Diel Oscillations in Whale Shark Vertical Movements Associated with Meso- and Bathypelagic Diving

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Abstract.—A female whale shark *Rhincodon typus* satellite tagged off the coast of Mozambique and moving to the east coast of Madagascar where the tag popped off after 87 d showed increased meso- and bathypelagic diving while crossing the bathymetrically nonconstraining southern part of the Mozambique Channel. After three weeks with daily maximum diving depths in the epipelagic zone at the beginning of the track, when the whale shark stayed close to the Mozambique coast, 44 and 19 d with maximum diving depths in the meso- and bathypelagic zones, respectively, were recorded. On a total of 10 d the whale shark dived to the maximum depth (1,285.7 m) the pop-off tag could record. Quantitative analysis of the diving time series using Fast Fourier Transform identified a diel cycle of vertical movements, with deeper depths occupied during the day and shallower depths during daytime. Using a single bandpass filter to identify where in the time series the diel oscillations were most pronounced showed that they were mostly associated with periods of meso- and bathypelagic diving during the oceanic phase of the long-distance movement. These data indicate that meso- and bathypelagic diving is common for whale sharks in bathymetrically nonconstraining habitat, expanding the habitat of this circumglobal species into the bathypelagic realm, and support the hypothesis that these were dives related to foraging behavior when crossing less productive deep oceanic waters.

Introduction

Deep diving behavior appears to be a ubiquitous search strategy for many large epipelagic vertebrates including both planktivores and macropredators (Carey and Scharold 1990; Block et al. 1992, 2001; Hooker and Baird 1999; Panigada et al. 1999; Boustany et al. 2002; Sims et al. 2003; Hays et al. 2006). However, while deep diving behavior is known to occur, it remains a relatively unexplored activity for the majority of species, and its exact function remains controversial (Carey and Scharold 1990; Bonfil et al. 2005).

Frequent vertical movements of epipelagic fish through the water column have

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been suggested as a strategy to (1) detect concentrations of prey (Josse et al. 1998) or the olfactory clues leading to them (Carey and Scharold 1990; Gunn et al. 1999); (2) to conserve energy, i.e. swim up and glide down strategy (Weihs 1973); (3) as a form of behavioral thermoregulation (Carey and Scharold 1990; Holland et al. 1992), or (4) as a way of orientation or navigation (Klimley et al. 2002). For example, vertical movements of plankton-feeding sharks have been shown to closely reflect the diel movements of zooplankton prey (Sims et al. 2005) while rapid ascents in some pelagic sharks and tuna may be undertaken as part of thermoregulatory behavior to regain heat loss at depth, or to re-oxygenate the gills following time spent in low oxygen layers in the water column, stratifications that are known to occur in tropical waters. Marine vertebrate predators may also exhibit plasticity in their diving and foraging behaviors in response to prey availability (Hays et al. 2006; Miller and Trivelpiece 2008). For example, sperm whales *Physeter macrocephalus* target epipelagic prey but also dive to very deep depths (>1000 m) to search for benthopelagic prey. It appears they feed on more sparsely distributed prey items during shallow dives and more densely distributed prey items during deep dives (Teloni et al. 2008).

One reason for distinct gaps in our knowledge of deep diving among species is that obtaining behavioral information when animals are in remote locations far from land is difficult. Much of the most detailed data on deep diving has been derived from animal-attached (external or implanted internal) data loggers that were physically recovered facilitating downloading of data (e.g., for Atlantic bluefin tuna *Thunnus thynnus thynnus*; Block et al. 2005). However, this is not a viable method for species studied in remote locations, where fishery recoveries are unlikely or where fisheries for certain species are not well developed. Consequently, one important goal is

to obtain behavioral information from diving animals in remote locations where data loggers cannot be recovered, for example, during long-distance migrations into the open ocean. The Argos system of receivers aboard polar-orbiting satellites allows remote collection of data from transmitter-tagged animals over many weeks or even months regardless of the remoteness of movements (Sims 2010).

As apex predators, elasmobranchs occupy a wide range of marine trophic niches from shallow coastal waters to meso- and bathypelagic depths in the open oceans. For fish, there is no constraint on foraging imposed by the need to surface to breathe, so the strategy on where to forage in the water column may be made simply on the basis of prey concentration (Sims and Quayle 1998; Sims 2000; Sims et al. 2003). The whale shark *Rhincodon typus* is a planktivorous epipelagic species that spends the majority of its time above 100 m and often at the water's surface feeding on plankton (Clark and Nelson 1997; Gunn et al. 1999; Eckert and Stewart 2001; Eckert et al. 2002; Graham et al. 2006; Wilson et al. 2006; Motta et al. 2010). But whale sharks are also known to show meso- and even bathypelagic diving when in bathymetrically nonconstraining habitats (Graham et al. 2006; Wilson et al. 2006; Brunnschweiler et al. 2009). Whale shark deep dives have been proposed to represent foraging dives that specifically target prey seeking refuge at depth and to exploit organisms of the deep scattering layer (Wilson et al. 2006). Nevertheless, deep diving by whale sharks is not known from all locations where they are known to occur so it is arguable how regular this behavior is. So, in addition to recent studies that have advanced the understanding of whale shark feeding behavior in relation to available prey resources and oceanographic factors (Nelson and Eckert 2007; Motta et al. 2010), there is a great need to better understand how whale sharks utilize deep water pelagic habitats in poorly studied locations.

In February 2006, a female whale shark was equipped with a pop-off satellite archival tag off the coast of Mozambique and, based on light-level longitude estimates that are typically accurate and robust (Teo et al. 2004), spent the first three weeks in shallow coastal habitat before moving into oceanic waters crossing the southern part of the Mozambique Channel and around the southern tip of Madagascar where the tag prematurely popped off after 87 d (Brunnschweiler et al. 2009). In bathymetrically nonconstraining habitat, this shark performed dives to depths well into the meso- and bathypelagic zones including the deepest dives so far recorded for the species. Here, detailed vertical movement data are provided that support the hypothesis that these were dives related to foraging behavior.

Methods

The female whale shark (estimated length 6–7 m) was equipped with a PTT-100 pop-off satellite archival tag (Microwave Telemetry Inc.) that archived pressure readings at a resolution of ±5.4 m every 15 min to a maximum depth of 1,285.7 m. An emergency release feature was enabled that detached it automatically when the shark was deeper than ~1,250 m for more than 15 min. After pop off, the tag relayed archived data via Argos, including daily maximum depths, archived pressure readings, and longitude estimates that were used for analysis. Due to the size limit of a single Argos transmission, the organization of depth data and their transmission to Argos satellites is optimized by the manufacturer so that a single Argos message can hold 24 readings. To achieve this, only the data recorded on the hours 0000, 0600, 1200 and 1800 and the 15 min readings on those hours are actual recorded values. Depth data recorded at any other time are transmitted as the difference between that time and the pre-

vious hour. This procedure results in a limit to the maximum range the tag can transmit from one depth reading to the next reading an hour later which is 166.8 m for descents and 172.2 m for ascents (Microwave Telemetry Inc., personal communication).

A total of 7,230 archived pressure readings (=87.2%) were transmitted for the time between 19 February and 16 May 2006. Full archival depth datasets (pressure readings every 15 min = 96 depth readings per 24 h) are available for 49 of the 87 consecutive days and, except for Fast Fourier Transform (FFT) analysis (see below), only those were used for analysis of individual dive profiles. Of all archived pressure readings received, 609 are excluded because the whale shark changed depth more than 166.8 m (descent) and 172.2 m (ascent) between hourly readings, respectively, and therefore pressure values do not represent true depth records (see previous paragraph). Overall, the whale shark spent a considerable amount of time in the first 10 m of the water column (Brunnschweiler et al. 2009). Throughout the entire track, 47.6% of the pressure readings were 0 and 5.4 m readings. These readings were defined as the whale shark being at the water surface. An individual dive was defined as the time between the whale shark descending from the water surface until reaching the water surface again. Based on the recorded maximum depth, individual dives were assigned to one of three categories: epipelagic dive (>0 m, <200 m), mesopelagic dive (>200 m, <1,000 m) and a bathypelagic dive (>1,000 m).

All times reported here are local times (GMT + 2–3 h). The whale shark moved in a south-westerly direction along the Mozambique coast before heading eastwards crossing the Mozambique Channel (Brunnschweiler et al. 2009). Time zones were assigned to locations by adding 0.5 h of time for each 7.5 degree increment in longitude. This gives local times of GMT + 2 h for positions between 30°E and 37.5°E, GMT + 2.5 h for positions

between 37.5°E and 45°E, and + 3 h for positions between 45°E and 52.5°E, respectively. Day was defined as the time between 0600 hours and 1759 hours and night as the time between 1800 hours and 0559 hours.

The frequency of dives during the long-distance horizontal movement of the whale shark was examined using FFT analysis (for description see Shepard et al. 2006). Briefly, FFT operates by approximating a function with a sum of different sine and cosine terms. The influence of each periodic component is indicated by the magnitude of the corresponding spectral peak in the periodogram. FFTs can identify periodicities up to the Nyquist frequency, which is half the sampling rate, which in this study was one cycle per 7.5 min (Chatfield 1996).

An FFT was applied to the full 87 (consecutive) day depth record using programming routines in MATLAB (Shepard et al. 2006). Due to Argos data transmission constraints some individual swimming depth data points (at 15 min intervals) were not received. We interpolated between missing data by assigning to the gap the mean of depth readings either side of the gap. The gaps never exceeded 45 min in length (2 consecutive data points missing). These gaps made up 1.3% of the total number of data points, with single missing data points making up a further 10% of the total. However, these were randomly distributed through the depth-time series so were unlikely to confound identification of broader temporal-scale frequency components. The finite, nonstationary nature of the data set means the FFT spectral components can interfere with each other, generating frequency peaks that do not represent true periodicity in dive behavior. Therefore, a 'hamming' window function was applied to reduce effects of adjacent spectral components and to help identify biologically meaningful peaks. In addition, a single band-pass filter was applied to each identified spectral frequency peak to indicate the strength (amplitude) of an identi-

fied frequency in the time domain of the dive series (Chatfield 1996). For example, a spectral frequency of 1 cycle per day (24 h) was used to filter the entire dive series to locate where in the time series a diel rhythm in dive activity was most pronounced.

Results

Epi-, meso- and bathypelagic dive performance

Regular diving behavior was recorded throughout the entire track (Figure 1). A total of 24 d with maximum diving depths in the epipelagic zone were recorded at the beginning of the track (19 February to 11 March) when the whale shark stayed close to the Mozambique coast at usually less than 10 m depth, and on 11 April and 9 and 11 May when the shark was in deep water (Figures 1 and 2a, b). The first mesopelagic dive to a maximum depth of 468.1 m was recorded on 12 March 2006. From then on, a total of 44 and 19 d with maximum diving depths in the meso- and bathypelagic zones, respectively, were recorded (Figure 1).

Epipelagic dives were performed all along the track with the majority of dives performed between 34°E and 37°E while the shark was in shallow coastal water and 47°E and 49°E while it was in the deep Madagascar Basin southeast of Madagascar, respectively (Figure 2a, 2b). Of a total of 129 epipelagic dives to depths >50 m, 79.1% were performed during the night and 14.7% during the day (descent and ascent between 1800 hours and 0559 hours and between 0600 hours and 1759 hours, respectively), indicating high epipelagic diving activity during the night (Figure 3a). Meso- and bathypelagic dives were recorded between longitudes 38°E and 51°E (Figure 2a) in deep water with bottom depths >4,000 m when the shark was either crossing the southern
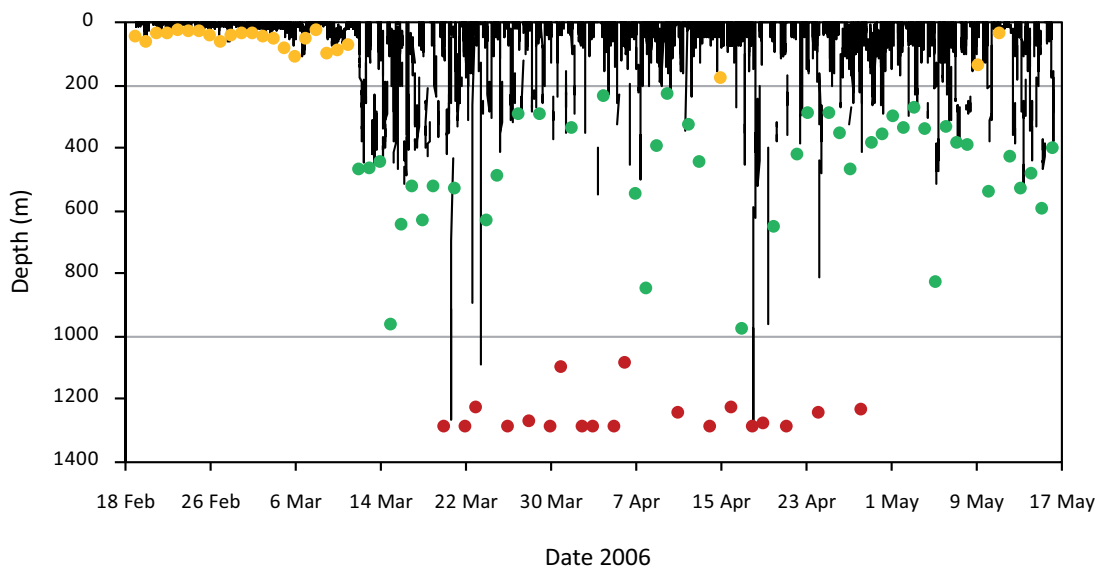
FIGURE 1. Time-depth series of the entire 87 d track (6,621 pressure readings; see Methods for details) and daily maximum depths recorded by the tag in the epipelagic (yellow), mesopelagic (green) and bathypelagic (red) zones. The two horizontal lines at 200 m and 1,000 m indicate the defined zones of diving depth.

part of the Mozambique Channel or was in the deep Madagascar Basin southeast of Madagascar (Figure 2b), near or in cyclonic (spiraling in clock-wise direction) or anti-cyclonic eddy systems (Figure 2c).

Fifty dive profiles included maximum depths in the meso- and bathypelagic zones. Of these, 44% were performed during the day and 10% during the night, indicating a higher deep diving activity during the day (Figure 3b). Except for four mesopelagic dives, all profiles showing the whale shark diving to the meso- or bathypelagic zones had pressure values of unknown depth (see Methods for details; maximum pressure readings unknown = 70%; mean ± SD = 33.2 ± 19%). In the majority of cases, readings that indicate the shark to be deeper than the transmitted depth value were recorded at the beginning of a dive whereas readings that indicate the fish to be less deep were recorded at the end of individual dives. Three dive profiles included actual recorded depths in the bathypelagic zone: on 20 March the whale shark

was recorded at 1,264.2 m at 2045 hours, on 23 March at 1,086.7 m at 1515 hours, and on 18 April at 1,285.7 at 0315 hours. Two of these profiles and one mesopelagic dive profile show that the whale shark dived from the epipelagic zone straight to or into the bathypelagic zone at an estimated swimming speed of ~0.9 m s⁻¹ (Figure 4).

Dive periodicity

The periodogram calculated for the whale shark had large spectral peaks near zero cycles per day (Figure 5a). This was a consequence of the dive data being offset by the mean dive depth, so only peaks following this initial slope represented periodic signals in the diving time series. Hence, those at or very near zero were ignored as they were not the product of biological signals. For the full dive record there was a pronounced spectral peak at a frequency of 24 h (1 cycle per day) (Figure 5a, 5b). The once daily (diel) signal was not strongly
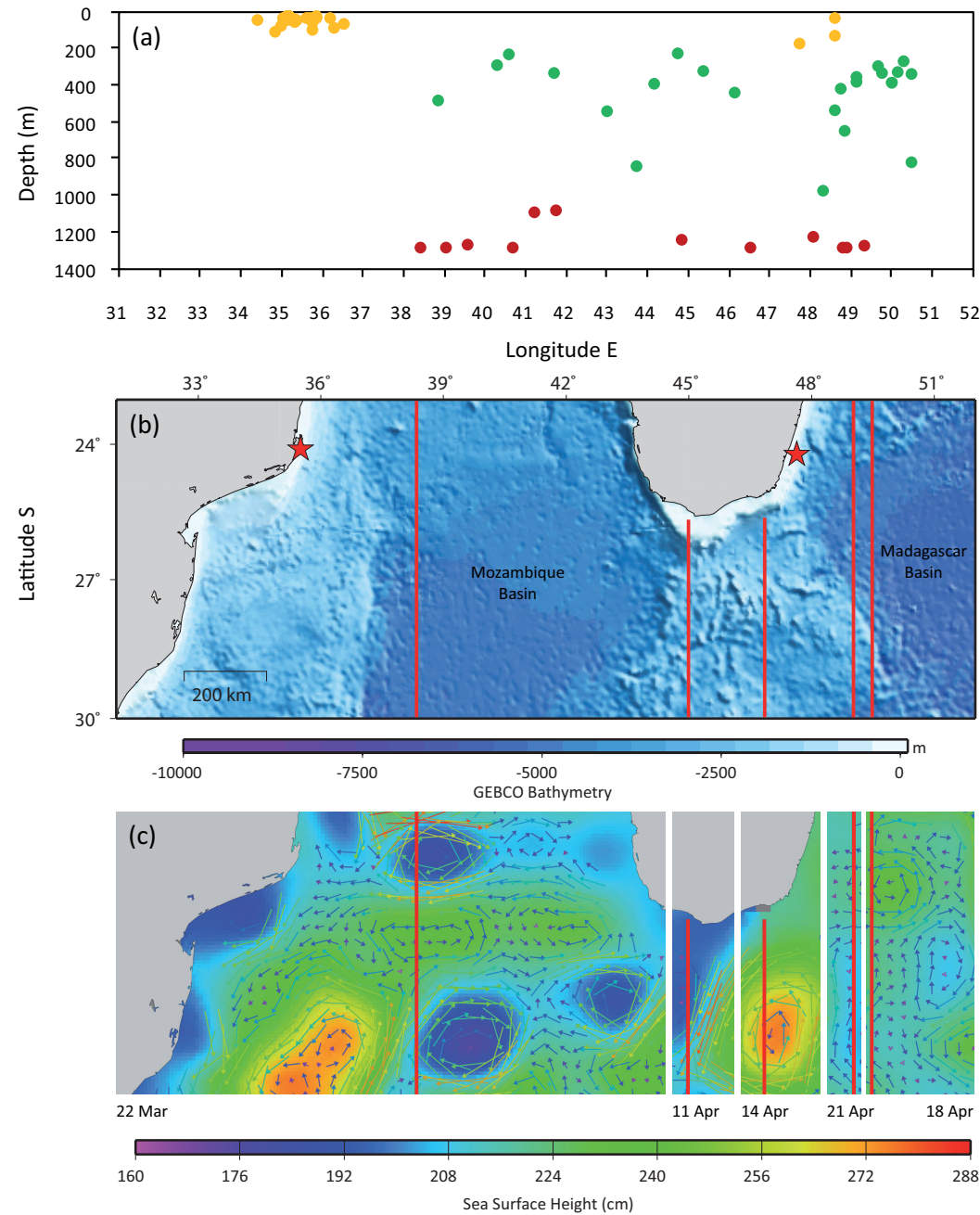
Figure 2. (a) Maximum depths in the epipelagic (yellow), mesopelagic (green) and bathypelagic (red) zones at daily longitude estimates (estimated error ± 0.5°). (b) Bathymetric map of the geographic area where the whale shark crossed the Mozambique Channel. The red stars off the coast of Mozambique and south-east of Madagascar indicate the positions where the shark was tagged and from where the first satellite uplink was received. (c) Longitudinal positions (red lines) on sea surface height and geostrophic current maps of five days with maximum diving depths of 1,285.7 m (22 March, 14, 18 and 21 April) and 1,242.8 m (11 April).
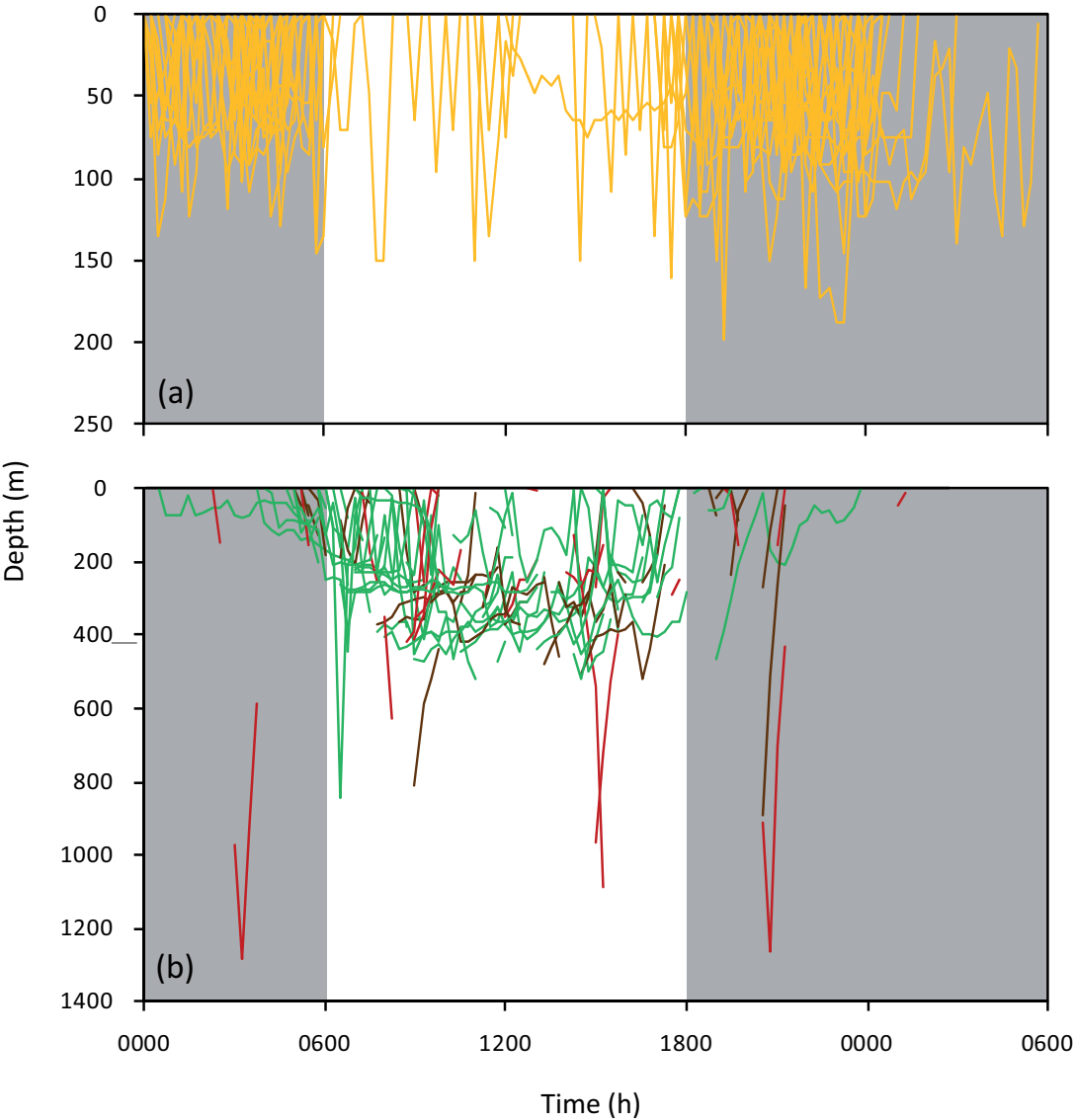
FIGURE 3. Depth profiles of (a) 129 epipelagic dives and (b) 28 mesopelagic (green), 10 bathypelagic (red) and 12 dives with maximum depths >200 m (brown). Gray shaded areas denote night.

present in the dive depths when the shark was on the Mozambique shelf, but was very strong when it moved into deep water and started the meso- and bathypelagic diving (Figure 5b, 5c). In support of this, the periodicity declined slightly in strength before becoming stronger when the second phase of bathypelagic diving occurred (Figure 5b, 5c).

Discussion

Detailed vertical movement data for sharks in deep oceanic waters are scarce. The deep diving profiles presented here are the first such data available for any shark species, including the deepest ever recorded dives to date for this circumglobal species, and therefore clearly expanding its habitat into the
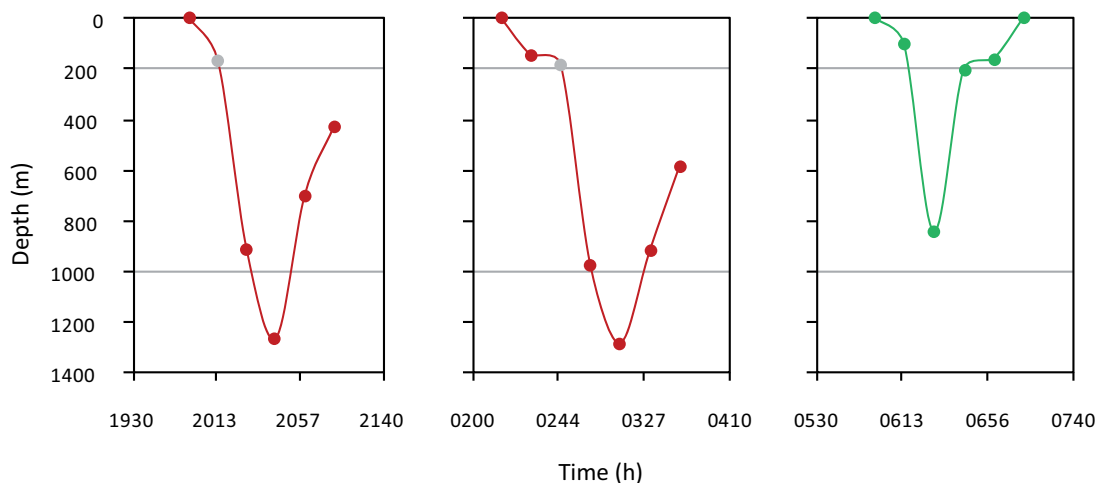
FIGURE 4. Two bathypelagic (red) dive profiles showing the descent to the maximum depth and one full mesopelagic (green) dive profile. Red and green dots represent archived depth readings every 15 min. Gray dots are minimum depth estimates and do not represent actual depth values (see Methods for details). The two horizontal lines at 200 m and 1,000 m indicate the defined zones of diving depth.

bathypelagic realm. The finding that on 22% of days the maximum dive depths were below 1,000 m indicates that such bathypelagic dives are common for whale sharks in bathymetrically nonconstraining habitat.

Overall, epipelagic dives were mostly observed during the night when plankton is generally closer to the water surface while considerably more meso- and bathypelagic dives were performed during the day (descent and ascent between 0600 hours and 1759 hours) when plankton can be found at greater depths compared to nighttime. This diel pattern was supported quantitatively by FFT analysis, and the pattern is consistent with other studies showing vertical behavior of planktivorous shark species to be a response to diel vertical migrations of their prey (Nelson et al. 1997; Sims et al. 2005; Wilson et al. 2006). The analysis of dive profiles can yield valuable information about the probable purpose of deep dives in marine vertebrates (Amano and Yoshioka 2003; Miller et al. 2004; Watwood et al. 2006, Bost et al. 2007), but because of missing actual depth values, it was not possible to reconstruct the majority of meso- and bathypelagic dive profiles with confidence in

this study. Nevertheless, the distribution of missing depth values within individual dive profiles, as well as three reconstructed profiles (Figure 4) indicate that the whale shark dived directly from the epipelagic zone to maximum dive depths at or in the bathypelagic zone at swimming speeds similar to that of surface feeding whale and basking sharks *Cetorhinus maximus* (Sims 2000; Motta et al. 2010). Additionally, the fact that, despite 19 d with maximum depths in the bathypelagic zone being recorded, the tag's emergency release feature was not triggered indicates that the shark only briefly dived into the bathypelagic zone.

The purpose of deep dives to mesopelagic habitats and beyond in this planktivorous shark species remains unknown but is consistent with a general pattern for behavioral plasticity known from a wide range of marine vertebrate predators (Bonfil et al. 2005; Hays et al. 2006; Wilson et al. 2006). Whale sharks are well known to feed on seasonal plankton-rich surface waters and predictable food sources close to coasts and/or reefs (Clark and Nelson 1997; Gunn et al. 1999; Heyman et al. 2001; Wilson et al. 2001; Graham et al.
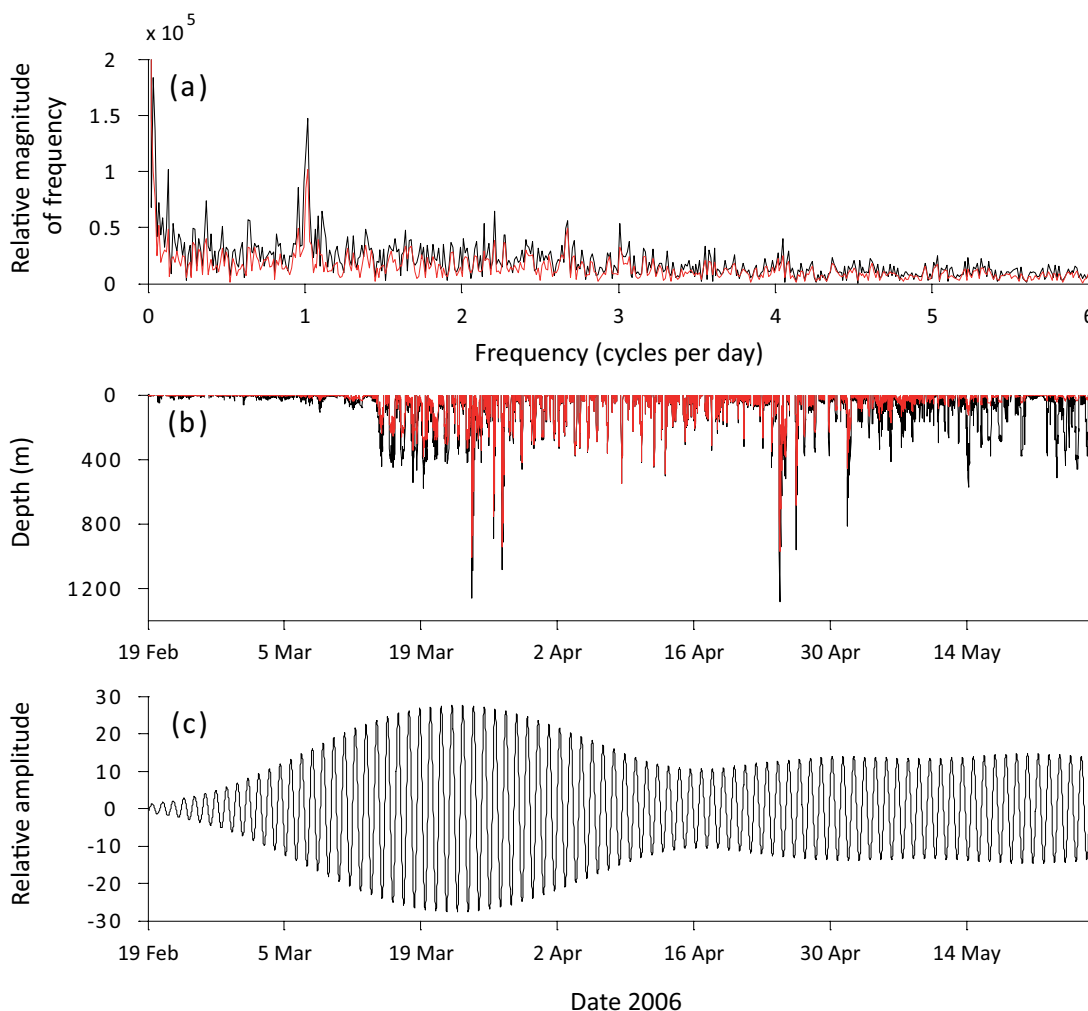
Figure 5. Diel oscillations during the oceanic phase of the whale shark's movement. (a) Fast-Fourier Transform generated periodogram for swimming depth indicates vertical movements with a period of 24 h (1 cycle per day). (b) The time series of swimming depths of the female whale shark. (c) Application of a single band-pass filter in the time domain for a periodicity of 1 cycle per day indicate diel dive patterns were most pronounced (greater y-axis amplitude) when meso- and bathypelagic diving occurred in the oceanic phase of long-distant movement. Red lines are results using the hamming window (see Methods for explanation).

2006; Nelson and Eckert 2007; Taylor 2007; Motta et al. 2010), but it remains largely unknown how whale sharks behave when moving between distant seasonal food patches. A possible hypothesis is that they cross less productive deep oceanic waters at relatively high speed to reach distant food-rich patches (Brunnschweiler et al. 2009; Sleeman et al. 2010). Crossing less productive deep oceanic surface waters might trigger deeper dives that aim to explore for feeding opportunities at greater depths. For example, the region south of Madagascar is a source of mesoscale eddies which drift westwards across the southern end of the Mozambique Channel reaching to the channel bottom and in which core water masses with different geophysical properties mix at various depths (de Rui-

jter et al. 2002, 2004; DiMarco et al. 2002; Quartly and Srokosz 2004). Such physical processes are known to have a structuring role on spatial dynamics and foraging strategy, influence movements and modify the diving behavior of marine predators (Cotté et al. 2007; Lambardi et al. 2008; Bailleul et al. 2010; Kai and Marsac 2010; Mencacci et al. 2010). Additionally, dissolved oxygen concentrations found at the southern end of the Mozambique Channel are generally higher compared to the northern tropical region (Di-Marco et al. 2002). For example, at 500 m, an oxygen maximum with high nutrient concentration levels (Wyrtki 1971) spanning the full width of the southern part of the channel can be observed. Such nutrient rich waters might attract planktivorous species resulting in increased deep diving by feeding whale sharks.

The clear diel oscillation in the depth record supports results found previously in quantitative analyses of dive patterns in whale sharks (Graham et al. 2006) and for basking sharks (Shepard et al. 2006). However, in this study it was evident that the diel rhythm was most pronounced when the female whale shark conducted deep diving to meso- and bathypelagic depths during the oceanic phase of the long-distance movement. The fact that the diving behavior of only one, presumably immature (Norman and Stevens 2007), individual was available for analysis precludes us from firmly concluding that foraging within the water column to great depths is a typical behavior of the whale shark. Intraspecific plasticity in behavior are known from a range of oceanic fishes (e.g., Pade et al. 2009; Sims et al. 2009; Queiroz et al. 2010) and we therefore strongly encourage future studies to analyze, where possible, individual deep diving profiles from whale sharks of different size classes and from different geographic areas to determine whether or not deep foraging dives constitute 'normal' behavior.

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