch was assigned the behavioral state which occupied more than 50% of the epoch time. Active waking (AW) was scored when the walrus was swimming, walking around the enclosure, feeding, sitting on the platform, being trained or when the pool was being cleaned. Quiet waking (QW) was scored when the walrus was lying or sitting quietly on the platform, occasionally looking around, moving its flippers or changing its posture more than 50% of the epoch time. The eyes were opened most of the time. In water QW was scored when the walrus was standing on the pool bottom (usually leaning against the fence wall) with its head or nostrils above the surface or floating at the surface with both eyes opened more than 50% of the epoch time.

Behavioral defined sleep on land was scored when the walrus was lying quietly on the platform on its sides or belly with its eyes closed (for W3 and W4) at least 50% of the epoch time. Sleep on land in W3 and W4 was subdivided into three stages: “light” quiet sleep (QS1), “deep” quiet sleep (QS2) and REM sleep. QS1 was scored when the walrus lay motionless for a minimum of 50% of each epoch with its eyes closed. In the remaining time the walrus might have moved its head, flippers or change body postures but those movements were brief. An epoch was considered QS2 if the walrus lay motionless with its eyes closed during the entire epoch. It is usually considered that QS represents SWS (or NREM sleep) and a portion of QW. Therefore, in our case QS1 largely included low voltage SWS and a portion of QW while QS2 primarily included high voltage and low voltage SWS. The REM sleep episode in the walrus was characterized by visually detectable postural changes (the neck extended and the head moved forward and rested on the platform), muscle and vibrissae jerks as well as rapid eye movements. Phasic events could occur continuously for several minutes. These episodes alternated with periods of complete immobility without muscle jerks or behavioral arousal (opening of the eyes or changing the posture). These alternated episodes represented a series of phasic and tonic periods within a single continuous REM sleep episode. An epoch was scored as REM if the described phasic and tonic events lasted a minimum of 30 s. Some apparent REM sleep episodes were shorter than 30 s (7.7% of total amount of REM sleep in W3 and 3.9% in W4). Those episodes were not considered when calculating the total amount of REM sleep to estimate the budget of time; however, those episodes were considered when calculating the average duration of individual REM sleep episodes in seconds (from the first phasic event or characteristic postural changes to behavioral arousal). The REM sleep episode was considered interrupted if phasic events had not been observed for more than 1 min and the last epoch was scored as QS or QW as described above. The sleep cycle was defined as the number of minutes between the beginning of QS and the end of the last REM episode in the series, followed by waking. When a sleep cycle started, a 2-min or less interruption by episodes of QW was allowed, considering that these episodes did not interrupt the sleep cycle. Similar criteria were used in previous studies [12,16,18,19,21,24]. As we mentioned above, W1 and W2 preferred sleeping on the side of the platform directing their heads toward the corner of the enclosure, so their eyes and muzzles were rarely seen at these times. This prevented the reliable identification of all REM sleep in these animals and subdivision of behavioral sleep into substages as it was done in W3 and W4.

Sleep in water was scored when the walrus was floating motionless at the surface, lying on the bottom or standing on the bottom leaning against the pool wall. Episodes of REM sleep in water were documented in all four walrus; however, REM sleep and QS were scored and quantified only in W3 and W4. The duration of QS (combined amount of QS1 and QS2) and REM sleep episodes in water was calculated in seconds as described. Due to the configuration of the platform in the pools where W1 and W2 were housed (it extended about 10 cm above the water surface along the longest side of the pool, so the walrus' heads were not visible when they floated close to the platform) we were not able to quantify all episodes of REM sleep in water in these animals.

All walrus alternated long periods of activity while in water with long periods of rest on the platform. The amount of time spent in water and on land during consecutive 1-h intervals was calculated. Each 1-h interval was then classified as “in water” or “on land” applying the 50% criteria. A 1-h interruption was allowed under the conditions that the amount of time spent “on land” per each hour during a period scored as “in water” and the time spent “in water” during the period scored as “on land” did not exceed 50% of each hour.

The breathing pattern was analyzed in W3 and W4 both on land and in water by recording the opening and closing of nostrils. Inter-breath interval durations were calculated for data collected during one night in W3 and W4.

2.5. Data analysis

All results are reported as mean \pm S.E.M. The correlation between the 24 h amounts of vigilance states and the temperature of water and air was examined using Pearson's correlation coefficients. The Mann–Whitney *U*-test was used to compare mean breathing pauses during QS and REM sleep. Differences in the distribution of breathing pauses between vigilance states were evaluated using the Chi² test.

3. Results

3.1. Vigilance states and episode duration

When walrus had access to water and land, they slept on average 17% of 24 h with the majority (on average 75% of behaviorally defined sleep which will be referred as to total sleep time, TST) of sleep occurring on land (Table 1). There was a wide range in TST between walrus (6.6% of 24 h or 95 min per day in W4 versus 23.1% of 24 h or 330 min per day in W2, with our observation times ranging from 6 to 11 days). In W1, W2 and W4 most sleep occurred during the nighttime (95, 78 and 100% of TST when averaged over the entire observation period, respectively). In W3, which showed the greatest amount of sleep on land (see 24-h activity profile), sleep was equally distributed between the daytime and nighttime.

In W3 and W4, sleep was subdivided into QS1, QS2 and REM sleep. QS2 (state of complete immobility) occupied on average about 40% of TST. Single QS2 episodes lasted up to 16 min in W3 (with the average duration of 3.1 ± 0.2 min, $n = 288$) and 12 min in W4 (2.3 ± 0.3 , $n = 78$). REM sleep occurred more often on land. It was characterized by intense jerks of the entire vibrissae area (including lips) and to a lesser extent by head, flipper and whole body jerks and twitches. Individual REM sleep episodes on land lasted from 5 to 611 s with 75 and 94% of all episodes in W3 and W4, respectively, being shorter than 3 min. The average duration of all REM sleep episodes recorded over the entire period of observation was 172 ± 25 s ($n = 37$) in W3 and 56 ± 7 s ($n = 40$) in W4. The average daily amount of REM sleep in W4 was one third that of W3 when single episodes shorter than 30 s were omitted (Table 1). The average amount of REM sleep increased only by 0.1% per day in each walrus reaching to 1.2% of 24 h in W3 (a total of 743 s per 11 days) and 0.5% in W4 (additional 292 s per 6 days), respectively, when all REM sleep episodes were considered.

REM sleep in walrus usually followed an episode of QS and consisted of 1–8 individual REM sleep episodes separated by QW or QS1. The mean sleep cycle duration was 40 ± 7 min ($n = 20$, max = 118 min) in W3 and 22 ± 3 min ($n = 14$, max = 52 min) in W4. The maximal number of sleep cycles and episodes of REM sleep per day were 12 and 22 in W3 and 11 and 40 in W4, respectively. The average sleep cycle included on average 1.8 ± 0.2 single REM sleep episodes in W4 (max 3 per cycle) and 2.9 ± 0.6 episodes in W4 (max 8 per cycle).

3.2. Variability in sleep time across days

There was significant variation in the daily amounts of sleep and waking states in walrus when they had access to both water and land (Figs. 1 and 2). This variation was greater in W3 and W4, which were housed in larger pools. In these animals TST calculated per observation day varied between 0 and 60% of 24 h. For instance, over the entire observation period (12 days), there were two occasions when sleep was not observed in W3 for a period of 58 and 60 h. They started on day 2 at 14:00 and day 6 at 20:00, respectively (Fig. 2). REM sleep in this animal was recorded largely during day 1 and day 6 (Fig. 1), comprising 4.7 and 4.1% of 24 h, respectively. At the same time, REM sleep occupied less than 0.2% of the total recording time over a period of 5 continuous days (days 7–11) and was not observed over a period of 3 consecutive days (days 3–5). In W4, REM sleep was not observed over a period of 4 continuous

Table 1
Vigilance states in four walrus presented as percent of 24 h.

Walrus	AW	QW	Behavioral sleep		QS1	QS2	REM
			TST				
			On land	In water			
W1 ($n = 9$)	68.8 ± 5.5 (48–89)	9.4 ± 2.9 (1–28)	21.8 ± 3.7 (10–39)	15.1 ± 5.2 (0–39)	–	–	–
W2 ($n = 7$)	67.1 ± 6.3 (41–88)	9.8 ± 2.3 (2–18)	23.1 ± 4.2 (9–41)	16.5 ± 6.1 (0–41)	–	–	–
W3 ($n = 11$)	79.2 ± 7.9 (22–99)	5.7 ± 1.7 (0–18)	15.1 ± 4.4 (0–61)	14.0 ± 6.1 (0–37)	7.8 ± 3.4 (0–23)	5.1 ± 2.3 (0–23)	1.1 ± 0.5 (0–4.7)
W4 ($n = 6$)	83.5 ± 9.4 (41–100)	9.9 ± 5.7 (0–37)	6.6 ± 3.7 (0–23)	6.6 ± 3.7 (0–23)	3.3 ± 2.0 (0–8)	2.8 ± 1.6 (0–8)	0.4 ± 0.4 (0–2.5)
W1 and W2 ($n = 2$)	68.0 ± 0.9	9.6 ± 0.2	22.5 ± 0.7	15.8 ± 0.7	–	–	–
W3 and W4 ($n = 2$)	81.4 ± 2.2	7.8 ± 2.1	10.9 ± 4.3	10.3 ± 3.7	5.6 ± 2.3	3.9 ± 1.2	0.8 ± 0.4
W1–W4 ($n = 4$)	74.7 ± 4.0	8.7 ± 1.0	16.7 ± 3.8	13.1 ± 2.2	–	–	–

Number of observation days in each animal is given in parentheses. The data are presented as mean \pm S.E.M. with minimal and maximal values given in parentheses for each animal and for the pairs of animals (W1 and W2 and W3 and W4). AW: active wakefulness, QW: quiet wakefulness, TST: total sleep time, REM: rapid eye movement sleep, and QS1 and QS2: light and deep quiet sleep, respectively.

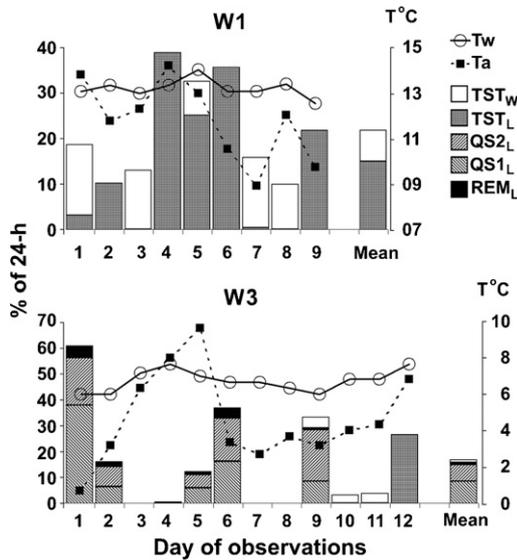


Fig. 1. Variability in daily amounts of vigilance states and mean air and water temperature in walrus 1 (W1) and walrus 3 (W3) across several consecutive days. Data are presented as percentage of 24 h. QS1: light quiet sleep; QS2: deep quiet sleep; REM: rapid eye movements sleep; TST: total sleep time; W: water; L: land; Tw and Ta: mean daily water and air temperature, respectively. In W3 behavioral sleep was subdivided into QS1, QS2 and REM sleep except for day 12. The average data (mean) are presented for 9 days in W1 and the first 11 days in W3.

days. The variation of TST in W1 and W2, kept in smaller pools, was considerably less (between 10 and 38% per day). The longest period of continuous waking in W1 and W2 lasted 23 h. It started on day 7 at 02:00 in W1 (Fig. 2).

3.3. 24-h activity profile

The walruses were in water 50 min or longer per hour during the great majority of all 1-h intervals scored as “in water” (91, 93 and 97% of 1-h intervals in W1, W3 and W4, respectively; 85% in W2). In 70% (W2) to 85% (W4) of all 1-h “in water” intervals the walruses were in water during all 60 min of each hour. During the entire observation period there were 4–6 periods (or bouts) “in water” and 3–6 periods “on land” (Fig. 2, Table 2). The longest “in water” period was recorded in W3 and continued for 84 h (3.5 days). In the three other animals the longest “in water” period varied between 36 and 54 h and the average values were two times shorter than in W3. During “in water” periods all walruses did spend most of the time in water (>55 min per hour or >90–95% of each hour) and they were predominantly active during these times. The walruses virtually swam continuously during these times; they usually circled from side to side (W1 and W2 along the longest side) or across a diagonal (W3 and W4) with an average speed of approximately 0.8 m/s. Walruses usually took one or occasionally two breaths per one complete circle surfacing in the same place every 5–15 s from circle to circle. When they surfaced, walruses briefly raised their head above the water, looked around, took a breath, made a U-turn and then continued swimming. When two eyes were seen they were always open. These periods of circular swimming occasionally alternated with short episodes of multidirectional active (or chaotic) swimming in the center of the pool or along the pool wall, or with short episodes of sleep at the surface. W1 and W2, housed in smaller pools were less active when in water (>88% of time in water or >53 min per hour) than W3 and W4. However, it was W1 who showed the longest period of continuous swimming (the 98% criteria, that is 59 min swimming per 1 h), which lasted almost 23 h.

Sleep in water was recorded in three walruses (W1–W3). They slept while floating at the surface, lying on the bottom or while

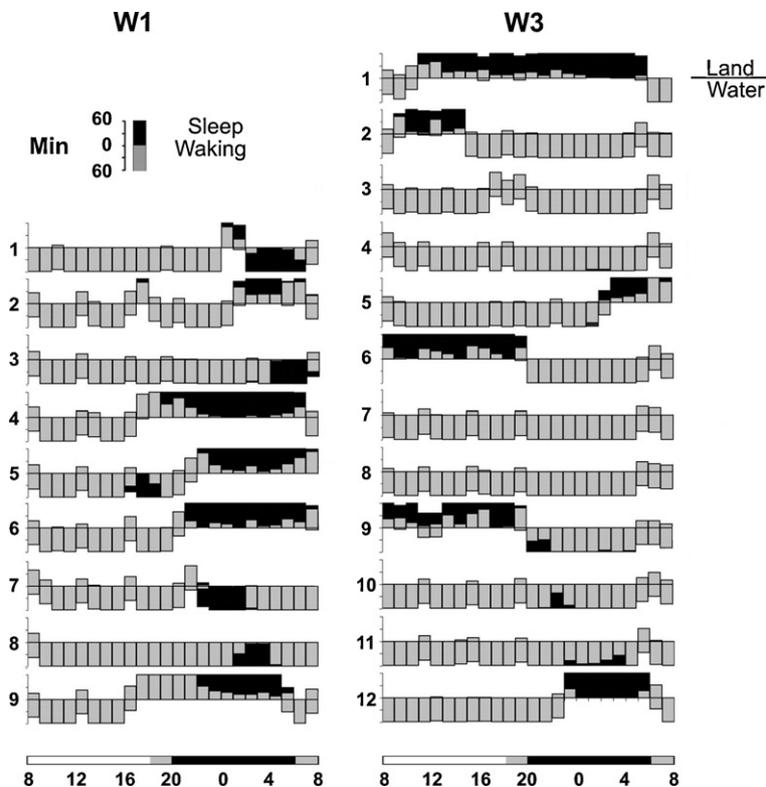


Fig. 2. Behavioral patterns in walruses 1 (W1) and 3 (W3). The time spent on land is shown above the x-axis and time spent in water is shown below. The black portion of the bar indicates behavioral sleep while the gray part indicates waking. The height of each portion of the bars is proportional to the number of minutes of each hour. The numbers are consecutive days of observation. The diagram below the graph shows the time of dark (black), light (white), and dusk and dawn (gray) hours.

Table 2
Characteristics of “in water” and “on land” periods in four walrus.

Parameter	W1	W2	W3	W4
Duration of observations (days)	9	7	12	6
“In water” period				
Total number of periods	5	6	4	4
Mean duration (h)	27.2 ± 7.7	17.7 ± 5.3	55.5 ± 18.2	29.8 ± 5.4
Duration range (min–max, h)	12–54	6–36	3–84	18–43
^a The longest episode of uninterrupted swimming (h)	23	8	17	9
Time spent in water (% of 1 h)	91.4 ± 1.5	90.1 ± 1.1	93.3 ± 0.6	95.1 ± 1.1
AW in water (% of 1 h)	80.7 ± 4.1	81.8 ± 4.9	91.9 ± 0.8	94.2 ± 1.1
AW in water (% of time in water)	88.2	90.8	98.4	99.0
Behavioral sleep (% of 1 h)	10.1 ± 2.9	7.2 ± 3.5	1.2 ± 0.9	0
“On land” period				
Total number of periods	6	5	5	3
Mean duration (h)	9.8 ± 2.0	8.8 ± 1.9	12.4 ± 2.5	8.3 ± 3.8
Duration range (min–max, h)	2–14	3–11	6–19	4–16
Time on land (% of 1 h)	96.3 ± 0.7	88.1 ± 3.4	96.0 ± 2.3	98.4 ± 1.0
AW on land (% of 1 h)	15.5 ± 3.4	21.0 ± 3.7	6.7 ± 1.4	7.4 ± 3.2
Behavioral sleep (% of 1 h)	50.0 ± 5.7	43.0 ± 4.4	71.6 ± 5.3	38.0 ± 6.7
Behavioral sleep (% of time on land)	51.9 ± 3.4	48.5 ± 3.8	73.8 ± 4.9	39.5 ± 6.6

The data are presented as mean ± S.E.M. AW: active wakefulness.

^a The 98% criterion was applied to determine these values (or 59 min per 1 h).

Table 3
Breathing parameters for two walrus (W3 and W4) during quiet sleep (QS) and REM sleep (REM) on land.

Parameter/test	State	W3	W4
Mean duration (s) of breathing pause (over entire nighttime)	QS	9.1 ± 0.2 (20, 243)	15.4 ± 0.4 (33, 254)
	REM	16.2 ± 2.6 (93, 157)	19.9 ± 1.3 (147, 91)
Mean duration (s) of breathing pause (by episodes)	QS	9.4 ± 0.5 (11.4, 6)	16.3 ± 1.1 (19.1, 6)
	REM	15.1 ± 3.2 (34.3, 7)	19.5 ± 1.4 (23.3, 5)
Mann-Whitney (<i>U</i> -test)		<i>p</i> < 0.05	ns
Percentage of breathing pauses <30 s	QS	100.0%	99.2%
	REM	96.8%	83.0%
Percentage of breathing pauses >60 s	QS	0.0%	0.0%
	REM	3.2%	3.4%
Chi ² test		<i>p</i> < 0.001 (<i>X</i> ² = 17.83, <i>df</i> = 2)	<i>p</i> < 0.001 (<i>X</i> ² = 41.45, <i>df</i> = 3)

In each walrus the data were collected during one night. Values are presented as mean ± S.E.M. Mean breathing pauses were calculated over the entire nighttime (maximal breathing pause and the number of pauses are given in parentheses) and by individual episodes of QS and REM sleep (maximal breathing pause and the number of sleep episodes are given in parentheses).

standing and leaning against the pool wall (for more details see *sleep in water*). In W1 and W2, housed in small pools, behavioral sleep occupied on average 10 and 7% of the time they were in water. In W3, sleep in water comprised on average only 1% of the entire period of observation or approximately 1 min per each hour spent in water (Table 2, Fig. 2).

“On land” periods lasted up to 19 h, with the longest episode being recorded in W3 (Table 2, Fig. 2). This animal also showed the longest period “in water”. The mean durations were similar in all walrus. In W3 and W4, which displayed little or no sleep in water, AW while on land did not exceed 7.5% of the observation time. In W1 and W2, AW lasted twice as long. While on land sleep occupied between 40 and 52% of the time in W1, W2 and W4. In W3, which displayed the longest periods “in water”, sleep on land comprised almost 75% of the time spent on the platform.

3.4. Pattern of breathing

The breathing pattern was analyzed in W3 and W4 for a period of one night when the walrus slept on the platform (Table 3, Fig. 3). During QS, the distribution range of breathing pauses was relatively narrow in both animals. All pauses (except for 2 out of 254 in W4) were shorter than 30 s. REM sleep was marked by a noticeable irregularity of breathing. The distribution of pauses was

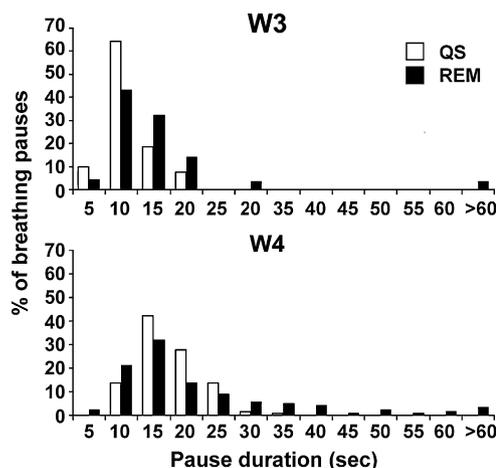


Fig. 3. Distribution of breathing pauses during quiet sleep (QS) and rapid eye movement sleep (REM) in walrus 3 and 4 (W3 and W4, respectively) while sleeping on land. The diagrams show data collected during one night in each walrus.

much wider than during QS and 3% of REM sleep pauses were longer than 60 s. In W3, three extended apneas were recorded, lasting 140, 142 and 157 s. Each occurred during different REM sleep episodes. The longest REM sleep apnea in W4 lasted 91 s. The difference in the distribution of respiratory pauses between QS and REM was highly significant in both animals (Chi² test, $p < 0.001$). The mean breathing pause during REM sleep was longer than during QS in both walrus. To avoid the inflated degrees of freedom resulting from large sample sizes, the average values for all recorded episodes of QS (6 episodes in both walrus) and REM sleep (7 episodes in W3 and 5 episodes in W4) were compared. The difference (measured by the Mann–Whitney test) was found to be significant in W4 only (Table 3).

3.5. Behavioral sleep in water

Sleep in W1 and W2, kept in small pools occurred mostly while they were standing on the bottom leaning against the wall and holding their heads and nostril above the surface. Several short episodes of REM lasting <1 min and accompanied by characteristic muscle jerks were observed. Due to the position of the cameras we were not able to quantify all episodes of REM sleep in water in W1 and W2.

When W3 had access to water and land, behavioral sleep occupied on average only 1.2% of 24 h (Table 2). To collect more data on sleep in water, W3 was kept afloat for 3 days by removing the platform. Under these conditions, sleep comprised 7.5% of the observation time. 69% of TST occurred when W3 was standing, leaning with its chest against the wall. Episodes of QS while standing lasted between 2 and 34 min (on average 14.3 ± 2.9 min, $n = 15$). The breathing pattern during QS represented an alternation of short pauses (<30 s; on average 10 ± 1 , $n = 31$) and apneas (>30 s) lasting up to 150 s (on average 67 ± 7 , $n = 24$). Both eyes were closed during this time. 13 episodes of REM were documented in the standing position. Single episodes lasted between 6 and 120 s (on average 47 ± 10 s) and occurred during one apnea. When the first muscle jerks occurred or several seconds before them, the walrus slowly slid down the wall and under the surface. The sleep episode continued with the animal under the water. When the walrus surfaced, it opened its eyes.

18% of TST in W3 occurred at the surface when the walrus briefly interrupted stereotypic swimming. The mean duration of QS was (6.1 ± 1.5 min, $n = 9$). No regular paddle movements were seen at this time. The breathing pattern during QS while floating was similar to that while standing with short breathing pauses (11 ± 3 s, $n = 17$) alternating with apneas, lasting up to 166 s (92 ± 22 s, $n = 5$). During apneas the walrus usually immersed its nostrils in the water. Three short REM sleep episodes (15, 29 and 47 s; an average of 30 ± 9 s) were observed during these apneas and accompanied by vibrissae and head jerks. REM sleep ended when the walrus raised its head above the surface, took a breath and began swimming.

27 sleep episodes (13% of TST in water) occurred while the walrus lay on the bottom of the pool. These episodes lasted 16–285 s (on average 1.5 ± 0.2 min). The walrus was not clearly visible while on the bottom. However, several times we noticed muscle jerks, suggesting that REM sleep occurred while lying on the bottom.

4. Discussion

Video recording of sleep behavior in zoos and laboratory-based monitoring of locomotor activity of a wide variety of terrestrial mammals has revealed that these animals slept every day, displaying both stages of sleep (SWS and REM sleep) during their usual sleep period (e.g., reviewed in Refs. [34,41]). In general prior reports have indicated that the variability in sleep parameters between

consecutive days in individual animals is low. The coefficient of variation (i.e., standard deviation/mean, calculated by the authors based on the published data) of total sleep time in individual animals ranges from 8 to 39% in elephants [37], 8–38% in giraffes [38], and 9–16% in baboons [27]. EEG studies on individually housed freely moving primates or herbivores also showed a relatively low level of variability in total sleep time (e.g., 4–14% in the *Macaca mulatta* [7]; 2–36% in ponies [8]; 23–41% in sheep [33]).

The variability of total sleep time in the four walrus studied here was considerably greater than that reported for the above mentioned terrestrial mammals: 48 and 51% in the two walrus housed in small pools and 97 and 137% in the two walrus in larger pools. In addition, they could spontaneously be almost continuously active for extended periods of time (up to 84 h) or asleep for up to 75% of the observation time with no evidence of REM sleep for a period of up to 4 days. It is known that dolphins can sleep unihemispherically while slowly swimming, and surfacing to breathe does not necessarily interrupt these sleep episodes [22,26]. Thus, the possibility that the walrus obtained some sleep while engaging in long bouts of swimming cannot be entirely excluded. However, while swimming, they usually made sharp U-turns on average every 5 s. Thus, the pattern of the walrus' swimming differed; being less stereotypic, from the slow "resting swimming" seen in dolphins when engaged in unihemispheric sleep. Even if the walrus did not surface for breathing each time they made U-turns, such sharp alterations in the trajectory of movement were likely to lead to awakening if the animals were asleep. Therefore, the amount of sleep obtained (if any) by walrus during these periods of uninterrupted swimming would be very small with these episodes lasting only a few seconds. Moreover, sleep while swimming was never recorded in one of these walrus (W4) during the following EEG study. While in water W4 slept only while floating motionlessly at the surface or lying on the bottom of the pool. EEG slow waves always developed bilaterally during these episodes and no noticeable EEG asymmetry was observed [23].

In addition to the walrus, other pinnipeds also show a high level of variability in total sleep time. In a study on 7 subadult fur seals it was shown that the daily amount of SWS and REM sleep while on land ranged from 13.5 to 33.6% (on average $23.7 \pm 3.0\%$ of 24 h) and 3.0–4.4% ($4.2 \pm 0.6\%$), respectively. However, in water the variability in sleep time increased. For instance, in one of these seals, which was kept afloat for 10 consecutive days, the amount of SWS measured over 5 days (day 1, 2, 4, 8 and 10) varied from 2.0 to 30.0% of 24 h (on average $14.3 \pm 4.5\%$, the coefficient of variation was 70%) and REM sleep from 0.0 to 0.6% of 24 h [16]. Therefore, similar to walrus, fur seals display extended periods of waking and a reduction of sleep time while in water. Our data are consistent with data collected in the wild. For instance, a walrus instrumented with a time–depth recorder and monitored for about 200 h kept diving continuously over several days, apparently feeding throughout this period [40]. The increased variability in sleep time and the ability to reduce or even eliminate sleep for a few days may be an adaptation of marine mammals to the nature of the aquatic environment they inhabit, namely 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.

It is known that seasonal changes in the daily duration of behavioral states occurs in mammals. These changes are thought to be triggered by changes in the photoperiod and ambient temperature [10] and mediated by changes in melatonin secretion and other processes [2]. There is clear evidence that some mammals (e.g., golden hamster, prosimians and elephants) spend a greater amount of time asleep in winter compared to summer [1,37,39]. Seasonal changes in the amount and the pattern of sleep has recently been shown in an avian species (*Zonotrichia leucophrys gambelii*), which migrates 4000 km twice per year. The amount of sleep during the migratory

state decreased by 70% compared to those in the non-migratory state [30].

We did not find a statistically significant correlation between the amount of vigilance states and the temperature fluctuation, even though the fluctuations were quiet substantial. Consequently, the behavioral pattern we observed in the walrus (alternation of activity periods in water and rest periods on land) may be related to their seasonal migratory behavior. In this study the longest periods of continuous swimming were most evident in W3, which was observed in spring (March–April). In the wild, most pacific walrus migrate during this time from the winter grounds in the Bering Sea to the northern shores of either eastern Siberia or Alaska [11]. However, unlike the changes described in sparrows and in terrestrial mammals, which reduced the daily amount of sleep or redistributed sleep between the light and dark time but slept every day, the walrus studied here alternated periods of almost continuous activity in water with periods of extended rest on land.

The walrus slept on average as much as 25% of 24 h and as little as 6% of 24 h (1 h and 40 min per day), a 400% difference. All animals had access to both water and land and three of them experienced the same range of environmental temperatures. The variations in the amount of sleep between individual walrus: (1) may have resulted because of the difference in pool dimensions in which they were housed or (2) were individual differences between the studied animals. In either case, the 400% difference in the amount of sleep between apparently healthy animals, well adapted to the experimental conditions suggests that total sleep time in these animals may be more closely correlated with environmental conditions than with a species specific daily need for sleep.

Most available data on the amount of sleep in animals have come from recordings performed on captive solitary animals. However, recent data collected in sloths (*Bradypus variegatus*) instrumented with digital EEG recorders in their natural habitat [31] indicate that in the wild these animals slept on average 6 h less than was measured in captive animals [9]. These sloth studies, as well as our data, emphasize the potential for variability in the amount of sleep. Data previously collected on captive, usually solitary caged animals should be treated with caution when estimating a species specific need for sleep. On the other hand, some species specific aspects of sleep appear to be predetermined genetically or insensitive to environmental conditions. For example, dolphins display unihemispheric SWS regardless of the experimental recording regime: lying in stretchers, tethered to the recording equipment and confined to small pools, or freely swimming in spacious enclosures (reviewed in Ref. [22]).

All studied phocids exhibited a similar respiratory pattern while resting or sleeping: periods of arrested breathing (apnea) alternated with periods of regular breathing [6,24,32,35]. For instance, captive harp seal pups (10 days to 3 months old), sleeping on ice or land exhibited apneas of maximal duration during SWS, ranging from 84 to 180 s in duration, with means ranging from 36 to 88 s. The mean inter-breath interval during non-apneic periods (regular breathing or eupneas) was 1.9–3.3 s. The majority of REM sleep episodes in harp seal and northern elephant seal pups on land and all REM sleep episodes in water occurred within one apnea [6,12,18]. Visual observations on wild elephant seals confirmed the results of EEG studies on captive animals. While resting on land elephant seals alternated apneas lasting up to 21 min with eupneas ranging from 2.2 to 5.1 min, with the number of breaths per min during eupneas varying from 4.4 to 20.5 per min [4].

In contrast, all studied otariids displayed a regular breathing pattern while sleeping on land. Mean breathing pauses during SWS varied from 16 to 25 s in three yearling southern sea lions [19], from 4 to 14 s in northern fur seals of different age–sex groups (from 10 days old to adults; a total of 15 animals), and from 7 to

20 s in Steller's sea lion pups [13,16]. In REM sleep on land, breathing became irregular in all studied otariids, however, most pauses were within 30 s and only rarely did apneas last longer than 1 min [15,16,19]. In water the pattern of breathing in fur seals was also regular with most pauses lasting less than 40 s. Longer pauses occurred only during episodes of REM sleep when the animal's head dropped into the water [16]. Therefore, although the breathing pauses in fur seals and sea lions became longer when they slept in water, extended inter-breath intervals of the sort recorded in phocids were rare and those apneas were considerably shorter.

The breathing pattern of walrus studied here has features of the patterns displayed by both otariids and phocids. While on land, the breathing of walrus was regular during QS and similar to that of terrestrial mammals and otariids. In REM sleep the breathing irregularity in walrus was greater than that seen in otariids; however, it did not reach the extent observed in phocids. While in water the breathing pattern of walrus was similar to that of phocids. Most phocids are Arctic and Antarctic species [5], so they live and sleep under the ice. It is usually emphasized that the interrupted pattern of breathing maximizes the time spent under water (e.g., [36]). However, maximizing the time under water may be important not only for more successful foraging but for sleep as well.

Walrus also spend a considerable amount of their yearly life cycle on ice. There is little information on the rest/sleep behavior in walrus in the wild. It is usually reported that they sleep in groups on ice floes or on land [11]. Walrus were also observed resting in water while using their tusks to hang from the ice floes [28]. As we show in this study and in our preliminary EEG study on one captive walrus [23], these animals can sleep in water. Sleep in water occurred while floating motionless at the surface, standing in a shallow area with their head above the water or lying on the bottom of the pool. Sleep at the surface in walrus is facilitated because of the thick blubber layer as well as because of the air sacs (extension of the pharynx) in adult animals [11]. Sleep while floating in an upright position (“bobbing”) has been observed in some phocids as well [24,32]. Therefore, according to the behavioral features (including the interrupted pattern of breathing), the walrus sleep more closely resembles the sleep of phocids [6,12,17,24,32]. It was shown that the majority of dives in walrus in the wild are to depths less than 100 m (on average 20 m) with the time spent foraging at the bottom up to 20 min [36,40]. However, as we show in this study, even young walrus can sleep during extended apneas lying on the bottom of the pool. Therefore, in the wild diving to depth would be an adaptive retreat for walrus from bad weather and potential predators (polar bears and in some places killer whales). It is hypothesized that some of the deep dives recorded in migrating elephant seals may be also performed for sleep [36].

The two most distinct hallmarks of walrus sleep are (1) immobility and (2) an interrupted breathing pattern. These features make walrus (as well as phocids) different from the otariids (particularly fur seals), which sleep in water at the surface maintaining motion and regular breathing. The behavioral pattern of sleep in fur seals in water is thought to be associated with the unusual nature of their sleep, which is asymmetrical SWS, similar to the unihemispheric sleep of cetaceans [22,25]. Unihemispheric sleep in cetaceans and asymmetrical SWS in fur seals [17] and in birds [29] have also been shown to be associated with asymmetrical eye state. In a recent pilot study in one walrus we documented several episodes of SWS with pronounced interhemispheric EEG asymmetry while the walrus was sleeping on land [23]. During these episodes the eye contralateral to the hemisphere in a state of low amplitude SWS was briefly opened periodically, as in fur seals. The other eye, which was contralateral to the hemisphere in a state of deeper SWS was directed to the platform and was not visible. Additional observations and EEG studies need to be done to understand

under what experimental (environmental) conditions this behavior occurs in walruses.

The available data (behavior and preliminary EEG data) suggest that the pattern of sleep and breathing in young walruses is similar to that of the Otariidae seals while on land and the Phocidae seals while in water. We find that walruses appear to share the unihemispheric sleep capability of the cetaceans (whales and dolphins) and Otariidae seals. Furthermore and most importantly we find that captive walruses spontaneously almost entirely cease sleeping for as long as 84 h, even when well adapted to an environment free of any threat and with *ad libitum* availability of food. This is another remarkable example of the diversity of sleep behaviors in aquatic mammals.

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