

Circadian and seasonal rhythms in the behavior of spinner dolphins (*Stenella longirostris*)

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ABSTRACT

The present study investigated both circadian and seasonal fluctuations in the daytime activities of the spinner dolphin, *Stenella longirostris*, from the Fernando de Noronha Archipelago in Brazil. The number of dolphins, and aerial, and reproductive activities were documented. The observations were carried out from January 1997 to December 2001. Temporal series and rhythmic characteristics (mesor, rhythmic percentage, and acrophase) were obtained by COSINOR analysis and later compared. The dolphins entered the bay in the morning, displayed aerial and reproductive activities during daytime, and left the bay in late afternoon to the open ocean. This study indicated that the rainy season affected the three behaviors investigated decreasing the rhythms parameter and advancing the beginning of these activities. The number of individuals was higher during the dry season and the animals stayed longer inside the bay. During the dry season, there was a bimodal expression of aerial activity, expressing a longer use of the temporal niche than in the rainy season. The phases with high frequencies of aerial activity seemed associated with those showing high reproductive activity, both with peak frequencies at about 0800. The results represent an important contribution to the advancement of chronobiological studies, and to the biology of cetaceans, considering that the existence of circadian and seasonal rhythms was proven in the behavior of spinner dolphins in an area of the SW Atlantic. Moreover, it allows restricting periods of the day for the activities of tourism as a form of minimizing the impacts of the boats on the dolphins.

Key words: Delphinidae, circadian rhythm, seasonal rhythm, daily and annual circarhythm activity, spinner dolphin, *Stenella longirostris*.

Organisms live in habitats with fluctuations in environmental factors, such as rain, day length, and temperature. These oscillations depend on the season and are a great selective force in the development of adaptive strategies and skills to cope with environmental challenges (Marques *et al.* 1997, Goldman 2001). This may explain why many biological activities, such as migration and reproduction, are restricted to a period of the year (Gwinner 1984).

The spinner dolphin, *Stenella longirostris*, is found in tropical waters of the Atlantic, Pacific, and Indian Oceans and frequently occurs in large groups far from the coast or close to oceanic islands (Norris *et al.* 1994a).

According to Norris *et al.* (1994a), the spinner dolphins in Hawaii feed during the night in the open ocean and rest inside bays in calm water during the day. While within bays, they swim in large groups with alternating periods of high and low aerial activity. At sunset, these groups leave the bays and return to the feeding areas where they forage at night. A similar behavior was described for spinner dolphins from Fernando de Noronha, Brazil, where behavior of dolphins move toward the bay (Baía dos Golfinhos) in the early morning and remain inshore resting, nursing, and mating until sunset (Sazima *et al.* 2003). However, there is no precise information on daily or seasonal rhythmic oscillations of their behavior for the southwest Atlantic region.

The aim of the present study was to verify the existence of behavioral circadian rhythmicity in spinner dolphins, specifically, the number of individuals, and aerial and reproductive activities, as well as to determine the existence of seasonal modulation in these behaviors in a region of the southwest Atlantic. We first assessed how the number of individuals and the frequency of aerial and reproductive activities of spinner dolphins varied over the light phase of the day. Secondly, we examined how these behaviors varied between the dry and rainy seasons.

The determination of the existence of circadian and seasonal rhythms is important for advancing the knowledge of the biological aspects of species, especially in tropical regions. In general, daily and seasonal variations in behavior occur only in species from temperate areas, where daily and seasonal oscillations of climatic factors such as rain, photoperiod, and temperature are more marked than in tropical regions (Gwinner 1984).

MATERIAL AND METHODS

Study Area and Animals

This study investigated a free-ranging population of spinner dolphin in a bay (Baía dos Golfinhos) located in the Fernando de Noronha Archipelago (03°51'S, 32°25'W), northeast Brazil (see Carleton and Olson 1999, for map and description). This bay is about 15–25 m in depth, 500 m maximum width, 1,000 m maximum length, and around 3 km² in area. The study area was marked visually by buoys used for delimiting navigation boundaries.

This is a tropical area with a wet season (autumn–winter) from March to August, and mean rainfall of approximately 1.93 mm d^{-1} , and a dry season (spring–summer) from September to February, with mean rainfall of around 0.8 mm d^{-1} .

Study Strategy

Both circadian and seasonal fluctuations in the number of dolphins inside the bay and aerial and reproductive activities were investigated over 4 years, from January 1997 to December 2001. Two observers were positioned at a fixed point on a cliff next to the bay from which all of the study area and its surroundings could be observed. Observations were made through binoculars (7×50) twice a week (Tuesdays and Thursdays) using scans at 5-min intervals between 0500 and 1800.

The scans were always made from the right to the left side of the bay. One observer counted the number of dolphins inside the bay with an event recorder, while the other recorded the number of aerial activities (frequency of total or partial exposure of the dolphin's body outside water, except when only the head was exposed for breathing), and the number of reproductive activities (identified when an individual was positioned underneath another individual and they swam with their bodies in contact for more than 5 s). These behaviors have been validated as evidence of copulation for this species in medium- and long-term underwater studies on spinner dolphins (Sazima *et al.* 2003, Silva Jr. and Sazima 2004, Silva Jr. *et al.* 2005). Because water in the study area was very clear, dolphins could also be observed underwater.

Data Analysis

To eliminate the influence of the number of individuals on the number of aerial and reproductive activities recorded, we calculated the relation between the sum of each of these variables and the number of individuals present in the bay at each observation period. Temporal series were constructed for each variable through the sum of the values recorded in the entire scan at 1-h intervals.

Temporal series were analyzed by COSINOR analysis ($P < 0.05$) to identify and describe rhythmic characteristics and also to identify temporal parameters: mesor (M), rhythmic percentage ($\%R$), and acrophase (φ) of the investigated variables (Nelson *et al.* 1979).

The COSINOR analysis consists of adjusting a function cosine to a temporal series of n data measured, and is described through the function cosine: $f(t) = M + A \cos(\omega t + \varphi)$ as a model of biologic rhythms where $f(t)$ is the value at time t of the function defined by parameters M (mesor = value about which oscillation occurs), A (amplitude = half the difference between the highest and lowest values of the adjusted curve), ω (angular frequency = degrees/unit time, with 360° representing a complete cycle) and φ (acrophase = mean time span between a reference moment and the phase in which the highest value of a variable is likely to be found from the adjusted sinusoidal curve of the data. In this case, the cycle duration (and ω) is given, on the basis of either prior knowledge or a reasonable assumption, (as a 24-h period in the case of animals or populations adhering to regular daily activity) whereas M , A , and φ are estimated (Nelson *et al.* 1979).

The statistical significance of the adjusted curve lies in calculating the descriptive level (P value) from the variability rate (VR), and comparing it with the significance level established in the test ($P < 0.05$ in the present study). The descriptive level

(P value) is calculated considering: $P \text{ value} = (1 - VR)^{\frac{N-3}{2}}$. The rhythmic percentage ($\%R$) analyzes how much of the temporal series can be explained by a cosine curve and is calculated by: $\%R = 100 VR$ (Nelson *et al.* 1979). It is accepted that the temporal series is explained by the cosine curve, therefore, having a rhythmic character when we obtain a $\%R$ above 15% for each temporal series analyzed (Enright 1989, Mikulecky 1991).

To describe the distribution variations and adjusted curves of the number of individuals, aerial activity and reproductive activity between the dry and rainy seasons, we also performed descriptive analyses in the temporal series obtained by the COSINOR test (Nelson *et al.* 1979).

Furthermore, the non-parametric Mann–Whitney U test was used to compare one variable with two categories, and Kruskal–Wallis ANOVA to compare one variable considering three or more categories. Statistical significance was considered at $\alpha = 0.05$.

RESULTS

Number of Dolphins

The COSINOR analysis in 24-h period for the number of individuals showed significant P values (COSINOR $P < 0.001$ for every month) and the rhythmic percentage was high (above 15%) throughout all the months, thus supporting a circadian rhythm in the number of dolphins within this bay (Table 1).

The temporal parameters obtained from COSINOR analysis for the number of individuals, except the acrophase (Mann–Whitney U , $P = 0.3465$), were significantly different between the seasons (mesor: Mann–Whitney U , $P = 0.0034$; rhythmic

Table 1. Circadian rhythm of the spinner dolphin numbers inside the bay.

Month	Season	Mesor	$\%R$	Mean acrophase ^a Time of day (lower–upper limits)
January	Dry	155.15 ^a	77.31 ^a	1011 (0946–1036)
February	Dry	133.69 ^a	71.53 ^a	1010 (0941–1040)
March	Rainy	84.13 ^b	58.15 ^b	0938 (0858–1017)
April	Rainy	26.36 ^b	39.81 ^b	0754 (0656–0851)
May	Rainy	43.56 ^b	49.53 ^b	0933 (0846–1020)
June	Rainy	26.03 ^b	67.16 ^b	0932 (0900–1004)
July	Rainy	62.94 ^b	63.83 ^b	0941 (0906–1016)
August	Rainy	96.46 ^a	75.47 ^a	1015 (0949–1042)
September	Dry	101.68 ^a	79.70 ^a	1055 (1032–1119)
October	Dry	106.51 ^a	70.87 ^a	1037 (1007–1107)
November	Dry	92.19 ^a	78.98 ^a	1053 (1029–1117)
December	Dry	155.73 ^a	83.59 ^a	1039 (1018–1100)

^aData from COSINOR analysis for 24 h obtained from 1997 to 2001.

^b $\%R$ = rhythm percentage; P value COSINOR < 0.001 for every month. Values followed by different small case letters are statistically different from each other. Comparisons between seasons (Mann–Whitney U , $P < 0.05$) and between months within a season (Kruskal–Wallis, $P < 0.05$).

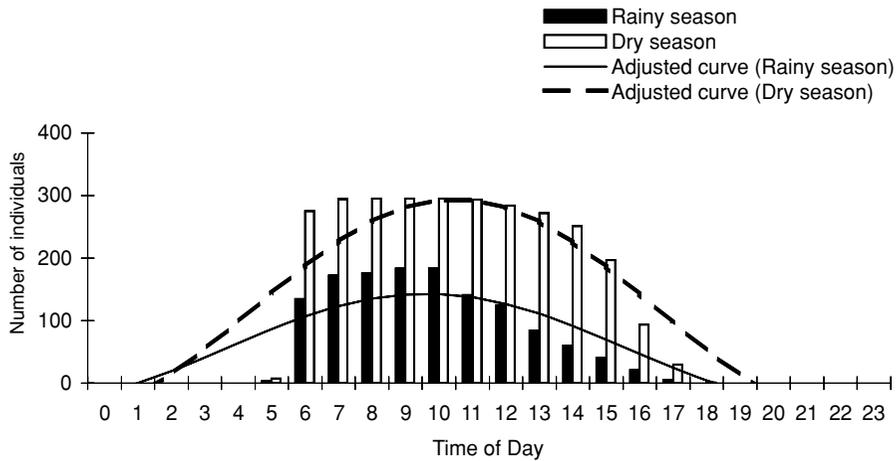


Figure 1. Distribution of number of dolphins according to season. Curves adjusted by COSINOR analysis for 24-h period ($P < 0.001$). Bars are means and the lines the adjusted curves.

percentage: Mann–Whitney U , $P = 0.0022$). On the other hand, these parameters showed no significant effect for a given month within any season (mesor: Kruskal–Wallis test, $P = 0.3003$; rhythmic percentage: Kruskal–Wallis test, $P = 0.3066$; acrophase: Kruskal–Wallis test, $P = 0.3062$) (Table 1).

Mesor, rhythmic percentage, and acrophase of the number of individuals were all reduced in the rainy season, whereas in the dry season these parameters were increased. Mesor and rhythmic percentage showed minimum values in April and maximum in December. Acrophase was minimal and maximal in April and September, respectively (Table 1).

Descriptive analyses also revealed a seasonal variation in the circadian rhythm of the number of dolphins. Accordingly, in the rainy season the number of individuals gradually increased from the appearance of the first dolphin group, maintaining this level for 2 h (from 0700 to 0900). The number of dolphins then decreased gradually until the group left the study area, which always occurred before 1800 (Fig. 1). However, in the dry season the number of individuals increased sharply in the second hour of observation (0600–0700) and this number was maintained over the next 7 h. From 1400, these values decreased gradually until the dolphins left the study area (in some cases after 1800) (Fig. 2). Moreover, the adjusted curve for the number of individuals was skewed to the right, as compared with the rainy season, thus showing a delay in the acrophase (Fig. 1).

Aerial Activity

P values were significant (COSINOR $P < 0.001$ for every month) and the rhythmic percentage was high (above 15%) for the 24-h period for all months, supporting a circadian rhythm in the aerial activities of the spinner dolphins (Table 2).

Considering the temporal parameters of the aerial activity, only the rhythmic percentage was significantly different between the rainy and dry seasons (Mann–Whitney U , $P = 0.0021$), but not within each season (Kruskal–Wallis test,

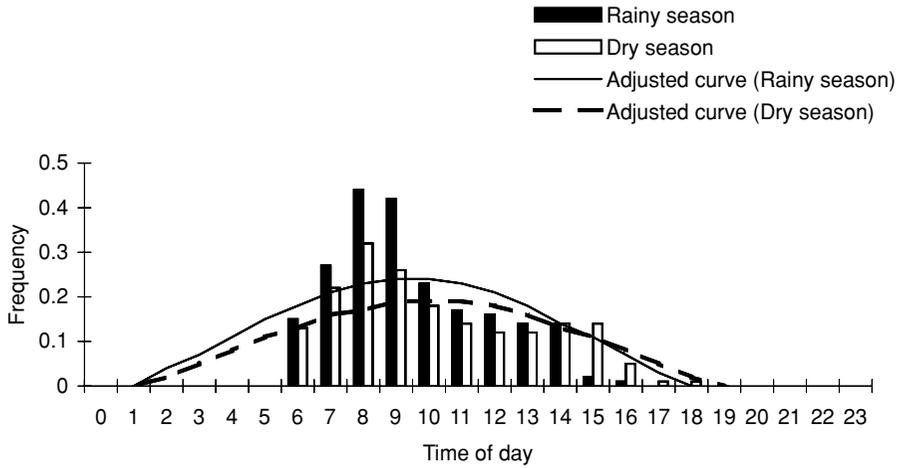


Figure 2. Hourly distribution of aerial activity for dry and rainy seasons. Bars are means and the lines the adjusted curves (COSINOR analysis for 24-h period; $P < 0.001$).

$P = 0.3062$) (Table 2). The rhythmic percentage was lower during the rainy season, with minimum values in March; higher values occurred in the dry season, with maximum values in November. Although no significant difference was found between the seasons (Mann–Whitney U , $P = 0.2001$), the acrophase was earlier in the rainy season but delayed in the dry season (Table 2).

Descriptive analyses also showed a variation in the circadian rhythm of aerial activity over the seasons. In the rainy season a peak was detected from 0800 to 0900, slowly decreasing over the next 5 h and then abruptly decreasing because the

Table 2. Circadian rhythm of aerial activity of spinner dolphin inside the bay.

Month	Season	Mesor	%R	Mean acrophase ^a Time of day (lower–upper limits)
January	Dry	0.07 ^a	55.14 ^a	1027 (0945–1109)
February	Dry	0.07 ^a	44.79 ^a	1020 (0928–1112)
March	Rainy	0.08 ^a	16.96 ^b	1056 (0912–1240)
April	Rainy	0.07 ^a	32.92 ^b	0810 (0705–0915)
May	Rainy	0.08 ^a	52.25 ^a	0936 (0852–1021)
June	Rainy	0.15 ^a	48.74 ^a	0914 (0826–1002)
July	Rainy	0.06 ^a	53.24 ^a	0933 (0849–1016)
August	Rainy	0.08 ^a	60.86 ^a	0956 (0919–1034)
September	Dry	0.06 ^a	55.18 ^a	0945 (0903–1026)
October	Dry	0.08 ^a	56.39 ^a	0949 (0908–1030)
November	Dry	0.07 ^a	62.12 ^a	0935 (0859–1011)
December	Dry	0.09 ^a	53.26 ^a	1012 (0928–1055)

^aData from COSINOR analysis for 24 h obtained from 1997 to 2001.

^b%R = rhythm percentage; P value COSINOR < 0.001 for every month. Values followed by different small case letters are statistically different from each other. Comparisons between seasons (Mann–Whitney U , $P < 0.05$) and between months within a season (Kruskal–Wallis, $P < 0.05$).

Table 3. Circadian rhythm of reproductive activity of spinner dolphin inside the bay.

Month	Season	Mesor	%R	Mean acrophase ^a
				Time of day (lower–upper limits)
January	Dry	0.13 ^a	28.46 ^a	0900 (0446–1014)
February	Dry	0.10 ^a	36.26 ^a	0947 (0846–1049)
March	Rainy	0.30 ^b	27.98 ^a	0902 (0747–1016)
April	Rainy	0.80 ^b	24.41 ^a	0829 (0707–0951)
May	Rainy	0.59 ^b	39.91 ^b	0908 (0811–1005)
June	Rainy	0.84 ^b	34.91 ^a	0908 (0805–1012)
July	Rainy	0.29 ^a	41.67 ^b	0854 (0759–0949)
August	Rainy	0.16 ^a	47.50 ^b	1007 (0918–1056)
September	Dry	0.56 ^b	60.63 ^b	1000 (0923–1038)
October	Dry	1.17 ^b	5.12 ^a	0808 (0447–1128)
November	Dry	0.42 ^a	38.92 ^b	0948 (0849–1046)
December	Dry	0.23 ^a	38.88 ^b	0923 (0824–1021)

^aData from COSINOR analysis for 24 h obtained from 1997 to 2001.

^b%R = rhythm percentage; *P* value COSINOR < 0.001 for every month. Values followed by different small case letters are statistically different from each other. Comparisons between seasons (Mann–Whitney *U*, *P* < 0.05) and between months within a season (Kruskal–Wallis, *P* < 0.05).

dolphins left the bay at around 1600. During the dry season, the aerial activity also gradually increased from the arrival of the dolphins inside the study area, reaching a peak at 0800. After that, these values decreased and remained until 1300, followed by another increase from 1400 to 1500 and then a slow decrease until the animals left the study site (which could take place even after 1800) (Fig. 2).

Reproductive Activity

The COSINOR analysis for the 24-h period showed significant *P* values (COSINOR *P* < 0.001 for every month) and high rhythmic percentages (above 15%) in all of the months, except October (5.12), thus supporting a circadian rhythm in the reproductive activity of the spinner dolphins (Table 3).

The temporal parameters for the reproductive activity was significantly different between the seasons (mesor: Mann–Whitney *U*, *P* = 0.0080; rhythmic percentage: Mann–Whitney *U*, *P* = 0.0087), except when considered in terms of acrophase (Mann–Whitney *U*, *P* = 0.5218). However, neither of the parameters was significantly different within each season (mesor: Kruskal–Wallis test, *P* = 0.3060; rhythmic percentage: Kruskal–Wallis test, *P* = 0.3063; acrophase: Kruskal–Wallis test, *P* = 0.3062) (Table 3).

Unlike the other two variables analyzed, mesor was high during April and June (rainy season) and in October, showing a tendency to decrease in the other months. In these other months, except in October, the rhythmic percentage of copulation was high. The minimum value occurred in April and the maximum in September. The beginning of the acrophase was advanced in the rainy season and delayed in the dry season (Table 3).

According to the descriptive analyses, the daily fluctuation of the reproductive activity exhibited a seasonal variation. In both seasons, reproductive activity was

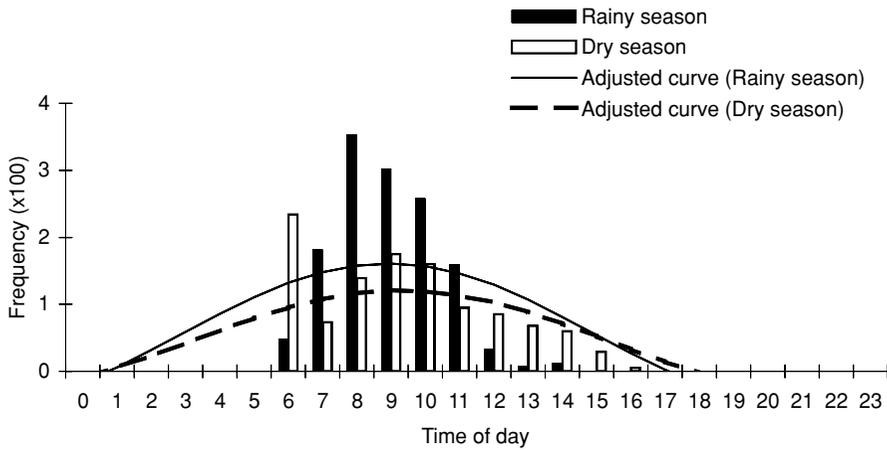


Figure 3. Hourly distribution of reproductive activity for dry and rainy seasons. Bars are means and the lines the adjusted curves (COSINOR analysis for 24-h period; $P < 0.001$). Values $\times 100$.

recorded 1 h after animals entered the bay. The reproductive activity increased in the rainy season after the dolphins entered the bay until the peak at 0900. Subsequently, these events decreased gradually until their end at about 1500 (Fig. 3).

On the other hand, in the dry season the peak of the reproductive activity occurred just after the animals entered the bay (0700). In the next hour, however, this activity diminished and then rose gradually reaching another peak at 1000; this behavior then decreased gradually until the last recorded event at 1700 (Fig. 3).

DISCUSSION

Clear circadian and seasonal rhythms were detected for the number of individuals, and aerial and reproductive activities, confirming both tested hypotheses, thus supporting cyclical behaviors in the spinner dolphins. Furthermore, this study indicated that the rainy season affected the three behaviors investigated usually decreasing the rhythms parameter (mesor, rhythmic percentage, and acrophase), and thus advancing the beginning of these activities (see Table 1–3).

Previous studies on a few other delphinids described daily time shifts and daily routine activities, mainly in terms of resting, feeding, and social behavior (see overview by Klinowska 1986). Bräger (1993) and Bearzi *et al.* (1999), as we found for spinners in the present study, found daily and seasonal fluctuations in the behavior of the bottlenose dolphin *Tursiops truncatus*. Würsig *et al.* (1994) described seasonal fluctuations in the behavior of the spinner dolphins in Kealahou Bay, Hawaii: time of movements into and out of the bay, time spent underwater, and aerial activity. Moreover, it has been reported that serum testosterone levels in male spinner dolphins begin to increase in March and peak in June and July, with a concurrent increase in sexual behavior (Wells 1984), supporting seasonal variation in reproduction based on endogenous factors.

In the present study, descriptive analysis of the temporal series and the respective adjusted curves showed that the number of individuals was higher and the adjusted

curve was skewed to the right during the dry season. This indicates a delay in the acrophase and a higher occupation of the temporal niche during this season (see Fig. 1).

During the dry season, there is a remarkable bimodal expression of aerial activity, expressing a longer use of the temporal niche than in the rainy season. Even considering the decreased number of individuals during the rainy season, aerial activity was maintained at higher levels. Moreover, the peak of the aerial activity during both seasons (dry and rainy) occurred 2 h after the entrance of the dolphins into the bay, followed by a decrease in this activity. During the dry season, however, a slight secondary peak occurred before the dolphins left the bay (between 1400 and 1500) (see Fig. 2).

The phases with high frequencies of aerial activity seem associated with those showing high reproductive activity, both with peak frequencies at about 0800 (Fig. 2, 3). The aerial activities of spinner dolphins are similar to acoustic signals used for communication among individuals in different behavioral contexts, including mainly reproductive activities (Norris *et al.* 1994b). The phases with lower frequencies of aerial activity found for spinners in the present study may be related to resting on the part of the dolphins, as described in our previous studies on underwater behavior in the area (Silva Jr. *et al.* 2005).

Our previous observations in the area during the dry season indicated an elevation in the transparency and surface temperature of the water, and of the photoperiod (length of the day). These factors may contribute jointly to the increased number of individuals and elevated frequency of aerial and reproductive activities in the dolphins. It is known that spinner dolphins occur mainly in areas of high water transparency (Perrin 2002). Moreover, earlier studies showed that the daily routine of spinner dolphins, both in other regions (Norris *et al.* 1994a) and in Fernando de Noronha (Sazima *et al.* 2003; Silva Jr. *et al.* 2004, 2005), involves nocturnal feeding and daytime reproduction and rest. During the dry season the increased length of the light phase may favor the longer period spent by the dolphins in the area, allowing them to make better use of the temporal niche for reproductive activities and other behaviors.

In general biological rhythms are associated with both geophysical cycles and endogenous control mechanisms. This association enables animals to improve physical and behavioral performance in response to environmental fluctuations and brings important adaptive gains. Moreover, the different rhythms of the behaviors may represent the maximum adjustment efficiency in response to environmental fluctuations (Aschoff 1984, Malpaux *et al.* 2001).

The results obtained in the present study represent an important contribution to the advance of chronobiological studies, and to the biology of cetaceans, considering that the existence of circadian and seasonal rhythms was proven in the behavior of spinner dolphins in an area of the SW Atlantic. In general, studies about biological rhythms indicate seasonal behavioral oscillations only in temperate regions.

Furthermore, this study may also contribute to the conservation of spinner dolphins and of other cetacean species. Spinner dolphins are the main tourist attraction in the Fernando de Noronha Archipelago. There are daily boat excursions, involving hundreds of tourists, to observe the dolphins. The norms currently in practice restrict the number of boats, as well as their velocity and proximity to the dolphins. In the present study we observed that the dolphins perform their aerial and reproductive activities more frequently between 0700 and 1100. Considering that these activities

are important for the animals' survival, the results found here suggest that restricting the hours (0700–1100) would minimize the impact of boat tours in the region.

Future studies will focus on confirming if the environmental factors photoperiod, rainfall, salinity, water temperature, and transparency influence the daily and seasonal behavioral variations of the dolphins.

ACKNOWLEDGMENTS

We thank Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis (IBAMA) and Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for allowing data collection in the Fernando de Noronha Archipelago, as well as PETROBRAS, VIVO, and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for financial support. We thank Maria Emilia Yamamoto and John Fontenele Araujo for earlier discussions on this paper.

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Received: 15 June 2007

Accepted: 19 July 2008