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Swimming with humans: biotelemetry reveals effects of “gold standard” regulated tourism on whale sharks

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ABSTRACT

Wildlife tourism can benefit conservation of target species, however, it can have detrimental effects on animal behaviour and physiology. Whale shark *Rhincodon typus* tourism has seen recent rapid growth globally, but methods and regulations vary widely. Ningaloo Reef, Australia is considered “gold standard” whale shark tourism management due to legal regulation, strict enforcement, and high compliance. Rather than relying on observational data, we used biotelemetry to collect high-resolution data (20 Hz) on whale sharks’ movement behaviour in the presence or absence of tourists. Tourism encounters lasted an average of 62 min and swimming with tourists increased the activity levels of larger (> 7 m) but not smaller sharks. Given that activity levels positively correlate with energetic costs, it is likely the 18% increase seen in activity of large sharks would have incurred additional energetic costs. However, when considered as a proportion of daily energy requirements, these additional costs were only incurred for an average of 4% of a whale shark’s day. The tourism-induced impacts we found on the endangered whale sharks at this highly regulated tourism site would not have been apparent from purely observational studies, highlighting the utility of biotelemetry to quantify tourism-related impacts on wildlife.

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Introduction

Wildlife tourism, in its broadest sense, includes both consumptive (e.g. hunting, fishing) and non-consumptive (e.g. viewing, photographing) use of wild animals in captive, semi-captive and natural settings (e.g. entertainment venues, zoos, wildlife refuges, national parks) (Newsome et al., 2005; Tisdell & Wilson, 2005), and is one of the most lucrative and popular tourism sectors in the world (Krüger, 2005). By definition, consumptive wildlife tourism has fatal consequences for individuals and can result in population declines and disruption of ecosystems. Claims of benefits to conservation have been made, but these are controversial (Lovelock, 2008). In contrast, the viewing of animals in their natural environment is considered relatively benign and can provide psychological health benefits for humans (Curtin, 2009), and positive conservation

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outcomes for wildlife by changing public attitudes towards the protection of species and habitats (Krüger, 2005; Macdonald et al., 2017). However, interactions with humans can cause behavioural responses, such as increased vigilance, fleeing and avoidance of tourism areas, and physiological responses, such as elevated levels of glucocorticoids (“stress” hormones, which can lead to immunosuppression and increased disease susceptibility), and increased heart rate, metabolic rate and energy expenditure (Bateman & Fleming, 2017). It is likely that all wildlife involved in tourism activities are impacted to some degree Macdonald et al., 2017). The tangible benefits of wildlife tourism to conservation are debated (Ardoin et al., 2015) and it is unclear whether any positive effects on target species and the environment compensate for direct and indirect negative effects (Semeniuk, 2021). Negative effects of tourism activities can be reduced with activity-specific management (Healy et al., 2020), but impacts remain difficult to quantify, assess and interpret (Bateman & Fleming, 2017; Gallagher et al., 2015).

Species from diverse taxa, both terrestrial and aquatic, are targeted for wildlife tourism, particularly large and charismatic species which can also be some of those most threatened with extinction (Gallagher & Hammerschlag, 2011). Marine vertebrates, including turtles, cetaceans (dolphins and whales) and elasmobranchs (sharks and rays) have become popular target species for non-consumptive wildlife tourism (Gallagher & Hammerschlag, 2011). Indeed, wildlife tourism that involves interacting with elasmobranchs has seen recent rapid growth globally (Gallagher & Hammerschlag, 2011; Huveneers et al., 2017) and is now offered commercially in at least 42 countries (Healy et al., 2020). Despite this rapid growth, and this taxon being one of the world’s most threatened vertebrate groups (Dulvy et al., 2021; IUCN, 2023), the responses of elasmobranchs to tourism-related activities have historically received less attention than those of other charismatic marine megafauna, such as cetaceans.

Tourism activities involving sharks and rays are often touted as encouraging conservation as the monetary gain from non-consumptive exploitation for tourism is greater than the once-only value of a dead animal (Gallagher et al., 2015; Vianna et al., 2012). However, elasmobranch tourism has the potential to result in negative consequences for both the target species and the ecosystem (Gallagher et al., 2015), and its effects vary depending on species and location (Healy et al., 2020). For example, tourism activities have produced increased swimming speeds and altered respiratory behaviour in grey nurse sharks *Carcharias taurus* (Barker et al., 2011), increased activity levels in white sharks *Carcharodon carcharias* (Huveneers et al., 2018), and caused degradation of coral reefs in the Philippines (Wong et al., 2019). Tourism-induced effects can also vary widely depending on the type of interactions and the regulations (and levels of enforcement and compliance) governing them (Healy et al., 2020). For example, provisioning caused physiological changes in stingrays *Dasyatis americana* (Semeniuk, 2021; Semeniuk et al., 2009), and touching of whale sharks *Rhincodon typus*, in contravention of codes of conduct, caused avoidance behaviours (Araujo et al., 2017). Management and regulation of wildlife tourism must balance the potential detrimental effects on the target species with the social and economic benefits to people and communities, and the potential conservation benefits for species and their habitats, to ensure that the industry can be sustained in the long-term (Meyer et al., 2021; Ziegler & Dearden, 2022).

Whale sharks, the world’s largest elasmobranch, aggregate and are reliably encountered at many coastal locations throughout the tropics (Norman et al., 2017a). As a result, tourism industries that benefit local economies have grown at many of these aggregation sites (Ziegler & Dearden, 2022). Whale shark tourism has become one of the most lucrative wildlife tourism sectors and the most popular form of shark-watching activity worldwide (Gallagher & Hammerschlag, 2011; Ziegler & Dearden, 2022). An estimated 900,000 tourists engage in non-captive tourism activities with whale sharks annually at more than 30 sites in 23 countries, worth almost US\$140 million (Ziegler & Dearden, 2022). However, the levels of economic development, management controls and methods used for interactions vary considerably in different sites and countries (Healy et al., 2020; Ziegler & Dearden, 2022). Many sites have little or no

official regulation or requirements for permits e.g. Madagascar, Thailand, Mozambique and Indonesia (Ziegler & Dearden, 2022), poor enforcement or compliance e.g. Mexico (Montero-Quintana et al., 2018) and the Philippines (Schleimer et al., 2015), and/or are newly established and growing faster than regulations can be enacted e.g. Madagascar (Ziegler et al., 2021). Some engage in provisioning (i.e. using food to attract sharks) e.g. the Philippines (Araujo et al., 2014; 2017) and Indonesia (Ziegler & Dearden, 2022), which remains controversial because of its effects on sharks' behaviour and physiology (Araujo et al., 2017; 2020; Barry et al., 2023; Legaspi et al., 2020; Penketh et al., 2020; Schleimer et al., 2015; Semeniuk, 2021; Ziegler & Dearden, 2022). Conversely, the tourism industry at Ningaloo Reef, Australia is well-established and has been highly regulated by the Western Australian (State) Government since 1993, with rules limiting the number of vessels and swimmers and their proximity to sharks (see Methods for more information) (Davis et al., 1997; Department of Biodiversity Conservation & Attractions, 2023; Department of Parks & Wildlife, 2013). Management of the whale shark tourism industry at Ningaloo Reef is considered the "gold standard" worldwide, with legal enforcement and high levels of monitoring and compliance (Ziegler & Dearden, 2022). However, the local management agency considers human disturbance from tourism the greatest threat to this endangered species (Pierce & Norman, 2016) in Western Australian waters, and recognises the need for ongoing research to assess and mitigate the impacts of swimmers and vessels (Department of Parks & Wildlife, 2013).

Most published studies assessing the effects of tourism-related activities on whale sharks have relied on observational data (e.g. watching ecotourism encounters in the water, or from a boat or aircraft). Responses include increased probability of disturbed behavioural state (Gayford et al., 2023), increased avoidance behaviours and directional changes (Haskell et al., 2014; Montero-Quintana et al., 2018; Pierce et al., 2010; Quiros, 2007), and decreases in interaction times (because sharks dive or otherwise avoid tourists) with greater proximity of vessels (Araujo et al., 2017; Pierce et al., 2010). A study at Ningaloo Reef between 2007 and 2009 observed 80 whale sharks from a light aircraft for up to 15-minute periods, either participating in tourism operations or not. Whale sharks changed direction more often when vessels were present, but maintained neutral behaviours (e.g. surface swimming) and remained at the surface for twice as long on average as sharks not involved in tourism operations (Raudino et al., 2016). Also at Ningaloo Reef, data from electronic monitoring systems of tourism vessels (Lester et al., 2019) and photo-identification records (Sanzogni et al., 2015) have been used to show that encounter duration, visitation rates and the likelihood of re-sighting individuals are not affected by the number of tourism interactions in which individual sharks have been involved. However, the lack of observable behavioural reactions, and the apparent tolerance of tourism that these results imply, do not preclude changes in fine-scale behaviour, activity levels or physiology that cannot be detected in these types of studies (Bateman & Fleming, 2017; Schleimer et al., 2015). Indeed, studies that rely on observational data of behavioural responses may fail to detect fine-scale changes and cannot measure physiological reactions (Bateman & Fleming, 2017; Gallagher & Huveneres, 2018)

Biotelemetry tags (animal-borne, electronic devices that record or transmit data) allow high-resolution data to be collected remotely, providing metrics for objectively quantifying disturbed and natural behaviours (Grainger et al., 2022). These tags also remove the potential for the subjectivity of observers to bias results or indeed influence animal responses with their presence. Data from biotelemetry tags can reveal effects of tourism that are not possible to discern from observations alone. Indeed, studies using temperature/depth recorders (Araujo et al., 2020) and accelerometer tags (Barry et al., 2023) have shown changes in whale shark habitat use and activity levels due to tourism operations at a site where sharks are provisioned in the Philippines.

The aim of this study was to use biotelemetry to assess the impacts of the "gold standard" whale shark tourism at Ningaloo Reef (Ziegler & Dearden, 2022). The Daily Diary (DD) (www.

wildbytetechnologies.com) is an archival, multi-sensor tag that incorporates a tri-axial magnetometer and a tri-axial accelerometer and can record data at up to 40 Hz, allowing it to quantify animal movement, derive orientation, estimate location (*via* dead-reckoning (Gunner et al., 2021)), and define behaviour (Shepard et al., 2008a, Wilson et al., 2008). We used DDs to investigate the effect of highly regulated tourism encounters on the activity levels, tortuosity of movements (how winding movements are), diving behaviour and vertical habitat use of whale sharks. We expected that if tourism was disturbing whale sharks, or they perceived people in the water as a threat, this would be evidenced by the expression of avoidance behaviours such as increases in acceleration, more frequent changes in direction (more tortuous movement paths), or increased diving (Haskell et al., 2014; Norman, 1999; Quiros, 2007). Therefore, we hypothesised that whale sharks' activity, tortuosity of movements and dive frequency would increase, and the proportion of time they spend at the surface would decrease, when exposed to tourism operations. Because smaller (i.e. younger) individuals are potentially more vulnerable and have less experience of people, we anticipated that they may perceive tourists as a greater threat, and therefore display a greater reaction to them than larger sharks. Using data collected *via* these animal-borne, behavioural data-logging tags, we aimed to gain insights into the effects of tourism on whale sharks that could not be achieved using observational data. By collecting data over periods when sharks were not involved with tourism interactions, we also obtained control data that are often lacking in studies of tourism impacts on wildlife (Ziegler & Dearden, 2022).

Materials and methods

Study site and the whale shark ecotourism industry

Ningaloo Reef, Western Australia, 21° 59' 57.84" S, 113° 54' 33.62" E (Figure 1) was the first place in the world where swimming with whale sharks was offered as a tourism experience, and whale sharks have become a tourism icon for the region (Catlin & Jones, 2010). Almost 2000 individual whale sharks have been identified at Ningaloo Reef (B. Norman, unpublished data from www.sharkbook.ai), with some individuals recorded there for periods of more than 20 years (Norman & Morgan, 2016). The whale shark ecotourism industry has operated there during the austral autumn and winter since 1989 (Catlin & Jones, 2010), although whale sharks are present year-round (Norman et al., 2017b, Reynolds et al., 2017). Tours are conducted seven days a week (weather dependent), primarily between March and August and more than 36,000 tourists swam with whale sharks in 2022 (Department of Biodiversity Conservation & Attractions, 2023). Since 1993, commercial whale shark ecotourism activities have been regulated and managed through a Western Australian State Government Department (Davis et al., 1997), currently called the Department of Biodiversity Conservation and Attractions (DBCA). The DBCA issues a limited number of licences (currently 15 i.e. 15 vessels, all powered and ~12–20 m in length) to tour operators who, in order to retain their licence to conduct tours, must adhere to rules (Code of Conduct) governing the interactions with whale sharks. Rules include limits on the proximity and speed of vessels during interactions (which are restricted to 90 min per vessel with each shark), and the number of people allowed to swim with the sharks at one time (10 tourists plus a guide and a photographer), as well as prohibiting swimmers touching, swimming in front of, or coming within 3 m of the sharks (Department of Biodiversity Conservation & Attractions, 2023; Department of Parks & Wildlife, 2013). The use of SCUBA when interacting with whale sharks is also prohibited, therefore interactions are restricted to periods when the sharks are swimming at the surface and come to an end when sharks dive too deep to be seen from the surface. Rules are strictly enforced and compliance is high due to monitoring by the DBCA and self-regulation by the operators themselves (Department of Biodiversity Conservation & Attractions, 2023; S. Reynolds and B. Norman pers. obs.).

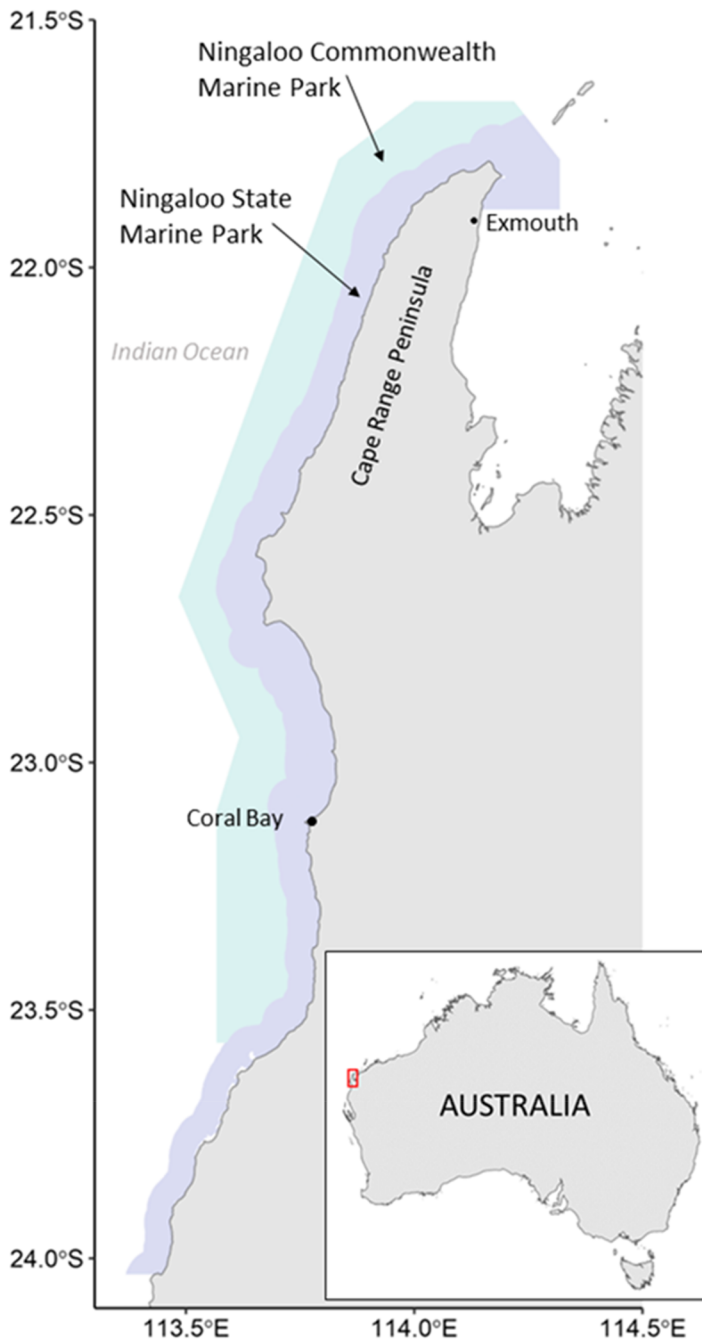


Figure 1. Map showing Ningaloo Marine Parks (Western Australian State waters and Commonwealth waters) where a highly regulated whale shark tourism industry operates during the austral autumn and winter from the towns of Exmouth and Coral Bay.

Daily Diary data collection

The DDs recorded magnetometry and accelerometry data at 8Hz and 20Hz respectively, and included other sensors to record environmental conditions such as temperature (2Hz) and pressure (2Hz). The data are recorded on a micro Secure Digital card and therefore the DD must be retrieved to recover the data (Wilson et al., 2008).

Data were collected over a 3 yr period from 24 “short-term” deployments of DDs on 23 whale sharks during the autumn/winter whale shark seasons (six in 2019, eight in 2020 and 10 in 2021, one shark was tagged in both 2020 and 2021). The tag package was attached to the first dorsal fin of the whale shark *via* a custom-made spring clamp deployed while swimming alongside the shark (Figure 2A). The package included the DD, two underwater video cameras (Paralenz; www.paralenz.com), and a continuous acoustic transmitter (V16-5H; www.innovasea.com), which allowed the shark to be actively tracked from a research vessel (at a distance of 100–300 m) using an acoustic receiver and directional hydrophone (VR100 and VH110; www.innovasea.com). Sharks were tracked for periods ranging from 59.5 min to 6 h (mean duration 3.63 h) and kept under constant observation so that the timings of in-water tourism encounters could be recorded (Figure 2B). All tag packages were manually retrieved by researchers at the end of each tracking period. The earliest tag deployment was at 09:15 and the latest tag retrieval time was 16:54 (UTC +08:00). Tagged sharks were photographed and individually identified *via* unique skin markings in *Sharkbook: Wildbook for Whale Sharks* (www.sharkbook.ai) (Arzoumanian et al., 2005).

To collect data on the behaviour of whale sharks on days when they were not involved in tourism interactions at all, 20 sharks were tagged with “long-term” DDs at Ningaloo Reef in 2021. Sharks were photographed for identification purposes but not actively tracked. Tags were retrieved the next time sharks were encountered by researchers or trained staff from tourism vessels after periods of between 1.8 and 39.9 days. We could be confident that sharks had not swum with tourists until the tags were retrieved because all tourism operators were cooperating with the research program and reported to researchers and DBCA when they encountered a tagged shark.

All spring clamps were designed with a corrodible section in the clamp so that the tag would detach from the shark within six months if not retrieved. The total length (TL) of each tagged shark was estimated (using boats or swimmers for scale (Sequeira et al., 2016)) and ranged from 5 to 9 m TL (mean 7.0 m TL).

Behavioural metrics and data analyses

High-resolution data collected by the DDs were visualised and initial analyses were performed using the custom, lab-built software Daily Diary Multiple Trace (DDMT) (www.wildbytetechologies.com) (Wilson et al., 2018). For the short-term deployments, the timings of tourism interactions recorded during field observations of each DD deployment were imported, synced to the DD data, and marked in DDMT, as periods *with tourists* and periods *without tourists*. Metrics derived

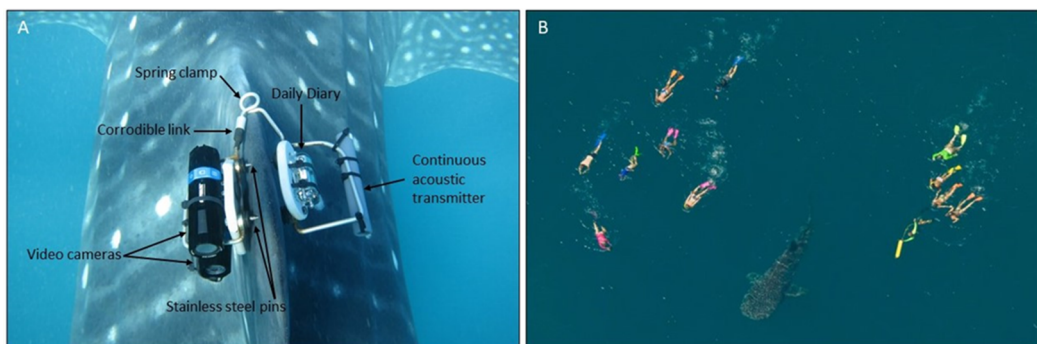


Figure 2. (A) Tag package used to collect data on tourism interactions, deployed on the first dorsal fin of a whale shark *Rhincodon typus* at Ningaloo Reef, Western Australia, using a custom-made spring clamp. Photo credit: Brad Norman, ECOCEAN. (B) Tourists swimming with a whale shark at Ningaloo Reef. Photo credit: Tiffany Klein, Ningaloo Aviation.

from the DD data, including the vector sum of the dynamic body acceleration (VeDBA), and pressure, were downloaded for each deployment with these marked observations. The proportion of time each shark spent with tourists was calculated by dividing the total duration of the deployment by the total duration of periods spent *with tourists*. For the long-term deployments, the same metrics were derived and exported from DDMT for the day after tagging because no tourism interactions with tagged sharks were reported by the tourism operators for each of those days, but from previous satellite tracking (Reynolds et al., 2017), active-acoustic tracking (B. Norman and S. Reynolds unpublished data) and dead-reckoning of DD data (J. Redcliffe unpublished data) we could be confident that the sharks were still in the Ningaloo Reef area. We included data only between 10:00 and 14:00 (UTC +08:00) because these are the typical operating times of the tourism vessels when the majority of interactions with whale sharks occur, and when most of the short-term tracking took place. Data were collated, sub-sampled to 1 Hz and further analysed in R (R Core Team, 2021).

We used VeDBA and tailbeat frequency (TBF) to provide a quantitative measure of shark activity, which we hypothesised would increase if whale sharks were disturbed by the presence of people in the water. VeDBA is a well-established measure of activity of tagged animals and can be used as a proxy for oxygen consumption (and therefore energy expenditure) (Qasem et al., 2012) if a calibration is made on the target (or similar) species (Halsey & Bryce, 2021; Lear et al., 2017). VeDBA is derived from the tri-axial accelerometry channels and was calculated directly in DDMT from the raw accelerometry data (20Hz) using the following equation:

$$\text{VeDBA} = \sqrt{(\text{DBAX})^2 + (\text{DBAY})^2 + (\text{DBAZ})^2}$$

where DBA is dynamic body acceleration in the three axes (X, Y and Z). The dynamic acceleration was calculated by subtracting static acceleration (the raw acceleration smoothed with a running mean over 4s intervals (Shepard et al., 2008b)) from the raw acceleration.

Sharks accelerate by increasing the frequency and amplitude of their tailbeat (sub-carangiform or carangiform swimming where the shark's head, body and tail swing from side to side). The amplitude and frequency of tail beats measured at the point of tag attachment i.e. the first dorsal fin, were derived from the tri-axial magnetometry data using DDMT (Williams et al., 2017). Before deployment, each DD was calibrated by putting it through a series of prescribed movements that could be recognised in DDMT and used to normalise the magnetometry data. This allows soft iron and sensitivity errors to be accounted for, and magnetometry data from individuals to be compared and appropriate metrics (e.g. heading) derived (Vasconcelos et al., 2011). The rate of change in heading across time periods was calculated using the normalised magnetometry data. Oscillations in animal heading (at the position of the first dorsal fin) were quantified according to the waveform apparent in the heading signal over time, giving both the period of the wave (e.g. peak to peak) and the amplitude of the movement at the site of the dorsal fin. Although this amplitude does not reflect the amplitude of the movement of the tail, it will scale proportionately. The body oscillation frequency though, will be the same as the tail beat frequency. This allowed magnetometer oscillations (our TBF) to be defined, marked, and counted (as waveforms per minute) in DDMT.

To investigate if the presence of tourists increased the tortuosity of sharks' movements, we reconstructed each animal's movement path from the magnetometry and accelerometry data *via* dead-reckoning (Bidder et al., 2015). Dead-reckoning uses vectors on speed, direction and change in depth to provide an animal's putative track within defined periods of time. We used this to determine a best estimate of each shark's track, split into minute-long sections. For each of these minutes, we calculated both the cumulative- and straight-line distance travelled by the sharks using the *fossil* package (Vavrek, 2011) in R. The former was divided by the latter to give a measure of relative tortuosity between 0 and 1, with 0 being straight-line travel and 1 being highly tortuous (with many deviations from a straight-line course).

For these three metrics (VeDBA, TBF, tortuosity), we constructed generalised linear mixed models (GLMMs) with the *lme4* package (Bates et al., 2015) to test the effect of tourism on whale shark activity. We used data from the short-term deployments only to compare whale shark activity between the two tourism states that had been marked in the data: *with tourists* or *without tourists*. Prior to analysis, we removed the first 15 min after the tag package was deployed on sharks (based on diving behaviour, see Results) to minimise potential tagging impacts affecting the results of our comparisons. However, in the analysis of VeDBA, we included the first 20 s after tag placement (*tagging*) as a third category (of tourism state) in our model, as we wanted to understand how swimming with tourists compared to more acute and intrusive disturbance. Because tourism activities only occur when sharks are swimming at the surface, and these metrics vary when sharks are descending, swimming at depth and ascending (Gleiss et al., 2011; Wilson et al., 2022), we also included data only when sharks were at the surface (above 3 m depth). Models with the response variables VeDBA and TBF had a gamma and a Poisson distribution respectively, both with log link, and included tourism state, the total body length (size) of each shark and the interaction of these as fixed explanatory variables. Because tortuosity was a relative measure bounded between 0 and 1, a beta regression model with logit link (Douma & Weedon, 2019) was constructed using the *glmmTMB* package (Brooks et al., 2017) to test the effect of tourism on the tortuosity of the sharks' tracks. The model had tortuosity as the response variable and included the same fixed explanatory variables as the previous models (tourism state, size and the interaction of these). The identity of each shark was included in all these models as a random effect to account for repeated measures from these individuals.

To investigate whether tourism affected the diving behaviour and vertical habitat use of whale sharks, we compared *tourism days* (i.e. data from the short-term deployments when whale sharks were subject to tourism operations) to *non-tourism days* (i.e. data from the long-term deployments). To make data from the short-term deployments more consistent with the long-term data, and to ensure we were capturing the effect of tourism operations on the sharks, we removed short-term deployments that lasted < 4 h duration and where sharks had spent < 20% of the deployment with tourists ($n = 13$). We hypothesised that whale sharks would dive more often and spend less time at the surface (above 3 m depth) on *tourism days*, in an effort to avoid tourists. For this analysis, a dive was defined as a descent from the surface to at least 10 m (a depth which would typically end a tourism encounter) and a subsequent return to the surface. Dives were identified and counted in DDMT, and the total number of dives during that deployment was divided by the duration of each deployment to give the number of dives per hour. A generalised linear model (GLM) was constructed using the *lme4* package, with the number of dives each shark made as the response variable, and the type of day (i.e. *tourism* or *non-tourism day*), the size of the shark, and the interaction of these as explanatory variables. The model had a Poisson distribution and log link, and an offset of unit of time (i.e. duration of deployment). The proportion of time each shark spent at the surface was calculated by dividing the total duration of these periods by the duration of the tag deployment. A beta regression model with logit link was constructed with the *betareg* package, because the response variable is a proportion (of time) (Douma & Weedon, 2019). It also included the type of day, the size of the shark, and the interaction of these as explanatory variables.

For all models, error distributions and link functions were chosen based on the type of response data and the normality of residuals in diagnostic plots. For each response variable, models that included all explanatory variables (and their interaction) as described above were run, then models excluding the interaction, and separate models for each explanatory variable alone were also run. Akaike information criterion (AIC) scores (and Δ AIC scores) were then used to compare full and reduced models, with the lowest AIC scores determining the most parsimonious model for each response variable (Supplementary Table S1). Means and 95% confidence intervals (CI) derived from the final models are reported, used for plotting and for assessing the differences between factors of the explanatory variables.

Results

Of the 24 short-term deployments of DDs on whale sharks (*Rhincodon typus*), one tag failed to record data on the accelerometry, magnetometry or pressure channels and could not be used in any analyses. Data from the remaining 23 tags were available for the analyses of VeDBA, diving behaviour and time at the surface. Of these 23 sharks, 15 initiated a dive within 20s of tagging, returning to the surface after an average of 9.4min and a maximum of 24.7min later. The remaining eight sharks did not dive immediately, but all did so within 15min of tagging (maximum duration between tagging and first dive was 14.5min). Data from five tags were excluded from the TBF analysis due to failure of the magnetometer channels.

Of the 20 long-term DDs deployed, 14 were retrieved and 12 had data suitable for our described analyses (2 tags failed to record data because of flooding of the housing and a faulty SD card respectively). At the start of the 4h period of interest (i.e. 10:00 (UTC +08:00) on the day after tagging), 3 of 12 tagged sharks were swimming at depth and did not ascend to the surface (above 3m depth) for the entire 4h. These three sharks were excluded from the analysis of diving behaviour (because, according to our definition of a dive, they did not make any) but were retained for the analysis of time spent at the surface.

Tourism interactions

Of the 23 sharks that were actively tracked during the short-term deployments, 20 were involved in successful interactions with swimmers from at least one tourism vessel. Attempts were made to interact with the remaining three sharks (i.e. tourists entered the water to swim with the shark) but the sharks dove or otherwise avoided the interaction soon after it started. The durations of these 23 short-term deployments ranged from 59.5 to 360.0min (i.e. 6h), with a mean deployment time of 217.7min (± 72.1 SD). The proportion of time sharks spent with tourists during these tracking periods ranged from 0.003 to 0.63 (mean 0.27 ± 0.22 SD), which equates to between 30s (when a tourism interaction was attempted but the shark dove almost immediately) and 2h 46min (mean 62.2min ± 55.0 SD). This means that when considered in the context of daily activity (i.e. over a period of 24h), sharks spent an average proportion of 0.04 (± 0.04 SD and range 0.0003 to 0.12), or 4% of a day when they were involved in tourism operations swimming with tourists.

Summed vector of the dynamic body acceleration (VeDBA)

Values of VeDBA recorded from the tagged sharks over both the entire durations of the short-term deployments and for the 4h periods of interest from the long-term deployments ranged from 0.013 to 0.627g (mean 0.041 ± 0.019 SD). Considering data only from when sharks were swimming at the surface, VeDBA ranged from 0.015 to 0.199g (mean 0.053 ± 0.017 SD). These values are comparable to the range of dynamic body acceleration measurements previously made on whale sharks (Barry et al., 2023; Gleiss et al., 2011; 2013; Sun, 2016).

The model which included tourism state (i.e. *with* or *without tourists* or *tagging*), size and the interaction of these had the lowest AIC value (Supplementary Table S1) and these factors were all retained in the final model. During the 20s immediately post-tagging, VeDBA was significantly greater than during periods with and without tourists, particularly amongst smaller sharks. Smaller sharks also had higher VeDBA without tourists than with tourists, while the opposite relationship was found in larger sharks (Figure 3A). For a 5m TL shark (the smallest size of sharks in our study), mean VeDBA decreased by 20%, from 0.056g (CI = 0.054 to 0.059g) when swimming with tourists, to 0.045g (CI = 0.043 to 0.047g) without tourists. However, during the initial reaction to tagging mean VeDBA was 134% higher than swimming without tourists

(mean 0.132 g; CI = 0.122 to 0.143 g). Mean VeDBA of the largest sharks in our study (9 m TL) was 18% higher when sharks were swimming with tourists than when swimming without tourists, increasing from 0.044 g (CI = 0.042 to 0.046 g) to 0.052 g (CI = 0.049 to 0.054 g) respectively, and increased by another 28% to 0.067 g (CI = 0.062 to 0.072 g) during the initial reaction to tagging (Figure 3A).

Tail beat frequency (TBF) and tortuosity

The final model for TBF (with the lowest AIC score) also included tourism state, shark size and their interaction (Supplementary Table S1). As for VeDBA, smaller sharks had higher TBF without tourists than with tourists and larger sharks had higher TBF with tourists than without tourists (Figure 3B). For 5 m TL sharks, mean TBF were 13.5% greater in the absence of tourists, increasing from 7.96 (CI = 2.62 to 24.21) when sharks were swimming with tourists to 9.03 (CI = 2.98 to 27.39) when swimming without tourists. The mean TBF of 9 m TL sharks increased by 13.4% in the presence of tourists, from 8.44 (CI = 2.63 to 27.10) when swimming without tourists to 9.57 (CI = 2.97 to 30.88) when swimming with tourists.

Tortuosity had the potential to range from 0 (straight-line travel) to 1 (highly tortuous movements), and the raw values of tortuosity recorded for all sharks per minute ranged from 0.00 to 0.99. The model which included tourism state only had the lowest AIC value (Supplementary Table S1), therefore whale shark size and the interaction of size and tourism state were removed

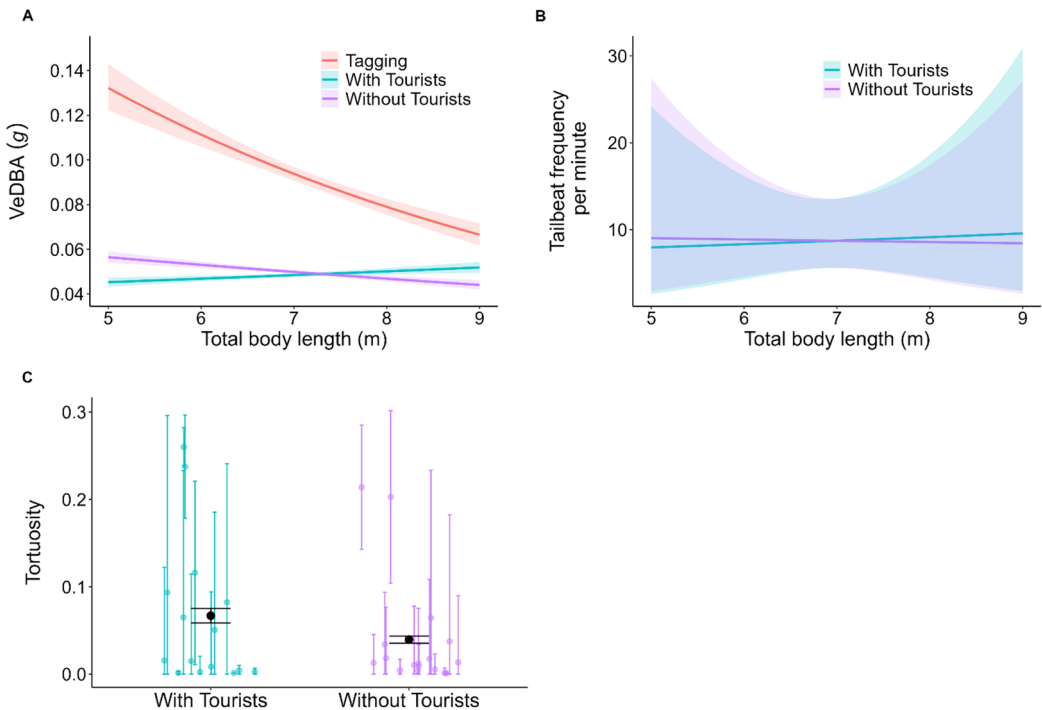


Figure 3. Activity levels of whale sharks *Rhincodon typus* at Ningaloo Reef, Australia between 2019 – 2021. (A and B) Results of generalised linear mixed models showing effect of the interaction of tourism state (*with* or *without tourists*, or *tagging*) and size on vectorial dynamic body acceleration (VeDBA) and tailbeat frequency respectively. Lines and ribbons are model-derived means and 95% confidence intervals (CIs). (C) Results of beta regression model showing effect of tourism on the tortuosity of sharks' movement paths. Tortuosity had the potential to range from 0 (straight-line travel) to 1 (highly tortuous movement). Coloured points and error bars show the means and standard deviations of individual sharks and black points and error bars show the model-derived means and CIs.

from the final model. The model-derived mean tortuosity when sharks were swimming without tourists was 0.04 (CI = 0.036 to 0.044) and increased by 69% to 0.07 (CI = 0.059 to 0.075) when swimming with tourists (Figure 3C). However, both means were < 0.1, indicating that the whale sharks' movement paths recorded by our DDs were all, on average, relatively straight.

Diving behaviour and vertical habitat use

For the short-term deployments (i.e. tourism days), 10 sharks had deployments lasting > 4h and/or spent > 20% of their tracked time with tourists. The proportion of time these sharks spent at the surface ranged from 0.47 to 0.82 and their number of dives per hour ranged from 1.90 to 3.70. During the 4h periods taken from the long-term deployments (i.e. non-tourism days), the proportion of time the 12 sharks spent at the surface ranged from 0 to 0.75. After removing data from the three sharks that remained at depth, the number of dives per hour made by the nine sharks ranged from 0.25 to 8.50.

Models with the lowest AIC values for the number of dives sharks made and the proportion of time they spent at the surface included only type of day (i.e. tourism or non-tourism day) (Supplementary Table S1). Size and the interaction of size and type of day were removed from the final models. Whale sharks made significantly fewer dives per hour and spent a significantly higher proportion of their time at the surface on tourism days than on non-tourism days. The average number of dives per hour sharks made decreased by 44% from 4.56 (CI = 3.35 to 6.19) on non-tourism days compared with 2.53 (CI = 1.71 to 3.73) on tourism days. Concurrently, the average proportion of time sharks spent at the surface on tourism days was 0.64 (CI = 0.573 to 0.711), an increase of 107% over non-tourism days when sharks spent an average proportion of 0.31 (CI = 0.167 to 0.448) of their time at the surface (Figure 4).

Discussion

Despite the growing popularity of whale shark tourism and concerns over its associated impacts on this endangered species, the majority of studies to date have relied purely on observations of behaviour. Our study is the first to use objective, high-resolution biotelemetry data to assess the effects of "gold standard" (Ziegler & Dearden, 2022) whale shark tourism at Ningaloo Reef on the activity, behaviour, and diving and vertical habitat use of whale sharks. Our results provide evidence of effects on whale sharks which would not have been apparent from observational studies. Contrary to our hypothesis, being subject to tourism activities did not increase the number of dives made by sharks or the amount of time they spent away from the surface. Rather, sharks dove more often and spent less time at the surface on days when they were not involved in tourism operations. However, although for smaller sharks, exposure to tourism correlated with decreases in activity (VeDBA and TBF), for larger sharks, VeDBA increased by 18% and TBF by 13% when swimming with tourists, and track tortuosity increased by 69% during tourism encounters across all sized sharks. While these differences were statistically significant, it is important to examine the biological significance of these results and what they mean for sharks' daily energy expenditure and in the context of whale shark tourism and conservation globally.

Our hypothesis that activity levels would increase in the presence of tourists was supported by the results from our analyses for larger sharks, but not for smaller sharks. We found that larger sharks had increased activity levels (VeDBA and TBF) when swimming with tourists compared to periods when swimmers were absent. Conversely, smaller sharks had lower VeDBA and fewer TBF when tourists were present. An increase in activity does translate to an increase in energy expenditure (Halsey & Bryce, 2021), therefore the increases in activity levels in larger sharks indicate that they were incurring a greater energetic cost during these tourism

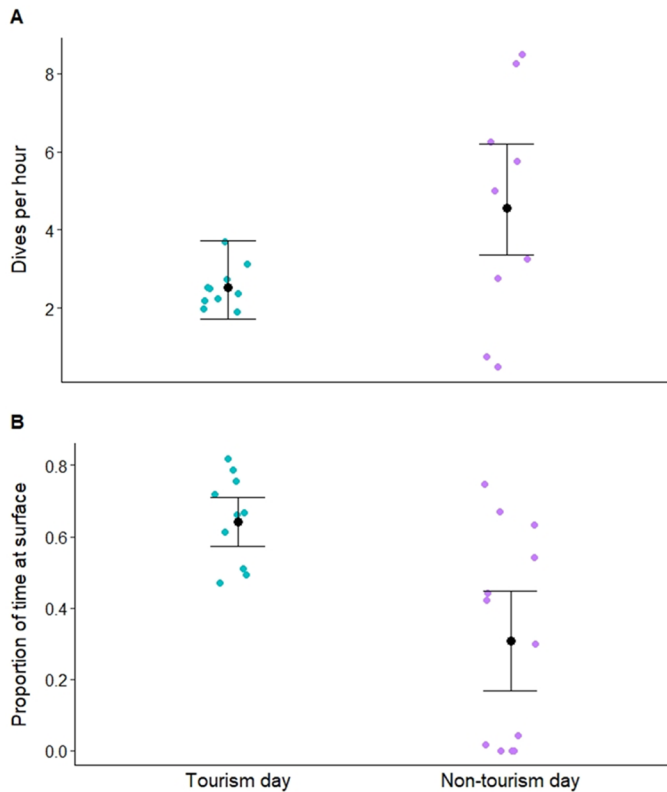


Figure 4. Diving behaviour and vertical habitat use of whale sharks *Rhincodon typus* at Ningaloo Reef, Australia between 2019 and 2021. (A) Results from a generalised linear mixed model showing the number of dives sharks made on days when they were subject to tourism operations and days when they were not. (B) Results from a beta regression model showing the proportion of time whale sharks spent at the surface on days when they were subject to tourism operations and days when they were not. Coloured points are the values for individual sharks and black points and error bars are the model-derived means and 95% confidence intervals.

interactions. However, because whale sharks' large size (currently) precludes the direct measurement of metabolic rate (Watanabe & Goldbogen, 2021), calibration of metrics from accelerometer tags with metrics of metabolic rate for the species is not possible. Without this calibration we cannot assume that the magnitude of the change in energy expenditure is the same as the change in the proxy (Halsey & Bryce, 2021), in this case an 18% increase in VeDBA for larger sharks, and a 20% decrease for smaller sharks, when swimming with tourists compared to without tourists. The increased activity of larger sharks may have incurred an increased energetic cost greater or lesser than 18%. However, an important consideration is the duration of the increase in activity, what proportion of daily activity this represents, and therefore, how much of a burden the increase places on an animal's overall daily energy budget. On tourism days, whale sharks spent up to 63% of the time for which we tracked them with tourists. When considered in the context of the total activity of whale sharks however, tourism encounters are often relatively short, and sharks may only be subject to tourism operations for a limited number of days per year. Sharks spent an average of 4% (62.2 min) of a tourism day swimming with tourists, although the longest amount of time a single shark spent with tourists was 2h 46 min, which is 12% of a day. Photo-identification records from tourism encounters at Ningaloo Reef indicate that individual sharks have limited exposure to tourism operations throughout the whale shark season, with 75–95% of sharks sighted for ≤ 3 days per year (B. Norman, unpublished data from www.sharkbook.ai). The regulations for tourism interactions

in place at Ningaloo Reef also limit the duration of interactions with individual sharks for each tourism vessel to 90 min (Department of Biodiversity Conservation & Attractions, 2023). However, on days when sharks are scarce, individuals are often shared between multiple vessels and this practice may need further scrutiny (Ziegler & Dearden, 2022) to ensure that the proportion of each day sharks spend with tourists remains low. Regulations restricting the amount of time whale sharks are exposed to tourism activities are important at all whale shark tourism sites for limiting the potential for tourism to negatively affect individuals' energy expenditure.

There were significant increases in VeDBA seen in all sized sharks during the initial reaction to tagging (Figure 3A), suggesting that the species is capable of high levels of activity when necessary. Indeed, VeDBA in whale sharks has been recorded up to 2.257 *g* during active feeding (Sun, 2016), more than three and half times greater than the highest value recorded in this study (0.627 *g*). The levels of VeDBA recorded from sharks during surface swimming, both with and without tourists, were low in comparison to these levels immediately post-tagging and during active feeding. This suggests that the energetic costs of interacting with tourists may also be relatively low. However, changes in behaviour resulting from tourism activities have the potential to increase energy expenditure (Araujo et al., 2020) and if this occurs in areas or at times when food resources are scarce, sharks subjected to tourism activities may be at a disadvantage, with their short-term energy budgets negatively impacted. Whale sharks at Oslob in the Philippines, spent more time in warmer waters on days when provisioning occurred, which the authors estimated could have increased their metabolic rate on those days by between 1 and 18% (based on increases in metabolic rate caused by warmer temperatures estimated from published Q_{10} values for ectotherms, but not including any increased energetic costs from higher activity levels) (Araujo et al., 2020). A further study at this site used accelerometers to reveal increases in activity levels of sharks during tourism periods, including a doubling of VeDBA compared to periods without tourists (Barry et al., 2023). Using this to inform a more complex bioenergetics model, the authors estimated that whale shark metabolic rates increased by between 56.7 and 71.6% during tourism operations, which, during the study, ran for four hours from 06:00 to 10:00. If we assume that the increase in VeDBA in our larger sharks at Ningaloo Reef equates to the same magnitude of increase in metabolic rate, then it is comparable with the higher value found in the first Oslob study (Araujo et al., 2020), although this increase only occurs for relatively short periods of time while sharks are interacting with tourists, not over the entire day (as described in Oslob). The larger increases in metabolic rate estimated by Barry et al. (2023) mean larger energetic costs. The authors concede that while the provisioning at Oslob probably compensates for this increased energy requirement, there may be other detrimental impacts from this practice, and they advocate operational changes to reduce the energy expenditure of whale sharks involved in tourism. At Ningaloo Reef, where provisioning does not occur, any increase in whale shark activity has the potential to place more of a burden on sharks' energy budgets.

However, the relatively small proportions of the day sharks spent swimming with tourists suggests that the increase in activity in larger sharks while swimming with tourists may contribute a relatively negligible amount to their total daily energy expenditure. The different relationships we found between activity levels and tourism depending on the size of the sharks at first seemed counter-intuitive, as we anticipated that smaller sharks (that are more vulnerable and potentially less-experienced with tourism activities) may have shown more of a reaction to tourists than larger sharks. However, it has been suggested that larger (i.e. older and more experienced) sharks may display avoidance learning (Quiros, 2007), which could explain the increase in VeDBA and TBF seen in these sharks in our study. Sharks at Oslob in the Philippines, where provisioning occurs, show signs of habituation i.e. sharks that have a longer resighting history show greater tolerance to the close proximity of tourists, indicating learning that has produced behavioural modification (Schleimer et al., 2015). Other studies in the Philippines (Araujo et al., 2017) and Mozambique (Haskell et al., 2014) have shown no relationship between

shark size and the length of tourism encounters, where the authors suggest that sharks are not learning to avoid tourists. Similarly, at Ningaloo Reef, encounter duration (Lester et al., 2019) and the likelihood of re-sighting individuals (Sanzogni et al., 2015) did not decline as the number of tourism encounters experienced by individual sharks increased. However, encounter duration and whether or not an individual returns to the tourism site may not be the best measures of tourism disturbance. Less-tolerant individuals may have already been displaced (Bejder et al., 2009) and apparent tolerance of tourism activity does not necessarily preclude other impacts on the animals. Using the fine-scale increase in the activities of whale sharks recorded by our DDs, rather than the length of tourism encounters or site fidelity as metrics for disturbance, allowed particular insight into the effects of tourism on these sharks and could be an indication of avoidance learning in larger sharks at Ningaloo Reef. Long-term photo-identification records of tagged individuals, in conjunction with the DD data, could provide further insights into the capacity of whale sharks to learn from previous encounters with swimmers, vessels, and other sources of disturbance.

Whale sharks use avoidance behaviours when they perceive a threat, including banking (i.e. turning their dorsal surface towards the threat), and changing direction (Norman, 1999; Quiros, 2007). In Mozambique, avoidance behaviours in response to tourists in the water have been observed in 65% of interactions (Haskell et al., 2014), and in Mexico the presence of both swimmers and vessels increases the probability that sharks will display “stress-related behaviours” including change of direction, diving and acceleration (Montero-Quintana et al., 2018). At Ningaloo Reef, sharks have been observed making more changes in direction when tourism vessels are operating in their vicinity (Raudino et al., 2016), and the frequency of avoidance behaviours during tourism encounters increased between 1995 and 1997 (Norman, 1999). Our results, showing that the tortuosity of whale sharks’ movement paths increased in the presence of tourists (but did not change with size), support these earlier findings. Increasing tortuosity would generally produce an increase in VeDBA because turning requires more energy than straight-line travel (Wilson et al., 2013). However, although tortuosity increased for all sized sharks in the presence of tourists, VeDBA increased only for larger sharks. Although we were unable to directly measure speed of travel, these results suggest that speed is driving the differences in VeDBA seen in the different-sized sharks. Larger sharks may be maintaining or increasing speed while turning, increasing their VeDBA, whereas smaller sharks may slow down as they turn in the presence of tourists which would decrease their VeDBA.

Mean tortuosity values for both *with* and *without tourists* were low on the relative scale (< 0.1 on a scale of 0–1), indicating that tagged whale sharks generally travelled in relatively straight paths. This straight-line travel corresponds to the movements of whale sharks typically observed at Ningaloo Reef, and on which the methods for interacting with whale sharks used by the tourism industry are based. Vessels drop tourists in the water in front of the shark and as the shark approaches, the swimmers are directed by the in-water guide to move to the sides of its path and swim alongside (Davis et al., 1997; Department of Biodiversity Conservation & Attractions, 2023). Sharks may turn to avoid tourists if they are slow to move out of their swimming path. Although it was outside the scope of this study to include analysis of videos from the on-animal cameras, future studies could incorporate data from these on number, proximity and behaviour of tourists in the water with the sharks to further elucidate the effects on their movements and behaviour. We were also unable to include data on the proximity of tourism vessels to sharks in our analyses, and it could be that sharks were responding to the presence of vessels rather than the presence of swimmers. However, when tourism operations involve both vessels and swimmers, it is difficult to separate the effects of each, and is probably not necessary for understanding the overall effects of tourism (Montero-Quintana et al., 2018).

Whale sharks are generally described as spending much of their time swimming near the surface, making them vulnerable to ship-strike (Pierce & Norman, 2016; Womersley et al., 2022), but also allowing tourism interactions, that rely on viewing, swimming or snorkelling with the

sharks while they are at the surface. Whale sharks can however, dive as deep as ~1900 m (Tyminski et al., 2015) and regularly move up and down the water column (Gleiss et al., 2011). A previous study at Ningaloo Reef found whale sharks spent more time at the surface when tourism vessels were operating in their vicinity than when vessels were absent. However, in order to contextualise these results, the authors recognised the need for further research to understand “typical” whale shark diving behaviour (Raudino et al., 2016). Our study provides further insight, finding that whale sharks dove more often and spent more time away from the surface on days when they were not subject to tourism operations (*non-tourism days*) compared to days when they were (*tourism days*). This finding was contrary to our expectations that if tourism was disturbing the sharks, the opposite would be the case, based on observations in the Philippines and the Seychelles where sharks repeatedly swum with by tourists were more likely to dive than those involved in tourism interactions for the first time (Quiros, 2007), and spent significantly less time swimming at the surface when tourist vessels were present (Rowat & Brooks, 2012). Our findings show that tourism operations at Ningaloo Reef do not increase the number of dives made or the time spent away from the surface by whale sharks. Rather, it seems that whether a whale shark is involved in tourism operations on a given day is determined by their differing diving behaviour and vertical habitat use on different days. It is also possible that weather and sea conditions could affect diving behaviour, although these were relatively similar over the days that data were collected and we did not include any environmental variables in our models. The fact that three of our sharks spent at least 4 h during the middle of the day swimming at depth (below 3 m) points to a more complex pattern of vertical habitat use than previously thought, even in relatively shallow waters. The depth and activity data collected by our long-term deployments of DDs provide the opportunity to further investigate the “typical” diving behaviour and vertical habitat use of whale sharks.

At many whale shark tourism sites globally, even in the absence of research showing clear effects of tourism, a precautionary approach has been adopted and codes of conduct (usually based on that in force at Ningaloo Reef) are now in place (Haskell et al., 2014; Montero-Quintana et al., 2018; Pierce et al., 2010; Schleimer et al., 2015; Ziegler et al., 2021; Ziegler & Dearden, 2022). However, compliance with these codes is mostly voluntary and even when they are legally binding, enforcement can be lax. In many countries permits to conduct whale shark tours are not required and overcrowding of both vessels and swimmers has been identified as a major issue, putting pressure on sharks and detracting from the tourism experience (Ziegler & Dearden, 2022). In Oslob, 93% of swimmers have been observed within 2 m of sharks (Legaspi et al., 2020), increasing the likelihood of physical contact with sharks (Schleimer et al., 2015). Indeed, 40% of tourists responding to a survey admitted to touching the sharks (Ziegler et al., 2019). The relatively high VeDBA values we found immediately post-tagging are likely a reaction to the shark’s fin being touched. Although tag attachment is likely more invasive than touching by tourist hands, due to the clamp attachment mechanism, we suggest that prohibition of touching sharks should be a priority for regulation and enforcement at all whale shark tourism sites.

Some tourism sites have seen declines in whale shark numbers (e.g. Tofo Beach, Mozambique (Rohner et al., 2013) and Phuket, Thailand (Theberge & Dearden, 2006)), and the whale shark tourism industry in the Seychelles has reportedly collapsed as whale sharks are no longer sighted in the area (Ziegler & Dearden, 2022). With the growing popularity of whale shark tourism globally (Gallagher & Hammerschlag, 2011; Ziegler & Dearden, 2022), it is essential that the social and economic benefits of tourism to people and local communities are balanced with the potential health and fitness impacts on the species. Good management will ensure the tourism industries are sustainable for both the sharks and the communities that rely on them for income (Legaspi et al., 2020; Montero-Quintana et al., 2018; Ziegler et al., 2021). It is also important to consider the impacts on, and risks to whale sharks from tourism relative to the threats facing the species and all elasmobranchs, such as ship-strike, fishing and climate

change (Pierce & Norman, 2016; Reynolds et al., 2022; Womersley et al., 2022). Conservation and management plans for whale sharks should consider tourism in the context of these global drivers of elasmobranch declines.

Conclusion

The effects of wildlife tourism vary among target species and are also highly dependent on the methods used for interactions, the regulations governing these and the levels of compliance and enforcement in place (Healy et al., 2020). We advocate the use of biotelemetry to reveal effects of tourism that cannot be detected in purely observational studies, especially on mobile marine species that are difficult to observe and follow. Standardisation of assessments of the impacts of tourism on target species will facilitate comparisons, both within and among species. We found evidence of some increases in activity levels and directional changes of sharks in response to tourism interactions at Ningaloo Reef, despite high levels of regulation and enforcement. The high-resolution data we collected with the use of innovative biotelemetry technology allowed these differences to be detected, when previous, observational studies have shown no effect of tourism on encounter duration (Lester et al., 2019), behavioural changes (Raudino et al., 2016), and probability of resighting (Sanzogni et al., 2015). The impacts of “gold standard” tourism probably represent a relatively small proportion of a whale shark’s total daily energetic cost, however, at other tourism sites where overcrowding, non-compliance with rules prohibiting close-proximity and touching the sharks, and provisioning are occurring, the impacts and costs of tourism may be much higher (Barry et al., 2023). Standardisation of research methods and metrics of disturbance are needed to definitively quantify this. Objective and standardised quantifications of tourism impacts should ultimately be used to formulate or refine management strategies that mitigate the effects of tourism on target species and their ecosystems, to ensure sustainable, minimal-impact wildlife tourism becomes ubiquitous.

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Data availability statement

The data that support the findings of this study are stored on The University of Queensland's Research Data Manager and available from the corresponding author, SDR, upon reasonable request.

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