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Use of an acceleration data logger to measure diel activity patterns in captive whitetip reef sharks, *Triaenodon obesus*

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Abstract – Traditional telemetry methods have been used to quantify the horizontal and vertical displacement of marine species, but are unable to identify specific physical activities such as swimming or gliding, resting, foraging, or spawning. We tested the utility of an acceleration data logger to quantify activity patterns of three captive whitetip reef sharks (*Triaenodon obesus*) in an enclosed lagoon using internal and external attachment methods. Data obtained using both attachment methods allowed swimming and resting behavior to be differentiated. All sharks showed constant swimming for 5–14 hours post-tagging before adopting a pattern of daytime rest and nocturnal activity throughout the 6–16 day deployments. Sharks showed a diel activity pattern, spending 10–24% of their time swimming during the day, and 42–67% swimming at night. Overall, sharks spent an average of 35 ± 11% (mean ± SD) of their time swimming. Mean tailbeat frequency was found to be 0.89 ± 0.03 beats s^{-1} in one shark for which it was measured. Respirometry experiments that measured the metabolic rate of two neonate whitetips showed significantly higher metabolic rates at night compared to the day. When taken in conjunction with the acceleration data, these results suggest that whitetips are nocturnally active and show diel circadian rhythms shortly after birth. Our study demonstrates that acceleration data loggers can be used to quantify activity patterns and offer promise for quantifying energy budgets of various reef sharks both in captivity and in the field.

Key words: Accelerometer / Respirometry / Diel cycles / Elasmobranch

1 Introduction

Understanding the activity patterns and energetic requirements of marine species is becoming increasingly important for modeling ecosystems and managing populations (Lowe and Goldman 2001; Kitchell et al. 2002; Lowe 2002; Shindler et al. 2002; Lowe and Bray 2006). Traditionally, acoustic and radio telemetry have been used to quantify the activity patterns of marine animals, but these provide relatively low resolution in regards to swimming speeds (typically measured as "speed over ground") and degree of activity. Although vertical movements can be measured with higher precision, it is usually not possible to infer specific physical activities (e.g. swimming versus gliding, resting versus foraging) from these data. A variety of sensors have been developed to more accurately quantify activity patterns, including those that measure swim speed, tailbeat frequency, muscle contractions, heart rate, and acceleration (Sundström and Gruber 1998; Lowe et al. 1998; Lowe and Goldman 2001; Green et al. 2002; Williams et al. 2004). However, several of these sensors require significant handling of the animal and surgical implantation of the sensor. One technique which is receiving attention in animal ecology is the use of acceleration sensors (Wilson et al. 2006). Acceleration data loggers are small, can be applied to an animal quickly and externally, and have been used with a variety of marine birds, mammals, and fishes to look at aspects of swimming performance, spawning behavior, foraging activity, and bioenergetics (e.g. Yoda et al. 1999; Tanaka et al. 2001; Williams et al. 2004; Tsuda et al. 2006; Wilson et al. 2006).

Many species of elasmobranch fishes are apex predators and may play important roles in the marine ecosystem (Cortes 1999), yet detailed studies of activity patterns have only been conducted on a couple of species (Sundström and Gruber 1998; Lowe 2002), and none have utilized acceleration sensors. The whitetip reef shark (*Triaenodon obesus*) is a large predator found in tropical coral reef ecosystems of the Pacific and Indian Oceans (Randall 1977). This species is not an obligate ram ventilator, and can be observed resting on the seafloor or lying in caves (Nelson and Johnson 1980). It is generally assumed that this species is nocturnally active, but empirical data

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are lacking. Because it is probable that whitetips alternate between distinct periods of active swimming and rest, they make an excellent candidate for testing acceleration loggers as tools for quantifying activity patterns and elucidating the bioenergetics of species that are difficult to observe in the wild.

The purpose of this study was to assess the effectiveness of acceleration data loggers in quantifying the activity patterns of free-swimming sharks, and to provide preliminary metabolic rate data for future studies that may integrate these two complementary techniques. Specifically we sought to 1) test the feasibility of two logger attachment techniques, 2) correlate visual observations of shark behavior (e.g. resting, active swimming) with acceleration data obtained from the logger 3) determine the diel activity cycles of captive whitetip reef sharks over multiple-day deployments, and 4) measure the diel metabolic rates of two neonate sharks to compare with diel activity cycles from the logger experiments, and to provide an example of how these could be used to determine the energy budgets of free-swimming sharks.

2 Methods

2.1 Subject animals and study location

Adult whitetip reef sharks (*Triaenodon obesus*) were maintained in a 22 × 100 m fenced enclosure of a lagoon in Kaneohe Bay at the Hawaii Institute of Marine Biology (HIMB). For accelerometer experiments, a shark was isolated in a 10 × 20 m section of the enclosure and allowed to acclimate for at least one week prior to accelerometer logger deployment. The enclosure consisted of a sand channel (max depth 3 m) flanked by coral and a shallow rubble flat (max depth 1 m). The enclosure experienced daily tidal flushing and represented a semi-natural habitat complete with reef fauna typical for Kaneohe Bay.

Respirometry experiments were conducted with two neonate whitetip reef sharks born in the seawater ponds at HIMB and then maintained in 4 m diameter (1 m deep) outdoor pools with flow-through seawater. All sharks were fed a diet of fish and squid *ad libitum* approximately three times per week prior to being used for experiments.

2.2 Acceleration logger experiments

The XYZ Acceleration Logger (VEMCO, Nova Scotia, Canada) consisted of a three dimensional acceleration sensor, a logger that recorded data to flash memory at user-selected intervals (100, 200, 500, or 1000 ms), and a replaceable battery pack. The entire package was contained in a 16 × 108 mm tube, weighed 35 g in air, and was slightly negatively buoyant in seawater. Of the three dimensions (X, Y, and Z) measured by the accelerometer sensor, the Y-axis was parallel to the length of the logger cylinder, while the X- and Z-axes were perpendicular to the length of the logger and to each other (Fig. 1). All three axes were calibrated by rotating the logger through each possible combination of pitch and roll so that the raw data output in millivolts could be converted into units of gravity (g) where 1 g is equal to 9.8 m s^{-2} of acceleration. When

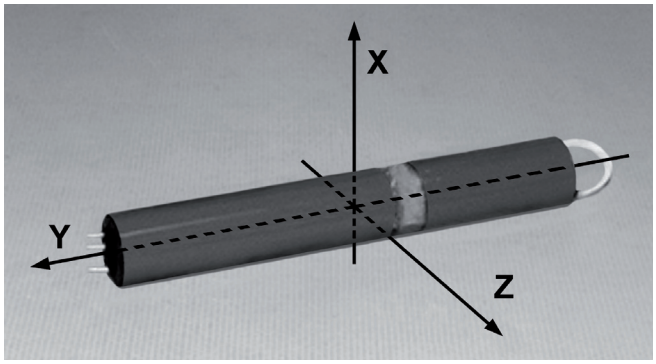

Fig. 1. Diagram of the *XYZ* acceleration logger showing the orientation of all three acceleration sensors (X, Y, and Z respectively). Courtesy of VEMCO (Nova Scotia, Canada).

the logger was stationary, each axis (X, Y, and Z) would record a value of 0 g if it was oriented parallel to the earth's gravitational pull, –1 g when oriented directly away from the earth, and +1 g when oriented directly toward the earth. For example, the logger orientation shown in Figure 1 would produce acceleration values of $X = -1$, $Y = 0$, and $Z = 0$. The values in g from each axis were integrated into a single absolute value reflecting whole logger acceleration using the equation:

$$|g| = [(Xg)^2 + (Yg)^2 + (Zg)^2]^{-2}.$$

Three adult male whitetip reef sharks were used for accelerometry experiments (Table 1). Both internal and external logger attachment techniques were used in this study. For the internal method, sharks were caught in a dip-net and then restrained in a stretcher. A siphon was used to pump tricaine methanesulfonate solution (MS 222, 0.15 g L^{-1}) over the gills. After the sharks were anaesthetized, a lubricated 3 cm diameter PVC pipe was gently inserted through the mouth into the stomach. The data logger was then dropped through the pipe into the stomach along with some bait fish to reduce the probability of immediate regurgitation (Papastamatiou et al. 2007a, 2007b). The pipe was then carefully removed and the shark artificially ventilated until it fully recovered from the anesthetic. The logger cylinder was assumed to lie parallel to the shark's body axis when in the stomach, and this was supported by data from the logger.

For external attachment, a stainless steel anchor barb (3.4× 0.8 mm, Hallprint, Victor Harbor, Australia) was inserted subdermally through a small incision at the base of the dorsal fin. A 3.5 cm leader attached to the anchor terminated in a loop to which the accelerometer tag could be attached. The shark was released and allowed to carry the barb and leader for at least one week to allow for acclimation and wound healing. The shark was then collected again and the logger attached to the leader using a stainless steel spiral ring clip. The negatively boyant logger hung vertically along the side of the shark during periods of rest, and moved back and forth from this position to a horizontal one when carried through the water during swimming.

Logger-equipped sharks were visually monitored at least once every other day over the course of the experiment to look for signs of tag regurgitation or shedding, and to record

Table 1. Shark characteristics and logistical details for three deployments of an acceleration logger.

	Sex	Total Length (cm)	Attachment method	Sampling interval (ms)	Experiment duration* (days)	Cause of ending experiment
Shark 4344	M	134	gastric insertion	500	7.5	logger regurgitated
Shark 0111	M	141	external	1000	17.3	anchor barb shed
Shark 0165	M	146	external	1000	14.6	logger battery died

* Durations are the full period for which the shark carried the logger. Days 1 and 2 were considered the acclimation period for each deployment and were excluded from analyses.

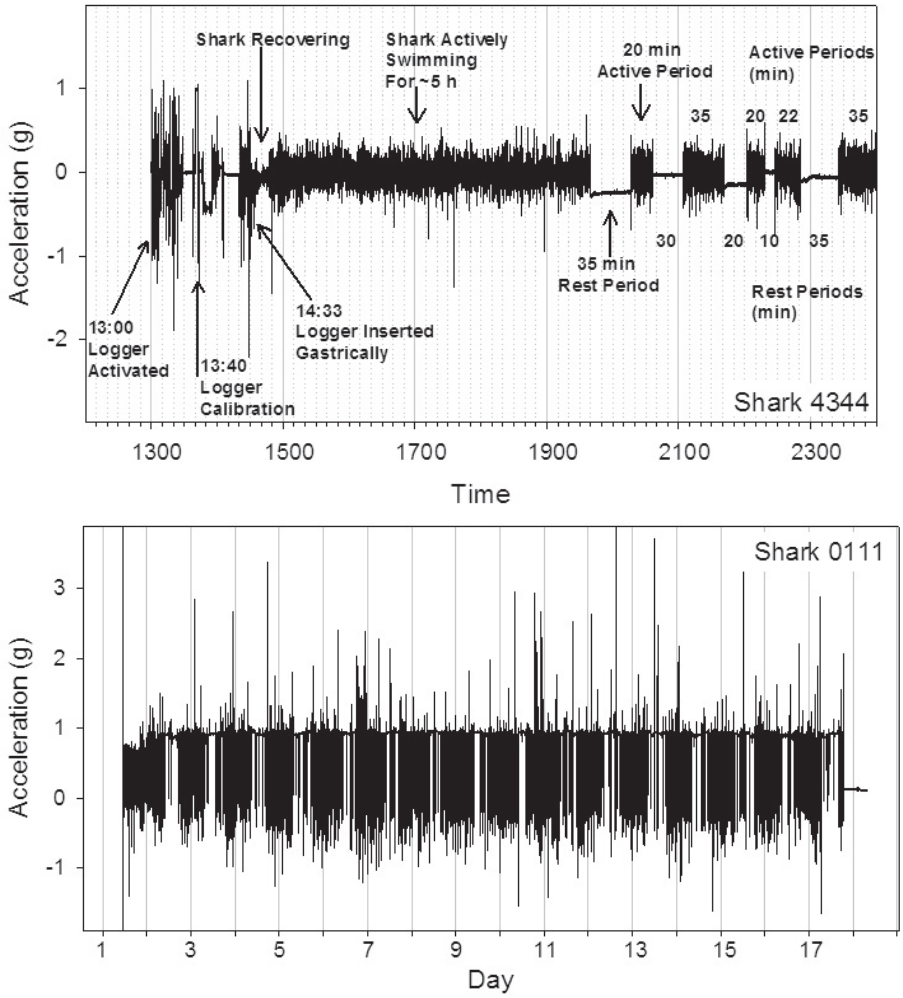

Fig. 2. a) Raw data (*Y*-axis only) from day one of acceleration logger deployment in Shark 4344 showing acceleration signature differences between active swimming and resting behavior. b) *Y*-axis data from the entire 17.3 day deployment for Shark 0111. Grid lines represent midnight.

behavioral observations. Observations lasted 10–30 min, and usually spanned at least one changeover from resting to swimming behavior (occasionally associated with controlled feedings) or vice versa. The time and duration of these behaviors were noted for corroboration with acceleration data. Tailbeat frequency (TBF) was measured for shark 4344 by analyzing video (15 frames s^{-1}) of the shark swimming within the experimental enclosure. Sharks were periodically fed meals of thawed mackerel or capelin to satiation.

At the end of each experiment, the logger was downloaded using a VEMCO computer interface and software which exported the raw data into ASCII files that could be imported into data analysis software. Acceleration data were plotted over time with grid lines at 10 min intervals (e.g. Fig. 2a). Each 10 min interval was visually scored as 1 if the shark was active (swimming) throughout the interval, 0 if the shark was resting, or 0.5 if the shark was active and resting for an equal amount of time over the 10 min period (intermediate proportions were

rounded to the nearest 0.5). These activity scores were then averaged to produce hourly mean proportion of activity values. These hourly values were used to calculate the mean proportion of time spent active for each day, and the mean proportion for each hour of the day averaged over the course of the experiment. Two-sample t-tests were used to compare day versus night (defined by local times of sunrise and sunset) activity levels. A Fast Fourier Transformation (FFT) was used to identify short-period cyclical patterns within bouts of activity in order to determine tailbeat frequency. An FFT decomposes time-series data into frequencies and identifies temporal periodicity in the data-set. A power spectrum is produced with sinusoidal waves of dominant frequencies represented by peaks in the spectrum (Chatfield 1996). All data were smoothed using a Hamming window before applying the FFT. Time series analysis was performed using Statistica (vers. 7.0, Statsoft Inc., Tulsa, OK, USA).

2.3 Respirometry experiments

Two 7-week-old whitetip reef sharks were used for respirometry experiments (Table 2). Both were fasted for 96 hours to ensure that they were in a post-absorptive state prior to being placed in the flume. Measurements of oxygen consumption were made in a 635 l Brett-style re-circulating flume. Details on the flume design are described in Lowe (1996). Sharks were placed in the flume and allowed to acclimate for two hours before the collection of data. Both sharks swam in a typical horizontal orientation or rested on the bottom, actively ventilating via buccal pumping. Water flow velocity was maintained at 20 to 30 cm s^{-1} for each shark. No solid blocking correction was applied because sharks occupied approximately 2% (<10%) of the cross-sectional space of the swimming chamber of the flume (Webb 1971; Lowe 1996).

Once the experiment was initiated, O_2 concentration, water temperature, buccal pumping rate, and swimming activity were recorded throughout. Dissolved oxygen concentration in the water was recorded using a Yellow Springs Instruments (YSI) BOD oxygen probe and a YSI model 57 oxygen meter. The oxygen meter was calibrated prior to each run using Winkler titration. Oxygen concentration, water temperature measurements, activity, and buccal pumping rate were taken every 5 min. Oxygen concentration in the flume was never allowed to drop below 80% saturation. At the completion of each experiment the shark was removed from the flume and a blank was run for 30 min to determine background respiration.

Oxygen consumption rate (MO_2) was calculated using the slope of the change in O_2 concentration over a period of 25 min or more in which the shark showed consistent behavior (actively swimming or resting on the bottom). Mean buccal pumping rate was then calculated for each of these intervals for comparison with MO_2. Standard metabolic rate for each shark was calculated from the interval of slowest linear decrease in O_2 concentration, whereas a measure of the maximum metabolic rate was calculated based on the interval of fastest decrease in O_2 concentration. Routine metabolic rate was based on the grand mean of the MO_2 for all intervals throughout the experiment. Values for day and night MO_2 were log transformed and compared for each shark using a two-sample *t*-test.

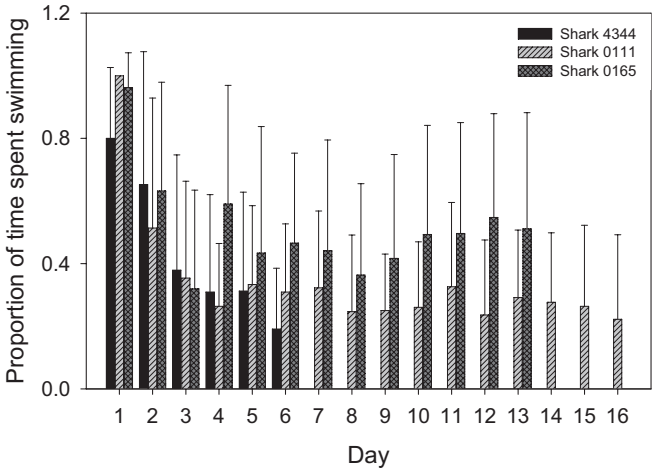

Fig. 3. Mean proportion of time ± SD spent swimming for each shark for all experiment days. Days one and two showed elevated activity levels for all sharks in response to tagging, and were therefore excluded from other analyses of diel activity patterns. The last day of each experiment is excluded because it did not represent a full cycle of diel activity.

3 Results

3.1 Acceleration logger experiments

External logger attachment produced longer deployments than gastric insertion (Table 1), but both methods produced accelerometry data that allowed for clear differentiation between swimming and resting behavior (Fig. 2). All three axes recorded sinusoidal movements during swimming. However, since single-point external attachment and gastric insertion both allowed the logger to roll or sway from water or stomach movements respectively, data from the logger's *X*- and *Z*-axes showed low levels of "noise" even when a shark was at rest. The *Y*-axis was more stable and thus provided a clearer reflection of shark activity because there was almost no movement along this axis when the shark was at rest. Thus only data from the *Y*-axis were used for categorizing swimming versus resting behavior. For the internally tagged animals, *Y*-axis values would typically be near 0 *g* when the shark was resting (Fig. 2a), indicating that the logger cylinder was lying in the shark's stomach parallel, or nearly parallel, to the length of the shark's body and the earth's surface. For externally tagged animals, *Y*-axis values were near +1 *g* when the shark was resting (Fig. 2b). This was due to the single-point attachment method which caused the logger to hang nearly vertically along the side of the shark's body whenever it came to rest.

All sharks showed long periods (5–14 h) of constant swimming immediately after logger insertion or attachment, and remained unusually active for up to 18 h post-tagging. Days 1 and 2 of each deployment thus had artificially high levels of activity (Fig. 3) and were therefore excluded from analyses of

Table 2. Shark characteristics, experiment duration, and metabolic rates (MR) calculated from respirometry. All rates are in units of MO_2 (mg $O_2 kg^{-1} h^{-1}$). Total length (TL).

	Sex	Wet mass (kg)	TL (cm)	Experiment Duration (h)	Standard MR	Routine MR	Maximum MR	Day MR	Night MR
Shark 1000	F	1.48	68	37.4	100.4	157.8	283.2	124.1	190.9
Shark 2000	M	1.60	67	36.0	52.4	82.98	147.6	63.3	101.8

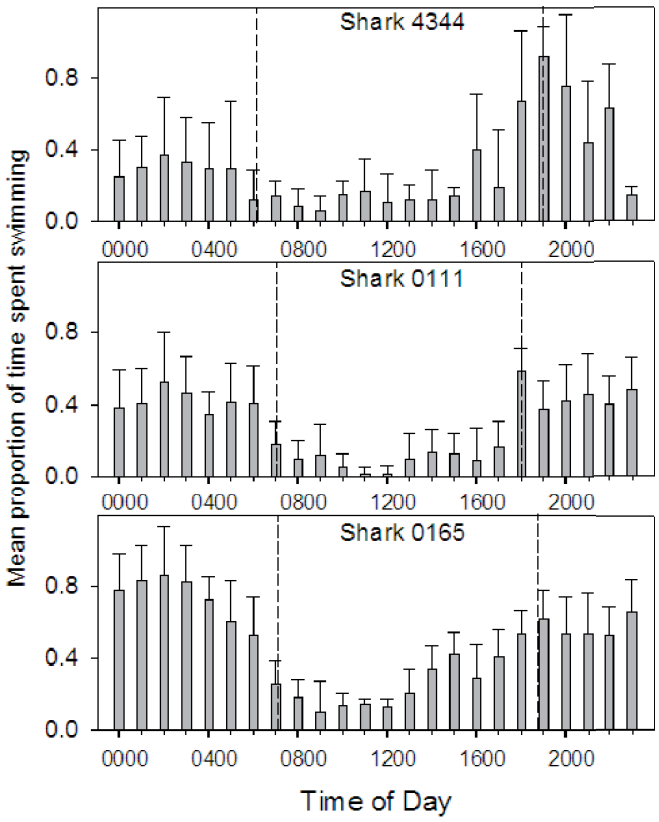

Fig. 4. Mean proportion of time ± SD spent swimming for each hour throughout the diel cycle for each shark. Dashed lines represent times of sunrise and sunset for each experiment.

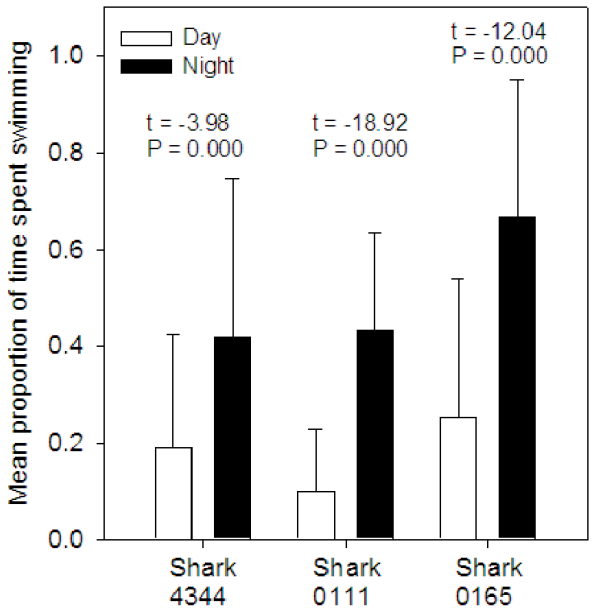

Fig. 5. Mean proportion of time ± SD spent swimming in day versus night from accelerometer experiments for all three sharks. Differences between day and night activity levels were statistically significant for all individuals.

diel activity patterns, as were the bouts of swimming (30 to 45 min) that occurred during controlled feedings.

All animals showed a diel pattern of activity characterized by long periods of resting with brief active periods during the day, and long bouts of swimming with comparatively little rest at night (Fig. 4). All showed relative peaks in activity around sunset, and Sharks 4344 and 0165 showed gradual increases in activity in the hours leading up to sunset. Sharks spent less time swimming during the day (10–24%) than at night (42–67%) and the difference was significant for each shark (Fig. 5). Overall, sharks spent an average of 35 ± 11% (mean ± 1 SD) of their time swimming.

FFT results showed clear peaks in the power spectrum corresponding to the period between tailbeats for the deployment in which a logger sampling rate of 500 ms was used (Shark 4344). These results showed a TBF of 0.89 ± 0.03 (mean ± 1 SD) beats s^{-1} for Shark 4344 based on 22 bouts of swimming over the duration of the deployment. This was consistent with the TBF of 0.9 beats s^{-1} measured from video analysis of brief bouts of swimming. Selection of the largest sampling interval (1000 ms) for the remaining deployments provided enough resolution for differentiating between active and inactive periods, and allowed for longer deployments (22 days of memory space as opposed to 11 days at the 500 ms sampling interval), but was insufficient for determining TBF using FFT.

3.2 Respirometry experiments

Sharks in the respirometry experiments spent most of the time at rest at the bottom of the swimming chamber, with occasional periods of activity that usually lasted less than five minutes in duration. Shark 1000 showed brief signs of agitation (head shaking and/or rapid circular swimming) periodically throughout the experiment, but otherwise showed similar behavior to Shark 2000. All metabolic rates for Shark 1000 were greater than the corresponding values for Shark 2000 by an average factor of 1.92 ± 0.03 (Table 2). Qualitative observations indicated that both sharks showed longer and more frequent periods of activity at night than during the day, producing significantly higher oxygen consumption rates at night (Fig. 6). There was no correlation between oxygen consumption and buccal pumping rate for either shark.

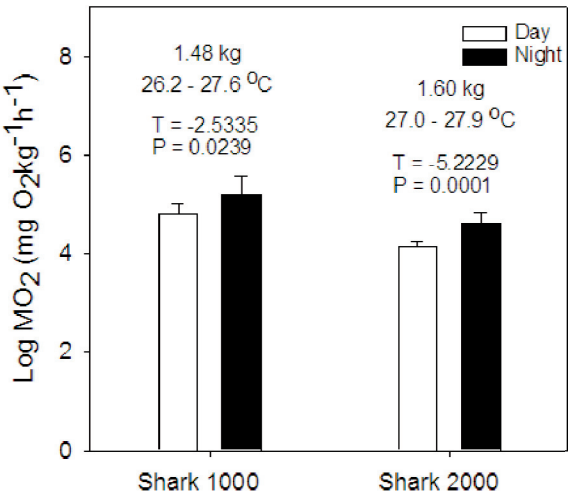

Fig. 6. Mean log oxygen consumption (MO_2) rates ± SD for day versus night from respirometry experiments on two sharks. Both individuals showed significantly higher rates of consumption at night.

4 Discussion

Results from this study show the utility of acceleration loggers in quantifying activity patterns in free-swimming elasmobranchs. Both attachment methods allowed for differentiation between swimming and resting activity, and the diel activity pattern shown by these captive sharks is consistent with observations of free-ranging whitetip reef sharks based on telemetry (Nelson and Johnson 1980) and anecdotal reports (Randall 1977). Increased nocturnal activity is likely an adaptation for foraging, and increases in late afternoon activity seen in Sharks 4344 and 0165 may represent anticipation of the evening crepuscular period and prey species transition (Hobson 1972). No such activity increase was seen at the morning transition.

The large difference in metabolic rates between sharks in the respirometry experiments may be attributable to elevated stress in Shark 1000 but natural variability between individuals cannot be ruled out. The range of SMRs found here overlaps the rate of 95 mg $O_2kg^{-1}h^{-1}$ reported for the lemon shark (*Negaprion brevirostris*; Bushnell et al. 1989), and is less than the 106 mg O_2 $kg^{-1}h^{-1}$ found for the nurse shark (*Ginglymostoma cirratum*; Fournier 1996), both of which are benthic tropical species like the whitetip reef shark. The lack of relationship between buccal pumping rate and MO_2 for either shark suggests that they increased oxygen consumption by increasing their respiratory volume (rather than ventilation rate) or by increasing lamellar recruitment.

Despite the behavioral differences between sharks in the respirometry experiments, both showed higher activity levels (qualitatively) and metabolic rates (quantitatively) at night than during the day. The diel activity patterns of these captive-born neonates thus coincided with those measured using accelerometry in adults, suggesting that these circadian rhythms may be present shortly after birth.

Future work should seek to directly couple accelerometry with respirometry experiments to quantify the relationship between acceleration and oxygen consumption so that energy budgets can be constructed for free-ranging animals. Such work has been done in one elasmobranch using a tail-beat transmitter (but acceleration was not measured, Lowe 2001; 2002), and in a cormorant species using an acceleration data logger (Wilson et al. 2006). The combination of accelerometry with metabolic rate measurements was not possible for this study, as the respirometer chamber could accommodate only very small sharks that could not have carried the logger at its current size. Smaller loggers are now available, but measuring oxygen consumption in adult sharks remains a challenge (Carlson et al. 2004).

The attachment methods and low (1000 ms) sampling intervals employed in this study can be used to measure long-term activity patterns in benthic species that periodically rest on the seafloor, to determine whether certain species are obligate ram ventilators (Lowe and Goldman 2001), or to test for endogenous circadian rhythms in captive studies with controlled light-dark cycles (Nelson and Johnson 1970; Finstad and Nelson 1975). Additional factors should be considered when choosing an attachment method for future studies. External logger attachment would be appropriate if there is a high probability of recapturing the animal, or if the accelerometer was coupled with an acoustic or radio transducer to telemeter acceleration data and eliminate the need for data logger recovery. Gastric insertion may be useful for short deployments in reef shark species, since it provides a natural mechanism (regurgitation) of logger detachment. Retrieval and re-use would then be possible if the logger was fixed to an acoustic transmitter to facilitate data logger relocation.

Multi-point attachment on or near the caudal peduncle and a higher sampling rate may be required to detect more subtle changes in activity in constantly swimming species (Lowe et al. 1998; Lowe 2002), or to quantify specific behaviors that are difficult to observe directly in elasmobranchs (e.g. feeding, agonistic interactions, courtship and mating). Acceleration signatures from these behaviors would need to be corroborated with direct observations initially (perhaps using captive animals), but may then be applicable across species. Mating in particular involves a suite of movements that are similar among different species (Pratt and Carrier 2001; Whitney et al. 2004) and likely to produce highly specific acceleration signatures relative to other behaviors.

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