

Resting behavior in a rehabilitating gray whale calf

O. I. Lyamin^{1,2}, L. M. Mukhametov¹, J. M. Siegel², P. R. Manger², and O.V. Shpak¹

¹Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninsky prospect, Moscow, 117071, Russia

²Department of Psychiatry, School of Medicine, UCLA and V.A. Greater Los Angeles Healthcare System, 16111 Plummer St, North Hills, CA 91343, USA

Abstract

We studied the behavior of a one-year old gray whale calf (*Eschrichtius robustus*) during its rehabilitation at SeaWorld of San Diego. Several behaviors in this whale were grouped into 3 stages: (1) active wakefulness (mean $37.9 \pm 1.7\%$ of 24 hr during 6 consecutive days) included episodes of swimming in the main pool and in the shallow channel; (2) transitional stage (mean $17.4 \pm 1.4\%$) was composed of quiescent at the surface or near the bottom and episodes of submerging and emerging to the surface; (3) rest on the bottom of the pool (mean $13.2 \pm 1.7\%$) or at the surface (mean $28.0 \pm 1.7\%$) during which the whale was almost completely immobile. Most apneas in this calf were <3 min. The mean respiratory pauses were 29.1 ± 0.5 s ($n=1615$) in active wakefulness; 21.8 ± 0.5 s ($n=407$) during series of submergings and emergings; 26.9 ± 1.4 s ($n=136$) during quiescence at the surface, 92.5 ± 2.5 s ($n=236$) near the bottom, 63.2 ± 0.9 s ($n=1030$) during rest at the surface, and 147.4 ± 5.0 s ($n=377$) on the bottom. In the rest stage, one eye could be open, tightly closed, or partially open. Characteristic muscle jerks and eyelid movements were documented in this whale during the rest stage. Most jerks were single, but in several cases jerks and eyelid movements followed each other resembling twitches characteristic of paradoxical sleep in terrestrial mammals. Our data suggested that large whales might have unihemispheric, slow-wave sleep and a low amount of paradoxical sleep, which occurs without muscle hypotonia, intensive jerks, and twitches.

Key words: gray whale, calf, rest, sleep.

Introduction

Most information about sleep in cetaceans comes from simple observations of captive or free-ranging

animals or a few electrophysiological studies, mostly of odontocete cetaceans. Generally, a quiescent posture is thought to be one of the most important behavioral criteria of sleep in mammals (Zepelin, 2000). Sleep in odontocetes; however, differs substantially from sleep in terrestrial mammals. Observations on behavior of bottlenoses dolphins (*Tursiops truncatus*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), belugas (*Delphinapterus leucas*), Amazon River dolphins (*Inia geoffrensis*), harbor porpoises (*Phocoena phocoena*), and Dall's porpoises (*Phocoenoides dalli*) showed they may rest while slowly swimming (Lilly, 1964; Flanigan, 1974a,b; 1975b,c; Mukhametov & Lyamin, 1994, 1997; Oleksenko *et al.*, 1996; Oleksenko & Lyamin, 1996; Goley, 1999).

Sleep in terrestrial mammals typically involves characteristic changes in the electrical activity of the brain as measured by electroencephalogram. Moreover, two stages of sleep have been distinguished, slow-wave sleep and paradoxical sleep. Brain wave activity during slow-wave sleep is characterized by high-amplitude slow-waves (1–4 Hz) in the electroencephalogram that contrast noticeably to the low-voltage, fast-wave patterns distinctive of paradoxical sleep and the waking state. Some other features of paradoxical sleep are the presence of periods of rapid eye movements (i.e., REM sleep), twitches, and the lack of skeletal muscle tone (Rechtschaffen & Siegel, 2000). The differences between the two stages of sleep are so significant that some researchers consider waking, slow-wave sleep, and paradoxical sleep as three distinctive behavioral states.

So far, electrophysiological studies have been made in the pilot whale, *Globicephala melaena*, (Shurley *et al.*, 1969), bottlenose dolphin, harbor porpoise (Mukhametov *et al.*, 1977, 1997; Mukhametov, 1984), Amazon River dolphin (Mukhametov, 1987), and recently in the beluga (Lyamin *et al.*, 2001). These studies showed that dolphins do sleep during slow-swimming and

exhibit 'unihemispheric' slow-wave sleep. That unihemispheric sleep is characterized by development of high-amplitude and low-frequency activity in one hemisphere of the brain (i.e., that hemisphere is asleep), while the other hemisphere is desynchronized and has low-amplitude and high-frequency activity.

The absence of typical polygraphic features of paradoxical sleep evidently is another intriguing feature of sleep in cetaceans (Mukhametov, 1984, 1987; Mukhametov *et al.*, 1977, 1997). Since recent studies of sleep in primitive, egg-laying monotremes revealed that the platypus, *Ornithorhynchus sp.*, and echidna, *Tachyglossus sp.*, exhibit a state resembling paradoxical sleep in terrestrial mammal (Siegel *et al.*, 1996; 1999), cetaceans appear to be the only mammals in which paradoxical sleep does not occur. Nonetheless, behavioral observations of muscle jerks and body twitches in belugas (Flanigan, 1974b, 1975b; Lyamin *et al.*, 1998), killer whales, *Orcinus orca*, (Flanigan, 1975a), bottlenose dolphins (Flanigan, 1974a; Mukhametov & Lyamin 1994, 1997), Pacific white-sided dolphins (Flanigan, 1975b; Nelson & Lein, 1994), and Amazon River dolphins (Oleksenko *et al.*, 1996) suggested that paradoxical sleep might occur in cetaceans, despite the absence of electrophysiological evidence.

Much less is known about resting behavior in large whales. Some evidently rest quietly at and near the sea-surface and perhaps even at-depth (e.g., Robbins *et al.* 1998; Watkins *et al.*, 1999). Here, we describe observations of rest and activity patterns in a California gray whale calf ('JJ'), *Eschrichtius robustus*, during rehabilitation at Sea-World of San Diego. Our goals were to describe the resting behavior and evaluate these behaviors for evidence of typical signs of paradoxical sleep.

Materials and Methods

We recorded JJ's behavior on a video recorder (Panasonic AG-6730E) for 9 days in early March 1998 (6 consecutive days of recording, 3 days of no recording, and then 3 consecutive days of recording) from two underwater and three aerial cameras (Samsung and Panasonic, sensitivity 0.08–0.15 Lux), which were connected to the recorder via a multiplexer (Panasonic WJ-FS20). JJ was approximately 14 months old during our observations. She was kept in a large pool (6400 m³, depth 3 to 12 m), where she spent most of the time in a shallow channel (approximately 10 × 10 m and depth between 3 and 6 m) isolated from the larger pool complex by two lattice gates. When in the channel, she stayed mostly in the same location with her head pointed at one of the gates. This allowed us to choose the position for two underwater cameras on opposite sides of the channel so

that when her head rested at the surface it filled most of the frame and was clearly visible from both sides. When JJ laid on the bottom of the pool, we were able to see only the right-side of her head. The pool was illuminated during all night observations (1830 to 0630 h) with two, 500 W lamps installed on the two sides of the channel. We habituated JJ to the lighting for three days before we began observations.

We observed and recorded JJ's behavior in real time when we reviewed the videotapes. We used the data from the first period (6 days) to characterize the amount of time she spent in different behavioral states. The data from the second period (3 days) were used to document eye state when JJ was resting. In the first stage of analysis, we documented all changes in her patterns of movements that lasted more than 5 s. Later, we excluded episodes <20 s, but considered all episodes of submergings and emergings. All these episodes were shorter than 20 s and signified transitions between the rest and wakefulness states (see Results). We also registered various features of JJ's activity, especially jerks of her head, body and appendages; the state of her eyes and eyelid movements when her eyes were clearly visible; and respirations.

Results

We identified several distinct behavioral patterns or styles of swimming and grouped them into three main stages: (1) active wakefulness (Fig 1A), (2) transitional stage (Fig 1B), and (3) rest (Fig. 1C). Most of the time JJ spent in the shallow channel. When JJ went to the main pool she usually made one cycle and then returned to the channel. However, JJ was not visible to our cameras when it was swimming in the main pool (ca 3.5% of the observation time), we always observed her and documented behavior.

She was awake and active (stage 1) about 33% to 45% (avg.=38%) of each 24-h period (Table 1). Activity then included swimming in the pool and in the channel, at various speeds and direction, and activities near the lattice gates. Both behavioral patterns were accompanied by different features of unambiguous behavioral activity: feeding, spinning, raising her head above water, rubbing on the walls or bottom of the pool, slapping her fluke or head on the surface, pushing the gates, loud exhalations, etc. Her eyes remained open and she often appeared to 'look at' humans near the pool. Most (75%) of these episodes lasted less than 2 min, whereas only about 5% were longer than 5 min. On the other hand, some periods of activity, which included alternating episodes of swimming in the pool, in the channel or near the gates lasted more than 1 h (Fig 2A). The average duration of episodes of swimming in the

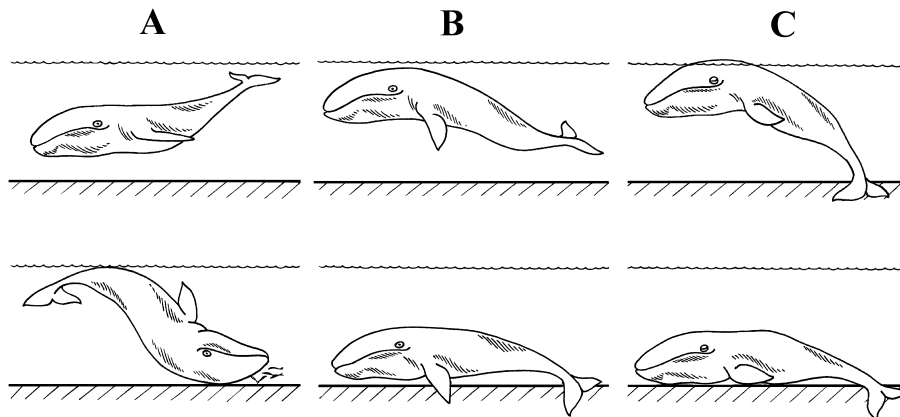


Figure 1. Main swimming styles and behavioral stages observed in JJ. (A)—swimming and feeding (stage 1, active wakefulness); (B)—quiescence at the surface and at the bottom (stage 2, transitional); (C)—rest at the surface and on the bottom (stage 3).

pool and activity near the gates (Table 2) were not different (Student's *t*-test, $P > 0.05$), nor were the distributions of durations of these two types of episodes (chi-squared test, $df = 13$; $P > 0.05$).

The transitional stage (stage 2) included four different behavioral patterns, which occurred only in the channel. On average, this stage accounted for 17.4% of each 24-hr period (Table 1). A portion of this time, JJ stayed at the bottom of the pool (mean $4.8 \pm 0.5\%$ of each 24-hr period) or near the surface (mean $4.0 \pm 0.6\%$). The mean durations (Table 2) and the distributions of episodes of these two types of swimming were very similar (chi-squared test, $\chi^2 = 12.9$, $df = 6$, $\chi^2_{0.05} = 12.6$). During all these episodes, JJ either moved her head, fin or flukes at least once every 20 s. Her eyes typically were open when they were visible. These episodes were usually

followed by slow submerging or emerging (mean $3.0 \pm 0.2\%$), which also were considered stage 2 episodes. Of all submerging or emerging episodes, 94% were < 20 s and 80% between 9 and 15 s. Occasionally, submergings and emergings followed each other without being separated by episodes of quiescence near the surface or on the bottom (mean $5.6 \pm 0.8\%$). These episodes lasted 21 to 463 s (Table 2). The distribution of durations of series of submergings and emergings differed significantly from the distributions of episodes of quiescence at the surface and near the bottom (chi-square test for both cases, $df = 7$, $P < 0.001$). Virtually every movement to the surface was accompanied by a breath. When series of submergings and emergings occurred, respiratory acts became more regular and sequential with brief inter-respiratory periods.

Table 1. Total duration of different patterns of behavior and activity and rest stages (mean and standard error) in 6 consecutive days in the gray whale (in % of 24-h)

Pattern of behavior and stage	Day of observations						Mean \pm SE
	1	2	3	4	5	6	
Swimming in the channel or in the pool	22.4	16.6	21.2	19.4	26.7	18.0	20.7 \pm 1.5
Activity near the gates	22.8	16.6	17.4	16.1	12.7	17.3	17.2 \pm 1.3
Active wakefulness (stage 1)	45.2	33.2	38.6	35.5	39.4	35.3	37.9 \pm 1.7
Emergings and submergings	2.4	3.8	3.1	3.4	2.7	2.7	3.0 \pm 0.2
Series of stereotypic emergings and submergings	4.5	7.2	7.3	7.5	3.7	3.5	5.6 \pm 0.8
Quiescence near the surface	6.5	4.5	2.7	3.2	4.3	2.4	4.0 \pm 0.6
Quiescence near the bottom	5.1	7.0	3.6	4.8	5.1	3.7	4.8 \pm 0.5
Transitional (stage 2)	18.5	22.5	16.7	18.9	15.8	12.3	17.4 \pm 1.4
Rest at the surface (stage 3a)	24.7	27.2	22.7	30.4	34.2	29.1	28.0 \pm 1.7
Rest on the bottom (stage 3b)	8.5	15.0	18.0	14.8	7.8	14.9	13.2 \pm 1.7
Rest (stage 3)	33.2	42.2	40.7	45.2	42.0	44.0	41.2 \pm 1.7
Unidentified	3.1	2.1	4.0	0.4	2.8	8.4	3.5 \pm 1.1

Table 2. Characteristic of activity and rest episodes in the gray whale (mean, standard error, median, mode and maximal duration of episodes are in seconds; number—the total number of episodes recorded in 6 consecutive days)

Pattern of behavior and stage	Statistical parameters				
	Mean \pm SE	Median	Mode	Maximum	Number
Swimming in the channel and in the pool	102 \pm 3	77	40	911	943
Activity near the gates	122 \pm 5	83	58	1235	728
Quiescence near the surface	58 \pm 2	42	20	310	351
Quiescence near the bottom	57 \pm 2	49	48	410	441
Emergings and submergings	11 \pm 1	11	10	80	1328
Series of stereotypic emergings and submergings	69 \pm 2	64	35	463	422
Rest at the surface (stage 3a)	363 \pm 36	109	64	5935	400
Rest on the bottom (stage 3b)	115 \pm 2	114	116	431	596

The rest stage (stage 3) included episodes when JJ was motionless at the surface (stage 3a) or on the bottom of the channel (stage 3b). This stage accounted for about 41% of each 24-hr period, on average (Table 1). These behaviors were not observed in the main pool. Either eye might be open, closed, or half-open. When resting at the surface, JJ clasped her pectoral fins tightly to her body while her flukes touched the bottom of the pool and were motionless. Practically all (96%) episodes of lying on the bottom lasted less than 3 min; the longest was 7 min (Table 2). Episodes of resting at the surface were distributed much more widely; 69% of them lasted less than 3 min and 14% were between 10 and 98 min. The distributions of the durations of stage 3a and stage 3b episodes differed significantly ($df=9$, $P<0.001$).

JJ was usually awake and active between 0600 and 1800 hr (Fig. 2A) when she was being fed or when observing humans nearby. During these times, she alternated swimming in the main pool, in the channel or near the gates (stage 1) with periods of quiescence near the bottom (stage 2). She was also active between 1800 and 2200 hr, although less active than during the day. In some days, JJ was active at night. These periods did not evidently correlate with any particular changes around the pool complex (e.g., activity of people or sounds of killer whales coming from the nearby pool complex). The transitional stage (stage 2) was distributed evenly during each 24-hr period. Periods of rest at the surface (Fig. 2B) occurred typically in late afternoon and throughout the night, rarely between 0700 and 1700 hr. In contrast, episodes of rest on the bottom were evenly distributed over each 24-hr period except between 0600 and 0800 hr during the first daily feeding (Fig. 2C).

JJ's respiration patterns depended on her behavior stage (Fig. 3). We did not document respiratory events when she was in the main pool. Virtually all (90%) respiratory pauses during swimming in the

pool or in the channel and activity near the gates lasted <1 min. The lengths of respiratory pauses during the two forms of active behavior were very similar and the distributions of pauses had maximums at 20–25 s. On the other hand, we found statistically significant difference in the distribution of respiratory pauses between these two styles of swimming ($P<0.001$, $df=14$). It resulted from the presence of short (<5 s, loud exhalations) and long (>40 s) respiratory pauses, which occurred more often during swimming in the pool or in the channel (Fig. 3A).

In stage 2 (Fig. 3B), respiratory rate was most regular during series of submergings and emergings (82% of all documented pauses lasted between 10 and 25 s). Similar to stage 1, most respiratory pauses documented during quiescence at the surface (95% of all pauses) were shorter than 1 min. During episodes of quiescence near the bottom pauses became longer and 97% of all apneas were between 30 and 180 with a maximum between 60 and 90 s.

The longest respiratory pauses were recorded during the rest stage (Fig. 3C). When JJ was resting at the surface, the number of pauses shorter than 1 min dropped to 25% compared to more than 90% during active swimming (stage 1) and quiescence at the surface (stage 2). When JJ rested on the bottom, 65% of apneas were longer than 2 min (compared to 40% during rest at the surface). On the other hand, all but one of these apneas were <5 min with the longest lasted 460 s.

The mean respiratory pause (all pauses documented during 4 consecutive days) was 29.1 ± 0.5 s ($n=1615$) in stage 1. In stage 2, the mean pause during a series of submergings and emergings was 21.8 ± 0.5 s ($n=407$), during quiescence at the surface was 26.9 ± 1.4 s ($n=136$), and during quiescence at the bottom was 92.5 ± 2.5 s ($n=236$). In stage 3, the average pause was 63.2 ± 0.9 s ($n=1030$) when JJ rested on the surface and was 147.4 ± 5.0 s ($n=377$) when JJ rested on the bottom.

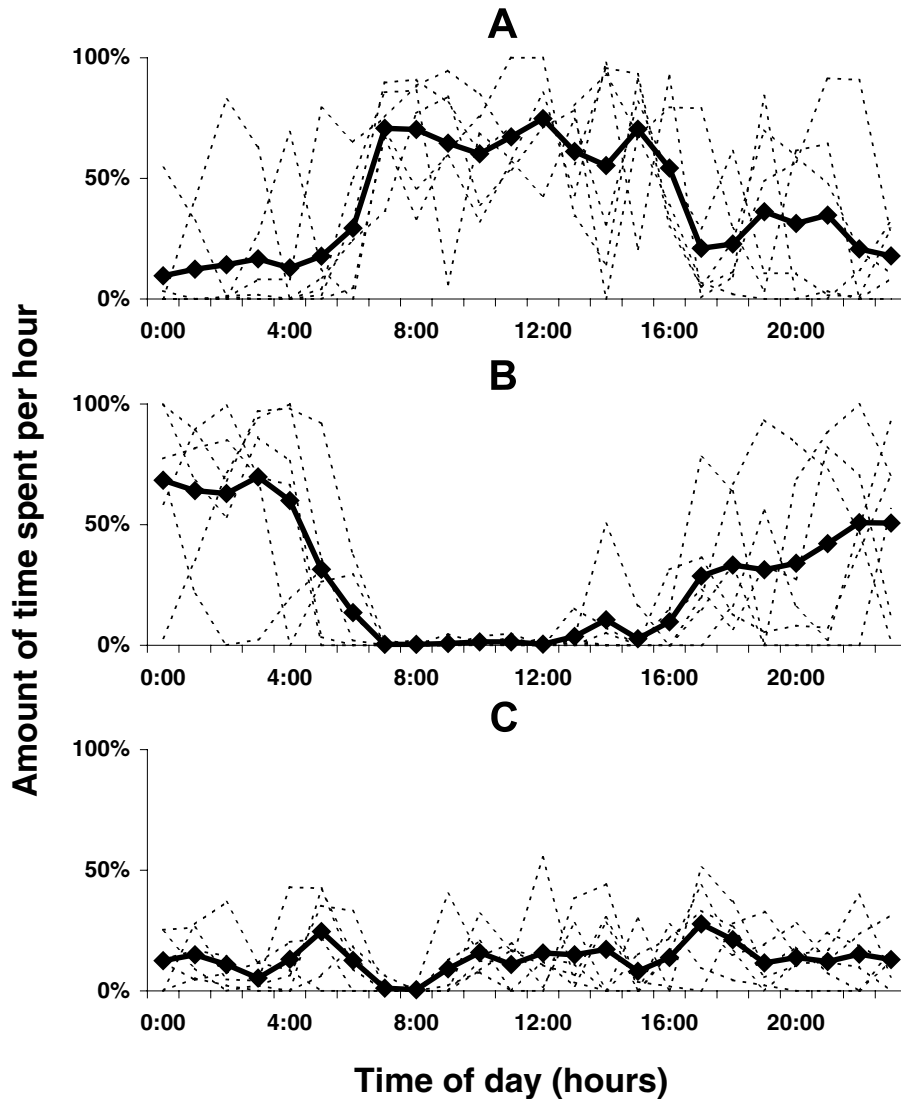


Figure 2. Distribution of active wakefulness and rest stages in the gray whale over the 24-hr period. The thin lines link the mean hourly values for 6 consecutive days. The thick lines—represent the average values for 6 days. (A)—active wakefulness (stage 1); (B)—rest at the surface (stage 3a), (C)—rest on the bottom (stage 3b).

It was not possible to observe both eyes continuously because the cameras were fixed in position at both sides of the channel. Therefore, we cannot quantify the time JJ spent in different eye states. However, our observations provided some information on the state of the eyes in this whale. When the eyes were visible in stages 1 and 2, they were usually open. Rarely, one or two eyes were closed and always for a short time. In stage 3, each eye could be open, closed, or in an intermediate (half-closed) state independent of the state of the other

eye. Figure 4 shows a representative episode of rest (0400–0600 hr) during which both eyes were visible for a significant amount of time (64% of the time) and the state of each eye was analyzed in real time second by second (a total of 1 hr and 17 min). As follows from this figure, at the beginning (0405–0515 hr) and at the end (0540–0600 hr) of this episode the left eye was usually closed while the right eye was closed or in the intermediate state. In the middle of this rest period (0520–0540 hr) the situation was opposite—the right eye was closed

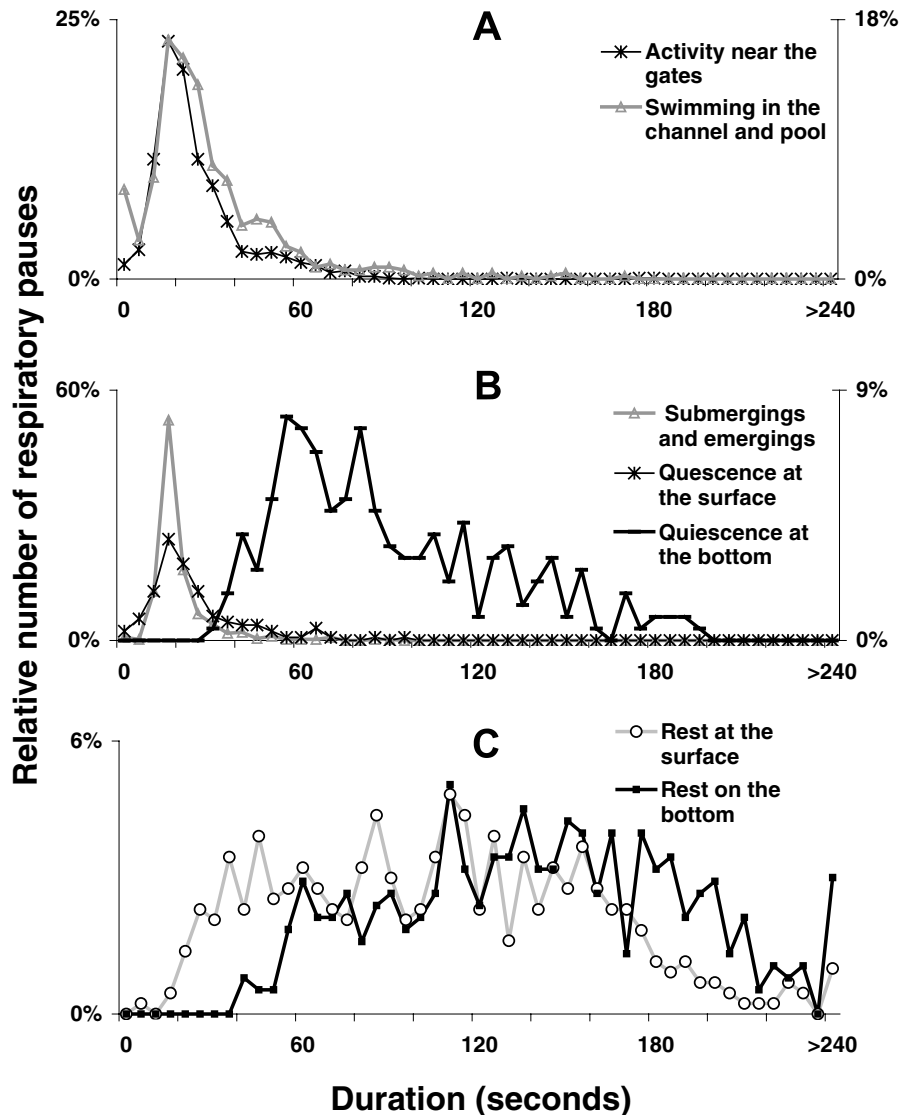


Figure 3. Distributions of respiratory pauses documented in different behavioral stages in the gray whale (as percentages of the total number of pauses documented in a given stage during two consecutive days). (A)—active wakefulness (stage 1); (B)—transitional stage (2); (C)—rest (stage 3). Note that the percentages of pauses during swimming in the channel and in the pool and during quiescence at the bottom are expressed on the right side axis.

more often, while the left eye was mostly open or in intermediate state. Moreover, in her typical rest posture, JJ's right eye, which was usually facing the observation booth, was closed slightly less often (56% of this episode time) than her left eye (63%), which faced the wall of the pool. Episodes of bilateral eye closure in JJ usually lasted for half as long (32% of this episode time) as when both eyes were in asymmetrical stages (61%, Fig. 4).

Muscle jerks, body twitches, rapid eye movements and muscle hypotonia are features of paradoxical sleep in mammals. We documented some of these events in JJ when she rested at the surface and on the bottom of the channel. We counted 48 single jerks of the head, rarely the whole body, during the first six-day observation period. Most (85%) occurred when JJ rested at the surface (stage 3a), 90% at night. About 25% of them occurred at the end of

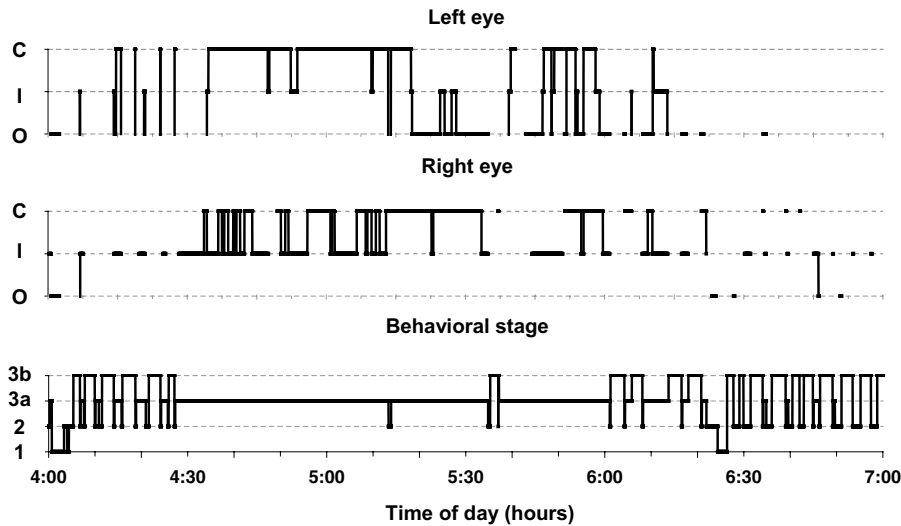


Figure 4. Simultaneous presentation of the state of both eyes and behavioral stage in JJ during a representative 3 hr night period. The state of eyes: O—open, I—intermediate and C—closed. The behavioral stage: 1—wakefulness, 2—transitional, 3a—rest at the surface, 3b—rest on the bottom.

rest episodes and they mostly were followed by episodes of active swimming in the pool or activity in the channel (wakefulness). The right eye, which we could see most of the time, was tightly closed or halfway open during 93% of all the head jerks observed. Most head jerks were single (43 of 48 or 90% of all jerks), only 5 (10%) occurred within 10 s of each other. There were two episodes of continuous head jerks over several seconds.

We observed eyelid movements when JJ was resting, though they were slower than in terrestrial mammals. We considered only those movements during which eyelids were tightly closed and were not followed by eye opening. Over the 6-day period we documented 131 single right eyelid movements and 34 series of such movements. In the last case, eyelids moved practically constantly during a period of 2 to 10 s and it was not possible to subdivide them into single movements. Both single eyelid movements and series were subdivided into 3 groups: slow (83% of all single and 15% of all series), fast (8% and 32%) and intermediate (9 and 53%). During slow movements, eyelids moved only in vertical directions up or down and then returned in the normal position. Each single movement lasted between 1 and 3 s. Fast movements were <1 s and the eyelids moved in all directions. These movements resembled jerks. The remaining movements could not be definitely classified as slow or fast. Serial movements lasted between 2 and 10 s and the average duration of all serial movements was 4.9 ± 0.4 s ($n=34$).

During the analysis we chose eleven episodes, in which muscle jerks or twitches (at least one event) were accompanied by eyelid movements and then were followed by behavioral arousal (e.g., opening one eye, loud respiration or falling on the side). All these episodes were observed when the whale rested at the surface. They lasted between 2 and 12 s. The total duration of these episodes measuring between the first and the last phasic events was 51 s. The total duration of these episodes measuring between the first event and behavioral arousal was 85 s or 0.02% of the 24-hr period. During five of these episodes, JJ was slowly rolling on her side with both pectoral fins tightly pressed against her body and then stayed motionless at the surface for several seconds. All these episodes were followed by long episodes of swimming in the main pool and had the most resemblance with episodes of paradoxical sleep in terrestrial mammals.

Discussion

JJ engaged in several distinct types of behavior, ranging from being unambiguously awake to resting at the surface or on the bottom of the pool, frequently almost completely immobile when she appeared to be sleeping. Quiescence at the surface ('hanging', 'floating') has been reported for several species of cetaceans in captivity (e.g., killer whales, Flanigan, 1975*a*; Pacific white-sided dolphins, Flanigan, 1975*b*; bottlenose dolphins, McCormick, 1969; Flanigan, 1974*a*; Mukhametov & Lyamin,

1994, 1997; Chinese river dolphins; Renjun *et al.*, 1994). Captive bottlenose dolphins spent between 4 and 53% of each 24-hr period (average of $25 \pm 10\%$ for four dolphins) resting at the surface (Mukhametov & Lyamin, 1997). In the ocean, this type of behavior is probably less typical of bottlenose dolphins (Shane *et al.*, 1986; Hanson & Defran, 1993). On the contrary, quiescence on the bottom has been observed only in a few captive cetaceans, including bottlenose dolphins (McCormick, 1969), Amazon River dolphins (Renjun *et al.*, 1994) and in one beluga whale (Lyamin *et al.*, 1998). Prolonged episodes of slow-swimming, as it has been shown in electrophysiological studies (Mukhametov 1974; 1987), is another form of sleeping behavior in dolphins and porpoises. This behavior was observed, for example, in captive bottlenose dolphins (Mukhametov & Lyamin, 1997), Pacific white-sided dolphins (Flanigan, 1975b; Goley, 1999), belugas (Flanigan, 1974b, 1975c), harbor porpoises (Mukhametov, 1974; Oleksenko & Lyamin, 1996), and Amazon River dolphins (Oleksenko *et al.*, 1996). In the wild, several odontocete species have been described to be engaged in a similar behavior—slow movements lacking behavioral components of evident activity (Klinowska, 1986; Shane *et al.*, 1986). However, we never observed JJ behave that way.

There is minimal information on resting behavior of large whales. Some observations indicate that southern right whales (*Eubalaena australis*) and Mediterranean fin whales, *Balaenoptera physalus*, lie motionless at the surface (Cassini & Vila, 1990; F. Ricciardi *et al.*, 2001). Sperm whales, *Physeter catodon*, can alternate long dives with periods near the surface, especially in daylight (Watkins *et al.*, 1999). Humpback whales 'log' at the surface and perform long dives always emerging for breathing at the same place. Underwater observations indicated that they are frequently motionless during these long dives, suggesting that this form of behavior can be a resting behavior (Robbins *et al.*, 1998; D. Mattila, P. Clapham, pers. comm.). Our observations of JJ collaborate these data, suggesting that large whales can sleep motionless at the surface and even at-depth.

Probably the most important difference between episodes of rest in JJ and those reported for dolphins and porpoises, was occasional long periods of almost complete immobility when she rested at the surface or on the bottom of the pool. These episodes occurred during respiratory pauses and lasted until the next respiration, when the whale needed to move to breathe. Even when resting at the surface, bottlenose dolphins and killer whales are never motionless more than a few seconds, but rather continue to move their fins and flukes

regularly (Flanigan, 1975a; Mukhametov, 1984; Mukhametov & Lyamin, 1997; Mukhametov *et al.*, 1997). A beluga we observed in the Moscow dolphinarium spent between 49 and 73% of the night time lying on the bottom of the pool and presumably was asleep, but it was practically never completely immobile slightly moving its head and fins (Lyamin *et al.*, 1998).

Therefore, unlike terrestrial mammals, which are mostly immobile during sleep (Zepelin, 2000), cetaceans can sleep both during swimming and while quiescent at the surface, at depth and even on the seabed. The data now available suggest that smaller cetaceans (porpoises and dolphins) sleep mostly or exclusively during swimming, while larger dolphins and whales sleep both during swimming and episodes of quiescence at the surface or at depth. This association between the size of cetaceans and sleeping behavior could be species-specific, related to their natural habits (e.g., inshore or oceanic species), or to their behavioral plasticity and capability for adaptation to captivity (Klinowska, 1986). In addition, we should not exclude the possibility that nearly continuous swimming in small porpoises could originate from the necessity to keep warm to compensate faster heat loss in comparison with larger whales. The data from JJ support this interpretation.

We found that JJ was active for about 38% and rested 41% of each 24-h period. Because she was entirely immobile during much of the rest stage, we think that she was indeed sleeping a significant portion of this time. However, because episodes of quiet wakefulness may not be distinguishable from episodes of slow-wave sleep in cetaceans (Mukhametov, 1984), these rest periods may not imply that JJ was sleeping the entire time. We cannot eliminate the possibility that JJ slept during a portion of the transitional stage (especially during emergings and submergings) because dolphins and porpoises have unilateral, slow-wave sleep when they surface to breathe, as well as during quiet stereotypic swimming (Mukhametov, 1984, 1987; Mukhametov *et al.*, 1997). Moreover, long episodes of quiescence near the bottom (scored here as stage 2) might be short episodes of sleep as well. Then the potential sleep time in JJ could be as much up to 58% of each 24-hr period. On the other hand, as follows from Fig. 3, the distributions of apneas in JJ during rest at the surface and on the bottom included both short and long episodes. This suggests that each of these behaviors grouped in different stages (2 and 3) might represent both wakefulness and sleep. Episodes of rest at the surface (stage 3) accompanied by faster and more regular respiration (e.g., pauses <60 s composing the peak between 40 and 60 s in Fig. 3C) could be arousals. Episodes of rest on the bottom were

evenly distributed over the 24-hr period and were present during the morning and daytime (0800 and 1600 hr; Fig. 2). At these times, JJ was maximally disturbed and did not rest at the surface. This suggests that most of these rest episodes represented wakefulness, but not sleep. If that is the case, then at least 33% of the quiescence and rest on the bottom and 21% of the rest at the surface should be excluded from the total rest time. This would decrease the potential sleep time in JJ from to 41% to 29% per 24 hr. Therefore, while according to our estimations JJ rested on average 41% of each 24-hr period, she might sleep up to 29–58% of each day.

We observed that JJ was awake and active mostly during the day and rested mostly at night (Fig. 2). Active wakefulness occurred during the day period, and rest mainly at night. Both in electrophysiological and behavioral studies, captive bottlenose dolphins have been observed sleeping in the afternoon and then again at night (Mukhametov & Lyamin, 1997; Mukhametov *et al.*, 1997). However, on some days JJ rested at the surface in the afternoon we did not see an evident afternoon napping. We think that this pattern of diurnal activity in JJ was related to patterns of human presence and activity near the pool. Almost every morning, a transition from rest to activity in JJ's behavior corresponded with an increase in noise associated with nearby preparation of her food. Consequently, we think that the nighttime rest period might have been longer if not interrupted by this activity. It is likely that afternoon napping would have been more prominent if had she been less disturbed during these hours.

JJ's breathing patterns were similar during periods of active wakefulness and most of the transitional stage (excluding quiescence at the surface), but it became more irregular during rest when longer respiratory pauses alternated with periods of ventilation, even while she rested at the surface. This pattern is typical for belugas (Lyamin *et al.*, 1998) and phocid seals (for review see, Castellini, 2001), which sleep both at the surface and while submerged. But the respiratory pauses of some other dolphins and porpoises that continue to swim while sleeping are usually <1 min (e.g., Mukhametov, 1984; Mukhametov & Lyamin, 1997). The fact that JJ did not exhibit long apneas (majority were <5 min) may be explained by young age and that she was accustomed to rest in the shallow channel.

We observed that JJ often alternated between closing one eye or the other during rest periods, similar to what was reported for other cetaceans. During our observations, JJ always rested with her right eye oriented toward the observation booth. Moreover, the right eye was more often observed open than the left eye, which was facing the wall of the channel. Earlier it was suggested that dolphins

might scan the environment with one eye open while sleeping (Lilly, 1964; McCormick, 1969). Several behavioral (Oleksenko *et al.*, 1996; Mukhametov & Lyamin, 1994; 1997; Goley, 1999) and several electrophysiological (Mukhametov *et al.*, 1997; S. Ridgway, pers. comm.) studies provided some evidences supporting this hypotheses. Recently, we recorded electroencephalogram and simultaneously documented the state of both eyes in one white whale. We found that the eye contralateral to the sleeping hemisphere during unihemispheric sleep was typically closed or in an intermediate (half-closed) state and the ipsilateral eye was mostly open (Lyamin *et al.*, 2001). This finding is the experimental confirmation the idea that unihemispheric sleep is a neurophysiological mechanism underlying visual monitoring of the environment during sleep in cetaceans. Therefore, we think that our observations of JJ's behavior (specifically, the presence of episodes of unilateral eye closure) suggest that unihemispheric sleep may occur in Mysticeti, as it does in Odontoceti whales. We make this suggestion because asymmetrical eye state appears to be closely associated with electroencephalogram asymmetry, not only in cetaceans, but in some pinnipeds (Lyamin & Chetyrbok, 1992) and birds (for review see Rattenborg *et al.*, 2000).

Muscle jerks during sleep have been observed in several species of captive cetaceans (Flanigan, 1974a, 1974b, 1975a, 1975b; Mukhametov & Lyamin, 1994; 1997; Nelson & Lein, 1994; Oleksenko *et al.*, 1996; Lyamin *et al.*, 1998). Although the number of jerks and their characteristics can vary substantially among species (e.g., 48 jerks per 6 days for JJ; 100–180 jerks per night for the beluga whale, Lyamin *et al.*, 1998), there are some apparent similarities. Jerks appeared to be related to resting behavior and occurred in prolonged rest episodes, usually at night. Some jerks occasionally follow other jerks, and resemble twitches. Jerks often were followed by behavioral activity or arousal which is consistent with the fact that paradoxical sleep in terrestrial mammals always follows slow-wave sleep (immobility) and is terminated by behavioral or electroencephalographic arousal (Zepelin, 2000). Therefore, some arguments obviously favor the hypothesis that paradoxical sleep is present in cetaceans, but in a modified form and in a significantly reduced amount, and this stage is not accompanied by intense phasic jerks as it takes place in most terrestrial mammals. Our data from JJ support this idea (specifically a low number of jerks during the rest stage compared to most terrestrial mammals). On the other hand, it is known that jerks during sleep in humans and animals can represent normal phasic muscle activity. They are typically present at sleep onset or during partial arousal from sleep. The

number of jerks decreases as slow-wave sleep deepens and then they reappear in paradoxical sleep or shortly before it (Carskadon & Dement, 2000). Both hypotheses need to be verified in future electrophysiological studies and observations of sleep and resting behavior in Cetaceans.

To summarize, our observations of JJ provided some additional information on the resting behavior of large whales. These findings suggested that, similar to other studied cetaceans (mostly Odontoceti), Mysticeti whales: (1) can sleep both at the surface and at depth; (2) likely have unihemispheric, slow-wave sleep and; (3) might have a small amount of paradoxical sleep, which occurs without pronounced muscle hypotonia and intensive jerks and twitches.

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