

Rest and activity states in a gray whale

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SUMMARY The behaviour of a female gray whale (*Eschrichtius robustus*) that had been rescued 14 months previously was recorded continuously on a video-recorder for 9 days at 'Sea World' in San Diego. On average, during the first six recording days, active wakefulness accounted for $37.9 \pm 1.7\%$ of each 24 h; transitional stage for $17.4 \pm 1.4\%$ and rest for $41.2 \pm 1.7\%$. In the rest stage the whale was lying on the bottom of the pool ($13.2 \pm 1.7\%$) or hanging on the surface ($28.0 \pm 1.7\%$). During the rest stage, it was immobile most of the time and moved only for respiration. In the rest stage both eyes could be open, one eye could be open while the other was closed or, more rarely, both eyes could be closed. Characteristic jerks of the head, neck and sometimes of the whole body were observed in the whale during the rest stage. Most jerks were single and only 10% of all jerks were serial (occurring within 10 s of a prior jerk). Eyelid movements accompanied 40% of jerks. In two episodes, intense jerks followed each other continuously for 3 and 4 s and were accompanied by eyelid movements. These jerks resembled the twitches characteristic of paradoxical sleep in terrestrial mammals. During these episodes the whale was falling slowly onto its side and subsequently started to swim in the pool.

KEYWORDS gray whale, rest, jerks, paradoxical sleep, REM sleep, Cetaceans

INTRODUCTION

Electrophysiological investigations of sleep in three species of dolphins (bottlenose dolphins, harbor porpoises and Amazonian dolphins) have identified three key characteristics of their sleep: (i) slow-wave sleep (SWS) in all studied species was characterized by profound interhemispheric EEG asymmetry and most of the time could be considered 'unihemispheric'; (ii) dolphins were never completely immobile during sleep, performing paddling movements (bottlenose dolphins) or even swimming almost 24 h per day (Amazonian dolphins, harbor porpoises); (iii) polygraphic features of paradoxical sleep (PS), including skeletal muscle atonia, muscle jerks, rapid eye movement (REM) and heart rate irregularity, traditionally found in most terrestrial mammals, were never observed in these species (Mukhametov *et al.* 1977; Mukhametov 1984, 1987).

Little is known about the resting behaviour of Cetaceans in the wild. Hawaiian spinner dolphins and dusky dolphins rest in

shallow lagoons, swimming slowly in tight formations with minimal echolocation activity (Norris and Dohl 1980; Wursig and Wursig 1980). Beluga whales have been described as lying quietly in formations at the surface or swimming slowly in tight groups along coastlines (Sjare and Smith 1986; Belkovich and Shchekotov 1990). Humpback whales are frequently observed motionless 'logging' at the surface or performing long dives always emerging for respiration in the same place (Robbins *et al.* 1998).

Visual observations of resting behaviour have been performed on several species of Cetaceans in captivity, including bottlenose dolphins (Flanigan 1974a; Mukhametov 1984; Mukhametov and Lyamin 1994, 1997), beluga whales (Flanigan 1974b, 1975c; Lyamin *et al.* 1998), Amazonian dolphins (Oleksenko *et al.* 1994, 1996), killer whales (Flanigan 1975a) and white-sided dolphins (Flanigan 1975b; Goley 1999). It appears that all of these species are able to sleep while swimming, which in captivity normally takes the form of slow swimming along the edge of the enclosure or in place. Therefore, visual observations confirm that immobility, one of the major criteria for sleep in terrestrial mammals, appears to not be a necessary feature of sleep in dolphins.

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jerks and occasionally twitches and even eye movements resembling those of REM sleep, were observed in bottlenose dolphins (Mukhametov and Lyamin 1994, 1997) and Amazonian dolphins (Oleksenko *et al.* 1994, 1996) during slow swimming or resting (hanging) on the surface. In one beluga whale the same type of behaviour was documented when the animal rested on the bottom of the pool (Lyamin *et al.* 1998). Recent studies of sleep in Monotremes have shown that a REM sleep-like state (rapid eye movements, twitches on the background of moderate and high-voltage EEG) is present in the platypus and a brainstem-activated state with some resemblance to REM is present in the echidna (Siegel *et al.* 1996, 1999). Therefore, the Cetacean order is now the only group of mammals in which the presence of PS is still under question.

A female gray whale (*Eschrichtius robustus*), named J.J. was rescued on 11 January 1997, near the California coast. It was thought to be 1 week old on the basis of its size and weight. The animal was extremely weak and exhausted, apparently because it had become separated from its mother. It was taken to 'Sea World' in San Diego, where it was bottle fed a special formula until September 1997. It was released into the ocean over 14 months later, on 31 March 1998. Having a gray whale in an artificial pool provided us with a unique opportunity to study the resting behaviour in the baleen whales (suborder Mysticeti) and to collect more data which might allow us to further investigate the presence or absence of PS and other aspects of sleep in Cetaceans. Polygraphic investigations of sleep in the gray whale, which would have required EEG recording from surgically implanted electrodes, were, of course, impossible.

METHODS

Continuous video-recordings and parallel visual observations of the whale were carried out for a total of 9 days (in periods of 6 and 3 consecutive days, separated by 3 days). At the time of observation, the whale was 15 months old, 9.4m long, and weighed 8618 kg. The animal was kept in a pool measuring =6400 m³ irregular in shape with a surface of =1100 m² and depth varying from 3 to 12m. Most of the time (> 90% of the 24-h period), the whale chose to stay in a shallow channel, which was =10 m long, 10 m wide and 5 m deep. Lattice gates at one end of the channel separated it from a "larger pool complex. The head of the whale was usually turned towards these gates. We placed two underwater and three aerial TV cameras on the sides of the channel which were connected to a video recorder (Panasonic AG-6730E) via a multiplexer (Panasonic WJ-FS20). These cameras allowed us to observe and videotape the animal in real time from different sides for almost all the time it spent in the channel or nearby.

Videotapes recorded during the first 6 days of continuous recording were scored visually in real time and all behavioural

acts. In the final stage of analysis all changes in behaviour excluding episodes of submergings and emergings lasting < 20 s were not considered (see below). The videos of the last 3 days were analysed mainly to study the state of the eyes during behavioural rest.

The pool was under constant illumination during the night. Two 500 W aerial lamps placed on each side of the channel were used to provide additional illumination in order to observe the behaviour of the whale in detail. Although the intensity of illumination varied between the surface and the bottom of the channel, at all depths it was darker than during the day. The animal was adapted to this additional illumination for 3 days before observation started. The illumination was turned on 30 min before sunset and turned off 30 min after sunrise (17.30 and 06.30, respectively).

The whale was fed 3-4 times daily between 07.00 and 17.00 in the main part of the pool. The food (krill, small fish, squid) was thrown on the bottom of the pool, and the animal could pick it up at any time. Divers in the middle of the day removed the food remains from the bottom of the pool. From =07.00 to 19.00, there were people (both visitors and trainers) constantly standing at the side of the pool.

RESULTS

From the point of view of the rest-activity cycle, the behaviour of the whale was divided into three stages.

Stage 1 - active wakefulness. The whale swam in the pool or channel with variable speed and trajectory (on average 20.7 ± 1.5% of 24-h during 6 consecutive days), or moved actively in one part of the channel: spun, raised its head above the water, put its head on the side of the channel, pushed the gates, etc. (17.2 ± 1.3%). On average this stage occupied 37.9% of the 24-h period for 6 days (Table 1). Both eyes were open. Stage 1, undoubtedly, constitutes active wakefulness.

Stage 2 - transitional stage. On average, this stage occupied 17.4% of the total time. The animal could be in one of two postures (Fig. 1): hanging with the rostral part of the back on the surface (4.0 ± 0.6%) or lying on the bottom with its back up (4.8 ± 0.5%). Even if the whale was hanging on the surface

Table 1 Duration of the behavioural stages in six consecutive days in the gray whale (as percentage of 24-h)

Stage	Days						Mean	SE
	1	2	3	4	5	6		
Stage 1	45.2	33.2	38.6	35.5	39.4	35.3	37.9	1.7
Stage 2	18.5	22.5	16.7	18.9	15.8	12.3	17.4	1.4
Stage 3a	24.7	27.2	22.7	30.4	34.2	29.1	28.0	1.7
Stage 3b	8.5	15.0	18.0	14.8	7.8	14.9	13.2	1.7
Unidentified	3.1	2.1	4.0	0.4	2.8	8.4	3.5	1.1

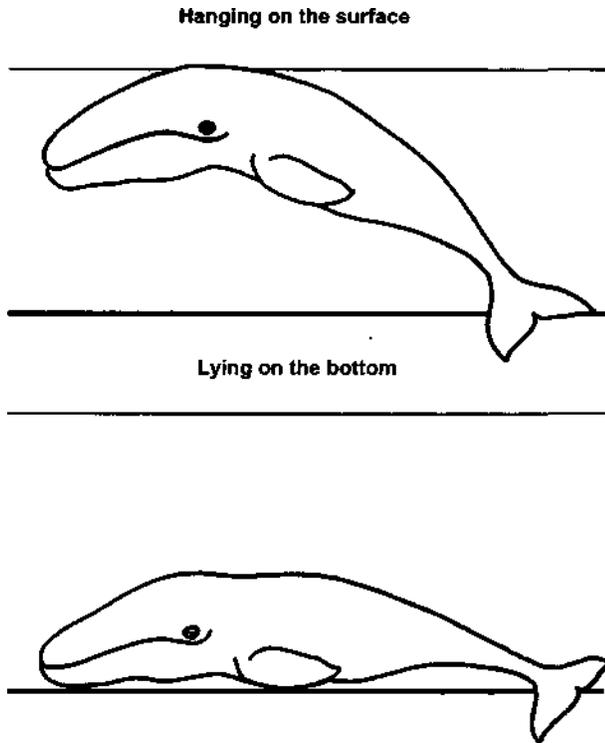


Figure 1. Two typical rest postures in the gray whale. The animal floated motionless on the surface with its fluke resting on the bottom of the pool or lay on the bottom of the pool on its belly. In both cases the fins were clasped to the whale's body.

the fluke was resting on the bottom most of the time. In both postures, slow movements of the fluke and fins or curving of the body were observed continuously. Both eyes were open. Slow stereotypic emergings and submergings that accompanied respiratory acts at the water surface also contributed to stage 2 ($3.0 \pm 0.2\%$). Sometimes, several series of such emergings and submergings followed each other without being separated by episodes of hanging on the surface or lying on the bottom ($5.6 \pm 0.8\%$). As a result, series of respiratory acts occurred without prolonged pauses.

Stage 3 - complete immobility interrupted only by movements, which were necessary for respiration (41.2% of the total time). The animal was in one of two postures, just as in stage 2 (Fig. 1), but its fins were clasped tightly to its body, and its fluke lay on the bottom. The body was motionless. Both eyes could be open but, more frequently, one or both were closed. Stage 3, appears to be a state of rest. Motionless hanging on the surface (stage 3a) occupied 28.0% and motionless lying on the bottom (stage 3b) occupied 13.2% of the 24-h period. Stages 2 and 3 were observed only when the animal was in the channel.

Occasionally, the whale was not visible at all or video-recording was interrupted for technical reasons. These episodes (unidentified stage) occupied 3.5% of the time on average.

As mentioned previously, all changes in the pattern of the gray whale behaviour, lasting a minimum of 20 s were scored

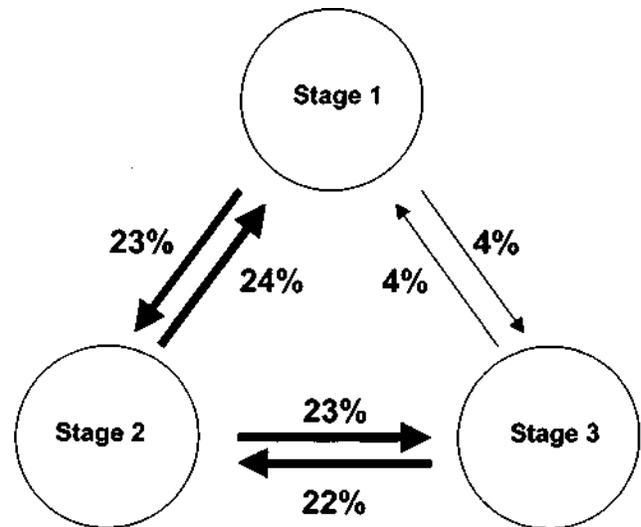


Figure 2. All transitions among stages 1, 2 and 3 (as a percentage of the total number of all transitions between stages for 6 consecutive days).

for analysis except episodes of submergings and emergings. Ninety-four per cent of all episodes of submergings and emergings were < 20 s (8-20 s). All were considered part of stage 2 because they always signified behavioural transitions, either between two substages of rest or between rest and active wakefulness. Analysis of transitions between separate episodes of three stages showed very few direct transitions between stages 1 and 3. Active wakefulness turned into rest after stage 2, confirming the transitional character of stage 2 (Fig. 2).

As follows from Fig. 3, active wakefulness was observed mainly during the day and the rest stage during the night. Nevertheless, stage 3b, immobility on the bottom, was also present during the day (Fig. 4).

Respiratory acts were registered continuously except during periods when the whale was outside the channel in the main pool or when there was human activity inside the pool (feeding, cleaning). In all these cases the whale was undoubtedly active (stage 1) but respiratory acts could not be documented reliably.

The pattern of respiration changed significantly depending on the behavioural stage (Fig. 5). Respiration was most frequent in stage 1 and 2.90% of all respiratory pauses recorded in both stages were < 1 min, compared with 43% and 4% of all recorded pauses, accordingly, recorded in stages 3a and 3b. However, the pattern of respiration became more frequent and regular when the whale moved from stage 1 to stage 2. Thus, only 37% of the pauses recorded in stage 1 were < 20 s compared with 62% in stage 2. The longest documented respiratory pause was recorded when the whale was lying on the bottom, 460 s. Seventy-one per cent of the respiratory pauses recorded in stage 3b were > 2 min compared with 7% during stage 3a, 0.5% during stage 1 and no pauses in stage 2. The differences in distribution of respiratory pauses between any given behavioural stages were highly significant

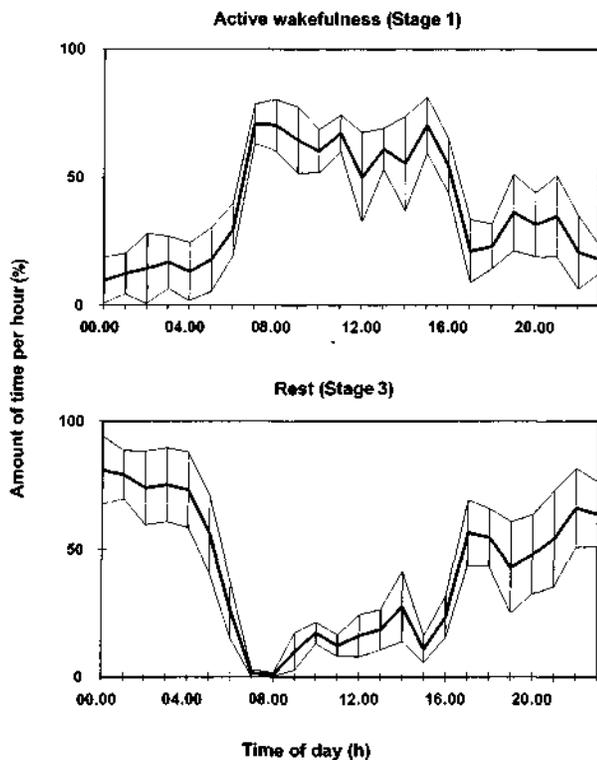


Figure 3. Distribution of active wakefulness and rest stage in the gray whale over the 24-h period. Average for 6 days. The thick lines link the mean hourly values representing the amount of time spent in a given stage as percentage of each hour. The standard error (SE) is marked with a thin line.

(Chi-squared test, $P < 0.001$ for all pairs). The mean duration of respiratory pauses calculated on two consecutive days were 29.8 ± 0.7 s ($i = 875$; in total 434 min) in stage 1, 23.1 ± 0.7 s ($n = 300$; 115 min) in stage 2, 67.5 ± 1.5 s ($n = 501$; 562 min) in stage 3a and 150.0 ± 3.6 s ($n = 240$; 600 min) in stage 3b.

During the last 3 days we paid special attention to the states of both eyes. Unfortunately, continuous video-recording of both eyes was not possible due to the fixed positions of the TV cameras, therefore, we cannot provide a quantitative 24-h description of the states of both eyes. However, we can draw conclusions about the state of the eyes during different behavioural stages. We scored the state of the eyes as open, closed or intermediate when the eye was not fully open or closed. Both eyes were open constantly in stage 1 and almost all the time in stage 2. In stage 3, both eyes could be open, closed or in asymmetrical states. Figure 6 shows the states of eyes during a period of rest when the whale rested mostly on the surface. Both eyes were healthy but the right eye, which in the typical rest posture was directed toward the observation booth, was closed a smaller proportion of the time than the left, which was directed toward the wall of the pool. Periods when both eyes were closed lasted for much shorter times than periods when only one eye was closed.

Also, during observations and analysis of videotapes, special consideration was given to short jerks of the head, neck and

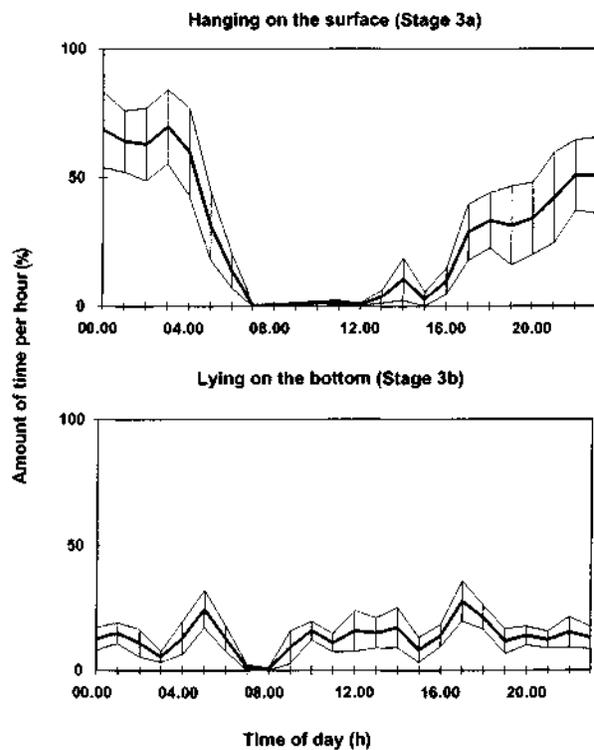


Figure 4. Distribution of two rest stages in the gray whale over the 24-h period. Average for 6 days. The thick lines link the mean hourly values representing the amount of time spent in a given stage as percentage of each hour. The standard error (SE) is marked with a thin line.

body muscles, and relatively fast movements of eyelids (either in the vertical or horizontal direction) observed during rest. Such movements are of special interest because they are characteristic of PS in terrestrial mammals. During these movements, the eyelids remained closed but the junctions between the eyelids shifted; such movements appeared to be the consequence of eyeball movements. Muscular jerks and eyelid twitches in the whale were not as fast and sharp as in terrestrial mammals.

In total, 48 jerks were registered in the gray whale during the first 6 days. The majority of jerks were single. Only five (10%) of the jerks followed each other within intervals < 10 s (1-8 s). They were considered serial jerks. The majority of the muscular jerks occurred at night (90%). Eighty-five per cent of jerks occurred in stage 3a, and 15% in stage 3b.

The average duration of stage 3a rest episodes during which one or more jerks occurred was 1904 ± 236 s ($n = 41$), whereas the average duration of all remaining stage 3a episodes was much shorter, -254 ± 20 s ($n = 374$). The distributions of episodes with jerks and without jerks differ significantly ($\chi^2 = 56.3$, d.f. = 5, $P < 0.001$) suggesting that there was a relationship between duration of the episode and the presence of jerks. Only a few jerks (seven) were recorded during stage 3b. The average duration of these episodes was very close to the average duration of all rest episodes, 137 ± 21 s ($n = 7$) and 114 ± 2 s ($n = 591$), respectively.

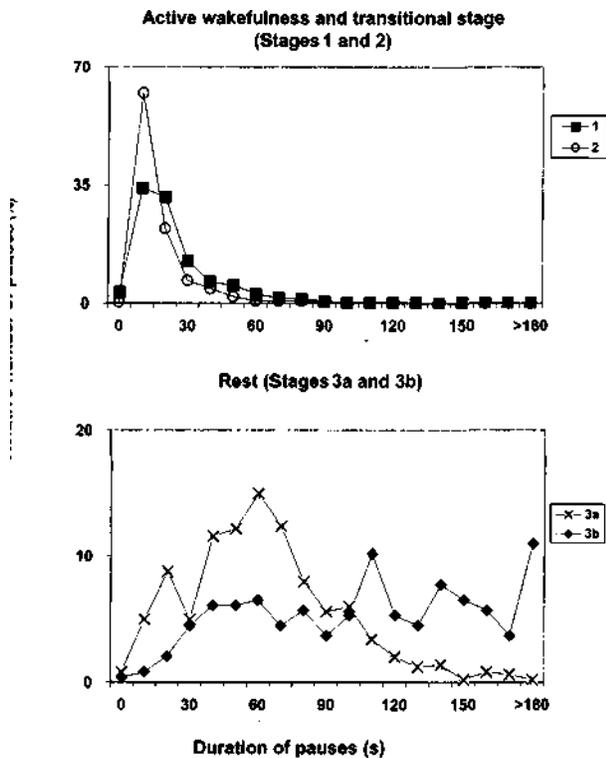


Figure 5. Distribution of respiratory pauses in different behavioural stages in the gray whale (as a percentage of the total number of pauses documented in a given stage during two consecutive days).

Twenty-five per cent of all jerks (12 of 48) occurred < 20 s before the end of the rest episode. Three of the 12 jerks were followed by episodes of unambiguous behavioural activity, swimming in the pool or in the channel. In three other cases the whale, simultaneously with jerks or shortly after, fell slowly onto its side, stayed motionless for several seconds afterwards and then started to swim in the pool. Six of the 12 jerks were followed by episodes of submergings and emergings (stage 2).

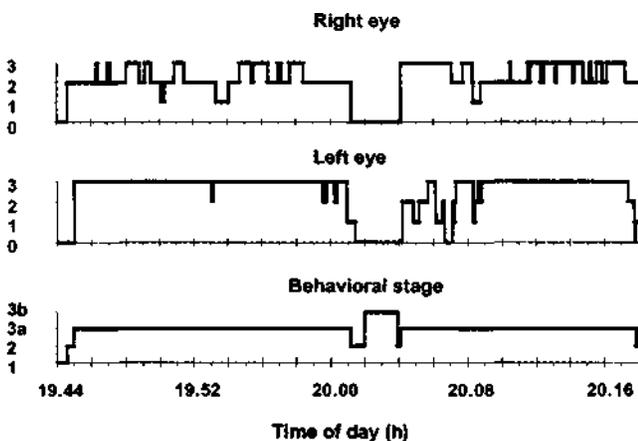


Figure 6. The states of eyes during one rest episode in the gray whale. y-Axis represents the state of each eye: 1, opened; 2, intermediate; 3, closed; 0, not seen.

In 86% of all jerks, the right eye, which could be seen almost all the time, was closed; it was intermediate in 7% and was not seen 7%. The right eye was never seen to be open during the jerks. Eyelid movements accompanied 40% of jerks. The jerks and eyelid movements were considered to accompany each other if they occurred within 10 s of each other.

We also documented two episodes (of 3 and 4 s duration) in which relatively intense jerks followed each other continuously (without noticeable pauses) and could not be separated into single jerks. In both these episodes, the right eye was closed, and eyelid movements were observed synchronously with jerks. The first episode started on the 11th min of stage 3a, and the second, 20 min after the first, also in stage 3a. Within 5 s after the second episode had ended, the whale began to swim in the main pool. In both cases, the whale was falling slowly on its side but the fins remained motionless. These two episodes showed the largest resemblance to episodes of PS with intense phasic phenomena seen in terrestrial mammals.

DISCUSSION

The main difference between rest states in the gray whale and dolphins that have been observed is the long duration of periods of immobility in the whale. Most studied species of dolphins were either never motionless or were immobile only for very short periods (Flanigan 1974b, 1975b,c; Mukhametov 1984; Oleksenko *et al.* 1996; Mukhametov and Lyamin 1997; Goley 1999). Only beluga whales could be rather inactive in captivity lying on the bottom of pools (Lyamin *et al.* 1998). It is obvious that the whale slept during a large portion of stage 3. However, we cannot exclude the possibility that some sleep also occurred in transitional stage 2, because in dolphins unilateral SWS occurs during their surfacing for respiration as well as during quiet stereotypic swimming (Mukhametov 1984; Mukhametov *et al.* 1997). Therefore, on average the total sleep time in the whale occupied =40% of each 24 h.

It is not quite clear whether such immobility is typical for gray whales in their natural environment and whether they can rest on the bottom when they are in shallow waters. One may expect that long periods of immobility in the studied whale were due to the whale spending most of the time in the shallow channel where it was able to lean its tail on the bottom. However, it is known that whales (e.g. the humpback whale) frequently 'log' at the surface at high latitudes in feeding grounds during calm water conditions. When they rest on the surface their respiratory rate is low. Any motions other than those related to breathing are not observed and sometimes it is possible to closely approach whales with a boat without them moving. During the breeding season in tropical waters it is rare to see them logging, probably because the sun is too hot (P. J. Clapham and D. K. Mattila, personal communication). Instead they perform long dives of up to 30 min duration, always emerging for respiration in the same place, with little horizontal change in position. Underwater observations indicate that they are mostly motionless during these long dives, and this pattern of behaviour is considered a resting behaviour

(Robbins *et al.* 1998). Therefore, Cetaceans demonstrate three different types of adaptation for sleep in water. They can sleep while swimming slowly near the surface, while motionless on the surface or they can hold their respiration for up to dozens of minutes and submerge. Further investigations need to be carried to determine why different marine mammal species sleep in different ways.

Active wakefulness occurred in the gray whale during the day, and rest mainly during the night (Figs 3, 4). There was no peak time for rest in the whale during the day. The whale lay on the bottom for extended periods during both the day and night. In contrast, afternoon sleep was prominent in the circadian profile of bottlenose dolphins and formed a second peak of rest in addition to one at night (Mukhametov and Lyamin 1997; Mukhametov *et al.* 1997). The pattern of activity that we observed in the gray whale appears to have been imposed by human activity near the pool. Almost every morning, a transition from rest to activity in the whale was caused by the noise made by trainers preparing food for the animal. It is likely that without this noise the rest state would have lasted longer despite the sunrise.

Analysis of the respiratory pattern in different stages has shown that the distribution of respiratory pauses was similar during active wakefulness and the transitional stage (stages 1 and 2), but the pattern of respiration changed significantly during rest (stage 3). It became more irregular and prolonged respiratory pauses alternated with periods of ventilation even while the whale rested on the surface. Such a pattern of respiration is very characteristic of beluga whales (Lyamin *et al.* 1998) and Phocidae seals (e.g. Lyamin 1993) which sleep both on the surface and submerged. This pattern of respiration appears to be a very important physiological adaptation for sleep in an aquatic environment. In contrast, other species of dolphins (Mukhametov 1984; Mukhametov and Lyamin 1997) and Otariidae seals (Lyamin and Chetyrbok 1992) which keep swimming slowly during their sleep or maintain paddling activity while sleeping on the surface usually do not display respiratory pauses longer than 1 min.

We observed the simultaneous closure of both eyes in the whale, which appears to occur in whales more frequently than in dolphins. Based on visual observation, there is no doubt that alternate eye closure was present in the gray whale. Lilly (1964) was the first to report that bottlenose dolphins usually slept with one eye open and the other closed. He hypothesized that dolphins scanned the environment during sleep. We performed experiments in which dolphins were presented a white and black chess board pattern to only one eye while they swam slowly in the enclosure and presumably were asleep (Oleksenko *et al.* 1996; Mukhametov and Lyamin 1997). We observed evident signs of behavioural arousal in most cases when the open eye could view the stimulus, supporting Lilly's hypotheses that the open eye does perform a guard function in sleeping dolphins. Recently Goley (1999) has shown that Pacific white-sided dolphins switch their positions in a sleeping formation in bouts and concurrently change the condition of

their eyes. They do it in such a way that the eye is more likely to be open toward schoolmates rather than toward the periphery of the school. During our observations, the gray whale always rested in a position that resulted in the right eye being orientated toward the observation booth. On the whole, the right eye was open a larger proportion of time than the left eye, which was directed toward the wall of the channel (Fig. 6). This supports the idea that open eye does control visual afferent input during sleep in Cetaceans and the open eye is a function of environmental conditions. There also appeared to be a correlation between alternate closure of eyes and unihemispheric deep SWS in dolphins (Mukhametov *et al.* 1997) and Otariidae seals (Lyamin and Chetyrbok 1992). The link between the open eye and more activated state of the contralateral hemisphere during SWS (interhemispheric EEG asymmetry) has also been found in birds, indicating that this form of sleep serves a predator detection function (Amlaner and Ball 1994; Rattenborg *et al.* 1999). Taken together, these data allow us to suggest that Mysticete whales might also have unihemispheric SWS.

We took special interest in observing any short muscular jerks and eyelid movements during rest, which would allow us to draw conclusions about the presence or absence of PS in the whale. Some of the observed jerks and eyelid movements differed from others for the following reasons: (i) they were recorded during the rest stage; (ii) they occurred at the end of the stage or were ended by arousal; (iii) the jerks occurred in series and were accompanied by eyelid movements (eyelids remained closed and probably corresponded to eyeball movements). Although such episodes were rare in the whale, and the jerks and eyelid movements were not as sharp and fast as in small terrestrial mammals, we suggest that some of these episodes might represent PS.

Obviously, it would be of great importance to subdivide stage 3 in the gray whale into two substages, with and without phasic events, in order to estimate the total duration of presumed PS in the gray whale. However, because most jerks were single short-lasting events, individual jerks could not be characterized in terms of duration. Most jerks were separated from each other by periods of minutes. For that reason, any estimations of the start and the end of putative PS episodes would be purely speculative because the beginning of a PS episode might not necessary coincide with the beginning of the jerk and the end of a PS episode may not always be followed by behavioural arousal. Because all eyelid movements observed in the gray whale were rather slow, the term 'REM' does not seem an appropriate description of these movements. Consequently, eyelid movements were also not very helpful in grouping phasic events into episodes. Another problem is that in comparison with bottlenose dolphins (Mukhametov and Lyamin 1994) and beluga whales (Lyamin *et al.* 1998), a significantly smaller number of jerks was recorded in the gray whale. Only 12 jerks in 6 days (two per day) were recorded at the end of the rest episode and only five of these jerks followed each other at intervals of several seconds. On only two occasions did jerks occur continuously

for a period of 3 and 4 s. Therefore, any estimation of total duration of putative PS episodes based on the appearance and disappearance of jerks gives us in total a maximum of 20-30 s of PS over the 6-day observation period.

To summarize, at this stage we can conclude that muscle jerks and eyelid movements did occur during rest in the gray whale. It is well known that not all animals and birds display all features of PS. Some species of mammals (e.g. rabbits; Pivik *et al.* 1981) and most birds (Amlaner and Ball 1994) do not have clear muscle tone hypotonia while they display evident phasic events such as REM and muscle jerks. Other mammals (e.g. Amazonian manatee; Mukhametov *et al.* 1992) show evident atonia but not REM or jerks. EEG desynchronization may not be the definite feature of PS either, because it does not appear during clear REM-like behaviour in primitive mammals (Siegel *et al.* 1996, 1999). Therefore, we think that the presence of jerks during rest in the gray whale, taken together with our previous data on three species of dolphins, allows us to suggest that short episodes of PS do exist in Cetaceans in a modified form that is not accompanied by the classical polygraphic or behavioural signs of PS observed in most terrestrial mammals.

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REFERENCES

- Amlaner, C. J. and Ball, N. J. Avian sleep. In: M. H. Kryger, T. Roth and W. C. Dement (Eds) *Principles and Practice of Sleep Medicine*. W.B. Saunders, Philadelphia, 1994: 81-94. Belkovich, V. M. and Shchekotov, M. H. *The Beluga Whale. The Behavior and Bioacoustic in the Wild*. Acoustic Institute of Russian Academy of Sciences, Moscow, 1990 (in Russian). Flanigan, W. F. Nocturnal behavior of small Cetaceans. I. The bottlenose porpoise, *Tursiops truncatus*. *Sleep Res.*, 1974a, 3: 84. Flanigan, W. F. Nocturnal behavior of small Cetaceans. II. The beluga whale, *Delphinapterus leucas*. *Sleep Res.*, 1974b, 3: 85. Flanigan, W. F. More nocturnal observations of captive, small Cetaceans. I. The killer whale, *Orcinus orca*. *Sleep Res.*, 1975a, 4: 139. Flanigan, W. F. More nocturnal observations of captive, small Cetaceans. II. The pacific white-sided dolphin, *Lagenorhynchus obliquidens*. *Sleep Res.*, 1975b, 4: 140. Flanigan, W. F. More nocturnal observations of captive, small Cetaceans. III. Further study of the beluga whale, *Delphinapterus leucas*. *Sleep Res.*, 1975c, 4: 141. Goley, P. G. Behavioral aspects of sleep in Pacific white-sided dolphins (*Lagenorhynchus obliquidens* Gill 1866. *Marine Mammal Sci.*, 1999, 15: 1054-1064.
- Lilly, J. C. Animals in aquatic environments: adaptation of mammals to the ocean. In: D. B. Dill (Ed) *Handbook of Physiology - Environment*. American Physiology Society, Washington, DC, 1964: 741-747. Lyamin, O. I. Sleep in the harp seal (*Pagophilus groenlandica*). Comparison of sleep on land and in water. *J. Sleep Res.*, 1993, 2: 170-174. Lyamin, O. I. and Chetyrbok, I. S. Unilateral EEG activation during sleep in the Cape fur seal, *Arctocephalus pusillus*. *Neurosci. Lett.*, 1992, 143: 263-266. Lyamin, O. I., Shpak, O. V., Nazarenko, E. A. and Mukhametov, L. M. Behavioral signs of paradoxical sleep in the beluga whale. *J. Sleep Res.*, 1998, 7 (Suppl. 2): 166. Mukhametov, L. M. Sleep in marine mammals. *Exp. Brain Res.*, 1984, 8 (Suppl.): 227-238. Mukhametov, L. M. Unihemispheric slow-wave sleep in the Amazonian dolphin, *Inia geoffrensis*. *Neurosci. Lett.*, 1987, 79: 128-132. Mukhametov, L. M. and Lyamin, O. I. Rest and active states in bottlenose dolphins (*Tursiops truncatus*). *J. Sleep Res.*, 1994, 3 (Suppl. 3): 174. Mukhametov, L. M. and Lyamin, O. I. The Black Sea bottlenose dolphin: the conditions of rest and activity. In: V. E. Sokolov and E. V. Romanenko (Eds) *The Black Sea Bottlenose Dolphin*. Nauka, Moscow, 1997: 650-668 (in Russian). Mukhametov, L. M., Lyamin, O. I., Chetyrbok, I. S., Vassilyev, A. A. and Diaz, R. P. Sleep in an Amazonian manatee, *Trichechus inunguis*. *Experientia*, 1992, 48: 417-419. Mukhametov, L. M., Oleksenko, A. I. and Polyakova, I. G. The Black Sea bottlenose dolphin: the structure of sleep. In: V. E. Sokolov and E. V. Romanenko (Eds) *The Black Sea Bottlenose Dolphin*. Nauka, Moscow, 1997: 492-512 (in Russian). Mukhametov, L. M., Supin, A. Y. and Polyakova, I. G. Interhemispheric asymmetry of the electroencephalographic sleep patterns in dolphins. *Brain Res.*, 1977, 134: 581-584. Norris, K. S. and Dohl, T. P. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fishery Bull. US*, 1980, 77: 821-849. Oleksenko, A. I., Chetyrbok, I. S., Polyakova, I. G. and Mukhametov, L. M. Rest and active states in Amazonian dolphins. *J. Sleep Res.*, 1994, 3 (Suppl. 1): 185. Oleksenko, A. I., Chetyrbok, I. S., Polyakova, I. G. and Mukhametov, L. M. Rest and active states in Amazonian dolphins. In: V. E. Sokolov (Ed) *The Amazonian Dolphin*. Nauka, Moscow, 1996: 257-266 (in Russian). Pivik, R. T., Sircar, S. and Braun, C. Nuchal muscle tonus during sleep, wakefulness and tonic immobility in the rabbit. *Physiol. Behav.*, 1981, 26: 13-20. Rattenborg, N. C., Lima, S. L. and Amlaner, C. J. Facultative control of avian unihemispheric sleep under the risk of predation. *Behav. Brain Res.*, 1999, 105: 163-172. Robbins, J., Mattila, D. K., Palsboll, P. J. and Berube, M. Asynchronous diving pairs of humpback whales: implications of a newly described behavior observed in the North Atlantic wintering grounds. *Abstract of the World Marine Mammals Science Conference, Monaco*, 1998: 20-24. Siegel, J. M., Manger, P. R., Nienhuis, R., Fahringer, H. M. and Pettigrew, J. D. The echidna *Tachyglossus aculeatus* combines REM and nonREM aspects in a single state: implication for the evolution of sleep. *J. Neurosci.*, 1996, 15: 3500-3506. Siegel, J. M., Manger, P. R., Nienhuis, R., Fahringer, H. M., Shalita, T. and Pettigrew, J. D. Sleep in the platypus. *Neuroscience*, 1999, 91: 391-400. Sjare, B. L. and Smith, T. G. The relation between behavioral activity and underwater vocalization of the white whale, *Delphinapterus leucas*. *Can. J. Zool.*, 1986, 64: 2824-2831. Wursig, B. and Wursig, M. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. *Fishery Bull. US*, 1980, 77: 871-890.