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Seasonal behavioral changes of a captive whale shark (*Rhincodon typus*) under variable temperature and light conditions

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Abstract—Long-term quantitative observations are essential for the conservation of the whale shark (*Rhincodon typus*), which requires a long time to grow and mature. In this study, a data logger was attached to a mature male whale shark that had been maintained in captivity for over 29 years at the Okinawa Churaumi Aquarium in Japan. Because long-term rearing of whale sharks in captivity is desirable, the effects of water temperature and light on the swimming behavior of the captive whale shark were investigated. Tail-beat frequencies (TBFs), activity levels, and frequencies of clasper crosses, which are thought to be a mating-like behavior, were calculated from the swimming data. In all seasons, TBF, swimming speed, and activity level of the shark were 4%–20% less during the nighttime than during the daytime, particularly at cool water temperatures (≤23.6°C). Furthermore, approximately 90% of the clasper crosses occurred during the daytime. These results indicate that the shark is active during the daytime, engaging in activities such as mating behavior. In contrast, during the nighttime, it rests while swimming, slowing down the beat of its caudal fin and lowering swimming speed to conserve energy. Therefore, we conclude that this individual has adopted this diurnal rhythm to adapt to its current rearing environment.

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The whale shark (*Rhincodon typus*) is a species within the order Orectolobiformes. Species of this order are predominantly benthic in nature; however, the whale shark is the only pelagic species within this order and, therefore, the only one that makes movements at the scale of an ocean basin. This species has become popular as an attraction for ecotourism activities, such as leisure diving (e.g., Gallagher and Hammerschlag, 2011; Legaspi et al., 2020; Reynolds et al., 2024). It is listed as endangered on the IUCN Red List of Threatened Species (Pierce and Norman, 2016); therefore, this species requires active protection and conservation. Long-term and wide-ranging tracking and other research are essential for improving understanding of the behavioral traits and ecology of the whale shark. Such knowledge can aid the conservation of this species, which migrates across long distances in the ocean, grows slowly, and takes a long time to reach maturity.

In cases where long-term and detailed observations in the field are difficult to collect, behavioral observations in captivity can help advance understanding of the swimming performance and reproductive ecology of a species, while also serving as a useful reference for interpreting the experimental observations of behavior gathered in field studies. The whale shark is difficult to keep in captivity; however, multiple individuals have been reared at the Okinawa Churaumi Aquarium (OCA). In particular, a male whale shark has been kept in the aquarium for more than 29 years, setting the world record for the longest period of captivity for this species. This individual is also the first in the world for which the sexual maturation process of a male whale shark was successfully observed (Matsumoto et al., 2019).

This species mainly occurs in waters with sea-surface temperatures ranging between 23°C and 30°C across the world's oceans (Hearn et al., 2021). Researchers have speculated that whale sharks may avoid prolonged exposure to excessively cool and warm water temperatures through vertical or extensive horizontal migration. This species is ectothermic and has the stability of its body temperature being derived from a large body that allows it to tolerate ambient water temperatures below 20°C for short periods of time (Nakamura et al., 2020); however, its long-term temperature tolerance has not been examined. Although water temperature is thought to significantly influence the behavior of this species, the range of suitable water temperatures for the whale shark still needs to be determined. Understanding how water temperature affects the swimming behavior of this ectothermic species is particularly important in the finite space of captivity, where deep diving and large-scale horizontal movements are not possible, and estimation of the range of suitable water temperatures is necessary to optimize the conditions of their captive environment.

Gleiss et al. (2013) found that this species increases its activity around sunrise and sunset in the wild, and its crepuscular pattern of locomotor activity is becoming better understood in Australia. However, the observed diel behavioral patterns of this species vary by region and location (Rohner et al., 2020), with some populations spending more time in shallow areas during the day and staying in deeper areas at night (Robinson et al., 2017; Araujo et al., 2018) and vice versa (Ramírez-Macías et al., 2017). However, the diel patterns of the whale shark's swimming behavior in captivity have only recently been explored (Gallimore et al., 2024).

One particularly unexplored aspect of the ecology of this species is its reproduction. Whale sharks are ovoviviparous, but only one case of a gravid female has been found in Taiwan (Joung et al., 1996), and other aspects, such as mating behavior, remain unclear. Since April 2012, the male whale shark at the OCA has been observed to perform one of its courtship behaviors, namely a large body rotation along with the crossing of both claspers (called a *clasper cross*), and because sperm release was also observed, it was reported that the individual reached sexual maturity in the same year (Sato et al., 2016; Matsumoto et al., 2019). During mating, male elasmobranchs usually maintain their position by biting the pectoral fins and trunk of the female and inserting their crossed claspers into the cloaca of females (Pratt and Carrier, 2001). This behavior is considered one of the reproductive behaviors of this species. Although such behavior, including the clasper cross, has been recorded by surveillance cameras, quantitative analysis of visual observations is needed for further evaluation.

To solve these problems, we used biologging to study the swimming behavior of whale sharks in captivity. The tools have been expanded to study various shark behaviors and to analyze activity patterns and energy use (Andrzejaczek et al., 2019).

Overall dynamic body acceleration (ODBA), a metric that Wilson et al. (2006) proposed as a substitute for rate of energy expenditure, has been found to be a useful measure of animal activity (Halsey et al., 2011), and results of experiments with 3 shark species indicate that ODBA was significantly correlated with energy consumption (Lear et al., 2017). More recently, measures of such activity levels have been quantified to indicate animal welfare in ecotourism and aquariums (Lauderdale et al., 2021; Barry et al., 2023).

We used relative entropy (RE) to detect specific behaviors like the clasper cross. When applied to animal behavior, higher RE values indicate that the target behavior is more specific than normal behavior (Kadota et al., 2011).

The objectives of this study were 1) to quantitatively evaluate the swimming characteristics of this species in captivity, 2) to obtain understanding of the effects of illumination and water temperature on the long-term swimming behavior of an individual, and 3) to contribute to the interpretation of the behaviors of this species. More specifically, the aims of this project were to examine the swimming behavior of an individual that has adapted to a captive environment (that has successfully been kept for the longest period of time in the world) and to evaluate the current rearing environment of the OCA. The results of this study will contribute to the development of captive conservation techniques by clarifying the rearing environment conditions that are appropriate for the whale shark, knowledge that is essential for the long-term rearing of this species.

Materials and methods

Experiment site, duration, specimens, and captivity conditions

An adult male whale shark, which had been kept in the tank at the OCA since 1995 and had a total length of 8.8 m and a body weight of approximately 6000 kg, was used in this study. The length was measured in 2020, and the weight was estimated on the basis of the regression equation of total length and weight used by Matsumoto et al. (2017). Data were collected in the Kuroshio Tank (width: 35 m; length: 27 m; depth: 10 m; and capacity: 7500 metric tons) at the OCA over 4 periods: 16–19 September 2020, 13–17 December 2020, 11–22 March 2021, and 6–9 June 2021.

During these periods, the Kuroshio Tank contained natural sea water pumped directly from the open sea; therefore, the temperature of the tank water was completely dependent on that of open sea water. The sea water in the tank was constantly circulated and replaced within approximately 2 h. Lighting was installed in the tanks and was turned on and off at predetermined times (0800 and 1850, respectively). Although sunlight shone through the top of the tank, light intensity measurements inside the tank, taken by using an illuminance logger, revealed an illuminance range of approximately 30–5000 lx during the daytime (when the lights were on) and 1–30 lx during the nighttime (when the lights were off). In addition to the individual that was the focus of our experiment, the tank also contained an immature female whale shark, Alfred manta (*Mobula alfredi*), and Pacific bluefin tuna (*Thunnus orientalis*). Approximately 60 other species were maintained in the Kuroshio Tank during the experiment (Okinawa Churaumi Aquarium[1]). Whale sharks were fed 4 times a day at fixed times, at approximately 0945, 1145, 1500, and 1700. The average ambient temperature of the water in the

[1] Okinawa Churaumi Aquarium. 2021. Churaumi Fish Encyclopedia. Search by area: The Kuroshio Sea. [Available from website, accessed March 2021.]

tank was measured with a data logger during each of the 4 observation periods of this study. These temperatures are listed in Table 1 along with the date and duration of each period of the experiment.

This study was conducted as part of the monitoring of the health of captive animals at the OCA. A separate or specific approval from any association was not required for this work. Maintenance, animal handling, and all procedures associated with this study were conducted in accordance with the ethical guidelines of the Okinawa Churashima Foundation.

Tagging and deployment

A data logger (ORI400-3MPD3GT[2], Little Leonardo Co., Tokyo, Japan; diameter: 16.5 mm; length: 83.5 mm; and weight in air: 42.4 g) was used to obtain information on the swimming behavior of the male whale shark. This data logger, which was attached to the shark, was used to measure the swimming speed (in meters per second), swimming depth (in meters), ambient water temperature (in degrees Celsius), triaxial acceleration (in g, with 1 g equal to 9.8 m/s^2), and triaxial magnetism (in micro Tesla). Swimming speeds, swimming depths, and ambient water temperatures were measured at 1-Hz intervals, and triaxial accelerations and triaxial magnetism were measured at 20-Hz intervals. The duration for recording these data was approximately 95 h when measurements were taken under these settings. The logger was fixed to a base fabricated by using a 3D printer, 2 suction cups were attached to the base, and instant glue applied to these suction cups was used to attach the logger to the shark (Fig. 1). The side of the logger with the propeller in it was attached to the anterior base of the first dorsal fin of the whale shark so that the position of the logger was as parallel to the body of the shark as possible (Fig. 1). By repeatedly attaching loggers to the same location on the shark during all experimental periods, it was possible to compare activity levels. Although no particular changes were observed in the swimming behavior of this individual as a result of the attachment and removal of loggers, the periods of approximately 20 min before and after the attachment and removal of loggers were excluded from analysis to avoid such effects. During analysis, some data were deemed to be unreliable because of missing or misaligned loggers, and these data were excluded.

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Data analysis

The data were analyzed by using Igor Pro analysis software (vers. 6.12; WaveMetrics, Portland, OR) and the add-on program Ethographer (Sakamoto et al., 2009). The raw acceleration data included data on static acceleration, which has 2 components that needed to be separated prior

Table 1

Dates, duration, and average water temperatures in the Kuroshio Tank, at the Okinawa Churaumi Aquarium in Japan, for an experiment during which the behavior of a male whale shark (*Rhincodon typus*) was observed in 2020 and 2021. Mean temperatures experienced by the whale shark in the tank are provided with standard deviations in parentheses.

Dates	Duration (h)	Temperature (°C)
16–19 September 2020	73	28.5 (0.1)
13–20 December 2020	143	23.6 (0.3)
11–22 March 2021	221	22.1 (0.3)
6–9 June 2021	57	26.8 (0.0)

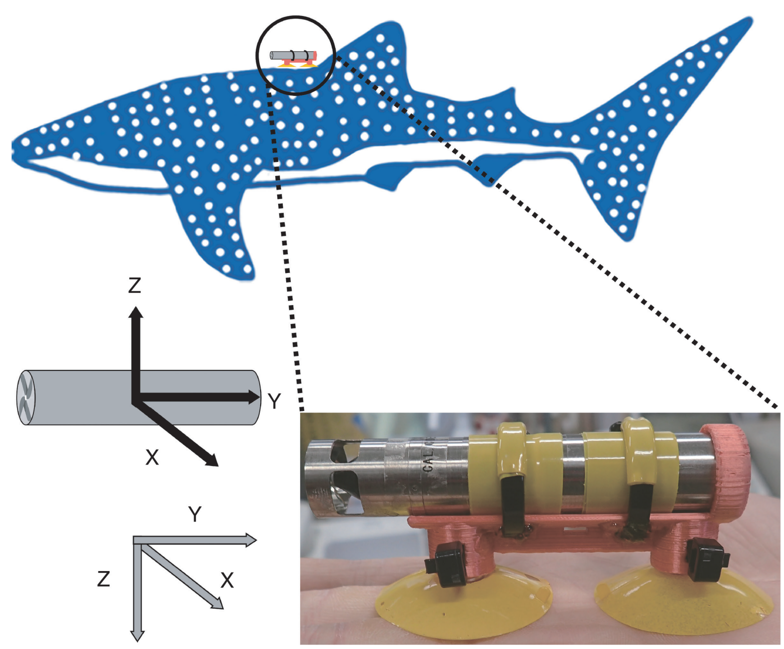

Figure 1

Diagram and photograph of the data logger attached to a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium in Japan during 4 experimental periods: 16–19 September 2020, 13–17 December 2020, 11–22 March 2021, and 6–9 June 2021. The diagram shows the mounting position of the data logger and direction of the device and logger axes. The black axis represents the direction of the acceleration, and the gray axis represents the geomagnetic direction. The *X*, *Y*, and *Z* labels represent the lateral (sway), longitudinal (surge), and dorsoventral (heave) axes, respectively.

to behavioral analysis: gravitational acceleration, caused by changes in the animal's posture, and dynamic acceleration, caused by the animal's movement (Sakamoto et al., 2009). To visualize the periodic components of the acceleration time series, a continuous wavelet transformation (CWT) was performed on all raw acceleration data. Results from the CWT indicate that most periodic components have peaks in periods less than 10 s in all acceleration data, the components with a period shorter than 10 s were classified as acceleration derived from the whale shark's motion (i.e., dynamic acceleration), and the components with a period longer than 10 s were classified as acceleration derived from its posture or body angle (i.e., static acceleration).

Next, by using the CWT Filter function in Ethographer, the dynamic and static accelerations were separated, and a CWT was applied to the x-axial (lateral) dynamic acceleration data separated from the raw acceleration data. The peak tracer function was then used to extract the dominant oscillation period component, which was considered the tail-beat period, and its reciprocal was calculated as the tail-beat frequency (TBF). We employed the k-means algorithm to cluster the tail-beat spectra at each second, to understand the characteristics of the tail beat. K-means clustering is an unsupervised, interactive algorithm that minimizes the within-cluster sum of squared Euclidean distances from the cluster centroids. For a detailed description of this algorithm, see Sakamoto et al. (2009).

The ODBA, an indicator of activity, was calculated by using the following equation:

$$ODBA = |D\alpha_x| + |D\alpha_y| + |D\alpha_z|, \tag{1}$$

where $D\alpha_x$ = the dynamic acceleration component in the lateral direction;
$D\alpha_y$ = the dynamic acceleration component in the longitudinal direction; and
$D\alpha_z$ = the dynamic acceleration component in the dorsoventral direction.

Statistical analysis was conducted by using 2-way analysis of variance and Mann–Whitney U tests, and the Bonferroni correction was used to compare the significance among swimming variables (swimming speed, TBF, and ODBA) in each month and during daytime and nighttime.

Furthermore, RE was calculated by using the calculated z-axis (heave) static acceleration (rotational posture) as an indicator for detection of a clasper cross, which is a mating-like behavior not observed during normal swimming. The sampling interval of the static acceleration of the z-axis was 20 Hz, but only the starting value of each second was taken from the calculated values, so that the analysis was performed on 1-Hz samples of data in the time series. In this study, the amount of change in rotational posture ($C\alpha_z$) was calculated by using the following equation:

$$C\alpha_z(t) = S\alpha_z(t) - S\alpha_z(t - \Delta t), \tag{2}$$

where $S\alpha_z$ = the static acceleration of the z-axis (i.e., the rotational posture); and
Δt = the measurement interval (in seconds; i.e., 1 s in this study).

The data in the time series were divided into bins with intervals of 20 s (number of bins=20). At each time t_k, the probability distribution followed by $C\alpha_z$ was assumed to be a normal distribution, and the statistical parameters μ and σ of each bin were estimated by using maximum likelihood estimation. The parameter μ represents the mean, and σ represents the standard deviation. The distribution $Q(C\alpha_z)$ for the entire measurement period was defined as the distribution form representing the average swimming state. Furthermore, the probability density functions were obtained for the continuous probability distributions $P(C\alpha_z, t_k)$ and $Q(C\alpha_z)$, and the RE was calculated for the time series by using the following equation:

$$\begin{aligned} RE(t_k) &= \int_{-\infty}^{\infty} P(C\alpha_z,\ t_k)\log\left(\frac{P(C\alpha_z,\ t_k)}{Q(C\alpha_z)}\right) S\alpha_z \\ &= \frac{1}{2}\left[\log\left(\frac{\sigma_q}{\sigma_p(t_k)}\right)^2 + \left(\frac{\sigma_p(t_k)}{\sigma_q}\right)^2 - 1\right] \\ &+ \frac{1}{2}\frac{(\mu_p(t_k) - \mu_p)^2}{\sigma_q^{\ 2}}. \end{aligned} \tag{3}$$

In this study, RE was high if the amount of change in rotational posture during a given 20-s period was extraordinarily active in comparison to the entire measurement period. Because the occurrence probability of such specific behavior is equivalent to the −RE power of the base e of the natural logarithm, it is considered to be equivalent to $P = e^{-20} = 2.06\times10^{-9}$, if RE is 20. In this study, the frequency of clasper crosses was determined by checking the video images of the surveillance camera when the RE value obtained with Equation 3 was high.

Results

Swimming behavior at ambient temperatures

In Figure 2, we provide, as an example of changes in the time series, a graphic representation of raw data of x-axis acceleration and x-axis dynamic acceleration, dynamic acceleration after CWT, swimming speed, TBF, and ODBA for a period of 3 d. The period of dynamic acceleration on the x-axis was typically in the range of 4–10 s, with some exceptions. Swimming speeds were higher at higher TBFs and lower at lower TBFs (coefficient of correlation [r]=0.43, $P<0.001$). The mean values of swimming speed, TBF, and ODBA in daytime and nighttime for each temperature during the experimental period, as well as the ratios of decreases from daytime to nighttime, are listed in Table 2. Swimming speed, TBF, and ODBA values were significantly lower during the nighttime than during the daytime across all experimental periods (speed: $U>5.5\times10^9$, $P<0.001$; TBF: $U>6.5\times10^8$, $P<0.001$; ODBA: $U>9.1\times10^8$, $P<0.001$) (Table 2, Fig. 3). The analysis of variance results indicate that month, time of day (daytime or nighttime), and their interaction significantly affected speed, TBF, and

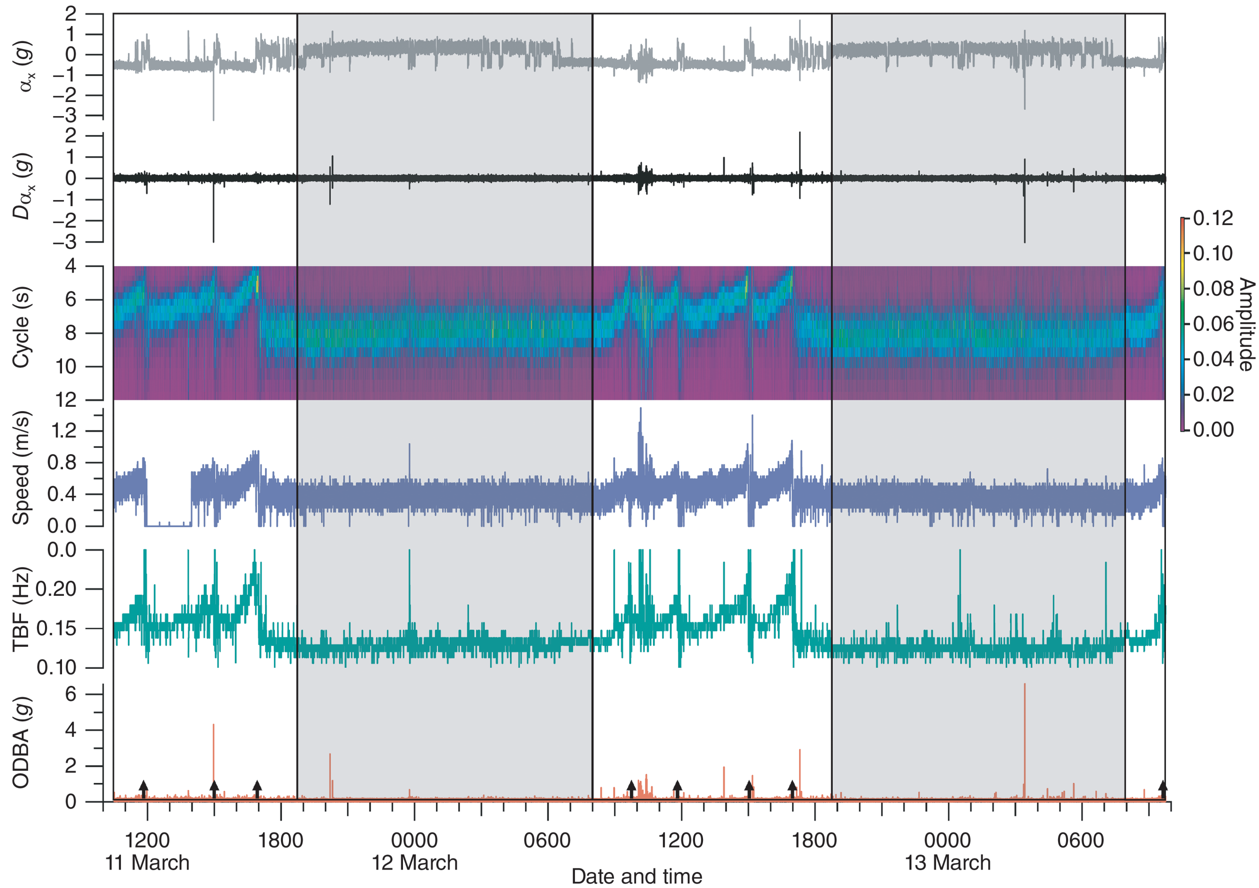

Figure 2

Movement and acceleration time series collected on 11–13 March 2021 with a data logger attached to a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium in Japan. The panels show, from the top, the raw data of *x*-axis acceleration (α_x) and dynamic acceleration on the *x*-axis ($D\alpha_x$, sway), a spectrogram of dynamic acceleration after continuous wavelet transformation (cycle, sway), swimming speed, tail-beat frequency (TBF, sway), and overall dynamic body acceleration (ODBA). The white and gray areas indicate periods of daytime and nighttime, respectively. The arrows above the *x*-axis indicate the feeding times. Note that 1 *g*, the unit of measure for α_x, $D\alpha_x$, and ODBA, is equal to 9.8 m/s^2.

ODBA, with the effect of time of day being particularly dominant (speed: $F(1, 1{,}299{,}893)=85{,}305.37$, $P<0.001$; TBF: $F(1, 1{,}588{,}564)=510{,}614.11$, $P<0.001$; ODBA: $F(1, 1{,}326{,}286)=52{,}872.65$, $P<0.001$).

The seasonal data indicate that swimming speed, TBF, and ODBA values were significantly lower during the cooler months of December and March than during the warmer months of June and September (speed: $U=1.5\times10^{11}$, $P<0.001$; TBF: $U=1.3\times10^{11}$, $P<0.001$; ODBA: $U=1.1\times10^{11}$, $P<0.001$) (Fig. 3). During the periods of cool water temperatures, the ratios of the decreases in swimming speed, TBF, and ODBA between daytime and nighttime ranged from 14.9% to 19.7%, 15.5% to 15.6%, and 15.9% to 21.0%, respectively. The ratios of the decreases between daytime and nighttime for all 3 parameters were greater in the period of cool water temperatures than in the period of warm water temperatures (Table 2). Box plots of ODBA by time of day for the entire period reveal that ODBA tended to be lower during the nighttime than during the daytime and was intermittently high at 0900, 1100, 1400, and 1600, times that correspond to the times before feeding (Fig. 4).

Because it was difficult to compare the characteristics of the TBFs for each condition (water temperature and light) by using only the average values, we used the *k*-means method for cluster analysis of the *x*-axis dynamic acceleration data. In all experimental periods, there were 2 distinct patterns of TBF: high and low frequency, representing fast and slow tail-beat movements (Fig. 5, A–D). The high-frequency peak, the low-frequency peak, and the difference between the 2 frequencies were 0.16 Hz, 0.14 Hz, and 0.02 Hz in September, 0.15 Hz, 0.13 Hz, and 0.02 Hz in December, 0.17 Hz, 0.13 Hz, and 0.04 Hz in March, and 0.17 Hz, 0.15 Hz, and 0.02 Hz in June, respectively. Furthermore, the occurrence ratios of the 2 TBF components were calculated for each minute, and almost

Table 2

Monthly mean swimming speed, tail-beat frequency (TBF), and overall dynamic body acceleration (ODBA) of a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium in Japan in September and December 2020 and March and June 2021, overall and during daytime and nighttime. Also provided for each month are the ratios of decreases in these measures from daytime to nighttime and the mean temperature. Means are given with standard deviations in parentheses. Note that 1 *g*, the unit of measure for ODBA, is equal to 9.8 m/s^2.

Index	Month	Temperature (°C)	Overall	Daytime	Nighttime	Ratio (%)
Speed (m/s)	Sept.	28.5 (0.1)	0.42 (0.10)	0.43 (0.12)	0.41 (0.08)	6.1
	Dec.	23.6 (0.3)	0.37 (0.11)	0.41 (0.12)	0.35 (0.08)	14.9
	March	22.1 (0.3)	0.40 (0.12)	0.46 (0.14)	0.37 (0.08)	19.7
	June	26.8 (0.0)	0.42 (0.11)	0.43 (0.13)	0.41 (0.11)	4.4
TBF (Hz)	Sept.	28.5 (0.1)	0.15 (0.02)	0.15 (0.02)	0.15 (0.01)	6.2
	Dec.	23.6 (0.3)	0.14 (0.02)	0.15 (0.02)	0.13 (0.01)	15.5
	March	22.1 (0.3)	0.14 (0.02)	0.15 (0.02)	0.13 (0.01)	15.6
	June	26.8 (0.0)	0.16 (0.02)	0.16 (0.02)	0.15 (0.02)	5.5
ODBA (*g*)	Sept.	28.5 (0.1)	0.088 (0.044)	0.090 (0.046)	0.086 (0.042)	4.4
	Dec.	23.6 (0.3)	0.075 (0.038)	0.082 (0.038)	0.069 (0.037)	15.9
	March	22.1 (0.3)	0.071 (0.036)	0.080 (0.038)	0.064 (0.034)	21.0
	June	26.8 (0.0)	0.084 (0.040)	0.088 (0.041)	0.080 (0.039)	9.1

all high-frequency tail beats occurred during the daytime, whereas almost all low-frequency tail beats occurred during the nighttime (Fig. 6). Strong pulse-like components of high-frequency tail beating were recorded intermittently during the nighttime, although most tail beats were recorded during slow swimming in periods of low-frequency tail beating (Fig. 6).

Calculation of clasper crosses

In all experimental periods, high values of RE were observed mostly during the daytime and rarely during the nighttime (Fig. 7). When the RE value was higher than 20, the behavior of the shark was checked on the video from the aquarium surveillance cameras. The shark was found to be engaged in a clasper cross in all cases during the experiment, with the exception of 4 cases when the shark was just changing direction. The counts of clasper crosses during each 24-h period indicate that 85.3% of the clasper crosses occurred during the daytime and 14.6% occurred during the nighttime (Fig. 8). The frequency of clasper crosses during each experimental period is shown in Table 3. The frequencies of clasper crosses per day were lower during periods of cool water temperatures (March and December) than during periods of warm water temperatures (June and September), and the highest frequency of clasper crosses per day was recorded in June (χ^2=10.18, P=0.00142) (Table 3).

Discussion

Comparisons of the swimming speed, TBF, and ODBA during each month and time of day (daytime and nighttime) revealed that month and light condition significantly affected the swimming behavior of the studied individual, with time of day exerting the greatest influence. Swimming speed, TBF, and ODBA values were lower in the nighttime than in the daytime, indicating that this individual tended to conserve energy during the nighttime.

During the experimental period, as mentioned previously, we recorded 2 distinct patterns of TBF, high and low frequency (i.e., fast and slow movements of the caudal fin). In the hourly ratio of these 2 frequencies, high-frequency tail beats were dominant in the daytime, and low-frequency tail beats were dominant in the nighttime. This individual used both fast and slow modes of tail beating and rested during the nighttime, when it mainly used the slow mode of tail beating. The intervals of low-frequency tail beating lasted about 50 min, and the pulse-like components of high-frequency tail beating, which indicate active, fast swimming, lasted from 1 to 5 min. This resting pattern indicates that the male whale shark has a rhythm of 50-min periods of sleep-like rest with slow swimming, interspersed with periods of 1–5 min of awake-like activity with fast swimming (Fig. 6). The metabolic rate of draughtsbroad sharks (*Cephaloscyllium isabellum*) decreases during sleep, and sleep plays a role in energy conservation (Kelly et al., 2022); however, few physiological studies have been conducted on sleep in elasmobranchs, especially by using electroencephalograms (Kelly et al., 2019). The diurnal circadian rhythm and nighttime resting of the male whale shark in our study differed from the findings of Gleiss et al. (2013), who reported that, in the wild, this species is more active around sunrise and sunset. The effects of fixed feeding times at the OCA for

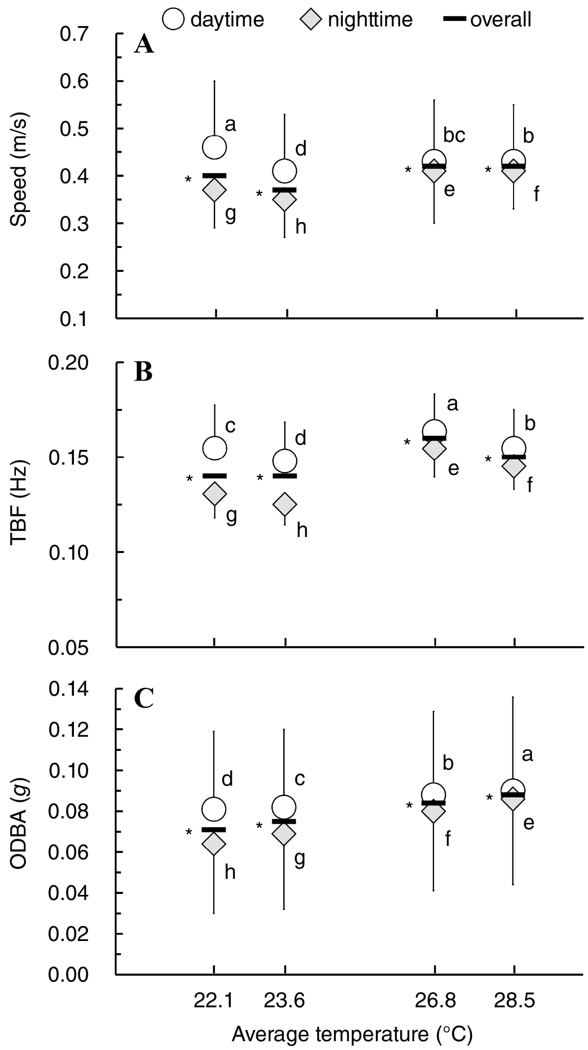

Figure 3

Relationships between average (overall) water temperature and daytime and nighttime (**A**) swimming speed, (**B**) tail-beat frequency (TBF), and (**C**) overall dynamic body acceleration (ODBA) for a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium, in Japan, over 4 experimental periods: 16–19 September 2020, 13–17 December 2020, 11–22 March 2021, and 6–9 June 2021. The temperatures of 22.1°C, 23.6°C, 26.8°C, and 28.5°C represent those in March, December, June, and September, respectively. Error bars indicate the standard deviations. Asterisks indicate that there was a significant difference ($P<0.01$) between daytime and nighttime. Different letters indicate significant differences between the groups of each condition (water temperature and time of day [daytime or nighttime]). Note that 1 *g*, the unit of measure for ODBA, is equal to 9.8 m/s^2.

whale sharks during only the daytime should be investigated in a future study.

The ODBA increased during the periods of warm water temperatures, indicating that the amount of energy consumed for swimming was higher in warm water. This finding is in accordance with the results of a previous study conducted at the OCA (Matsumoto et al., 2018). In that study, during the period of warm water temperatures, the male whale shark fed more, but the ratio of girth to total length, which is one of the fatness indices, decreased. On the other hand, during the period of cool water temperatures, this ratio increased even though the food intake of this fish was not as high as that during the warm temperature period.

Nakamura et al. (2020) found that, in the wild, the TBF of this species also decreased with decreasing muscle temperature, indicating that this individual also experienced a decrease in TBF due to a reduction in muscle temperature during the period when the water was cool. Particularly, during the periods of cool water temperatures, the ratios of decreases in ODBAs were 15%–20% and clearly high (Table 2, Fig. 3C); therefore, the whale shark could easily rest in the nighttime under cool temperature conditions. In contrast, under temperatures at more than 28°C in September, the ratio of decrease in ODBA was as low as 4.4%, indicating that it was difficult for the whale shark to rest and save energy during the nighttime in warm temperature conditions. It has been suggested that this species behaviorally thermoregulates by deep diving (Thums et al., 2013; Robinson et al., 2017). However, our results were obtained in limited space and temperature ranges because deep diving is not possible under captive conditions. The aquarium staff reported that this species is prone to feeding problems during the summer, indicating that in captivity, it struggles to adapt to warm water temperatures in summer, when the in-tank water temperature can exceed 28°C, and that it adapts to low water temperatures by decreasing its activity level. Given the findings of Ryan et al. (2017), which indicate that this species spends approximately 75% of its time in water with temperatures of 22°C–26°C and tends to inhabit waters with stable temperatures averaging 25°C, we estimated the optimal range of water temperatures for this species in captivity as approximately 22°C–27°C.

The clasper cross, a mating-like behavior, tended to occur mostly during the daytime. This result indicates that this behavior is affected by illumination. It had been reported that vision of the whale shark plays an important role in short-range perception (Martin, 2007; Tomita et al., 2020). Therefore, we suggest that the male whale shark engages in clasper crosses during the daytime to make courtship visually appealing to the female whale shark.

Our results indicate that the frequency of clasper crosses was lower in the cool temperature periods than in the warm temperature periods; the highest clasper-cross frequency was observed in June (when the water temperature was around 26°C). Matsumoto et al. (2021) reported that the highest clasper-cross frequency occurred in early summer from May through July, when the water temperature in the aquarium was approximately 25°C, a finding that is quite close to the results of this study. Increased blood levels of testosterone have

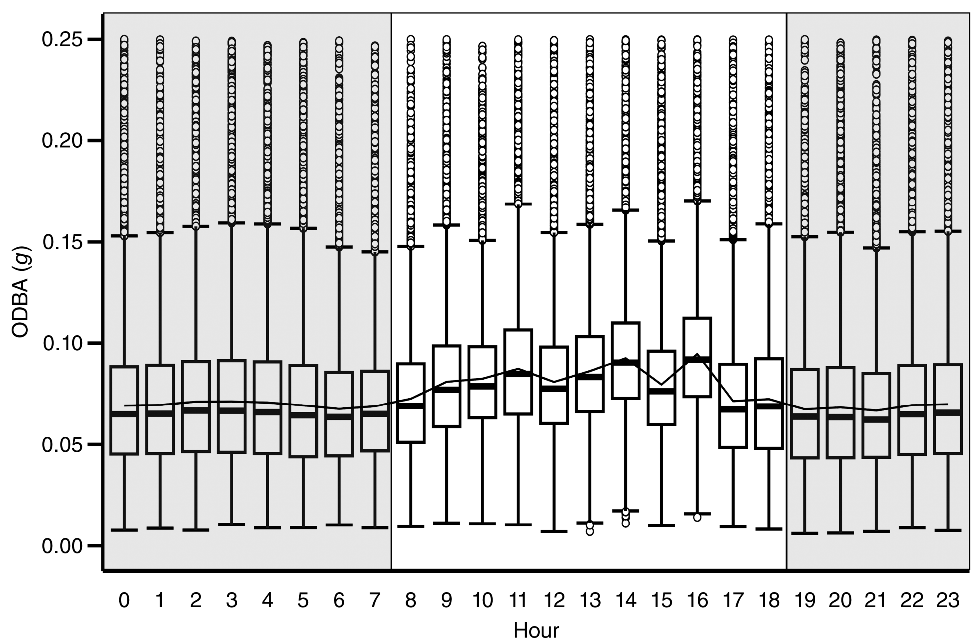

Figure 4

Box plots of overall dynamic body acceleration (ODBA) by hour of day for a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium, in Japan, during an experiment conducted in September and December 2020 and March and June 2021. The trend line indicates average values. The thick line in each box indicates the median, and the ends of the box represent the upper and lower quartiles. The whiskers indicate the highest and lowest values, excluding the outliers (circles). The white and gray areas indicate periods of daytime and nighttime, respectively. Note that 1 *g*, the unit of measure for ODBA, is equal to 9.8 m/s^2.

also been observed for this individual within this water temperature range, indicating a relationship between the elevation of this hormone and the rise in the number of clasper crosses (Matsumoto et al., 2021). Therefore, we speculate that reproductive behavior is greatly affected by ambient water temperature and that the optimal reproductive water temperature for this species may be approximately 26°C.

The findings of our study indicate that the behavior of the male whale shark is significantly affected by ambient water temperature and illumination. The studied shark successfully adapted to the current rearing environment by managing swimming and resting while conserving activity and energy, a flexibility that is thought to be one of the reasons for the long-term success in rearing of this species at the OCA. In particular, a period of cool temperatures is considered more suitable for resting than a period of warm temperatures, and the frequency of clasper crosses during cool temperature periods is about half that during warm temperature periods. Therefore, there seems to be a trade-off between rest for saving energy and mating-like behaviors. All of these results indicate that, in order to promote growth, maturity, and ultimately successful breeding of this species in captivity, water temperature should be allowed to fluctuate within a range of approximately 22°C–27°C, as it is in the current rearing environment at the OCA, rather than kept at a constant level.

Conclusions

The results of this study, in which detailed data from long-term biologging were used to quantify the behavior of a whale shark successfully adapted to captive conditions, provide an important basis for developing captive conservation methods for this species. In particular, the findings of this study indicate that 2 factors are key to long-term rearing of this species: 1) active swimming during the daytime and resting at nighttime and 2) seasonal changes in the water temperature of the aquarium (i.e., allowing the fish to experience cool water conditions). In the future, staff of other aquariums should consider the nighttime resting behavior of this species and how to manage water temperature, in order to aid health management and to enable long-term rearing of this species. Long-term rearing of this species will reduce the

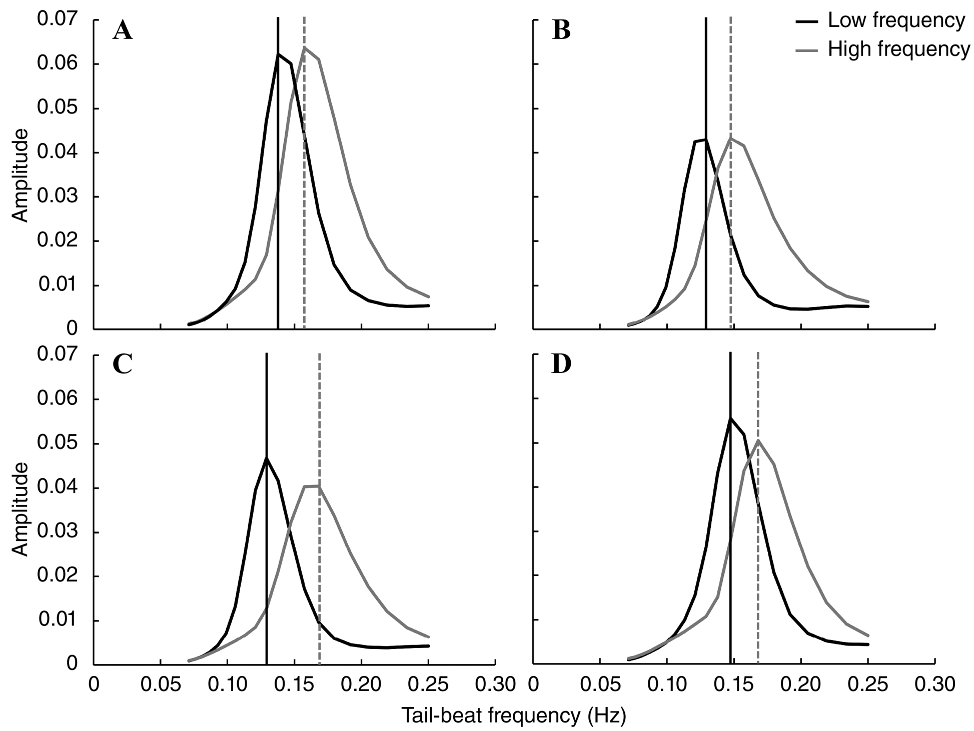

Figure 5

Results of cluster analysis, with the *k*-means method, of oscillations of the caudal fin of a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium in Japan during 4 periods: (**A**) 16–19 September 2020, (**B**) 13–17 December 2020, (**C**) 11–22 March 2021, and (**D**) 6–9 June 2021. The vertical axis represents the amplitude strength, and the horizontal axis represents the tail-beat frequency. The gray and black dashed lines represent the high- and low-frequency peaks in oscillations, respectively.

need to take more individuals from the wild, leading to resource conservation.

Resumen

Las observaciones cuantitativas a largo plazo son esenciales para la conservación del tiburón ballena (*Rhincodon typus*), el cual necesita mucho tiempo para crecer y madurar. En este estudio, se colocó un dispositivo de registro de datos en un tiburón ballena macho maduro que se había mantenido en cautiverio durante más de 29 años en el Acuario Churaumi de Okinawa (Japón). Debido a que es deseable la crianza a largo plazo del tiburón ballena en cautiverio, se investigaron los efectos de la temperatura del agua y la luz sobre el comportamiento de natación del tiburón ballena en cautiverio. A partir de los datos de natación, se calcularon las frecuencias de los latidos de la cola (TBF), los niveles de actividad y la frecuencia de cruces de los claspers, que se considera un comportamiento similar al apareamiento. En todas las estaciones, la TBF, la velocidad de nado y el nivel de actividad del tiburón fueron entre un 4% y un 20% menores durante la noche que durante el día, especialmente a temperaturas de agua frías (≤23.6°C). Además, aproximadamente el 90% de los cruces del claspers se produjeron durante el día. Estos resultados indican que el tiburón está activo durante el día, realizando actividades como el apareamiento. Por el contrario, durante la noche descansa mientras nada, ralentizando el batido de su aleta caudal y reduciendo la velocidad de nado para conservar energía. Por lo tanto, concluimos que este individuo ha adoptado este ritmo diurno para adaptarse a su actual entorno de cría.

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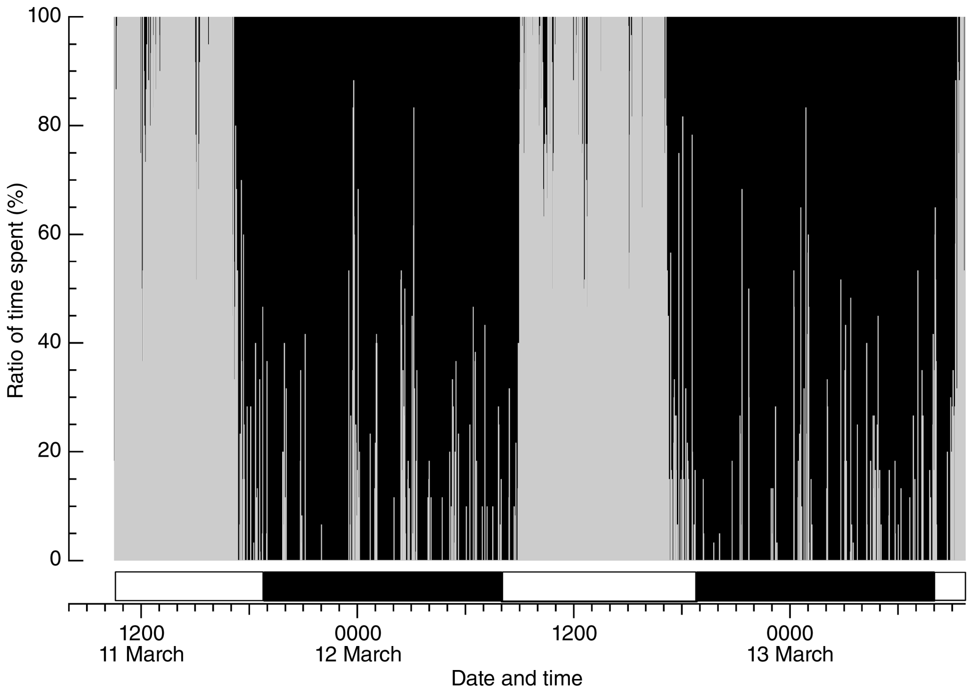

Figure 6

Ratio of time occupied by 2 types of tail-beat frequencies in 1 min of data from the data logger attached to a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium, in Japan, during 11–13 March 2021. The gray part of the graph represents the time with high-frequency tail beats, classified by using the *k*-means method, and the black part represents the time with low-frequency tail beats. The white and black horizontal bars at the bottom of the graph indicate periods of daytime and nighttime, respectively.

Table 3

Frequency and duration of clasper crosses of a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium in Japan during September and December 2020 and March and June 2021. Mean temperatures in the tank for each month are also provided, with standard deviations in parentheses. A clasper cross is a mating-like behavior that includes a large body rotation and a crossing of both claspers.

Month	Temperature (°C)	Duration (h)	Frequency of clasper crosses	Frequency of clasper crosses per day
Sept.	28.5 (0.1)	23.2	4	4.1
Dec.	23.6 (0.3)	119.0	10	2.0
March	22.1 (0.3)	220.2	14	1.5
June	26.8 (0.0)	56.3	13	5.5

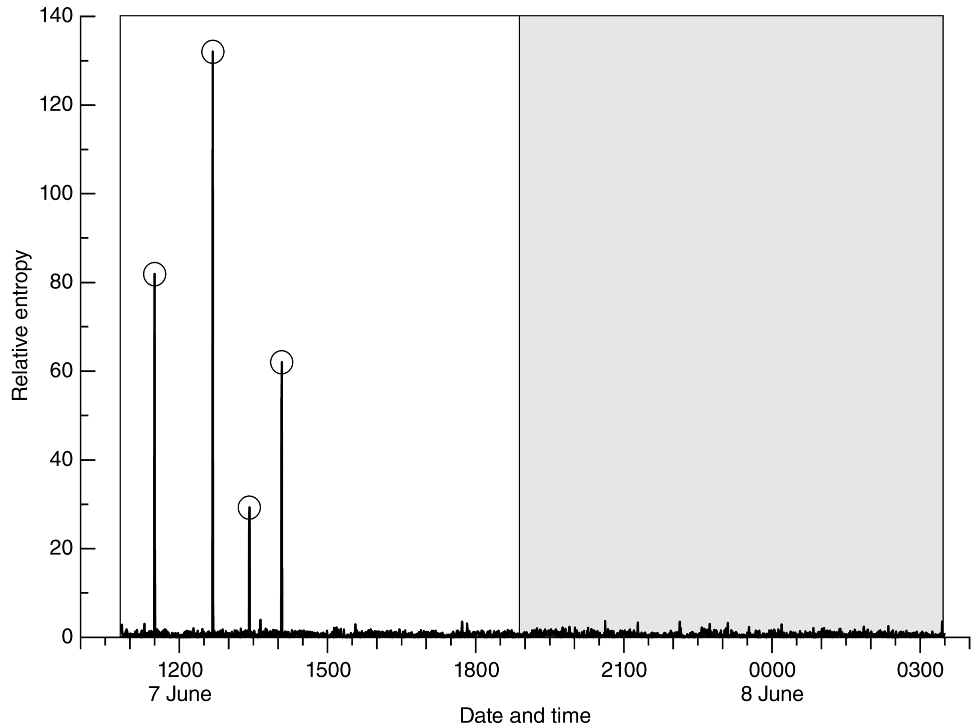

Figure 7

Variation in relative entropy values calculated from static acceleration on the *z*-axis for a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium in Japan during 7–8 June 2021. The relative entropy values >20 indicate a clasper cross, a mating-like behavior that includes a large body rotation and a crossing of both claspers (white circles). Relative entropy values <4 indicate normal behavior. The white and gray areas indicate periods of daytime and nighttime, respectively.

Literature cited

Andrzejaczek, S., A. C. Gleiss, K. O. Lear, C. B. Pattiaratchi, T. K. Chapple, and M. G. Meekan.
2019. Biologging tags reveal links between fine-scale horizontal and vertical movement behaviors in tiger sharks (*Galeocerdo cuvier*). Front. Mar. Sci. 6:229. Crossref

Araujo, G., C. A. Rohner, J. Labaja, S. J. Conales, S. J. Snow, R. Murray, S. J. Pierce, and A. Ponzo.
2018. Satellite tracking of juvenile whale sharks in the Sulu and Bohol Seas, Philippines. PeerJ 6:e5231. Crossref

Barry, C., C. Legaspi, T. M. Clarke, G. Araujo, C. J. A. Bradshaw, A. C. Gleiss, L. Meyer, and C. Huveneers.
2023. Estimating the energetic cost of whale shark tourism. Biol. Conserv. 284:110164. Crossref

Gallagher, A. J., and N. Hammerschlag.
2011. Global shark currency: the distribution, frequency, and economic value of shark ecotourism. Current Issues Tour. 14:797–812. Crossref

Gallimore, C. G., C. Walton, R. Nugent, M. Fradkin, L. Poppell, C. Schreiber, C. Coco, M. Grober, B. Carlson, A. D. M. Dove, et al.
2024. A longitudinal behavioral analysis of aquarium whale sharks (*Rhincodon typus*): insights into anticipatory cues, individual variation, and social interaction. Front. Mar. Sci. 11:1418002. Crossref

Gleiss, A. C., S. Wright, N. Liebsch, R. P. Wilson, and B. Norman.
2013. Contrasting diel patterns in vertical movement and locomotor activity of whale sharks at Ningaloo Reef. Mar. Biol. 160:2981–2992. Crossref

Halsey, L. G., E. L. C. Shepard, and R. P. Wilson.
2011. Assessing the development and application of the accelerometry technique for estimating energy expenditure. Comp. Biochem. Physiol. A 158:305–314. Crossref

Hearn, A. R., J. R. Green, C. R. Peñaherrera-Palma, S. Reynolds, C. A. Rohner, M. Román, and A. M. M. Sequeira.
2021. Whale shark movements and migrations. *In* Whale sharks: biology, ecology, and conservation (A. D. M. Dove and S. J. Pierce, eds.), p. 105–128. CRC Press, Boca Raton, FL.

Joung, S.-J., C.-T. Chen, E. Clark, S. Uchida, and W. Y. P. Huang.
1996. The whale shark, *Rhincodon typus*, is a livebearer: 300 embryos found in one 'megamamma' supreme. Environ. Biol. Fishes 46:219–223. Crossref

Kadota, M., E. J. White, S. Torisawa, K. Komeyama, and T. Takagi.
2011. Employing relative entropy techniques for assessing modifications in animal behavior. PLoS ONE 6(12):e28241. Crossref

Kelly, M. L., S. P. Collin, J. M. Hemmi, and J. A. Lesku.
2019. Evidence for sleep in sharks and rays: behavioural, physiological, and evolutionary considerations. Brain Behav. Evol. 94:37–50. Crossref

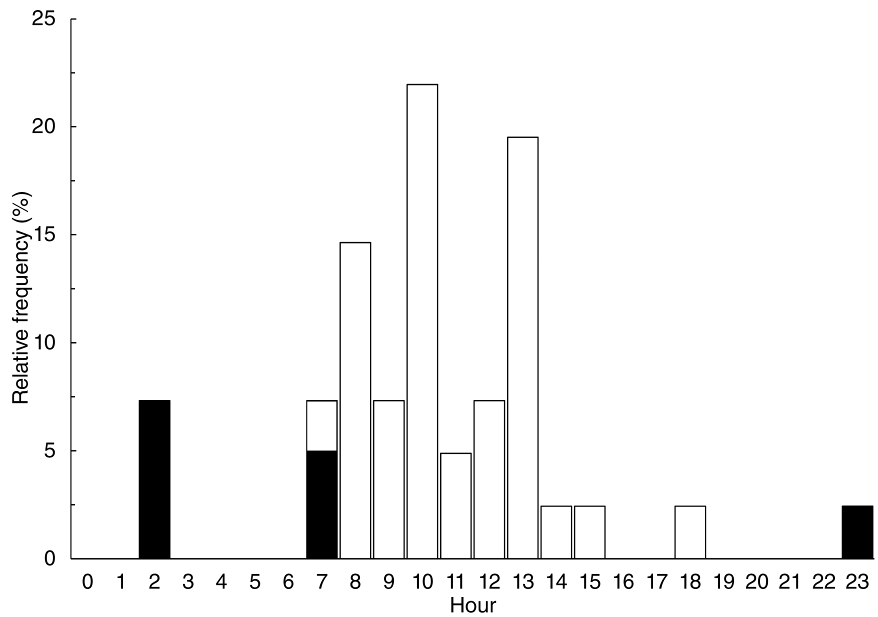

Figure 8

Relative frequency of clasper crosses (number observed=41) by hour of day for a male whale shark (*Rhincodon typus*) in the Kuroshio Tank at the Okinawa Churaumi Aquarium, in Japan, during September and December 2020 and March and June 2021. A clasper cross is a mating-like behavior that includes a large body rotation and a crossing of both claspers. The white and black bars indicate the relative frequencies of clasper crosses that occurred during daytime and nighttime, respectively.

Kelly, M. L., S. P. Collins, J. A. Lesku, J. M. Hemmi, S. P. Collin, and C. A. Radford.
2022. Energy conservation characterizes sleep in sharks. Biol. Lett. 18:20210259. Crossref

Lauderdale, L. K., K. A. Shorter, D. Zhang, J. Gabaldon, J. D. Mellen, M. T. Walsh, D. A. Granger, and L. J. Miller.
2021. Bottlenose dolphin habitat and management factors related to activity and distance traveled in zoos and aquariums. PLoS ONE 16(8):e0250687. Crossref

Lear, K. O., N. M. Whitney, L. R. Brewster, J. J. Morris, R. E. Hueter, and A. C. Gleiss.
2017. Correlations of metabolic rate and body acceleration in three species of coastal sharks under contrasting temperature regimes. J. Exp. Biol. 220:397–407. Crossref

Legaspi, C., J. Miranda, J. Labaja, S. Snow, A. Ponzo, and G. Araujo.
2020. In-water observations highlight the effects of provisioning on whale shark behaviour at the world's largest whale shark tourism destination. R. Soc. Open Sci. 7:200392. Crossref

Martin, R. A.
2007. A review of behavioural ecology of whale sharks (*Rhincodon typus*). Fish. Res. 84:10–16. Crossref

Matsumoto, R., M. Toda, Y. Matsumoto, K. Ueda, M. Nakazato, K. Sato, and S. Uchida.
2017. Notes on husbandry of whale sharks, *Rhincodon typus*. *In* Elasmobranch husbandry manual II: recent advances in the care of sharks, rays and their relatives (M. Smith, D. Warmolts, D. Thoney, R. Hueter, M. Murray, and J. Ezcurra, eds.), p. 15–22. Ohio Biol. Survey, Columbus, OH.

Matsumoto, R., K. Murakumo, R. Furuyama, and S. Matsuzaki.
2018. Effects of energy intake and water temperature on the body shape of whale sharks at the Okinawa Churaumi Aquarium. *In* Proceedings of 10th International Aquarium Congress Fukushima 2018; Fukushima, 7–10 November, p. 80–84. Int. Aquar. Congr.

Matsumoto, R., Y. Matsumoto, K. Ueda, M. Suzuki, K. Asahina, and K. Sato.
2019. Sexual maturation in a male whale shark (*Rhincodon typus*) based on observations made over 20 years of captivity. Fish. Bull. 117:78–86. Crossref

Matsumoto, R., K. Murakumo, R. Nozu, T. Tomita, and K. Sato.
2021. Observation on the reproductive behaviors of a captive male whale shark. *In* Proceedings of the Elasmobranch Symposium 2021; Chiba, 17 December, p. 8. Jpn. Soc. Elasmobranch Stud., Chiba, Japan. [In Japanese.]

Nakamura, I., R. Matsumoto, and K. Sato.
2020. Body temperature stability in the whale shark, the world's largest fish. J. Exp. Biol. 223(11):jeb210286. Crossref

Pierce, S. J., and B. Norman.
2016. *Rhincodon typus*. The IUCN Red List of Threatened Species 2016:e.T19488A2365291. [Available from website, accessed November 2021].

Pratt, H. L., Jr., and J. C. Carrier.
2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. Environ. Biol. Fishes 60:157–188. Crossref

Ramírez-Macías, D., N. Queiroz, S. J. Pierce, N. E. Humphries, D. W. Sims, and J. M. Brunnschweiler.
2017. Oceanic adults, coastal juveniles: tracking the habitat use of whale sharks off the Pacific coast of Mexico. PeerJ 5:e3271. Crossref

Reynolds, S. D., J. Redcliffe, B. M. Norman, R. P. Wilson, M. Holton, C. E. Franklin, and R. G. Dwyer.
2024. Swimming with humans: biotelemetry reveals effects of "gold standard" regulated tourism on whale sharks. J. Sustain. Tour. 1–20. Crossref

Robinson, D. P., M. Y. Jaidah, S. S. Bach, C. A. Rohner, R. W. Jabado, R. Ormond, and S. J. Pierce.
2017. Some like it hot: repeat migration and residency of whale sharks within an extreme natural environment. PLoS ONE 12(9):e0185360. Crossref

Rohner, C. A., J. E. M. Cochran, E. F. Cagua, C. E. M. Prebble, S. K. Venables, M. L. Berumen, B. L. Kuguru, J. Rubens, J. M. Brunnschweiler, and S. J. Pierce.
2020. No place like home? High residency and predictable seasonal movement of whale sharks off Tanzania. Front. Mar. Sci. 7:423. Crossref

Ryan, J. P., J. R. Green, E. Espinoza, and A. R. Hearn.
2017. Association of whale sharks (*Rhincodon typus*) with thermo-biological frontal systems of the eastern tropical Pacific. PLoS ONE 12(8):e0182599. Crossref

Sakamoto, K. Q., K. Sato, M. Ishizuka, Y. Watanuki, A. Takahashi, F. Daunt, and S. Wanless.
2009. Can ethograms be automatically generated using body acceleration data from free-ranging birds? PLoS ONE 4(4):e5379. Crossref

Sato, K., R. Matsumoto, K. Murakumo, and K. Asahina.
2016. Long-term husbandry and physical observation of the whale sharks in Okinawa Churaumi Aquarium. QScience Proc. (4th International Whale Shark Conference). 2016:iwsc4.56. [Available from website.]

Thums, M., M. Meekan, J. Stevens, S. Wilson, and J. Polovina.
2013. Evidence for behavioural thermoregulation by the world's largest fish. J. R. Soc. Interface 10:20120477. Crossref

Tomita, T., K. Murakumo, S. Komoto, A. Dove, M. Kino, K. Miyamoto, and M. Toda.
2020. Armored eyes of the whale shark. PLoS ONE 15(6):e0235342. Crossref

Wilson, R. P., C. R. White, F. Quintana, L. G. Halsey, N. Liebsch, G. R. Martin, and P. J. Butler.
2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. J. Anim. Ecol. 75:1081–1090. Crossref