Behavioral aspects of sleep in bottlenose dolphin mothers and their calves

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Abstract

Adult dolphins are capable of sleeping with one eye open and exhibiting slow wave activity in the electroencephalogram (EEG) of one hemisphere at a time. The aim of this study was to examine the postpartum sleep behavior of bottlenose dolphin calves and their mothers. The behavior of three dolphin mother–calf pairs was monitored from birth to 13 months postpartum. Dolphin mothers and their calves exhibited a complete disappearance of rest at the surface for a minimum of 2 months postpartum, swimming in echelon formation on average in 97–100% of the observation time. Calves surfaced to breathe more often than their mothers between the postpartum age of 2 and 8 weeks. During the first postpartum month two dolphin mothers surfaced with both eyes open on average in 93 and 98% of the time while in their calves both eyes were open in 90 and 60% of the cases. In calves, the eye directed toward the mother was open more often (on average in 95% of all observations in calf 1 and 99% in calf 2) than the eye directed to the opposite side (82% in calf 1 and 60% in calf 2). Our data indicate that dolphin mothers and calves are highly active and vigilant during the initial period of the calf's life, continuously monitoring their position relative to each other by sight during wakefulness and sleep. We hypothesize that episodes of EEG slow wave activity at this time are likely to be brief, fragmenting EEG defined sleep into short episodes.
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1. Introduction

All terrestrial mammals studied to date exhibit minimal activity and maximal total sleep amounts at birth, with sleep gradually decreasing, and activity gradually increasing to adult levels as the animal grows to maturity [1]. In contrast to terrestrial mammals, killer whale (*Orcinus orca*) and bottlenose dolphin (*Tursiops truncatus*) neonates are highly active after birth, with their mothers not resting at the surface during the first 3 weeks postpartum [2,3]. This surface behavior is a common rest behavior in captive killer whales and dolphins [2–7]. Previous studies have noted a high level of activity in dolphin calves when compared to their mothers but did not examine this behavior in detail [8,9].

Terrestrial mammals have been shown to remain immobile during sleep with both eyes closed at all times. However, dolphins are capable of sleeping during swimming and exhibiting slow wave activity in one hemisphere while the other hemisphere displays low voltage activity [10]. The eye which is opposite to the sleeping hemisphere is predominantly closed or in an intermediate state while the eye opposite to the waking hemisphere is more frequently open [11–13]. To date, an association between rest behavior and eye state, in freely swimming dolphins, has been studied in only one species — the pacific white-sided dolphin (*Lagenorhynchus obliquidens*, [14]). During slow echelon swimming, when dolphins switched their positions, they also switched eye state in such a way, that the open eye was always directed toward their schoolmates. Similar, but limited, observations were also obtained from bottlenose dolphins [8,9]. Lilly [15] speculated that dolphins need to keep one eye open to scan their environment to avoid predation, while Goley [14] suggested that the open eye allows them to maintain visual contact with group members. Sekiguchi and Kohshima [9] suggested that captive bottlenose dolphins keep one eye open to avoid collisions with the pool wall. Although these hypotheses differ in minor details, they clearly emphasize the sentinel function of the asymmetrical eye state in sleeping dolphins and the ability of dolphins to be asleep and vigilant simultaneously.

The maintenance of visual contact should be of even greater importance to cetacean mothers and their newborn calves.

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However, the behavioral aspects of sleep in dolphin neonates and their mothers have not been examined in detail. In the present study we paid particular attention to the eye state of bottlenose dolphin mothers and their calves, as this parameter has been shown to be a useful indicator of behavioral state [12].

2. Materials and methods

2.1. Subjects and experimental conditions

The behavior of three bottlenose dolphin calves and their mothers was videotaped and visually monitored from birth to 13 months of age. The behavior of 2 non-pregnant females, one pregnant female, and one adult male was also examined for comparison. The observations were conducted in accordance with the National Institute of Health *Guide for the Care and Use of Experimental Animals* and were approved by VA GLAHS Sepulveda and UCLA Animal Research Committees. The characteristics of the dolphins and the timing of the observations are presented in Table 1.

Pair 1 was housed at the Utrish Marine Station of the Russian Academy of Sciences (Novorossiysk, Russia) in a circular tank 13 m in diameter and 4.5 m deep. This pair was alone in the pool during the first 2 months postpartum and together with two adult females during most of the 3rd month after that. Pairs 2 and 3 were housed at the Gelendgick Dolphinarium (Gelendgick, Russia) in an indoor rectangular pool, 25 m × 14 m, with depth ranging from 1.5 to 3.5 m. Calves 2 and 3 were born in the dolphinarium, 15 months apart. Each pair was kept alone in the pool during the first 3 days postpartum. Afterwards, both pairs were housed together with 2–3 adult dolphins.

Over the entire observation period, the illumination was natural during the daytime at both sites. In order to observe the dolphins at night, additional illumination was turned on above the pools (<200 lx at the water surface in pair 1 and approximately 300 lx in pairs 2 and 3) during the night (20:00–08:00). Dolphins were adapted to this level of illumination because it was set by the dolphinarium at least 1 month prior to each calf's

birth to continuously monitor the dolphin female during the last portion of her pregnancy. The lights continued to be on at night during the first month postpartum for continuous observation of the neonate performed by the personnel of the dolphinarium and 2 days prior to each subsequent series of observations after that, at our request.

The pool at Utrish (pair 1) was cleaned and refilled with fresh seawater 2–3 times per week. The dolphins were fed 3–4 times/day between 08:00 and 20:00. This pair was not disturbed at any other time. Dolphins housed in the Gelendgick Dolphinarium (pairs 2 and 3) were trained and fed 3–4 times/day between 9:00 and 19:00 and were not disturbed between 20:00 and 07:00. During the daytime, all dolphins were generally active at this site because of the presence of personnel and visitors in the vicinity of the pool. Females 2 and 3 participated in 1-h shows, 1–5 times/day depending on the season, starting at the postpartum age of 2 weeks. The temperature of water in the pool varied between 20 and 24 °C in Utrish (pair 1) and between 18 and 22 °C in Gelendgick (pairs 2 and 3). However, the temperature did not change more than 2 °C within one night.

2.2. Video recording and observation of behavior

Behavior of dolphin mothers and their calves was observed (videotaped and visually monitored) both during the day and nighttime at different postpartum ages beginning from several hours after birth until calves were 13 months of age (Table 1). The behavior of female 2 (mother of calf 2) was also videotaped for 2 consecutive nights when she was pregnant (2 months prior to the calf's birth). We also monitored the behavior of 2 non-pregnant females and one adult male when they were housed in the same pool for 2 consecutive nights.

2.3. Observation of eye state

In addition to videotaping the dolphin behavior, the state of both eyes was documented in two mother–calf pairs (1 and 2) from 1 week to 3 months postpartum during slow resting circular

Table 1
Time and duration of video recording and visual observations

Dolphins	Status at the time of observations	Time resident in the facility and age	Video recording: postpartum age (for pairs) and duration	Eye state observations: postpartum age and duration
Female 1	Mother	1/10 years	1–3 days: 58 h including 3 nights (22–07 h)	3–10 weeks: for 3–5 h continuously
			14 days: 1 night (22–07 h)	between 05 and 21 h
Calf 1	Born to female 1	≤8 weeks	28 days: 2 nights (22–07 h)	3–10 weeks: for 3–5 h continuously
			57 days: 48 h including 2 nights (22–07 h)	between 05 and 21 h
Female 2	Mother	5/9 years	2–4 days: 40 h including 3 nights (22–07 h)	2–4 days: 2 nights (00–06 h)
			8–9 days: 2 nights (22–07 h)	8–9 days: 2 nights (00–06 h)
Calf 2	Born to female 2	≤5 weeks	17 days: 36 h including 2 nights (22–07 h)	28–29 days: 2 nights (00–06 h)
			28 days: 2 nights (22–07 h)	
Female 3	Mother	8/13 years	3–6 days: 24 h including 3 nights (21–06 h)	–
			20 days: 3 nights (22–07 h)	
Calf 3	Born to female 3	≤54 weeks	15 weeks: 3 nights (22–07 h)	–
			54 weeks: 2 nights (22–07)	
Female 2	Pregnant	5/9 years	36 h, including 2 nights (22–07 h)	–
Female 4	Non-pregnant	4/8 years	36 h, including 2 nights (22–07 h)	–
Female 5	Non-pregnant	4/6 years	36 h, including 2 nights (22–07 h)	–
Male	Father of calves 2,3	9/18 years	36 h, including 2 nights (22–07 h)	–

swimming. To accomplish this, two observers took positions at opposite ends of the pool. On average, in 74% of all observations, the state of eyes was noted when dolphins surfaced to breathe and in the remaining cases when the dolphins swam near the observers close to the water surface. Observation of eye state in pair 1 was conducted between 05:00 and 22:00 for 3–5 h/day. The time of observations in this pair was changed randomly from day to day, so that the entire observation period (05:00–22:00) was covered two times at the postpartum age of 3–4 weeks and two times at the age of 7–10 weeks. Recording of eye state in pair 2 was performed during most of the nighttime (00:00–06:00). The detailed timing of the observations is given in Table 1. During analysis we considered only those cases in which two eyes were observed within an interval of less than 15 s. The eye states in pair 1 were analyzed separately for the postpartum ages of 3–4 and 7–10 weeks. The eye state data for pair 2 was calculated separately for 3 postpartum ages (1, 2 and 4 weeks) based on the data collected during two consecutive nights in each case. The total eye state observation time was 53 h in pair 1 and 48 h in pair 2.

2.4. Scoring of behavior

The behavior of all dolphins was scored from videotapes in real time as active swimming, circular swimming, and floating (or resting) at the surface if an uninterrupted episode continued for at least 10 s, as described in other publications [5–7,9,16]. Active swimming was marked by variable speed, irregular trajectory, and evident features of activity, such as eating, association with conspecifics, emission of sounds, etc. Circular swimming was scored when dolphins swam at least one complete circle without evidence of active behavior as described above. Dolphins were considered floating and resting at the surface if they stopped at the surface with their dorsal fin above the water or slowly drifted without evident paddle movements. We also continuously noted respiration acts of the mothers and their calves.

2.5. Data analysis

The high level of daytime activity (approximately between 08:00 and 21:00) in dolphins housed in the Gelendgick Dolphinarium was confirmed with 24-h video recordings. Therefore, only the nighttime data collected between 22:00 and 07:00 was used for comparison. All data for the dolphin mothers and their calves were grouped by weeks of postpartum age studied (e.g., animals of 1–7 days of age were grouped into the 1-week category). Average numbers are reported as mean±standard error (SE). Analyses of several thousands of individual breaths in dolphin mothers and their calves were averaged to create the means, comprised ten 20-min intervals (5 per each of two consecutive nights in the series of observations), each started at the beginning of every hour between 01:00 and 05:00. This averaging technique was used to avoid the inflated degrees of freedom resulting from very large sample sizes. Differences in the mean breathing pauses between the calves and their mothers were evaluated by paired *T*-test. We

also calculated the percentage of apneas (breathing pauses longer than 40 s). Dolphin pairs 2 and 3 rarely exhibited breathing pauses longer than 60 s (<3% of the total number of all pauses in females 2 and 3). Therefore, the 40-s criteria were chosen because this apnea duration was found to be approximately twice as long as the average breathing pause in pairs 2 and 3 and 1.5 times longer in pair 1 during most observation periods. One and two way ANOVAs were performed to assess the difference between the state of two eyes in dolphin mothers and their calves. Because of the small number of subjects and the fact that the observations were conducted at different experimental conditions we were limited in the usage of statistical tests.

3. Results

3.1. Continuous swimming

Although captive adult dolphins spend a significant portion of time resting at the surface, this behavior was not observed in dolphin mothers during the initial postpartum period. Calves swam in continuous formation with their mothers at all times.

Table 2
Total duration of the behaviors documented in adult bottlenose dolphins (females without calves, male, females with calves) and calves at different postpartum ages as percent of the nighttime

Dolphins	Age (weeks)/ status	Active swimming	Circular swimming	Rest at the surface
Pair 1				
Mother	1	6.4±3.2	93.6±3.2	0.0
Calf		6.9±3.2	93.1±3.2	0.0
Mother	2	4.9±0.6	95.1±0.6	0.0
Calf		5.1±0.6	93.9±0.6	0.0
Mother	4	4.4±3.1	95.6±3.1	0.0
Calf		4.7±3.1	95.3±3.1	0.0
Mother	8	14.1±3.5	85.6±3.9	0.3±0.3
Calf		16.5±4.7	83.5±4.9	0.0
Pair 2				
Mother	1	22.8±2.4	76.7±2.7	0.5±0.3
Calf		31.7±0.7	68.2±0.8	0.1±0.1
Mother	2	9.4±4.5	89.7±4.3	0.9±0.1
Calf		10.4±4.4	89.5±4.3	0.1±0.1
Mother	3	14.8±5.9	82.6±6.0	2.6±0.3
Calf		27.3±3.6	72.7±3.6	0.0
Mother	4	23.5±3.6	73.9±4.3	2.6±0.4
Calf		32.6±6.0	67.4±6.1	0.0
Pair 3				
Mother	1	2.6±1.2	97.4±1.2	0.0
Calf		9.0±2.0	91.0±2.0	0.0
Mother	3	3.3±0.7	95.7±1.5	1.0±0.5
Calf		16.0±1.5	83.5±2.6	0.5±0.3
Mother	15	12.9±3.5	64.7±10.0	22.4±2.0
Calf		41.8±7.8	54.1±8.9	4.1±0.7
Mother	54	18.3±1.3	67.7±2.1	14.0±0.3
Calf		39.4±1.9	58.0±2.8	2.6±0.6
Female 2	Pregnant	27.0±2.6	0.0	73.0±2.6
Female 4	Non-pregnant	31.9±2.9	16.4±1.2	51.7±1.8
Female 5	Non-pregnant	28.8±2.2	2.2±0.6	69.0±2.8
Male	–	27.4±4.8	14.1±1.1	58.5±5.9

Each number is average of 2 consecutive nights (22.00–07.00). The values are presented as mean±standard error (SE).

Each pair often changed the trajectory and speed of swimming (especially during the first 2 weeks postpartum), and displayed an immediate orienting response to changes in the behavior of other animals and to all events in the vicinity of pool (e.g., presence of personnel). The calves also frequently changed positions next to their mothers.

Mother 1 was not observed floating at the surface throughout the entire period of observation except for a few stops at the surface at 8 weeks postpartum (Table 2). Two other mothers resumed resting at the surface (floating time was greater than 1% of the nighttime) when their calves were 3 weeks of age (mother 2) or older (mother 3). In mother 2, rest at the surface occupied less than 3% of the nighttime between 3 and 4 weeks postpartum. The duration of rest at the surface was greatest in mother 3 at 15 weeks postpartum. However, the greatest measured amount of rest at the surface in mother 3 (22.4% of the nighttime) was significantly less than that observed for females without calves and in one adult male (52–73% of the nighttime). There was a considerable difference between the time spent resting at the surface in dolphin females without calves (females 2, 4 and 5, on average 64.6±6.5% of the observation time) and in mothers 1–3 at the postpartum age of 1 week (on average 0.2±0.2%, $n = 3$), 2–4 weeks (0.9±0.5%). Calves 1 and 2 swam continuously during the entire observation period. The duration of time they briefly stopped at the surface was less than 0.1% of the nighttime. Calf 3 rested at the surface 3–4% of the observation time at the postpartum ages of 15 weeks and 13 months. The total duration of floating time in this calf was only 18% of that of its mother. Because of the small number of subjects we did not have enough power to evaluate the significance of the developmental changes of the behavioral pattern in the studied calves and their mothers.

3.2. Breathing pattern

During the first two weeks postpartum, mothers and calves surfaced to breathe and submerged synchronously, breathing within 5 s of each other on average in 90, 95 and 96% of cases (pairs 1–3, respectively). In most of the remaining cases dolphin calves surfaced alone breaking the synchrony while the mother took a longer pause and continued swimming. Over at least the first 4 weeks postpartum, the mothers exhibited a greater number of apneas (pauses longer than 40 s) compared to their calves, except at the age of 1 week in pair 1 (Fig. 1). The mean duration of breathing pauses in each calf was shorter than that in its mother at the same postpartum age, except at 1week postpartum (Fig. 1). When the calves were between 2 and 15 weeks old the difference between the average breathing pause in the mother and her calf was statistically significant with T-test for 7 out of 8 comparisons. The mean breathing pause and percentage of apneas did not change substantially in the mothers and their calves during the first 8 weeks postpartum. Mother 3 noticeably increased the duration of intervals between surfacing for breathing and the percentage of apneas at the postpartum age of 15 weeks and older compared to 1–3 weeks postpartum.

3.3. State of two eyes in dolphins mothers and calves

In pair 1 the state of both eyes was documented 870 times in the calf (on average 35 times per hour) and 600 times in the mother (44 times per hour). In pair 2 the state of two eyes was noted during 1140 times in the calf (on average 72 times per hour) and 1570 times in the mother (50 times per hour, 200–550 times/night) over the entire period. The average
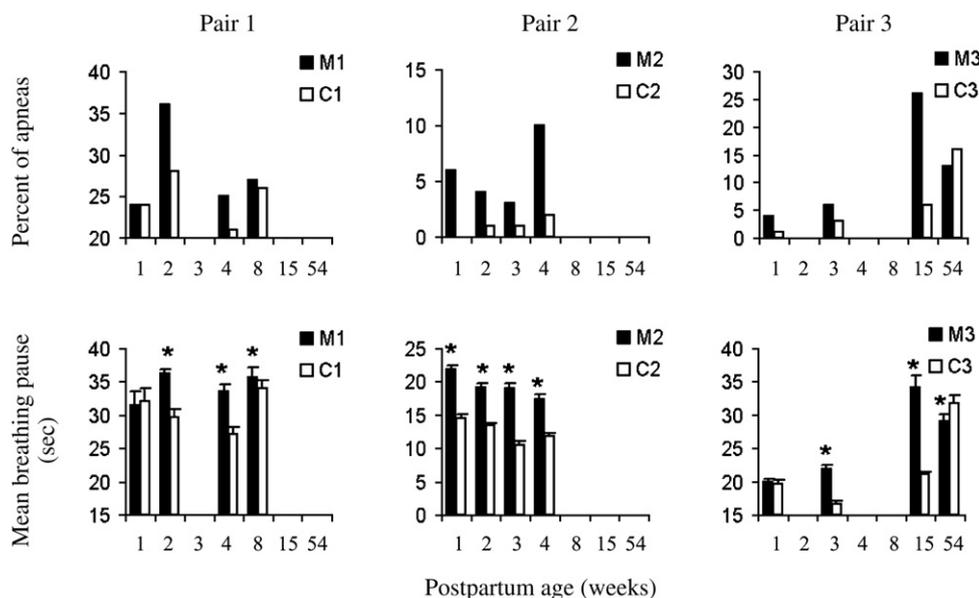

Fig. 1. Characteristics of the breathing pattern in bottlenose dolphin mothers and their calves. Top diagrams show proportion of apneas (pauses longer than 40 s) in mothers (M1–M3) and in calves (C1–C3) as percent of all breathing pauses during the observation period. The bottom diagrams are mean breathing pauses±standard error (SE). The means are the average of 10 measurements as described in Materials and methods. Asterisks indicate a significant difference ($p < 0.05$) between mothers and their calves.
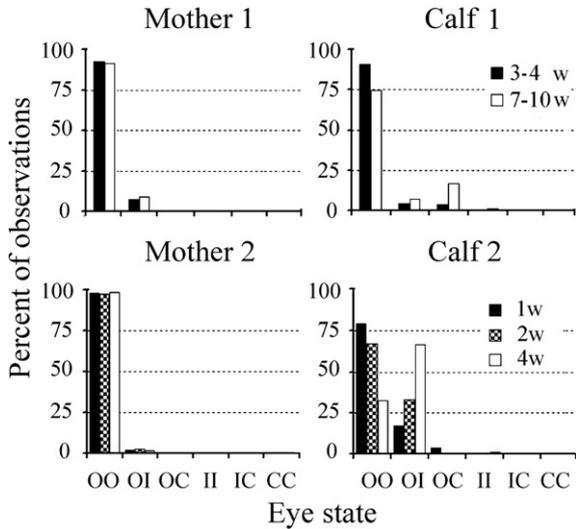
Fig. 2. State of two eyes in two bottlenose dolphin mother–calf pairs (pair 1 and 2) at different postpartum age. The first letter signifies the state of one eye (O — open, I — intermediate, C — closed) and the second letter marks the state of the other eye. W is age in weeks. For each period of observation the data is presented as percent of all cases in which both eyes were seen simultaneously (in most cases within intervals less than 10 s). There was no difference between the states of the right and left eye (see the text). Note that the amount of eye closure (complete or intermediate) increased during the first 3 months postpartum in both calves.

interval between observing both eyes was 11 s in pair 1 (56% of all intervals in the calf and 86% of all intervals in the mother were shorter than 10 s) and 7 s in pair 2 (87% and 81% of the intervals were shorter than 10 s in the calf and the mother, respectively).

During the entire period of observation, dolphin mothers were observed surfacing or swimming mostly with both eyes open (91–100% of the time during different observation

periods, Fig. 2). During the first postpartum month, female 1 was observed with both eyes open in 93% of the cases (percentage of all observations at 3–4 weeks postpartum) and female 2 on average in $97.8 \pm 0.2\%$ of the cases (3 periods of observations at 1–4 weeks postpartum). Over the entire period of observation, for both females, one eye was rarely seen in an intermediate state (on average in 8% of the time in mother 1 and 2% in mother 2), while the other eye was open. Only on a few occasions (<0.4%) was one eye noted to be closed in mother 1 while the other eye was open.

Calves also surfaced most often with both eyes open, particularly at younger ages (Fig. 2). In calf 1, which was observed mostly during the light hours, the percentage of instances of surfacing with both eyes open, at the postpartum age of 3–4 weeks, was similar to that of its mother (90% of the observation time in the calf and 93% in the mother). In the remaining cases, the calf was seen with only one eye in a closed or intermediate position while the other eye was open (4 and 5% of the observations, respectively). During several surfacings (approximately 1% of all cases) one eye was closed while the other eye was in an intermediate position. When the calf was 7–10 weeks old, the percentage of surfacings with both eyes open decreased by approximately 15%. At this time, the calf surfaced with one eye closed four times more often than when it was younger (4% at the age of 3–4 weeks and 17% at the age of 7–10 weeks). At the same time, the percentage of surfacings with both eyes open in the mother did not change compared to the period when the calf was 3–4 weeks old.

In calf 2, which was observed during the nighttime, the percentage of surfacing with both eyes open varied between 32 and 79% of the observation cases (on average $59 \pm 14\%$ for 3 age periods) with the greatest value recorded at the calf's youngest age (Fig. 2). During other time calf 2 was seen
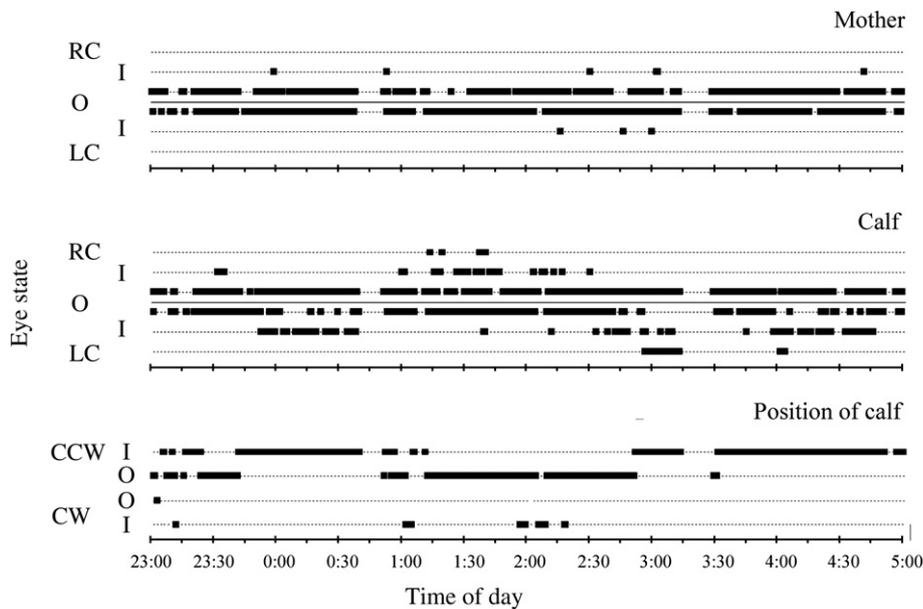

Fig. 3. Simultaneous recording of eye state in a bottlenose dolphin mother and her calf (pair 2) during slow circular swimming. The state of each eye (R — right, L — left) is marked as open (O), closed (C) or intermediate (I). The position of the calf relative to its mother is shown as inner (I) or outer (O). The direction of swimming in the dolphin pair is marked as counterclockwise (CCW) or clockwise (CW). Interruptions in the record of eye state and calf position (at 0:45 and 3:15) represented gross periods of activity during which time dolphin eyes could not be continuously monitored. However, when visible, both eyes were open at these times.

with one eye open while the other eye was in an interme-diate state (on average $39 \pm 14\%$, $n=3$), or occasionally closed ($1.4 \pm 1.1\%$). Rarely (<2% of the observations on different nights) was calf 2 seen with both eyes in an intermediate position or with one eye in an intermediate state and the other eye closed. At all time points this calf was observed with two eyes open less frequently than its mother.

We found no difference between the percentage of cases when the right and left eyes were seen open in both mothers (one way ANOVA, mother 1: $F_{1,2}=1.81$, $p=.31$, mother 2: $F_{1,2}=3.45$, $p=.14$) and their calves (calf 1: $F_{1,2}=5.75$, $p=.14$, calf 2: $F_{1,2}=7.71$, $p=.54$) during different periods of observa-tions. This indicates an absence of asymmetry in the state of two eyes in the calves and their mothers at the time of surfacing. Over the entire observation period, bilateral eye closure was not observed in mothers or their calves when they were engaged in slow circular swimming.

3.4. State of eyes and position of the dolphin mother and calf

Both mother–calf pairs swam predominantly in a counter-clockwise direction (>97% of the observation time). During periods of slow circular swimming calves took position next to their mothers, swimming along either the inner or outer circle in bouts and tended to resume position on the same side, even when they surfaced to breathe alone. The asymmetry in eye state in the calf occurred in bouts. The eye state of calves changed depending on their position next to their mothers, in such a way, that the eye directed to the mother was open more often than the eye directed to the opposite side (Fig. 3). As shown in Table 3, in both calves the eye directed to the mother was predominantly open (91–97% of the observations in calf 1 and 99–100% in calf 2). The opposite eye (directed to the center of the pool or the pool wall) was observed open in a smaller proportion of cases (68%–93% in calf 1 and 35–90% in calf 2). In the remaining cases, the eye not directed to the mother was in

an intermediate (on average $12 \pm 4\%$ in calf 1, $n=4$, 2 eyes and 2 observation periods; $38 \pm 9\%$ in calf 2, 2 eyes and 3 observation periods) or closed state (on average $5 \pm 1\%$ and $1 \pm 1\%$, respectively in calf 1 and 2). When analyzed for the entire periods of observation, the difference in the state of two eyes in the calves reached significance for the factor "direction" (toward the mother or opposite side; two way ANOVA, $F_{1,4}=7.72$, $p=.05$) but no difference was found between the state of the right and left eyes ($F_{1,4}=0.02$, $p=.89$). The eyes in the dolphin mothers were open most of the time (Figs. 2 and 3, Table 3). There was no difference between the states of the right and the left eye in both mothers regardless of whether the eye was directed to her calf or to the opposite side (factor "direction": $F_{1,4}=0.74$, $p=.43$; factor "eye": $F_{1,4}=1.07$, $p=.35$).

4. Discussion

Continuous swimming is a remarkable feature of the dolphin neonate and their mother behavior as shown in this study. High level of activity of bottlenose dolphin calves and almost complete absence of rest at the surface for several postpartum months were mentioned in several publications (e.g., [8,9,17–19]) but have not been documented in detail prior to this study. We [2,3] and others [20] noted that similar changes occur in killer whales. All these data have important implications for our understanding of the functions of sleep in cetaceans and of sleep in general.

Sleep as defined by EEG slow waves can occur in ceta-ceans during floating at the surface, slow stereotypic swimming, and also while lying on the bottom [10,21]. Near continuous swimming appears to be characteristic of all small adult ceta-ceans and their calves (e.g., the Commerson's dolphin, *Ce-phalorhynchus commersonii* [22]; harbor porpoise, *Phocoena phocoena* [23,24]; white-sided dolphin [14]; Amazonian river dolphin, *Inia geoffrensis* [25]). All these species weigh less than

Table 3
State of eye in dolphin mothers and their calves as function of their relative positions and the age of calves

Dolphin pair/age in weeks	Calves				Mothers			
	Eye directed to the mother		Eye directed to the opposite side		Eye directed to the calf		Eye directed to the opposite side	
	Right	Left	Right	Left	Right	Left	Right	Left
Pair 1								
3–4 weeks	95% (137)	97% (219)	88% (206)	93% (235)	98% (221)	96% (165)	94% (164)	90% (222)
7–10 weeks	91% (227)	97% (256)	68% (227)	81% (311)	97% (323)	95% (312)	96% (329)	92% (321)
Mean ($n=2$)	93 ± 2	97 ± 0	78 ± 10	87 ± 6	98 ± 1	96 ± 1	95 ± 1	91 ± 1
Pair 2								
1 week	100% (412)	99% (753)	90% (605)	60% (321)	98% (548)	99% (371)	96% (348)	100% (883)
2 weeks	100% (450)	100% (490)	79% (424)	55% (429)	100% (321)	100% (477)	95% (307)	100% (610)
4 weeks	99% (399)	99% (265)	42% (404)	35% (253)	100% (148)	100% (179)	99% (163)	95% (65)
Mean ($n=3$)	100 ± 0	99 ± 0	70 ± 15	50 ± 8	99 ± 1	100 ± 0	97 ± 1	98 ± 2
Mean for both eyes								
Pair 1 ($n=4$)	95.0 ± 1.4		82.5 ± 5.4		96.5 ± 0.6		93.0 ± 1.3	
Pair 2 ($n=6$)	99.5 ± 0.2		60.2 ± 9.5		99.5 ± 0.4		97.5 ± 1.1	

The data are presented as percentage of the cases in which the eye was seen open. The total number of observations is given in parenthesis. The average values are mean ± standard error (SE).

150 kg [26]. Almost continuous swimming is also a behavioral feature of calves of larger size cetacean species and their mothers (e.g., the bottlenose dolphin and killer whale [2,3]; 1-month old calves weigh 50–80 kg and 150–200 kg, respectively, with lengths less than 1 and 2 m [26]), indicating that sleep in all these animals must occur during swimming. In contrast, long periods of immobility while floating at the surface or lying on the bottom of pools are characteristic of all large cetaceans studied to date (e.g. beluga, *Delphinapterus leucas* [27], killer whale [2,3], gray whale, *Eschrichtius robustus* [28]; adult belugas weigh 500–1400 kg, killer whales weigh 2600–9000 kg, and gray whales reach 35,000 kg [26]). Rest at the surface has also been reported to be among the most typical sleep behavior in middle size cetaceans such as adult bottlenose dolphins in captivity [4,5,7,9,16]. As we showed in this study it may occupy between 50 and 70% of the nighttime in adult dolphins. The available data suggests that the length and weight of the animal, rather than the developmental status of dolphins and whales, determine whether continuous swimming occurs or not. Therefore, according to behavioral criteria, large dolphins and whales more closely resemble terrestrial mammals, indicating that motion is not a necessary feature of sleep for all cetacean species.

One obvious danger for infant dolphins born in captivity is collision with the walls of the pool. This happened to one of the calves in this study, several hours after its birth, when the mother made a sharp turn too close to the corner of the pool. However, we did not see any evidence that dolphin (this study) or killer whale [3] mothers tried to prevent their calves from swimming outside of the circle followed by the mother, where the calves could potentially hit the wall. As we mentioned in the Results section, all 3 dolphin mothers swam predominantly in a counterclockwise direction. At the same time the calves swam an approximately similar amount of time both along the inner and outer circles (Fig. 3). It is also important to emphasize that both dolphin and killer whale mothers resumed resting at the surface when their calves still remained in motion almost 24/h/day, swimming near their mothers or joining other dolphins swimming at that time. There is no question that calves followed their mother but the data available suggest that dolphin calves also have an "internal drive" for continuous swimming during the initial period of their lives.

Although several studies have reported continuous swimming in captive cetaceans, we are aware of only one study by Mann and Smuts [29], which attempted to quantify rest behavior in dolphin infants in the wild. This was done in Shark Bay, Australia. In this study, rest behavior was defined as "slow travel, <2 mph, frequent floating at the surface, frequent direction changes" which is a more general definition than the criteria we used in this study. It has been reported that neonatal bottlenose dolphins did not stop moving for more than a few seconds during the first postpartum week, however older calves floated on the surface for up to several minutes. These data are in full agreement with ours, indicating that continuous swimming is characteristic of infant dolphins born both in captivity and in the wild. On the other hand, when the data collected in Shark Bay were averaged for the whole period of observation (postpartum age of 1–10 weeks) the rest time in the calves occupied on average 21 and 50% of the time in two areas of observations (non-provisioning and provisioning). These data indicate that calves in the wild may spend a larger portion of time resting at the surface for reasons unknown to us. On the other hand, the estimate of the total duration of rest behavior in wild calves cannot be directly compared with our data on captive animals because a great deal of slow swimming was included in the rest behavior category in the study by Mann and Smuts [29].

The essential point we emphasize here is that the bottlenose dolphin and killer whale mothers and their calves become "obligate swimmers" for the initial postpartum period displaying only one of the cetacean sleep behaviors. Therefore, if EEG defined sleep occurs during the initial period of the calf's life, it must occur during swimming. Continuous swimming may be required for thermoregulation [12,30] because cetacean neonates have larger surface area to volume ratios than adults and their blubber is not specialized to provide enhanced thermal insulation [31]. Both factors result in greater amounts of heat loss to the environment compared to that in adults. Neonates also appear not to be able to control buoyancy well and are therefore unable to easily float at the surface as adults do [3,29]. Although we do not know exactly what physiological mechanisms trigger continuous swimming in cetacean mothers and their calves, the ability to remain active and responsive after birth has several advantages for newborn cetaceans. Increased motor activity likely reduces the risk of predation in the wild, and helps the calves to maintain body temperature until their body mass has increased and their insulating blubber has developed. Accordingly, it is reasonable to suggest that large cetaceans do not need to move as much as calves and smaller dolphins do because of enhanced insulation and buoyancy.

The second major finding of the present study is that dolphin mothers and their calves continuously monitored their position relative to each other by sight. This occurred both during active waking and slow resting swimming. Asymmetrical eye closure has been recently observed in slowly swimming bottlenose dolphin neonates and their mothers in a different study [18]. Similar observations were conducted earlier in adult dolphins of two cetacean species — the pacific white-sided dolphin [14] and bottlenose dolphin [8,9,15]. Asymmetrical eye closure was also documented in solitary held adult bottlenose dolphins [12], belugas [11,27] and in a 1-year old gray whale [28] while they were resting at the surface or lying on the bottom of pools. Electrophysiological studies have indicated that the studied beluga and dolphins had unihemispheric EEG slow waves during a significant portion of this time [12,21]. Therefore, maintenance of visual contact with conspecifics or monitoring of the environment is another distinctive feature of cetacean sleep behavior.

Asymmetrical eye state has been shown to be indicative of sleep (unihemispheric or highly asymmetrical slow wave sleep) in adult bottlenose dolphins and belugas with a probability of 80 and 91%, respectively [12]. Electrophysiological studies in the same cetacean species also showed that opening of both eyes is highly indicative of waking (approximately 80% of the time

when both eyes were open). Therefore, we can hypothesize that episodes of swimming followed by surfacing with one eye closed and the other eye open, observed in both calves in this study, may have been accompanied by slow waves in EEG during at least some portion of this time. Swimming with asymmetrical eye states in the mothers was rarer than in their calves. These data suggest a high degree of vigilance and a low amount of sleep in two of the studied dolphin mothers during at least the first two months postpartum.

Another feature of continuous swimming in bottlenose dolphin and killer whale neonates is more frequent surfacing for breathing compared to their mothers. Similar findings have been obtained in the wild [29]. Electrophysiological studies have demonstrated that breathing acts in dolphins are fully compatible with uninterrupted unihemispheric EEG sleep [10]. However, the majority of this data was collected in solitary dolphins floating and swimming in shallow pools. The behavior of dolphins under these conditions is stereotypic and monot-onous, and the level of their vigilance is likely reduced com-pared to that in the wild and in females with calves. Our recent recordings indicate that the amplitude of slow wave EEG frequently decreased at the time of respiratory acts in one beluga, which was floating at the surface (unpublished data). Therefore, the likelihood of EEG defined awakening in sleeping cetaceans during surfacing for breathing appears to be related to the nature of the movements they must accomplish in order to surface and the social interactions between dolphins.

It is difficult to estimate total sleep time in freely swimming dolphins, on the basis of behavioral criteria. Asymmetrical eye state in dolphins engaged in resting behavior is the only known behavioral indicator of their sleep. While the opening of one eye and the closure of the opposite eye in dolphins and belugas are highly indicative of sleep, this association is less prominent when the eye state asymmetry is less expressed (one eye open and the other eye in the transitional state) [12]. As we see, dolphin neonate 2 surfaced with both eyes open in 80% of the cases at the postpartum age of 1 week (Fig. 2). It should be emphasized that these data were collected during the nighttime period when captive dolphins are less active compared to the daytime, when they are usually disturbed in captivity. In the majority of the remaining cases, one eye was open in this calf while the opposite eye was in an intermediate position, which is less indicative of sleep in dolphins. In only 5% of the cases one eye was open and the other was closed. Only full closure of one eye was shown to be indicative of sleep in dolphins, with a probability of about 80% [12]. It is also quite intriguing that the percentage of surfacing with two eyes open (indicative of waking) was maximal in both calves at the youngest age. We believe that the presence of moderate light illumination at night might have only a minor quantitative effect on the state of eyes during surfacing because the dolphin mothers and calves were adapted to the exposed level of illumination. Moreover, the calves showed behavioral sleep under these conditions based on the presence of asymmetrical eye state during slow swimming next to their mothers.

The data we report here were collected on 3 mother–calf pairs, which is a small sample size. On the other hand, sev-

eral trends we observed allow us to speculate that the total consolidated sleep time in dolphin neonates may be very small during at least the first 1–2 weeks postpartum. This would be the opposite to the developmental pattern in all previously studied terrestrial mammals, which displayed maximal amounts of rest, sleep and immobility after birth, gradually decreasing with age [1]. Experiments with deprivation of sleep in neonatal terrestrial mammals suggest that sleep serves important functions in developing animals and that a deficit of sleep early in development can produce long lasting behavioral, morphological and biochemical abnormalities [32,33]. Our data indicate that brain development appears to not require consolidated sleep in the cetacean neonate. It is hard to imag-ine that the calf was continuously asleep when it surfaced to breathe with two eyes open on average every 10–30 s. More-over, in cases where calves came to the surface alone breaking synchrony with their mother, they had to accelerate to catch up with their mother and to assume the echelon position. EEG synchrony occurring at this time would likely be brief, breaking sleep into short episodes. No known terrestrial mammal is capable of sleeping and being engaged in visually coordinated locomotion at the same time. Moreover, at least two species of dolphins have been reported to emit sounds while engaged in continuous swimming [18,34]. We neither excluded that EEG slow waves occur in calves and their mother while they were swimming at depth nor suggested this in our earlier publications that calves do not sleep at all [2,3]. However, based on our present knowledge it is very likely that the muscular activation and sensorimotor coordination seen in dolphin calves and their mothers are not possible without extensive activation of the brainstem and forebrain neurons. This is the opposite of what has so far been considered the most essential feature of sleep in terrestrial mammals [35,36]. Therefore, if slow wave EEG activity occurs in the dolphin cortex during the initial post-partum period, the accompanying motor behavior indi-cates that other brain areas must be active. This pattern is fundamentally different from the extended periods of slow wave sleep observed in terrestrial mammals.

Acknowledgments

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