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## REPORT

## Diving behaviour of whale sharks in relation to a predictable food pulse

Rachel T. Graham<sup>1,†</sup>, Callum M. Roberts<sup>2</sup>  
and James C. R. Smart<sup>2</sup>

<sup>1</sup> Wildlife Conservation Society, PO Box 37,  
Punta Gorda, Belize

<sup>2</sup> Environment Department, University of York,  
York YO10 5DD, UK

We present diving data for four whale sharks in relation to a predictable food pulse (reef fish spawn) and an analysis of the longest continuous fine-resolution diving record for a planktivorous shark. Fine-resolution pressure data from a recovered pop-up archival satellite tag deployed for 206 days on a whale shark were analysed using the fast Fourier Transform method for frequency domain analysis of time-series. The results demonstrated that a free-ranging whale shark displays ultradian, diel and circa-lunar rhythmicity of diving behaviour. Whale sharks dive to over 979.5 m and can tolerate a temperature range of 26.4 °C. The whale sharks made primarily diurnal deep dives and remained in relatively shallow waters at night. Whale shark diving patterns are influenced by a seasonally predictable food source, with shallower dives made during fish spawning periods.

**Keywords:** elasmobranch; circadian; rhythmicity; Fourier transform; satellite telemetry; diving behaviour

Whale sharks are coastal-pelagic zooplanktivores distributed throughout the world's tropical seas (Gudger 1915; Colman 1997). A highly migratory species capable of transoceanic movements (Eckert & Stewart 2001), whale sharks are threatened by overfishing, primarily taking place in SE Asia and the Indian Ocean (Fowler 2000). Whale sharks are designated as globally 'vulnerable' to extinction by the World Conservation Union in the 2000 Red List of Endangered Species of Fauna and Flora (Hilton-Taylor 2000) and are one of three shark species to be listed on Appendix II of the Convention for the International Trade in Endangered Species which monitors and regulates the trade in designated species.

Knowledge of the whale shark's ecology and behaviour remains limited particularly regarding its diving behaviour. Three studies using acoustic telemetry and satellite tags, respectively, have yielded

data on diving patterns suggesting that whale sharks are a shallow epipelagic species that spend the majority of their time above 240 m (Gunn *et al.* 1999; Eckert & Stewart 2001; Eckert *et al.* 2002). They further make brief oscillatory or 'yo-yo' dives interspersed with less frequent deep dives (Eckert & Stewart 2001), a form of diving found in several species of sharks (Carey & Scharold 1990; Nelson *et al.* 1997; Klimley *et al.* 2002). These diving patterns in sharks are thought to be regulated by circadian rhythms (Finstad & Nelson 1975), which may be synchronized by the environmental light : dark cycle (Carey & Scharold 1990; Nelson *et al.* 1997).

To investigate the patterns of diving in whale sharks on the Mesoamerican Barrier Reef, particularly in relation to a predictable food source, nine whale sharks were tagged with 11 pop-up archival satellite tags (PAT-Models 1 and 2; Wildlife Computers, Redmond, WA, USA) at the Gladden Spit Marine Reserve, Belize, in 2000 and 2001 (table 1). Of these, four tags yielded 3 h histogram summary data on temperature (°C), depth (m) and irradiance (wavelength of 550 nm) for a total of 15, 40, 188 and 206 days, respectively. The depth sensors are calibrated from 0 to 100 m accurate to  $\pm 1$  m, and 100 to 1000 m accurate to  $\pm 1\% + 0.5$  m, and temperature sensors are calibrated to  $\pm 0.2$  °C. Archived data recorded maximum dive depth to 979.5 m. The tags and sensors were pressure tested to 1500 m by the manufacturer. The release mechanism on shark S4 attached on 11 April 2001 malfunctioned and the tag was opportunistically removed from the juvenile male whale shark (6.7 m total length) following its return to the Gladden Spit on the 28 March 2002. S4 yielded a full archival data set of the ambient depth, temperature and light levels recorded every 60 s for 206 days while deployed on the shark. Tag deployments coincided with the predictable near-surface spawning aggregation of snappers *Lutjanus cyanopterus* and *L. jocu* following the full moon (FM) periods in March through June. The spawn produced by the reproducing snappers attracts a seasonal feeding aggregation of whale sharks (Heyman *et al.* 2001).

The data on depths and temperatures were extracted from the tags using the manufacturer's software (PAT Host v. 1.1, Wildlife Computers, Redmond, WA). S4's archival data revealed that the whale shark dived to over 979.5 m—representing the manufacturer's maximum depth recording for archival data—six times over the course of 206 days and tolerated a temperature range of 26.4 °C (range: 30.8–4.4 °C). By comparison, the endothermic white shark (*Carcharodon carcharias*) reaches a depth of 680 m and tolerates a temperature range of 21.2 °C (Boustany *et al.* 2002). Sharks S1–S3 also made dives beyond 979.5 m to temperatures below 7.6 °C. A whale shark may be able to withstand low temperatures due to its subcutaneous fat layer (Graham 2003). Moreover, it is highly likely that S4 dived to beyond the tag sensor's depth limitations (1500 m) as the tag recorded a seventh and final deep dive on 30 October 2001, after which all sensors and the release mechanism failed and no further data were recorded (R. Hill, Wildlife Computers, 2002, personal communication).

Sharks S1–S4 spent the greatest proportion of their time in 50–250 m based on a comparison of time spent

<sup>†</sup>Author for correspondence (rgraham@wcs.org).

Table 1. Summary of 11 PAT tag deployments and detachments for nine whale sharks. (All deployments took place at Gladden Spit at 16° 30' N, 87° 57' W. JM, juvenile male; MM, mature male; ?, sex unknown; NA, data not available.)

satellite tag number and model	size (m) <sup>a</sup>	sex	original duration of deployment (days)	deploy date	pop-up date	maximum depth (m)	maximum water temperature (°C)	minimum water temperature (°C)
S1 (PAT 1)	5.5	JM	14	23 Apr 2000	7 May 2000	>980	>30.0	<7.6
S2 (PAT 1)	3.6	JM	40	23 Apr 2000	2 Jun 2000	>980	28.6	<7.6
S3 (PAT 2)	9.7	MM	188	11 Apr 2001	15 Oct 2001	>980	30.6	<7.6
S4 <sup>a</sup> (PAT 2)	6.7	JM	248	11 Apr 2001	removed	>980	30.8	4.4
S5 <sup>b</sup> (PAT 1)	6.7	JM	14	21 Apr 2000	6 May 2000	>650	>30.0	<12.6
S6 <sup>c</sup> (PAT 1)	5.5	?	105	25 Apr 2000	8 Aug 2000	NA	NA	NA
S7 <sup>c</sup> (PAT 1)	5.5	?	40	25 Apr 2000	12 Jun 2000	NA	NA	NA
S8 <sup>d</sup> (PAT 2)	5.2	JM	127	16 Mar 2001	31 July 2001	NA	NA	NA
S9 <sup>d</sup> (PAT 2)	6.7	JM	187	11 Apr 2001	30 Jun 2001	NA	NA	NA
S10 <sup>d</sup> (PAT 2)	5.2	JM	163	11 Apr 2001	–	NA	NA	NA
S11 <sup>e</sup> (PAT 2)	5.5	?	249	10 May 2001	3 July 2001	NA	NA	NA

<sup>a</sup> Tag was recovered directly from the shark in March 2002.<sup>b</sup> Tag provided pop-off location and an incomplete set of data only.<sup>c</sup> Tag fell off prematurely, sank to the sea-floor but popped off on time and reported data.<sup>d</sup> Tag failed to report position and data.<sup>e</sup> Tag reported position but failed to report data.

in five depth bins (0–50, 50–250, 250–500, 500–1000, >1000 m; Kruskal–Wallis test:  $\chi^2_4=320.2$ ;  $p<0.001$ ) and S4's longer term deployment revealed a mean depth of  $58\pm 44$  m s.d., indicating that the whale sharks are primarily epipelagic. S1–S4 spent over 80% of their time in waters 25–30 °C, which further suggests that whale sharks are spending the majority of their time above 100 m based on tag records of temperatures at depth noted for all sharks.

Three of S4's six >979.5 m dives recorded occurred within a six-day period (dates in 2001: 29 May; 1 July; 25 July; 28 July; 31 July; 14 September). In deep dives, ascents were significantly faster than descents (descent: range 38–98 min,  $\bar{X} 52.9$  min  $\pm 22.2$  s.d.; ascent: range 32–72 min,  $\bar{X} 29.7$  min  $\pm 15.3$  s.d.; Wilcoxon paired ranks test:  $z=-1.992$ ;  $p<0.05$ ). The fastest ascent recorded from dives >979.5 m ( $n=6$ ) to the surface was 32 min,  $25.5$  m min $^{-1}$  or  $3.8$  BL min $^{-1}$  (body-length min $^{-1}$ ) or  $0.06$  BL s $^{-1}$  for the 6.7 m shark. Rapid ascents might be undertaken as part of thermoregulatory behaviour, 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 (Conkright *et al.* 2002).

Several shark species display differences in day versus night diving patterns (Carey & Scharold 1990; Klimley *et al.* 2002). To test whether whale sharks displayed the same behaviour, diving depths attained during night and day were compared. Sharks S1–S4 dived significantly deeper during the day than at night (3 h data summaries: day  $N=905$ , night  $N=887$ ; Mann–Whitney  $U$  test:  $z=-8.460$ ;  $p<0.001$ ). Not all days of deployment provided usable data due to data dropout during transmission.

Since 1999, researchers, fishermen and tour operators have noted that fewer sharks were sighted in the two-week period following the cessation of snapper spawning. This roughly coincides with the new moon (NM) and first quarter moons of April to June as compared to the FM and last quarter moon (LQ) periods

(R. Graham, E. Cuevas, E. Leslie and G. Eiley, personal observation). To determine whether whale sharks modulate their diving behaviour in relation to snapper spawning and the lunar phase, maximum dive depths for S1–S4 were compared within spawning and non-spawning periods. Peak snapper spawning periods from March through June 2000 and 2001 are based on cumulative monthly underwater observations of snapper spawning periodicity at Gladden Spit, Belize (Graham 2003). Dive depths during the FM and LQ phases were compared to depths recorded during the NM and first quarter moon (FQ) phases. These periods coincide with the onset and duration of snapper spawning and the absence of spawning, respectively. Between April and June 2000 and 2001, S1–S4 dived significantly deeper in the new moon–first quarter (NMFQ) periods once spawning was no longer occurring (Wilcoxon's test;  $z=-4.089$ ;  $p<0.001$ ) and spent longer at depth. Outside the peak snapper spawning season, (from July 2001 onwards), there was no significant difference in maximum depths reached for S3 and S4 during the FM and NM periods (paired samples  $t$ -test;  $t(73)=-0.026$ ;  $p=0.979$ ). The magnitude of differences in the means was very small ( $\eta^2=0.000\ 01$ ) indicating that the shark's diving behaviour is linked to timing of snapper spawning but is probably not directly influenced by the lunar phase outside of the spawning season.

Archival depth data for S4 ( $N=252\ 429$  data points) were further analysed using the fast Fourier Transform (FFT) technique (Lynn 1973). The FFTs are used widely in time series analysis (Greene 2003) and population studies (Krebs 1989) to identify rhythmic patterns (periodicities) within time series data. The FFT decomposes a stream of time series data into a constituent spectrum of sinusoidal components of different frequencies, and hence different periodicities (e.g. figure 1). The strength of each periodicity within the time series data is indicated by the magnitude of the corresponding frequency in the frequency spectrum (frequency = 1/period). A purely sinusoidal periodicity

in the time series data generates a single component in the frequency spectrum, whereas non-sinusoidal patterns, such as a regularly spaced sequence of steep-sided notches, generate a whole series of harmonic components in the frequency spectrum. The magnitude of these harmonics reduces as harmonic frequency increases (Lynn 1973).

The maximum frequency which the FFT reports reliably in the frequency spectrum is half that of the time series data collection (i.e.  $f_{\text{sampling}}/2$ ). The resolution between adjacent frequencies in the frequency spectrum ( $\Delta f$ ) is dictated by the length of the data collection sequence ( $N$ ) and the sampling frequency

$$\Delta f = \frac{f_{\text{sampling}}}{N}.$$

The FFT-generated spectrum contains  $N/2$  frequency components, separated by  $\Delta f$ , over the frequency range  $0-(1/f_{\text{sampling}})$  (Hz). The frequency spectrum produced from our full S4 dataset ( $N=252\,429$ ,  $f_{\text{sampling}}=1/60$  Hz), thus contains 126 214 separate frequency components, separated by  $6.6 \times 10^{-8}$  Hz, over the frequency range  $6.6 \times 10^{-8}$ – $8.3 \times 10^{-3}$  Hz (corresponding to periodicities of 175.3 days–2 min, respectively).

## 1. FFT ANALYSIS

Straightforward application of a MATLAB FFT routine (The Mathworks, Natick, MA; Duhamel & Vetterli 1990) to the full record of depth data produced a frequency spectrum with prominent peaks at periods of 45 min, 8 h, 24 h and a ‘monthly’ periodicity (figure 1). This indicates that strong rhythmic components at these periodicities were present within the depth record of this whale shark. The depth data were sub-divided (‘windowed’) (a) by time and (b) by depth to provide further insights into behaviour.

### 1.1. Windowing by time

Depth data collected during full moon–last quarter (FMLQ) lunar half-cycles were separated from data collected during NMFQ lunar half-cycles. The full data record covered six complete lunar months, producing 12 separate lunar half cycles in all. The peak spawning period of the snapper spp. occurred during the FMLQ lunar half-cycle during only the first three of these lunar months. Separate frequency spectra were generated by FFT for each lunar half-cycle. The results are shown for lunar months which contained peak snapper spawning aggregations (figure 2) and those which did not (figure 3). Frequency spectra for the FMLQ lunar half-cycles clearly differ from those during NMFQ half-cycles in months when peak spawning aggregations occurred (paired samples *t*-test on mean magnitude of spectral components over frequency range 0–50 cycles per day between FMLQ and NMFQ lunar half cycles:  $t=4.35$ ,  $d.f.=2$ ,  $p=0.049$ ). No such difference is evident in lunar months which contained little or no spawning activity ( $t=-0.34$ ,  $d.f.=2$ ,  $p=0.763$ ). The reduced magnitude evident across the frequency spectrum during FMLQ in lunar months with spawning aggregations is consistent

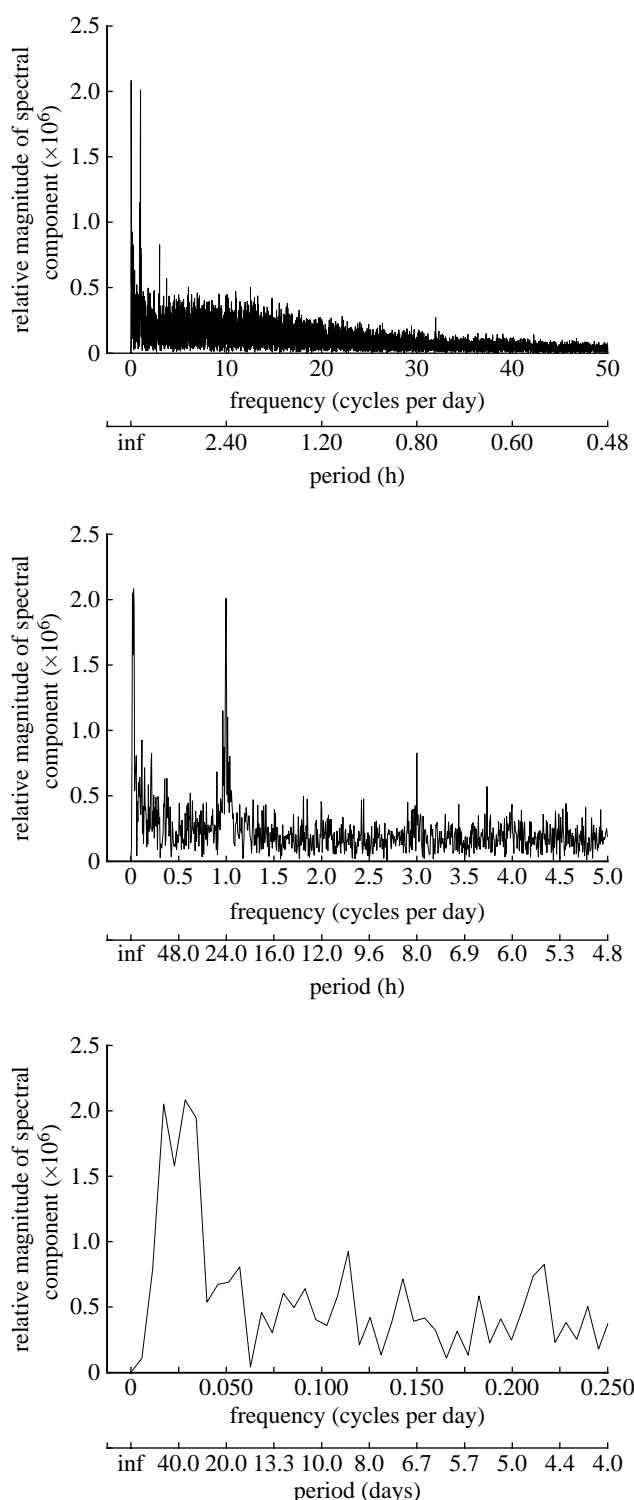


Figure 1. Frequency spectrum produced by FFT from the depth record of a tagged whale shark. Spectrum displayed with different horizontal expansion.

with observed behaviour, i.e. increased time spent near the surface. These results are supported by the non-archived summary PAT tag data from three whale sharks where relaxation of deep diving occurred during snapper spawning periods.

### 1.2. Windowing by depth

The full S4 depth record was truncated separately at depths of 500, 400, 300, 200, 100 and 50 m. In each

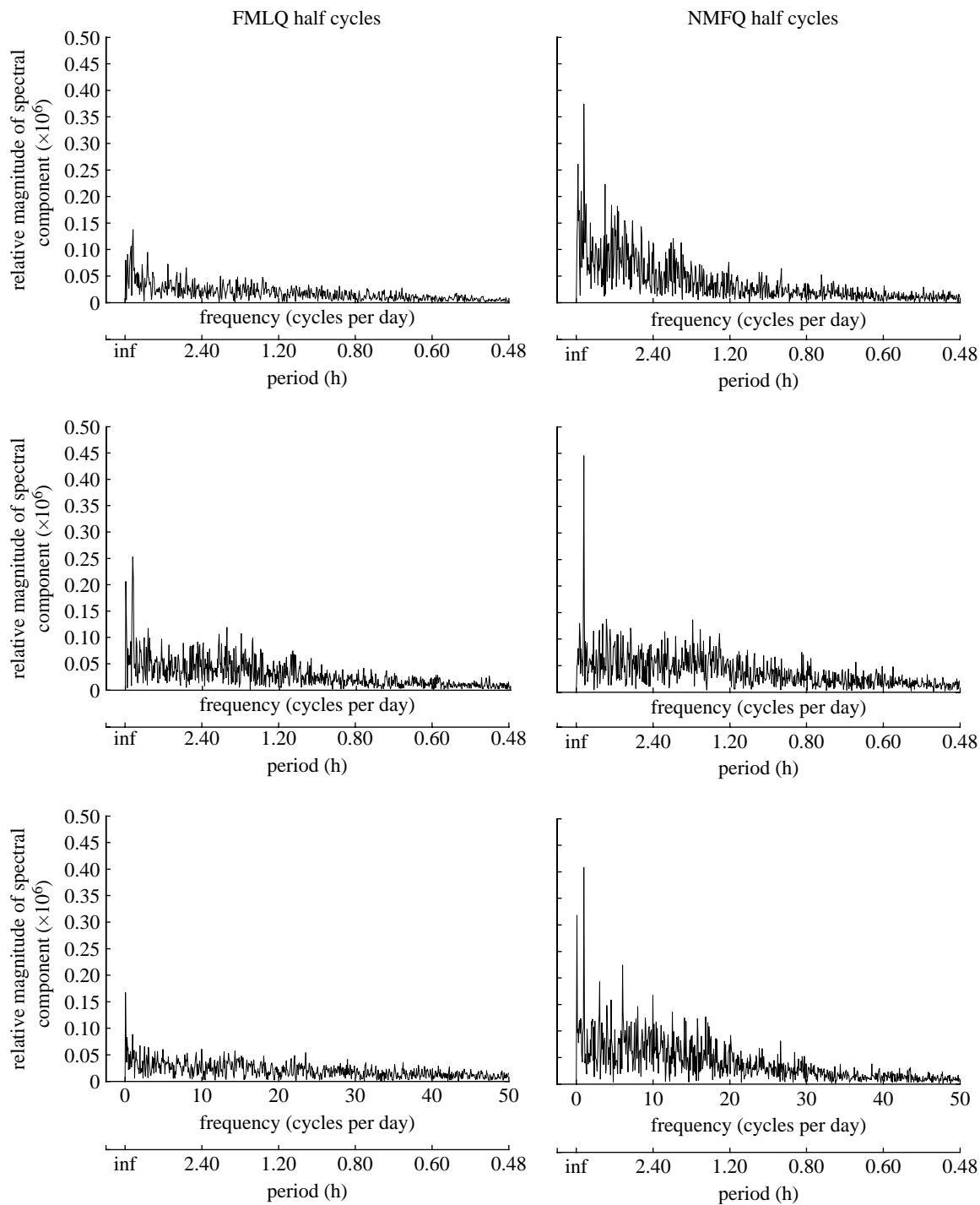


Figure 2. Frequency spectra of whale shark depth record for lunar half phases (FMLQ versus NMFQ) for lunar months in which a snapper spawning aggregation occurs during the FMLQ half phase.

case, depths below the truncation depth in the data record were replaced by the truncation depth itself. This simple truncation preserved the time relationship between data points at shallower depths in all cases. The separate frequency spectra were generated by FFT for each of these truncated depth records (figure 4). The 45 min, 8 h, 24 h and 'monthly' periodicities were present in the <500, <400 and <300 m depth spectra at magnitudes which are almost identical to those in the non-truncated data, suggesting that these periodicities are primarily upper water phenomena, associated with movements at less than 300 m depth (figures 1 and 4). The successive truncation of the data at depths of 200,

100 and 50 m reduced the strength of all these periodicities (figure 4). The 45 min periodicity disappeared completely when the data were truncated at 50 m, suggesting that this periodicity is associated with movements between 50 and 300 m.

## 2. ANALYSIS OF DEEP DIVING

The time series depth data contained 49 deep dives to below 500 m lasting 5 min or more (Graham 2003). If the deep dives were distributed at random throughout the depth record then the time intervals between successive deep dives would be distributed according to the

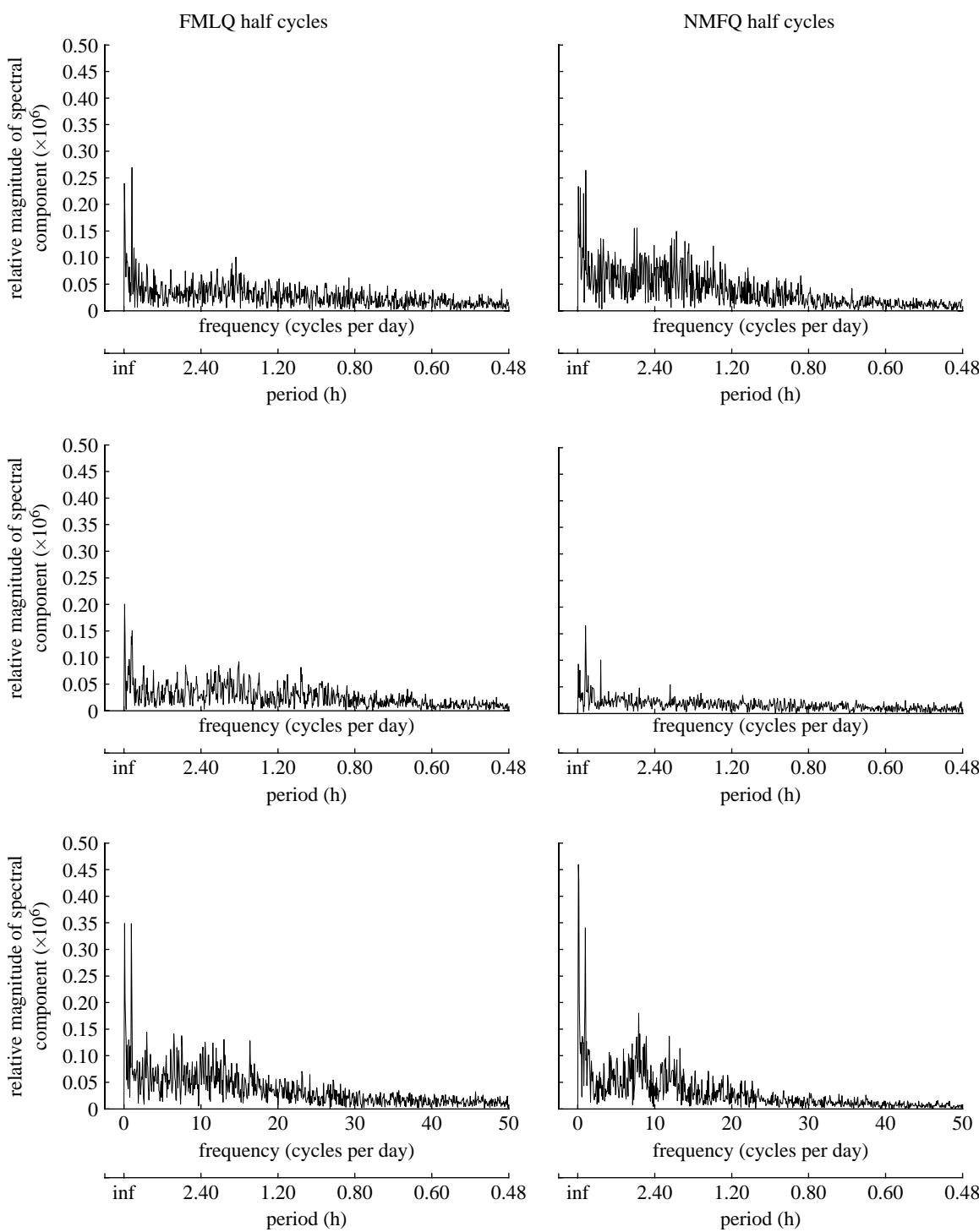


Figure 3. Frequency spectra of whale shark depth record for lunar half phases (FMLQ versus NMHQ) for lunar months in which a snapper spawning aggregation does not occur.

exponential probability distribution ( $f(x) = \lambda e^{-\lambda x}$ ), where  $x$  is the inter-dive interval and  $\lambda$  is 1/mean inter-dive interval; Cooper 1981; Klimley *et al.* 1992). A Kolmogorov–Smirnov test can be used to compare the observed cumulative distribution of inter-dive intervals with the cumulative exponential distribution ( $F(x) = 1 - e^{-\lambda x}$ ) to quantify the deviation of inter-dive intervals from exponential random (Conover 1998). Deep dives were distributed non-randomly through the depth record, occurring more frequently than random in some sections of the depth record, and less frequently

than random in others (Kolmogorov–Smirnov test on cumulative distribution of inter-dive intervals  $D=0.204$ , 48 data points,  $p<0.01$ ). Combined with time windowing results and the maximum depths recorded for all sharks throughout their deployment periods, deep dive analysis results suggest that S4 concentrated its deep diving outside of the peak snapper spawning periods when the predictable food source was no longer available.

The FFT technique reveals periodicities within time-series data, and indicates the relative magnitude of

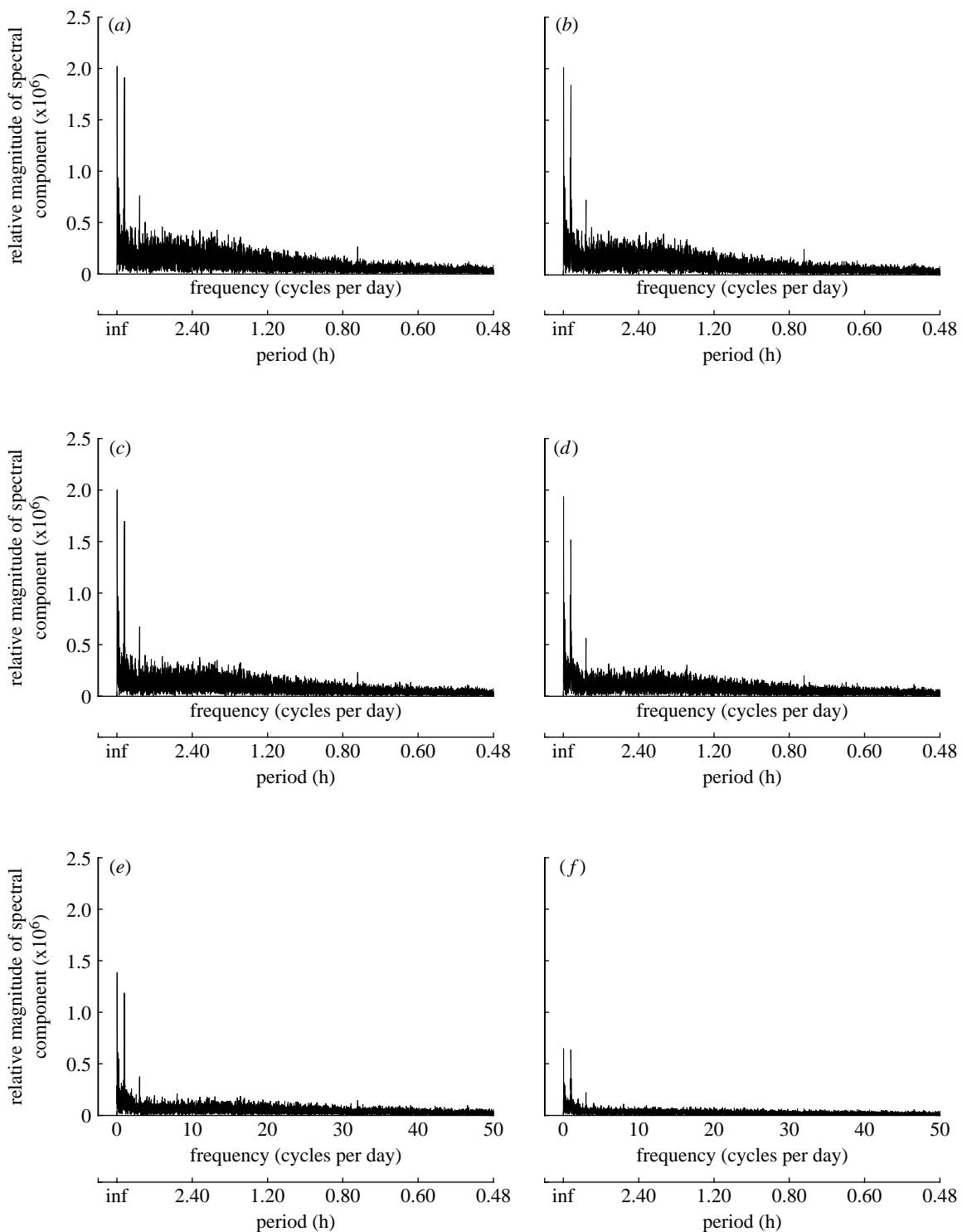


Figure 4. Frequency spectra of whale shark depth record truncated at depths of (a) 500, (b) 400, (c) 300, (d) 200, (e) 100 and (f) 50 m.

periodic components. Clear periodicities indicate rhythmic behaviour, but it is not always possible to determine why an animal is acting in a rhythmic manner. The whale shark's diving behaviour is not random and an examination of overlays of 206 days of diel dive data reveals a deep diving pattern, primarily undertaken during the day with distinct depth change events that often encompassed sunset and sunrise (figure 5a and b). The deep diving pattern that takes place at dawn may coincide with the strong 24 h periodicities revealed by the FFT analysis. However, it is unlikely that the 29-day rhythm coincides

with a deep diving excursion and instead may be linked to the lunar-modulated snapper-spawning events. The spectral components of the ultradian rhythms of 8 h and 45 min are not as strong as the diel rhythms, but are nonetheless distinct. The 45-min periodicity appears to be linked to oscillatory diving, which takes place primarily in the upper 300 m of the water column, and example of which is clearly seen in figure 5b. There are no clear explanations as yet for the shark's 8 h rhythms.

The rhythmic behaviour and patterns of activity linked to feeding behaviour have been documented for a

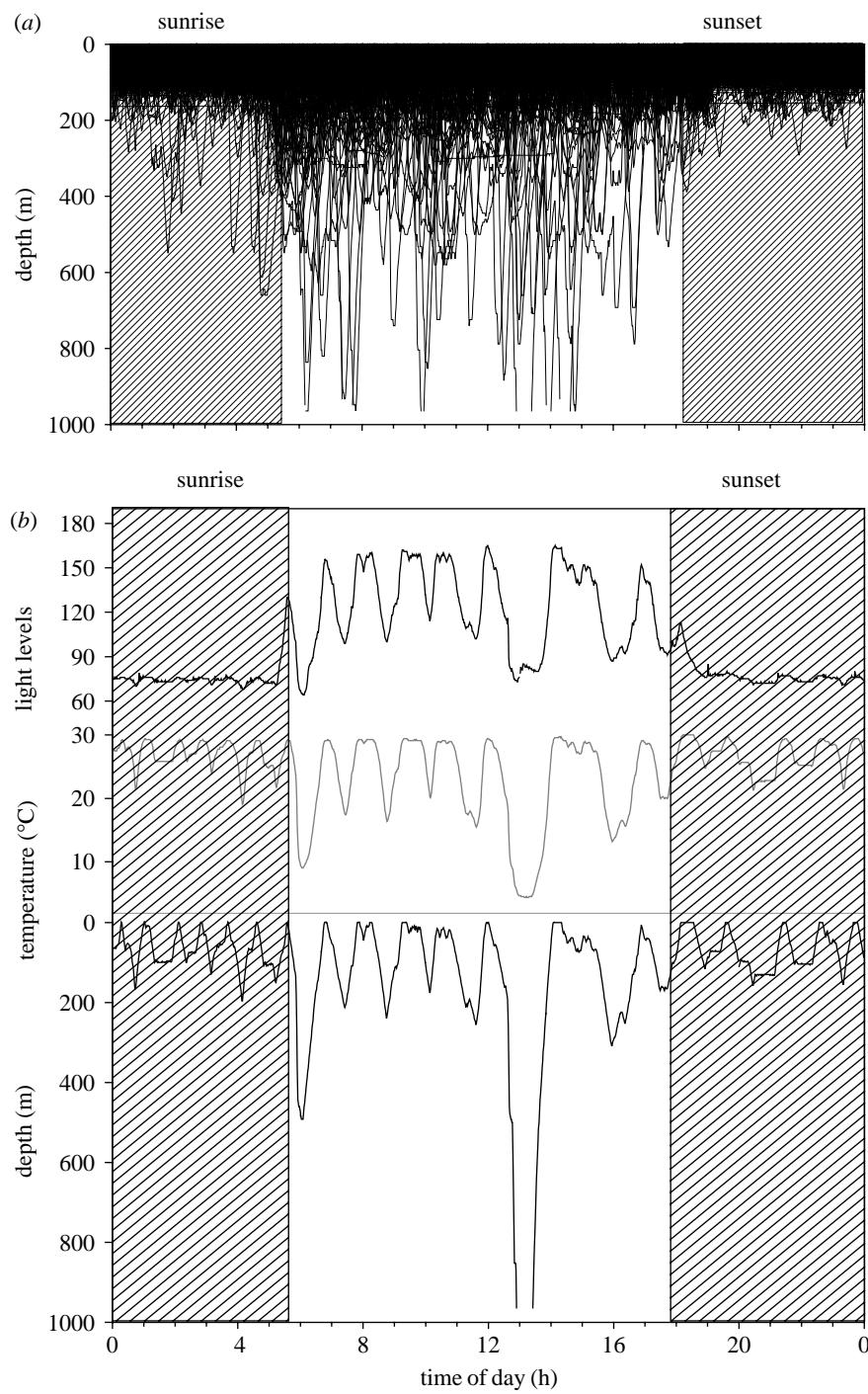


Figure 5. (a) 206 days of diving data overlaid during a 24 h period from the recovered pop-up archival satellite tag deployed on a 6.7 m juvenile male whale shark off the coast of Belize. Hatched areas represent night time. Time of day is in local Belize time (GMT–6 h). (b) Example of a diving profile with recorded ambient temperature and light levels over a 24 h period for whale shark S4 (14 September 2001). This date falls outside of the peak snapper spawning-season, 13 days after the September FM. The tail of the deep dive is not included as no depths are recorded with precision beyond 980 m.

range of fish species (Boujard 1995; Heilman & Spieler 1999; Boujard *et al.* 2000) including a range of shark species that are known to make oscillatory dives, potentially in search of prey (Carey & Scharold 1990; Sims *et al.* 2003). Sharks' cyclic diving patterns may be linked to the diel vertical migrations of zooplankton that usually aggregate near the surface by night and descend to deeper depths during the day (Folt & Burns 1999). Diel zooplankton vertical migrations or changes of light level during twilight periods may therefore modulate whale shark diving behaviour leading to

patterns of shallow dives at night and deeper dives during the day. Although no data on migratory behaviour of zooplankton were available for the Belize barrier reef or the Western Caribbean that would help to assess if the whale shark's dives were made in relation to the presence of dense layers of zooplankton, several other studies on diving behaviour in sharks have suggested similar patterns over a short time period. Gunn *et al.* (1999) found that four whale sharks tracked with short-term acoustic tags at Ningaloo reef spent more time close to the surface at night than during the

day. A 4.9 m megamouth (*Megachasma pelagios*) tracked acoustically for 50.5 h showed that the shark stayed shallow at night above 25 m and went deeper 120–166 m during the day, with depth largely dictated by light level (Nelson *et al.* 1997). Light levels are also known to trigger the onset of activity under natural and laboratory conditions in horn sharks (*Heterodontus francisci*; Finstad & Nelson 1975) and are plausible cues for diving behaviour in whale sharks.

Future studies need to determine with greater specificity why whale sharks are undertaking any of the cyclic diving behaviours, particularly in relation to the spatial and temporal distribution of zooplankton and oceanographic parameters such as levels of dissolved oxygen. This study's findings will help to focus management and conservation efforts for the globally vulnerable whale shark and other free-ranging sharks through a better understanding of their diving abilities and the modulation of their vertical movements and foraging behaviour, both in response to predictable food pulses and in relation to the spatio-temporal distribution of fishing effort.

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## REFERENCES

Boujard, T. 1995 Diel rhythms of feeding activity in the European catfish, *Silurus glanis*. *Physiol. Behav.* **58**, 641–645. (doi:10.1016/0031-9384(95)00109-V)

Boujard, T., Gelineau, A., Corraze, G., Kaushik, S., Gasset, E., Coves, D. & Dutto, G. 2000 Effect of dietary lipid content on circadian rhythm of feeding activity in European sea bass. *Physiol. Behav.* **68**, 683–689. (doi:10.1016/S0031-9384(99)00234-6)

Boustany, A. M., Davis, S. F., Pyle, P., Anderson, S. D., Le Boeuf, B. J. & Block, B. A. 2002 Satellite tagging: expanded niche for white sharks. *Nature* **415**, 35–36. (doi:10.1038/415035b)

Carey, F. G. & Scharold, J. V. 1990 Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* **106**, 329–342. (doi:10.1007/BF01344309)

Colman, J. G. 1997 A review of the biology and ecology of the whale shark. *J. Fish Biol.* **51**, 1219–1234. (doi:10.1111/j.1095-8649.1997.tb01138.x)

Conkright, M. E., Locarnini, R. A., Garcia, H. E., O'Brien, T. D., Boyer, T. P., Stephens, C. & Antonov, J. I. 2002 *World oceans atlas 2001: objective analyses, data statistics, and figures, CD-ROM documentation*. Silver Spring, MD: National Oceanographic Data Center.

Conover, W. J. 1998 *Practical non-parametric statistics*, p. 584. New York: Wiley.

Cooper, R. B. 1981 *Introduction to queuing theory*. Amsterdam: North-Holland.

Duhamel, P. & Vetterli, M. 1990 Fast Fourier Transforms: a tutorial review and a state of the art. *Signal Process.* **19**, 259–299. (doi:10.1016/0165-1684(90)90158-U)

Eckert, S. A. & Stewart, B. S. 2001 Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the sea of Cortez, Mexico, and the north Pacific ocean. *Environ. Biol. Fish.* **60**, 299–308. (doi:10.1023/A:1007674716437)

Eckert, S. A., Dolar, L. L., Kooyman, G. L., Perrin, W. & Rahman, R. A. 2002 Movement of whale sharks (*Rhincodon typus*) in South-East Asian waters as determined by satellite telemetry. *J. Zool.* **257**, 111–115. (doi:10.1017/S0952836902000705)

Finstad, W. O. & Nelson, D. R. 1975 Circadian activity rhythm in the horn shark *Heterodontus francisci*: effect of light intensity. *Bull. South. Calif. Acad. Sci.* **74**, 20–26.

Folt, C. L. & Burns, C. W. 1999 Biological drivers of zooplankton patchiness. *Trends Ecol. Evol.* **14**, 300–305. (doi:10.1016/S0169-5347(99)01616-X)

Fowler, S. L. 2000 Whale sharks *Rhincodon typus* policy research and scoping study, p. 27. UK: The Nature Conservation Bureau.

Graham, R. T. 2003 *Behaviour and conservation of whale sharks on the Belize barrier reef*. York: University of York.

Greene, W. H. 2003 *Econometric analysis*. New Jersey: Prentice Hall.

Gudger, E. W. 1915 Natural history of the whale shark, *Rhineodon typus* Smith. *Zoologica* **1**, 345–389.

Gunn, J. S., Stevens, J. D., Davis, T. L. O. & Norman, B. M. 1999 Observations on the short-term movements and behaviour of whale sharks (*Rhincodon typus*) at Ningaloo reef, Western Australia. *Mar. Biol.* **135**, 553–559. (doi:10.1007/s002270050656)

Heilman, M. J. & Spieler, R. E. 1999 The daily feeding rhythm to demand feeders and the effects of timed meal-feeding on the growth of juvenile Florida pompano, *Trachinotus carolinus*. *Aquaculture* **180**, 53–64. (doi:10.1016/S0044-8486(99)00140-4)

Heyman, W. D., Graham, R. T., Kjerfve, B. & Johannes, R. E. 2001 Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Mar. Ecol. Prog. Ser.* **215**, 275–282.

Hilton-Taylor, C. (compiler) 2000 *2000 IUCN red list of threatened species*. Gland, Switzerland and Cambridge, UK: IUCN/SSC.

Klimley, A. P., Anderson, S. D., Pyle, P. & Henderson, R. P. 1992 Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia* **1992**, 680–690.

Klimley, A. P., Beavers, S. C., Curtis, T. H. & Jorgensen, S. J. 2002 Movements and swimming behaviour of three species of sharks in La Jolla Canyon, California. *Environ. Biol. Fish.* **63**, 117–135. (doi:10.1023/A:1014200301213)

Krebs, C. J. 1989 *Ecological methodology*. New York: Harper Collins.

Lynn, P. A. 1973 *An introduction to the analysis and processing of signals*, p. 222. New York: Wiley.

Nelson, D. R., McKibben, J. N., Strong, W. R., Lowe, C. G., Sisneros, J. A., Schroeder, D. M. & Lavenberg, R. J. 1997 An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environ. Biol. Fish.* **49**, 389–399. (doi:10.1023/A:1007369619576)

Sims, D. W., Southall, E. J., Richardson, A. J., Reid, P. C. & Metcalfe, J. D. 2003 Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Mar. Ecol. Prog. Ser.* **248**, 187–196.