Whale shark behavioural responses to tourism interactions in Ningaloo Marine Park and implications for future management

HOLLY RAUDINO, DANI ROB, PETER BARNES, ROLAND MAU, EMILY WILSON, SARAH GARDNER AND KELLY WAPLES

Science and Conservation Division, Department of Parks and Wildlife, Locked Bag 104, Bentley Delivery Centre, Western Australia, 6983

Corresponding author: holly.raudino@dpaw.wa.gov.au

ABSTRACT

This study examined whale shark behaviour using fixed-wing aerial surveys in Ningaloo Marine Park between 2007 and 2009. The aims of the project were to develop and trial a method to test for impacts of tourism vessels and swimmers on whale shark behaviour. Whale sharks made significantly more directional changes when vessels were present, with approximately twice as many changes in direction observed per scan when a vessel was present. Whale sharks also maintained neutral behaviours, such as surface swimming, swimming at depth, resurfacing, or no reaction during interactions and, notably, more of these were recorded when a vessel was present. This suggests that, while behaviours were maintained regardless of the presence of vessels, whale sharks may have still responded to vessels by changing direction more frequently. The aerial observations were effective in detecting an increase in directional changes but further behavioural studies are required to improve our understanding of natural diving and surfacing behaviour in whale sharks. Alternative research platforms and technologies may be necessary to investigate whale shark behaviour in more detail and to further evaluate potential impacts of tourism interactions on whale sharks.

Keywords: behaviour, ecotourism, management, whale shark.

INTRODUCTION

Whale sharks (*Rhincodon typus*) are appreciated worldwide for their size, colouration patterns and generally harmless nature. They have become a focus of tourism interactions in areas where they are known to aggregate, including the Seychelles, Philippines, Mozambique, Mexico and Ningaloo Marine Park (NMP) in Western Australia (WA) (Coleman 1997; Davis et al. 1997; Pierce et al. 2010; Gallagher & Hammerschlag 2011). Typically between March and July each year, whale sharks aggregate in NMP and the surrounding area to feed in the nutrient-rich waters created by upwelling and plankton blooms associated with coral spawning (Taylor 1996). A nature-based tourism industry has developed around the predictable presence of these animals, taking people to view and snorkel with the whale sharks. This growing industry has been carefully managed at NMP under what is considered to be a sustainable best practice management program (Coleman 1997; Mau 2008; Rowat & Brooks 2012).

The whale shark is considered at international and national levels to be a threatened species given the pressures upon it across its range. It is listed as Vulnerable on the Red List of Threatened Species by the International Union for the Conservation of Nature (IUCN) and under the Australian *Environment Protection and Biodiversity Conservation Act 1999* (*EPBC Act 1999*). In WA, it is a protected species under the *Wildlife Conservation Act 1950*. The main recognised human pressures upon whale sharks are hunting and boat strike in international waters. Given that most whale sharks likely spend much of their time outside of WA state waters, the Department of Parks and Wildlife (Parks and Wildlife) can significantly contribute to an international effort for their conservation through effective local management based on understanding and reducing pressures in state waters through education, raising public awareness and community engagement. Understanding changes in population abundance or condition in state waters can be conveyed to federal authorities so that they can pursue national and international conservation initiatives.

Human disturbance, i.e. direct contact through boat strike or close proximity of boats and swimmers, is

Recommended citation: Raudino H, Rob D, Barnes P, Mau R, Wilson E, Gardner S, Waples K (2016) Whale shark behavioural responses to tourism interactions in Ningaloo Marine Park and implications for future management. *Conservation Science Western Australia* **10**: 2 [online]. https://www.dpaw.wa.gov.au/CSWAjournal

recognised as the most relevant anthropogenic pressure on whale sharks in WA (Department of Parks and Wildlife 2013). As there is a nature-based tourism industry reliant on interaction of tourists and whale sharks in NMP, it is important that these pressures are monitored and minimised where relevant (Department of Parks and Wildlife 2013). To address this, Parks and Wildlife developed and implemented a species management program in 1997 specific to the whale shark industry in NMP ('Management Program'; Coleman 1997). The Management Program includes a licensing system for tourism operators in NMP and a code of conduct (see https://www.dpaw.wa.gov.au/management/marine/marine-wildlife/whale-sharks?showall=&start=2) to manage interactions of vessels and people with whale sharks. In 2012 the Management Program was reviewed to evaluate its effectiveness along with the status of the tourism industry, and an updated Management Program published in 2013 ('Management Program 2013'; Department of Parks and Wildlife 2013). The Management Program 2013 identified strategies for research, including the need to assess the impact of vessels and swimmers on whale shark behaviour, and recommends the ongoing review and use of research and monitoring outcomes to inform management strategies, particularly to minimise impacts.

There has been substantial research on whale sharks in NMP (e.g. Meekan et al. 2006; Wilson et al. 2006; Bradshaw et al. 2008; Speed et al. 2008; Sleeman et al. 2010; Thums et al. 2013) and more broadly throughout the Indian Ocean (Rowat et al. 2009; Rowat & Brooks 2012) over the past 15 years. While much of this research has focussed on understanding whale shark biology and distribution patterns, there have been several studies on the whale shark tourism industry (Davis et al. 1997; Patton & Marsh 2005; Mau 2007; Anderson et al. 2014) and in particular on the impact of swimmers and vessels on whale sharks (Quiros 2007; Pierce et al. 2010; Haskell et al. 2014). However, these latter studies used an in-water observer to collect data, thus the observer could have potentially affected whale shark behaviour, thereby limiting the scientific validity of data collected. To date there has been limited research emphasis on the effectiveness of the Management Program at NMP.

A pilot research project was undertaken in NMP between 2007 and 2009 to assess the potential impacts of vessel and swimmer interactions on the behaviour of whale sharks and the consequent effectiveness of the Management Program using aerial surveys. Here we use this existing behavioural dataset compiled from 2007 to 2009 to:

1. assess the impact of interactions with tourism vessels on whale shark behaviour; and
2. assess the survey methods for their suitability in evaluating the impacts of tourist interactions on whale sharks.

This research will enable a better understanding of whale shark response to vessels, including whether the code of conduct minimises disturbance. This information will directly support the Management Program 2013 by evaluating the existing code of conduct and governance structures in place and identifying whether modifications to the code of conduct or protocols for monitoring interactions is warranted to fully meet the objectives of the Management Program 2013. Furthermore, information from this project will support improved whale shark conservation and management of whale shark tourism in NMP as well as inform conservation management options for whale sharks in other jurisdictions.

METHODS

Aerial surveys

Aerial surveys were conducted during the whale shark aggregation periods at NMP between 2007 and 2009 to assess whale shark behavioural responses to vessels and swimmers. Surveys were conducted on 11 days in 2007, seven days in 2008 and six days in 2009. All surveys were completed following a standard operating procedure (see supplementary material) with two observers and a pilot present on each survey.

Data were collected for both 'interaction' events (commercial tour vessel and/or swimmers within 250 m of whale shark) and 'control' events (no vessels or swimmers within 250 m of whale shark). When a whale shark was first sighted, a GPS location, initial directional heading, behaviour, estimated size and whether an interaction was occurring were recorded. Following the initial observation, the directional movement, behaviour and interaction details were recorded for a minimum of 15 minutes at approximate intervals of 30 seconds to one minute, unless visual contact of the whale shark was lost. Whale shark behaviours included: swam at the surface, swam at depth, increased speed, decreased speed, circled, dived deep, resurfaced, investigated and no reaction. Whale shark direction of movement was recorded in conjunction with behaviour with these headings using compass point directions (e.g. N, NW, NE, etc.; see supplementary material).

During interactions the vessel identity (although vessel anonymity was maintained in the data analysis), the vessel position relative to the whale shark, distance from the whale shark and whether the vessel was moving or stationary were recorded. An interaction was defined as the vessel and/or swimmers in the water within 250 m of the whale shark. Individual whale sharks could not be identified from the aircraft and therefore independence between observations is assumed but cumulative interactions with individual sharks may be a confounding factor.

Data Analysis

Due to the small sample size, recorded behaviours were pooled into three categories for analysis (Table 1). Change in direction of movement was rarely

Table 1

Categories of observed behaviours.

Observed behaviours	Explanation of behaviour
Dived deep Increased speed	Behaviours that reduced the likelihood of or shortened the duration of an interaction by increasing the distance between whale shark and vessel/swimmer.
Surface swam Swam at depth No reaction Resurfaced	Neutral.
Decreased speed Circled Investigated	Behaviours that maintained the likelihood of or increased the duration of an interaction by reducing the distance between whale shark and vessel/swimmer.

recorded as a behaviour as per the standard operating procedure (see supplementary material), however, could be assessed through analysis of the directional heading recorded at each sample point. Thus, change in directional heading was included in analysis as a separate variable.

Poisson regression was used to explore the relationship between response variables such as the rates of change in behaviour and directional headings of the whale shark and the presence or absence of a vessel. Poisson regression models are a type of generalised linear model commonly used to analyse count data (Zuur et al. 2013). The Poisson regression expresses the probability of a given number of events occurring in a fixed interval of time and/or space if these events occur with a known average rate. That is, it predicts the degree of spread around a known average rate of occurrence. Counts of different types of occurrences were modelled assuming a Poisson distribution and using a quasi-likelihood approach to allow for over dispersion. An offset of log (number of scans) was included to allow for the differing numbers of scans for respective counts, effectively modelling a rate of occurrence of each type (number per scan observed).

RESULTS

All three years of aerial survey data were included in the analysis (2007–2009). Due to the small sample sizes of sharks observed per year, data were pooled across years for the purpose of analysis. A total of 80 whale sharks were observed and recorded over the three years. Thirty three were 'control' events where no vessels and/or swimmers were within 250 m and 47 were 'interaction' events where a vessel and/or swimmers were within 250 m (Table 2). Whale shark behaviour was observed for a total of 28 hours with an average 40 scan samples (approximately 20 minutes) per observed shark.

Table 2

Number of control and interaction events recorded each year during the study.

Year	'Control' events	'Interaction' events
2007	18	19
2008	5	16
2009	10	12
Total	33	47

Effect of presence and number of vessels on changes in whale shark behaviour and direction of movement

There was no statistically significant effect of presence of a vessel ($p = 0.239$) nor of a linear trend in the number of changes in whale shark behaviour with the number of vessels present ($p = 0.942$). However, there were significantly more changes in whale shark directional movement in the presence of a vessel ($p = 0.038$). There was no statistically significant linear trend in the number of direction changes by whale sharks in relation to the number of vessels present ($p = 0.851$). The fitted mean number of changes in direction per scan was 0.119 when no vessel was present and 0.223 when a vessel was present. Thus, approximately twice as many changes in whale shark direction were observed per scan when a vessel was present.

Effect of presence and number of vessels on whale shark behaviour type

There was no statistically significant effect of presence of a vessel ($p = 0.782$), and no statistically significant linear trend with number of vessels present ($p = 0.424$) on behaviours that maintained an interaction; however, the infrequency of these behaviours limit our analysis power. There was a linear correlation between interaction duration and number of behavioural changes per scan ($r^2 = 0.52$, $p < 0.0001$).

There was a statistically significant effect of presence of a vessel on neutral behaviour ($p = 0.013$), with whale sharks that had a vessel present displaying more neutral behaviours. The fitted mean number of neutral behaviours per scan was 0.752 when no vessel present, and 0.873 when a vessel was present. There was also a statistically significant increasing linear trend in the number of vessels present ($p = 0.020$), i.e. neutral behaviours were recorded more per scan as the number of boats increased. Similarly, there was a statistically significant effect of presence of a vessel on behaviours that reduced an interaction ($p = 0.013$), but no statistically significant linear trend with the number of vessels present ($p = 0.075$). The fitted mean number of behaviours that reduced an interaction per scan was 0.188 when no vessel was present, and 0.085 when a vessel was present, therefore fewer behaviours

Table 3

Summary of the final behaviour observed for each whale shark observation in the absence or presence of a vessel. The total number of interactions when vessels were absent was 33, and when a vessel was present was 46.

Final Behaviour	No Vessel	Vessel present
Dived deep	21	24
Decreased speed	1	0
Resurfaced	0	1
Swam at depth	2	8
Swam at surface	9	13

that reduced an interaction were apparent with vessel presence.

In 45 of the 79 interactions where a final behaviour was recorded the observation ended with the whale shark in a deep dive (Table 3). The mean time to deep dive was 12.5 min (SE ± 1.4 min) in the absence of vessels (n = 21) and 21 min (SE ± 2.5 min) in the presence of vessels (n = 25), i.e. whale sharks remained at the surface twice as long, on average, when a vessel was present. There was no statistically significant difference between end behaviour in the presence or absence of a vessel (chi-square test 2.581 with 2 degrees of freedom; p= 0.275).

DISCUSSION

Effect of presence and number of vessels on changes in whale shark behaviour and directional movement

Whale sharks changed direction more often when vessels were present. The number of behavioural changes was also correlated to the interaction duration, with more changes observed for longer interactions. Another study investigating the impact of tourism and swimmers on whale sharks in the Philippines found directional changes increased when swimmers obstructed the whale shark's path or approached too closely (Quiros 2007). While we were unable to assess swimmer or vessel position or proximity due to the way this information was recorded, and can therefore not assess their influence on whale shark response, increase in directional changes may be a widespread response.

Understanding typical whale shark diving and surfacing behaviour is important in interpreting these results. Whale sharks have protracted surface swims following dives for the purpose of thermoregulation (Thums et al. 2013). They can also favour shallow water during food pulses e.g. fish spawning events (Graham et al. 2006). It is possible that whale sharks may tolerate the presence of a vessel, thus maintaining their behaviour, if the need to thermoregulate or feed is critical, as observed in this study with the high number of 'neutral' behaviours. However the potential ramifications of increased directional changes, vessel collisions and the associated fitness costs are unknown (Speed et al. 2008). Similarly, for NMP, the impact of vessel and/or swimmer proximity and position on this response are also unknown, but could have implications in evaluation of the existing code of conduct and its implementation.

Interactions were often noted to end with a 'deep dive' when the whale shark was no longer visible to the observer. However, on average it took twice as long for a whale shark to dive deep and the observation to end in the presence, rather than absence of a vessel. It should be noted that whale sharks did make multiple deep dives in some interactions before resurfacing and resuming surface swimming. However, understanding the proportions of surface versus subsurface time spent by whale sharks at NMP would be useful in determining whether whale sharks spend more overall time swimming at depth when a vessel is present. Such information could be gained from archival tags that record time and depth, thus providing an indication of the animal's movement patterns over a diurnal cycle (e.g. Wilson et al. 2006; Rowat & Gore 2007; Wilson et al. 2008; Gleiss et al. 2013).

Martin (2007) found that whale sharks sometimes appear to avoid boats by diving slowly toward the seabed, usually without noticeably changing their speed, presumably in response to the noise of the boat. Similarly, Quiros (2007) found that whale sharks that had been exposed to repeated interactions or were feeding were more likely to dive in response to the presence of a vessel. In our study we were unable to confirm whether the whale sharks had been interacted with previously and therefore the interactions were assumed to be independent. Confirming whale shark identity could be considered in future to ensure cumulative interactions with the same individual whale shark is not affecting behaviour and confounding results.

Limitations of sampling protocol and research platform

Research platforms and methods all come with particular limitations that need to be taken into account in relation to the research question and in survey design. An aerial platform was chosen for this study as it was a cost-effective option and addressed the specific research question about the impact of tour operations on whale shark behaviour by providing a neutral platform that would not have an added impact on the whale sharks. However, some limitations were identified by using this platform and the associated protocols. While methods should always be chosen appropriate to the research question(s) being asked, future studies could build on this pilot study by considering the following factors in protocol design and data collection.

The standard operating procedure did not prescribe point sampling (Martin & Bateson 1993), but rather observations were recorded as a scan sample anytime within a 30-second period, leading to inconsistencies in sampling. Further, for many scans data were missed or the whale shark was not visible to the observer. This reduced the amount of usable data on interactions and behaviours and quantitative analysis of time.

While the aerial platform offers a broad-scale and unobstructed view of the whale shark, vessels and swimmers, some fine-scale information cannot be collected with this technique. A comprehensive ethogram of whale shark behaviours, including banking, eye rolling, gulping, degree of mouth opening and gill flushing/coughing, has been described by Quiros (2007), who used boat-based or in-water observations to monitor whale shark behaviour in the Philippines. Some of these behaviours are indicative of feeding, which is an important consideration as whale shark fitness may be reduced if their feeding is repeatedly disrupted, while other behaviours were linked to avoidance. However, the aerial platform used in this study did not allow for such fine-scale detection of behaviours. Similarly, other behavioural changes that were of interest, such as increases and decreases in swimming speed, were more difficult to observe than anticipated owing to the speed at which the fixed-wing aircraft was moving. This loss of fine detail is a trade-off in having an independent platform removed from the interaction zone of the whale shark, and therefore use of this platform may be limited to examining broad-scale questions of behaviour.

Some limitations to the aerial surveys identified in this study can be overcome somewhat by a cooperative approach linking tour boat or in-water observations with simultaneous aerial observations. This would be more straightforward given the current use of an on-board electronic monitoring system (EMS) on tour boats, combined with the growing use of photo identification to identify individual animals. Novel aerial research platforms such as blimps (Hodgson 2007; Hodgson & Marsh 2007) and unmanned aerial vehicles (Hodgson et al. 2013) may have merit in assessing impacts as they record and store data that can later be reviewed and analysed. Regardless of the research platform, to be able to accurately measure behaviour, sampling must be standardised, e.g. point samples collected consistently and at set intervals (Martin & Bateson 1993) to allow quantitative analysis.

Future Research

It is apparent from this study that vessel presence is having an influence on whale shark behavioural response. This leads to additional questions of whale shark response that, if understood, could benefit the management of tourism impacts on whale sharks. For example, do the increased changes in direction by whale sharks equate to an energetic cost and subsequent reduction in fitness through impacts on critical behaviours such as thermoregulation and feeding? Long-term changes in localised behaviour of white sharks (Carcharodon carcharias) have been detected in response to cage-diving tourism interaction (Bruce & Bradford 2013; Huveneers et al. 2013). Further, an evaluation of the code of conduct and its implementation may be warranted to determine whether the position and proximity of either vessels or swimmers is having an influence on whale shark behavioural response.

The research techniques used to explore these questions need to be carefully considered. While an aerial platform used for multiple purposes may be cost-effective, and provides an independent platform to reduce responsive movement of whale sharks, it does have its limitations. Martin (2007) suggests that data collected by the whale shark tourism industry could help fill some knowledge gaps about the behavioural ecology of this species. Tour vessels can offer another cost-effective platform for data collection. A recent study at Ningaloo that used tour boats as the research platform investigated residency time and inter-season return rate of individual whale sharks that were encountered during nature-based tourism interactions. The study found no evidence that interactions with tourists affected the probability of whale shark re-encounters and that instead, physical, biological and environmental factors better explained visitation rates of whale sharks (Sanzogni 2012; Sanzogni et al. 2015)

Behavioural information could be collected directly from tour vessels, and used to develop a more comprehensive ethogram of whale shark behaviour, as well as to evaluate the impact of swimmers and vessels on critical behaviour. However, this would likely require involvement of an independent observer, particularly to address questions relating to evaluation of the tourism industry and Management Program to remove any inherent bias.

Finally, potential impacts on whale sharks from vessel interactions could be investigated through other means, such as the presence of unique scarring on some whale shark individuals, which is an indicator of previous vessel strikes (Speed et al. 2008). This could be done using data from the on-board electronic monitoring system (EMS), coupled with photo-identification data to assess the relationship between quantity and severity of scarring with the length of interaction and number of repeated interactions per individual shark, and whether this varies over time. Our study demonstrated that it is possible to detect directional and some behavioural changes in whale sharks from aerial surveys and this research could be extended through alternative research platforms.

ACKNOWLEDGEMENTS

NorWest AirWorks provided fixed-wing aircrafts and pilots. We thank the following observers from Parks and Wildlife's Exmouth District Office for their diligent data collection: Tegan Gourlay, Tristan Simpson, Naysa B, Brooke Halkyard, Kevin Hughes, Keely Markovina, Tony Howard. Matthew Williams provided advice on data processing and analysis. Corrine Severin graciously formatted the manuscript for publication.

REFERENCES

Anderson DJ, Kobryn HT, Norman BM, Bejder L, Tyne JA, Loneragan NR (2014) Spatial and temporal patterns of nature-based tourism interactions with whale sharks (Rhincodon typus) at Ningaloo Reef, Western Australia. *Estuarine, Coastal and Shelf Science* **148**, 109–119.

Bradshaw CJA, Fitzpatrick BM, Steinberg CC, Brook BW, Meekan MG (2008) Decline in whale shark size and abundance at Ningaloo Reef over the past decade: The world's largest fish is getting smaller. *Biological Conservation* **141**, 1894–1905.

Bruce BD, Bradford RW (2013) The effects of shark cage-diving operations on the behaviour and movements of white sharks, *Carcharodon carcharias*, at the Neptune Islands, South Australia. *Marine Biology* **160**, 889–907.

Coleman J (1997) *Whale Shark Interaction Management with Particular Reference to Ningaloo Marine Park 1997–2007 Wildlife Management Program No. 27*. Department of Conservation and Land Management, Perth.

Davis D, Banks S, Birtles A, Valentine P, Cuthill M (1997) Whale sharks in Ningaloo Marine Park: managing tourism in an Australian marine protected area. *Tourism Management* **18**, 259–271.

Department of Parks and Wildlife (2013) *Whale Shark Management with Particular Reference to Ningaloo Marine Park 2013, Wildlife Management Program No. 57*. Department of Parks and Wildlife, Perth.

Gallagher AJ, Hammerschlag N (2011) Global shark currency: the distribution, frequency, and economic value of shark ecotourism. *Current Issues in Tourism* **14**, 797–812.

Gleiss A, Wright S, Liebsch N, Wilson R, Norman B (2013) Contrasting diel patterns in vertical movement and locomotor activity of whale sharks at Ningaloo Reef. *Marine Biology* **160**, 2981–2992.

Graham RT, Roberts CM, Smart JCR (2006) Diving behaviour of whale sharks in relation to a predictable food pulse. *Journal of the Royal Society Interface* **3**, 109–116.

Haskell PJ, Mcgowan A, Westling A, Méndez-Jiménez A, Rohner CA, Collins K, Rosero-Caicedo M, Salmond J, Monadjem A, Marshall AD, Pierce SJ (2014) Monitoring tourism impacts on whale shark behaviour in Mozambique. *Oryx* **49**, 492–499.

Hodgson A, Kelly N, Peel D (2013) Unmanned aerial vehicles (UAVs) for surveying marine fauna: A dugong case study. *PLoS ONE* **8**, e79556.

Hodgson AJ (2007) 'The distribution, abundance and conservation of dugongs and other marine megafauna in Shark Bay Marine Park, Ningaloo Reef Marine Park and Exmouth Gulf'. Department of Environment and Conservation and James Cook University.

Hodgson AJ, Marsh H (2007) Response of dugongs to boat traffic: The risk of disturbance and displacement. *Journal of Experimental Marine Biology and Ecology* **340**, 50–61.

Huveneers C, Rogers PJ, Beckmann C, Semmens JM, Bruce BD, Seuront L (2013) The effects of cage-diving activities on the fine-scale swimming behaviour and space use of white sharks. *Marine Biology* **160**, 2863–2875.

Martin P, Bateson P (1993) *Measuring Behaviour, An Introductory Guide*. Cambridge University Press, Cambridge UK.

Martin RA (2007) A review of behavioural ecology of whale sharks (*Rhincodon typus*). *Fisheries Research* **84**, 10–16.

Mau R (2007) Industry trends and whale shark ecology based on tourism operator logbooks at Ningaloo Marine Park. In *The First International Whale Shark Conference: Promoting International Collaboration in Whale Shark Conservation, Science and Management* (eds TR Irvine, JK Keesing). Perth 9–12 May 2005. Available at http://www.srfme.org.au/news/1stInterWhaleSharkconf.pdf [accessed 16 December 2015].

Mau R (2008) Managing for conservation and recreation: The Ningaloo whale shark Experience. *Journal of Ecotourism* **7**, 213–225.

Meekan MG, Bradshaw CJA, Press M, Mclean C, Richards A, Quasnichk S, Taylor JG (2006) Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. *Marine Ecology Progress Series* **319**, 275–285.

Patton S, Marsh H (2005) 'Assessing the potential for logbook data collected in Ningaloo Marine Park by spotter pilots and tour boat operators to provide robust whale shark monitoring information'. James Cook University, Townsville.

Pierce SJ, Mendezjimenez A, Collins K, Rosero-Caicedo M, Monadje A (2010) Developing a Code of Conduct for whale shark interactions in Mozambique. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**, 782–788.

Quiros AL (2007) Tourist compliance to a Code of Conduct and the resulting effects on whale shark (*Rhincodon typus*) behavior in Donsol, Philippines. *Fisheries Research* **8**, 102–108.

Rowat D, Brooks KS (2012) A review of the biology, fisheries and conservation of the whale shark *Rhincodon typus. Journal of Fish Biology* **80**, 1019–1056.

Rowat D, Gore M (2007) Regional scale horizontal and local scale vertical movements of whale sharks in the Indian Ocean off Seychelles. *Fisheries Research* **84**, 32–40.

Rowat D, Gore M, Meekan MG, Lawler IR, Bradshaw CJA (2009) Aerial survey as a tool to estimate whale shark abundance trends. *Journal of Experimental Marine Biology and Ecology* **368**, 1–8.

Sanzogni RL (2012) 'Does love hurt? A study of inter-annual ecotourism impacts on whale sharks at Ningaloo Reef, Western Australia'. Bachelor of Science (Honours) Thesis, University of Western Australia, Perth.

Sanzogni RL, Meekan MG, Meeuwig JJ (2015) Multi-year impacts of ecotourism on whale shark (*Rhincodon typus*) visitation at Ningaloo Reef, Western Australia. *PLoS ONE* **10**, e0127345.

Sleeman JC, Meekan MG, Wilson SG, Polovina JJ, Stevens JD, Boggs GS, Bradshaw CJA (2010) To go or not to go with the flow: Environmental influences on whale shark movement patterns. *Journal of Experimental Marine Biology and Ecology* **390**, 84–98.

Speed CW, Meekan MG, Rowat D, Pierce SJ, Marshall AD, Bradshaw CJA (2008) Scarring patterns and relative mortality rates of Indian Ocean whale sharks. *Journal of Fish Biology* **72**, 1488–1503.

Taylor JG (1996) Seasonal occurrence, distribution and movements of the whale shark, (*Rhincodon typus*), at Ningaloo Reef, Western Australia. *Marine and Freshwater Research* **47**, 637–642.

Thums M, Meekan M, Stevens J, Wilson S, Polovina J (2013) Evidence for behavioural thermoregulation by the world's largest fish. *Journal of The Royal Society Interface* **10**, 20120477.

Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**, 123–137.

Wilson SG, Polovina JJ, Stewart BS, Meekan MG (2006) Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology* **148**, 1157–1166.

Zuur AF, Hilbe J, Ieno EN (2013) *A Beginner's Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists*. Highland Statistics, Newburgh UK.