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EDITED BY

Edson Gandiwa,
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United States
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Murdoch University, Australia
Naomi N Moswete,
University of Botswana, Botswana

*CORRESPONDENCE

Julian A. Tyne

✉ Julian.tyne@dbca.wa.gov.au

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Ningaloo Marine Park management program best practice for whale shark (*Rhincodon typus*) conservation

Julian A. Tyne^{1*}, Holly Raudino¹, Emily Lester²,
Gemma Francis³, Peter Barnes³ and Kelly Waples¹

¹Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia, ²Australian Institute of Marine Science, Crawley, WA, Australia, ³Parks and Wildlife, Department of Biodiversity, Conservation and Attractions, Exmouth, WA, Australia

The predictable nature of whale shark (*Rhincodon typus*) aggregations around the world forms the basis for nature-based tourism. The Ningaloo Marine Park (NMP), Western Australia is one of those locations and a management program has been in place since 1993. Measuring the effectiveness of the management program is important to minimise potential impacts on the whale sharks. In NMP tour operator vessels are equipped with an Electronic Management System (EMS) to collect data during whale shark encounters. Using EMS data and associated images of identified whale sharks from the months of March to July between 2011 to 2019, Generalised Additive Mixed Models (GAMMs) and Generalised Linear Mixed Effect Models (GLMMs) assessed the variation in duration of whale shark encounters. Using EMS data from 2010 to 2023 we mapped the density distribution of all whale shark encounters to identify hotspots. From the 44,017 whale shark encounters between 2011 to 2019, 7585 involved 986 individuals. On average individual sharks were encountered 4.30 times per day (\pm SD 3.15), with a mean duration of 15.30 mins (\pm SD 13.17). In Tantabiddi, daily encounters, distance, Southern Oscillation Index (SOI), habitat and vessel were important in predicting the variation in encounter duration, whereas in Coral Bay daily encounters, encounter number, SOI, sex and vessel were important at predicting the variation in encounter duration. There was no evidence to suggest a significant variation in whale shark encounter duration between days after repeated encounters in Tantabiddi or Coral Bay. However, some individuals were repeatedly encountered in a day with a cumulative encounter duration up to 224 minutes. A significant negative relationship between encounter duration and number of daily encounters was identified for Tantabiddi -0.073 , p -value < 0.001 , Coral Bay -12.3 , p -value < 0.001 and for NMP overall -0.083 , p -value < 0.001 . A G_i^* statistic identified significant whale shark encounter hotspots where commercial whale shark encounters occur in higher densities. Our findings support the best practice standard of the whale shark management program in the NMP, however the potential pressure of prolonged cumulative whale shark encounter durations, and the high density of the whale shark encounters in some areas warrants further investigation.

KEYWORDS

whale shark (*Rhincodon typus*), best practice, human-wildlife interactions, nature-based tourism, spatial density distribution, Ningaloo Marine Park

Introduction

The whale shark (*Rhincodon typus*) is listed as “Endangered” globally on the Red List of Threatened Species by the International Union for the Conservation of Nature (IUCN) and is considered “Largely Depleted” (Green Status Assessment that assesses the impact of past, present and future conservation actions) (Pierce et al., 2021). Pressures on whale sharks include commercial harvesting and by-catch (Rowat and Brooks, 2012; Rowat et al., 2021), large vessel strikes (Womersley et al., 2022, 2024), pollution and marine debris (Germanov et al., 2019) and tourism (Araujo et al., 2017). The Convention on Migratory Species (CMS) provides a framework within which signatories may tackle pressures that exist throughout the whale shark’s range. As a migratory species, whale sharks are wide-ranging filter-feeders that occur throughout the world’s tropical and warm-temperate oceans (Meekan et al., 2006; Holmberg et al., 2009; Sequeira et al., 2014; Andrzejczak et al., 2016). Globally there are two subpopulations of whale sharks, one in the Indo-Pacific and the other in the Atlantic Ocean (Vignaud et al., 2014). Individuals from these subpopulations aggregate seasonally to feed at many locations around the world, linked with an increase in productivity, including India, the Maldives, South Africa, St Helena, Belize, Mexico, the Galapagos Islands, Southeast Asia, Indonesia, and Australia (Norman et al., 2017). The predictable nature of these aggregations provides the basis for nature-based tourism opportunities that offer the possibility to swim with whale sharks.

Nature-based tourism operations that observe and interact with marine megafauna (e.g. marine mammals and sharks) have increased globally (O’connor et al., 2009; Tyne et al., 2014; Gallagher et al., 2015; Healy et al., 2020). Consequently, concerns have been raised regarding the impact that the lack of appropriate management of nature-based tourism operations might have on targeted populations (Lusseau, 2004; Williams et al., 2006; Healy et al., 2020). For example, the duration of encounters with whale sharks in the Philippines decreases when motorised vessels are in close proximity and when the encounters occur in deep water (Araujo et al., 2017). Whale sharks can change behaviour in the presence of vessels and swimmers (Araujo et al., 2017; Blanchard et al., 2020), which can detract from other fitness-related activities, such as foraging and resting and possibly impacting reproduction and survival. Forty two countries offer opportunities with commercial tour operators to interact with sharks (Healy et al., 2020), however 32% of those operations are apparently unmanaged (Healy et al., 2020).

Whale sharks are widely distributed in Australian waters where they are listed as ‘vulnerable’ and ‘migratory’ under the Australian *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act 1999). In Western Australia, the whale shark is a specially protected species under the *Biodiversity Conservation Act 2016*. One of the most predictable annual aggregations of whale sharks occurs in Ningaloo Marine Park (NMP) located in the Ningaloo Coast World Heritage Area, in Western Australia (Colman, 1997; Mau, 2007). Whale sharks are thought to prefer surface sea-water temperatures between 21 to 25°C and generally appear at locations where seasonal food “pulses” are known to

occur (Heyman et al., 2001; Wilson et al., 2001; Sleeman et al., 2010a; Jaramillo-Gil et al., 2023). The predictable annual whale shark aggregation in NMP has been closely linked with an increase in productivity of the region which is associated with a mass coral spawning that occurs each year (Taylor, 1996) The coral spawning has been linked with elevated levels of zooplankton and whale sharks are known to feed on the dense assemblages of krill *Pseudeuphausia latifrons*, rather than directly on the coral spawn (Jarman and Wilson, 2004; Gleiss et al., 2013).

While whale sharks aggregate each year in NMP, the number of whale sharks observed in the aggregations varies from year to year (Wilson et al., 2001). Large fluctuations in these aggregations have been identified between 2007 and 2012, from a high of 967 individuals in 2010 to a low of 164 in 2012 (Lester, 2015). The Western Australian coast is influenced by the Leeuwin Current, a warm water nutrient poor southerly flowing current that originates in the tropical waters to the north of Australia (Wilson et al., 2001; Feng et al., 2009). In La Niña years the Leeuwin Current is stronger and transports more warm water south increasing the water temperatures at Ningaloo Reef (Wilson et al., 2001; Feng et al., 2009). When the Southern Oscillation Index (SOI), a measure of the El Niño-Southern Oscillation Index (ENSO), and mean Sea Surface Temperature (SST) are high the whale sharks appear to stay longer in the NMP, thus being encountered more often or later in the year (Sanzogni et al., 2015), which can be a consequence of a La Niña event (Doi et al., 2013). Whale shark abundance in NMP is known to be higher in La Niña years rather than El Niño years and modelling by Sleeman et al., 2010a, indicated that the SOI best explained whale shark abundance during the peak of the season. SOI influences the strength of the Leeuwin Current and sea level along the Western Australia coastline (Pearce and Phillips, 1988). During a La Niña year, the strength of the Leeuwin Current increases, driving patterns of higher productivity along the central WA coast. Conversely, current strength and productivity decline in El Niño years. Sleeman et al., 2010a, suggested that these changes in productivity associated with the ENSO phenomenon could drive changes in the abundance and residency patterns of whale sharks along the Western Australian coast including at Ningaloo.

The predictable nature of these whale shark aggregations in NMP initiated and supports a growing nature-based tourism industry. Commercial tours in NMP have provided visitors with the opportunity to swim with whale sharks (Colman, 1997; Department of Parks and Wildlife, 2013) since 1989. Western Australian State regulations implemented in 1993 require all commercial activities in marine reserves to be licenced, including commercial whale shark tours operating in NMP (Colman, 1997).

The Department of Biodiversity, Conservation and Attractions (DBCA) administers these licences which include specific conditions that commercial tour operators must adhere to. Licence conditions are designed to minimise disturbances to whale sharks which could affect their welfare and population whilst providing a safe and enjoyable experience for visitors. A whale shark management program was first developed in 1997 and updated in 2013 and provides a framework for administration, compliance, education, research and monitoring, and actions to be followed to help ensure that human-whale shark interactions in

marine reserves are environmentally sustainable (Colman, 1997; Department of Parks and Wildlife, 2013). The whale shark tourism industry in NMP is considered best practice and has set the benchmark for managing whale shark interaction activities globally (Ziegler and Dearden, 2022; Reynolds, 2023). However, the number of people wanting to experience close-up in-water encounters with whale sharks continues to increase, making it important to regularly evaluate the effectiveness of the management program.

Short-term impacts on whale sharks in NMP from commercial in-water interactions have been detected in the past, such as eye-rolling, banking, rapid diving and avoidance strategies which may disrupt the effective feeding strategies of whale sharks (Norman, 1999). Consequently, long term effects may include disruption of normal feeding activities, avoidance or displacement from areas, stress, injury and even mortality (Norman, 2002). However, (Sanzogni, 2012) found that levels of interactions at that time were unlikely to decrease the chances of a whale shark interaction in subsequent years, suggesting that long-term impacts on the whale sharks from levels of commercial in-water interactions at the time were unlikely. More recently, Reynolds et al. (2024a) found no short term impacts on whale sharks in NMP from tourist interactions. There has been suggestion that individual whale sharks that visit NMP may become accustomed to the in-water interactions, which may make them more vulnerable to human threats, such as commercial fishing, outside of Australian waters.

Currently, there are 15 commercial licences available for in-water whale shark encounters in NMP. Commercial tour operators holding these licenses are required to submit daily data to DBCA on their encounters. The number of tours has consistently increased since the recording of tours commenced in 2000, from 251 tours per year in 2000 to 2,182 tours in 2023 (DBCA, unpublished data). Similarly, the number of people swimming with whale sharks has also increased over time from 3,061 in 2000 to 39,300 in 2023 (DBCA, unpublished data). In the 2018-19 financial year it was estimated that 218,000 people visited the Ningaloo Coast (Deloitte, 2020). The effectiveness of the whale shark management program has been tested many times at previous levels of pressure. Each time, the program was found to be effective at managing these pressures, with minimal detectable impacts and best practice applied (Sanzogni, 2012; Techera and Klein, 2013; Sanzogni et al., 2015; Raudino et al., 2016; Lester et al., 2019; Reynolds et al., 2024a). With increasing pressures from tourism, and to provide a world class visitor experience, combined with a changing environment and the need to protect the whale shark, it is important to have continued confidence in the efficacy of the management program, it is therefore essential that the program's effectiveness continues to be evaluated and adapted as needed.

To assess the effectiveness of the whale shark management program in NMP, we built on a previous study that used Electronic Management System (EMS) data collected by each licenced commercial whale shark tour operator in the NMP to investigate whether repeated encounters with individual whale sharks affected the encounter duration between 2011 and 2012 (Lester et al., 2019). Here we extend this evaluation using EMS data and individually identified whale sharks over a longer period to ask whether whale

shark encounter duration has changed over time and use these data as a measure/indicator of potential impacts on whale sharks in NMP during those encounters. We also investigate the spatial distribution of the whale shark encounters and attempt to identify hotspots where higher densities of the whale shark encounters may occur.

Materials and methods

Study site

Ningaloo Reef is a World Heritage listed fringing reef in the northwest of Australia (United Nations Educational Scientific and Cultural Organization, 2011). The reef runs parallel with the coast and extends approximately 300km from Bundegi in the north, around the North West Cape to Red Bluff in the south and includes the State and Commonwealth waters of NMP (Figure 1). The licenced activity is permitted in two operational areas; 12 licensed vessels are permitted to launch in the northern operational region, Tantabiddi, and 3 licensed vessels are permitted to launch in the southern operational region, Coral Bay.

Whale shark encounters and their effect on encounter duration data

In NMP the commercial whale shark encounter data were collected using an EMS installed on each licensed commercial tour vessel. The data used to investigate the effects of whale shark encounters on the whale shark encounter duration, were collected during the whale shark tourism season between March and July and from 2011 to 2019. In addition, commercial tour operators were required to provide underwater photographs of the area between the top and bottom of the fifth gill slit and the posterior of the pectoral fin on the left side of the whale sharks (Arzoumanian et al., 2005) they encountered.

EMS data were filtered for errors in latitude, longitude, encounter start time and encounter end time and the errors were removed from the dataset. Photographs taken of the whale sharks, were qualitatively graded and, if of sufficient quality, linked with the relevant EMS encounter data. Only whale shark encounter data linked with whale shark images of sufficient quality were used in the analysis.

The patterns of spots and stripes on the whale shark skin is unique to each animal and does not appear to change over time, therefore the area between the top and bottom of the fifth gill slit and the posterior of the pectoral fin on the left side is used to identify individuals (Norman, 1999; Arzoumanian et al., 2005; Meenakshisundaram et al., 2021). In this study, once the whale shark photographs were linked to the EMS data of the encounter, the whale shark photographs were uploaded to Sharkbook: Wildbook for Sharks <https://www.sharkbook.ai/database> (a global photo identification catalogue for whale sharks) and the photographs were then used to determine the identity of the individual animal.

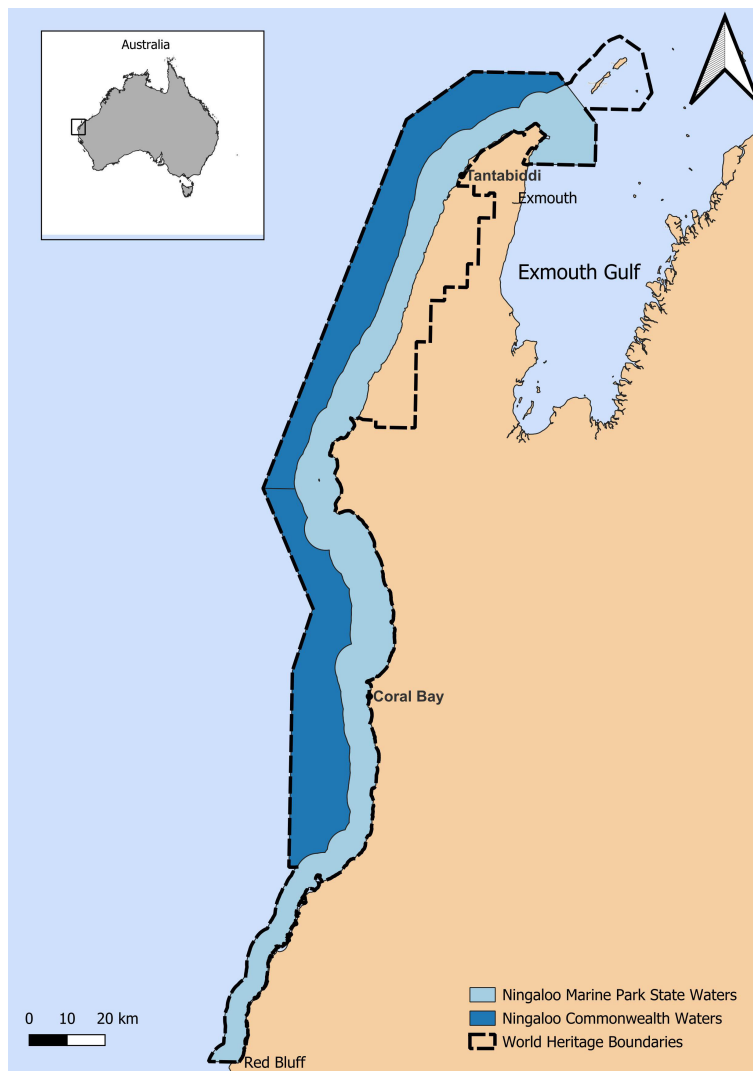


FIGURE 1
World Heritage listed Ningaloo Reef showing the Commonwealth and State waters of the Ningaloo Marine Park.

Data analysis

All statistical analyses were conducted in R (R Development Core Team, 2024). Whale shark encounter durations were compared across the study period at Tantabiddi and Coral Bay with several predictor variables (Table 1). Contingency tables and X^2 analysis were used to investigate the independence of categorical variables. The variance inflation factor (VIF) was used to investigate collinearity between the explanatory variables in the models. Scatter plots of residuals versus fitted values and residuals against each explanatory variable were used to test the assumption of equal variances (i.e. homogeneity of variance) in the models (Zuur et al., 2010). Normality of residuals was interpreted from quantile–quantile plots and from residual histograms. Over-dispersion was tested for each model by dividing the residual deviance by the residual degrees of freedom and a value of greater than 1.5 was used to indicate over-dispersion. Statistical tests on the variation in whale shark encounter duration were conducted in ANOVA or the non-parametric Kruskal-Wallis tests.

Generalised Additive Mixed Effect Models (GAMMs) were fitted using a full-subset information theoretic approach (Burnham and Anderson, 2002) to construct, fit and compare all combinations of predictor variables (Table 1) using the FSSgam package; (Fisher et al., 2018) to examine their relationship to whale shark encounter duration. This approach also calculates the correlation between predictor variables and removes those variables above a correlation threshold from the models (Fisher et al., 2018), in this study no models contain predictor variables above a correlation threshold of 0.28 (Graham, 2003). To control for temporal autocorrelation arising from repeated measures on the same shark, the unique shark identification code was included in the models as a random effect.

The most parsimonious model was the model with the lowest AIC and fewest predictor variables (Burnham and Anderson, 2002). Models within ≤ 2 of the lowest AIC of the most parsimonious model were also considered to have comparable support. Akaike weights (ω AICc) were calculated for each model to provide a measure of strength for each model (Burnham and Anderson, 2002).

TABLE 1 Description of the predictor variables used in the GAMM modelling approach in this study.

Predictor Variable	Source	Description
ID	Sharkbook, Wildbook for sharks	Individual whale shark identification.
Vessel	EMS	Name of the commercial tour operator's vessel.
Month	EMS	Month of whale shark encounter.
Year	EMS	Year of whale shark encounter.
Daily Encounters	EMS derived	Number of daily encounters for each individual whale shark.
Encounter	EMS derived	Encounter number for the individual whale shark.
Duration	EMS	Duration of whale shark encounter.
Location	EMS	Latitude and longitude of whale shark encounter.
Sex	EMS	Sex of whale shark encountered.
Southern Oscillation Index (SOI)	Bureau Of Meteorology	Provides an indication of the development and intensity of the El Niño Southern Oscillation (ENSO) phases at the time of the whale shark encounter. Sustained positive SOI values >+8 indicate a La Niña event while sustained negative values < -8 indicate an El Niño.
Depth	High resolution AusBathyTopo 250m (Australia) 2023 grid depth model for Australia (Bearman, 2023).	The overall water depth in metres at the location where each whale shark was encountered.
Distance	QGIS and EMS derived	Distance (as the crow flies) in kilometres from the vessel launch site to the whale shark encounter.
Habitat - Bare reef	Seamap DPAW Marine Habitats	Located in subtidal areas with either sedimentary, igneous or metamorphic substratum, either as pavement or boulder (> 25 cm) fields; typically, bare but macroalgae, or sparse invertebrates, including sponges, octocorals, soft corals, and ascidians.
Habitat -Coral reef communities (subtidal)	Seamap DPAW Marine Habitats	Located in the subtidal zone; includes the upper seaward reef slope, sheltered back reef, deep lagoonal reef, and bommie clusters; high live coral cover with macroalgal turf and coralline algae covering areas of reef not occupied by living corals; sand patches, bare pavement, and rubble may be present.
Habitat - Mixed filter feeding community	Seamap DPAW Marine Habitats	Located in the subtidal zone; typically experiencing high water motion; high diversity of sessile invertebrates, including sponges, ascidians, gorgonians, bryozoans, sea pens, soft and hard corals; macroalgal turf, coralline algae, sand, and bare reef pavement may be present in areas of reef not occupied by the filter feeder community.
Habitat - Pelagic	Seamap DPAW Marine Habitats	Located in > 50 m depth; dominated by life in the water column, including pelagic fish, pelagic invertebrates, zooplankton and phytoplankton.
Habitat - Sand	Seamap DPAW Marine Habitats	Located in subtidal areas; predominantly white carbonate sand (0.1 - 2 mm grain size) substrate, which is constantly being moved by currents or wave action; typically bare, but seagrass, macroalgae, and invertebrates, including scallops, seastars, and sea urchins may be present.
Grid cells 1km ²	QGIS	Created using the vector create grid tool in QGIS to investigate the spatial density distribution of the whale shark encounters with commercial tour operators.

To investigate the effects of multiple whale shark encounters per day on the duration of those whale shark encounters. We developed a Generalised Linear Mixed Effect Model (GLMM) using the encounter duration as the response variable and the number of encounters per day as the predictor variable, with a negative binomial distribution to account for overdispersion and using the whale shark identity as the random effect variable to account for repeated measures on the same whale shark.

Spatial density distribution data

The data to investigate the spatial density distribution of the whale shark encounters was collected between 2010 and 2023. The EMS whale shark encounter location data (latitude and longitude)

were overlaid upon a map of NMP and map of 1 km² grid cells. Kernel densities of the number of encounters per km² were calculated in QGIS using Python 3.7 using cell sizes of 500m x 500m and a search radius of 1000m (from the centre of the grid cell). Maps of the kernel densities were produced of all years combined. A threshold of the mean density of whale shark encounters plus two standard deviations was calculated for Tantabiddi and Coral Bay. Using the R package *sfhotspot* (Ashby, 2023) we calculated the G_i^* statistic (Getis and Ord, 1992) which identifies high and low cluster values spatially. We used the G_i^* statistic via the *hotspot_gistar* function in the *sfhotspot* R package, in combination with the density threshold to identify significant hotspots of whale shark encounters across all years combined for Tantabiddi and Coral Bay. The number of distinct commercial tour operator vessels were counted in each grid cell and overlaid to

show the number of vessels involved in the whale shark encounters for each grid cell.

Results

From March to July in the years between 2010 and 2023 a total of 16,933 whale shark tours were conducted in NMP and included 67,945 whale shark encounters. From March to July in the years between 2011 and 2019 a total of 11,321 whale shark tours were conducted in NMP (Table 2). Although the maximum number of licences to conduct commercial whale shark tours is 15, changes in licences over time have resulted in a varying number of vessels. These tours were conducted from 23 vessels that launched from Tantabiddi and four vessels that launched from Coral Bay. There was an increase of 68% in whale shark tours from 921 in 2011 to 1551 in 2019. These tours involved 44,017 whale shark encounters that were recorded using the EMS onboard each vessel. The number of whale shark encounters per year increased from 3211 in 2011 to 5914 in 2019, an increase of 84% (Figure 2). Of these whale shark encounters, 7585 included 986 individual whale sharks identified using the Sharkbook database (Arzoumanian et al., 2005) from the photographs taken by the tour photographer/videographer. There were 114 individual whale sharks observed only in Coral Bay, and 619 individual whale sharks observed only in Tantabiddi with 253 observed in both areas. Of the 986 individual whale sharks identified during these encounters 36% (n=354) were encountered only once, while 64% (n=632) were encountered on multiple occasions. Of the 632 individual whale sharks encountered on multiple occasions 98 were encountered on multiple occasions but on a single day, while 534 individuals were encountered on multiple occasions across multiple days. On average individual identified whale sharks were encountered 4.30 times per day (\pm SD 3.15) across the study period and area. Identified whale sharks were observed across multiple years. While 546 whale sharks were seen in only one year, 440 individual whale sharks were recorded in multiple years between 2011 and 2019, and three whale sharks were observed in each year from 2011 to 2019. There were 414 individuals encountered multiple times a day, on three occasions individual whale sharks were encountered 18 times in one day. One of those individuals was encountered 18 times a day twice, with a total cumulative encounter duration of 3 hours 44 minutes and 3 hours 39 minutes on each day, the second individual encountered 18 times in a single day had a cumulative encounter duration of 2 hours 54 minutes. However, during those cumulative encounter

durations no single encounter was longer than the maximum permitted whale shark encounter duration of 60 mins, the encounter durations ranged between 3 to 34 mins. All but one of these encounters involved in the cumulative encounters ended in the whale shark being passed to another vessel, the remaining encounter ended when the whale shark dived. One individual whale shark was encountered on 96 occasions across the study period. The mean whale shark encounter duration across the study period was 15.30 mins (\pm SD 13.17). A correlation matrix was used to identify the relationship between predictor variables used in the modelling approach (Table 3).

The most parsimonious model for Tantabiddi explained 21% of the variation in whale shark encounter duration and included number of daily encounters, distance to boat ramp, SOI, habitat and vessel name (Table 4). The number of daily encounters was also included in the most parsimonious model in Coral Bay which explained 35% of the variation in whale shark encounter duration, in addition to encounter, sex, SOI and vessel (Table 4). However, there were five models that were within two of the most parsimonious model AIC, suggesting that any of these models are appropriate for explaining the variation in the whale shark encounter duration.

The number of daily whale shark encounters and vessel are important variables in explaining the variation in whale shark encounter duration. There was no significant difference between the mean whale shark encounter duration for each vessel at Tantabiddi (ANOVA $F_{(1,21)} = 0.18$, $p=0.67$) or at Coral Bay (ANOVA $F_{(1,2)} = 5.23$, $p=0.15$). There was no significant difference in whale shark encounter duration between days after repeated encounters in Tantabiddi (Kruskal-Wallis chi-squared test: $df=40$, $p = 0.43$) or Coral Bay (Kruskal-Wallis chi-squared test: $df=15$, $p = 0.45$). The GLMM showed a significant negative relationship between an increase in the number of daily whale shark encounters and the whale shark encounter duration. The fixed effect estimates of the number of encounters per day were for Tantabiddi -0.073 , p -value < 0.001 , Coral Bay -12.3 , p -value < 0.001 and for the NMP -0.083 , p -value < 0.001 . Suggesting that for every increase of one encounter with an individual whale shark per day there would be a 7% decrease in whale shark encounter duration for Tantabiddi, a 12% decrease in whale shark encounter duration for Coral Bay and an 8% decrease in whale shark encounter duration for the NMP. The whale shark encounter duration decreased quite rapidly between one and seven encounters per day (Figures 3A, B), after seven encounters per day the encounter duration continued to decrease, but more gradually (Figures 3A, B).

TABLE 2 Commercial whale shark tours and encounter summary between 1st March – 31st July 2011 and 2019 in NMP, Western Australia.

Study area	Whale shark tours	Whale shark encounters	Individual whale sharks	Daily mean whale shark encounters	Mean whale shark encounter duration (mins)	Daily range of whale shark encounters
NMP	11,321	44,017	986	7.30 (\pm SD 5.69)	15.30 (\pm SD 13.17)	1 - 18
Tantabiddi	9,197	36,223	872 (619)	6.56 (\pm SD 5.18)	16.16 (\pm SD 13.43)	1 - 18
Coral Bay	2,124	7,794	367 (114)	2.90 (\pm SD 1.35)	10.98 (\pm SD 10.85)	1 - 12

Individual whale shark numbers in brackets reference individuals only observed in Tantabiddi or Coral Bay.

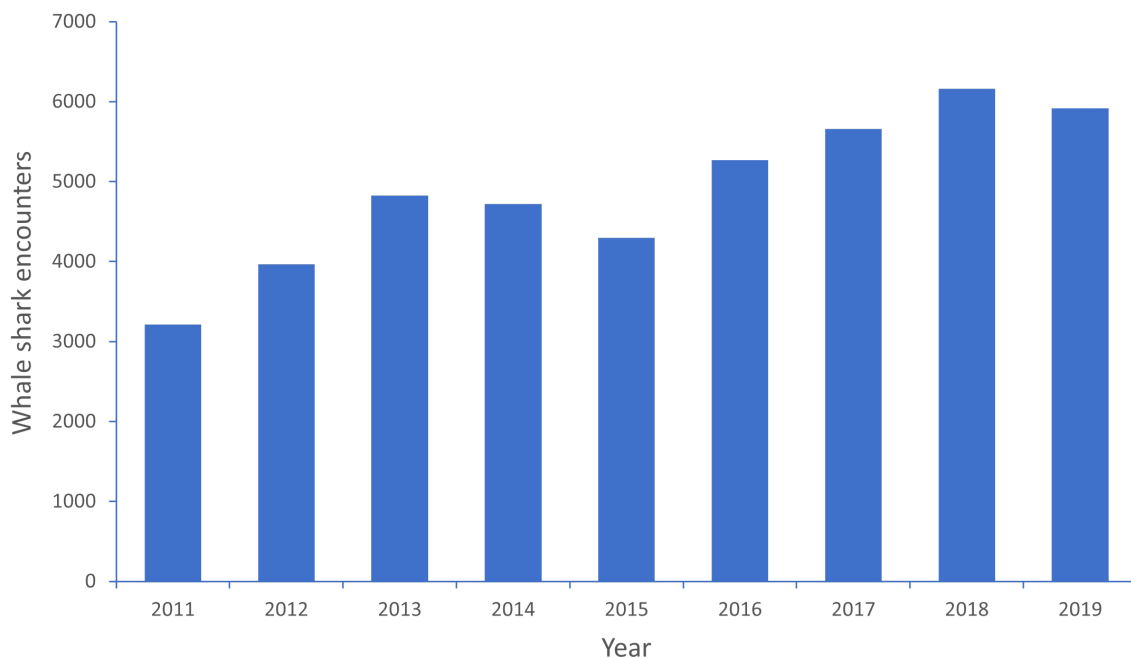


FIGURE 2

Number of commercial whale shark encounters from March to July between 2011 to 2019 in NMP Western Australia.

Spatial density patterns of whale shark encounters

The kernel density analysis shows the spatial density distribution of the whale shark encounters in 1 km² grid cells between 2010 and 2023. There is a uniform density distribution in Tantabiddi and Coral Bay (Figures 4A, B). With a Gi* statistic > 0 and a p-value < 0.05 and a mean density threshold > 652 for Tantabiddi and 51 for Coral Bay, significant whale shark encounter hotspots are identified by having borders around the grid cells (Figures 4A, B). The hotspot threshold varies between areas with a greater density for Tantabiddi than Coral Bay (Figures 4A, B). The number of vessels involved in whale shark encounters in the significant hotspots is generally higher than in other grid cells in both Tantabiddi and Coral Bay (Figures 4A, B).

Discussion

Encounter duration was used as an indicator of potential disruption of whale shark behaviour during an encounter with a commercial tour operator. If the encounter duration increased over time and after repeated encounters there could be evidence of whale sharks becoming habituated. Conversely, if the encounter duration decreased over time and after repeated encounters there could be evidence of avoidance of the commercial tour operators and a potential impact to the whale sharks.

From the EMS data and photographs of whale sharks collected by commercial tour operators during encounters from March 1st to July 31st and between 2011 and 2019 in NMP, we found no evidence to suggest that there has been a significant change in the

duration of whale shark encounters between days from repeated encounters with the same individual whale sharks at either Tantabiddi or Coral Bay. While some of the variables in the models showed a minor variation in whale shark encounter duration between days, no significant differences were detected. However, this study raised concerns of the daily cumulative duration of whale shark encounters, and we found that the whale shark encounter duration decreased significantly as the number of whale shark encounters per day increased in Tantabiddi, Coral Bay and across the NMP. The tour vessels in NMP, can legally spend no more than 90 minutes in the contact zone of a whale shark and must ensure that the swimmers spend no more than 60 minutes in the water from first swimmer entry for each whale shark encounter (Department of Parks and Wildlife, 2013). However, tour operators are permitted to 'handball' a whale shark to a second tour operator i.e. communicating their intention to depart after an encounter over radio and inviting a waiting vessel into the whale shark contact zone to then undertake its own encounter with the same whale shark (Department of Parks and Wildlife, 2013). Even though encounter duration time limits are in place for an individual vessel, the whale shark, if transferred to another tour operator, can be involved in several consecutive encounters, taking the cumulative whale shark encounter duration above that permitted. Of the individual whale sharks that were engaged in multiple encounters per day two individuals were involved in 18 encounters in a day. One individual experienced 18 encounters on two days, with a cumulative encounter duration of 3 hours 44 minutes and 3 hours 39 minutes on each day respectively. The second individual encountered 18 times in a single day had a cumulative encounter duration of 2 hours 54 minutes. This also indicates that the same vessel is conducting multiple encounters with the same whale shark

TABLE 3 Correlation matrix showing the relationship between variables for inclusion in the generalised additive mixed models (GAMMS) for Tantabiddi and Coral Bay.

Tantabiddi											
Variable	Encounter	Daily Enc	Depth	Distance	SOI	Vessel	Month	Year	Sex	Habitat	ENSO
Encounter	1										
Daily Enc	0.34	1									
Depth	-0.14	-0.12	1								
Distance	0.01	0.06	-0.17	1							
SOI	0.06	0.09	-0.02	0.10	1						
Vessel	0.31	0.23	0.10	0.24	0.20	1					
Month	0.27	0.26	0.13	0.13	0.29	0.19	1				
Year	0.42	0.27	0.11	0.25	0.58	0.58	0.10	1			
Sex	0.03	0.03	0.05	0.13	0.14	0.33	0.06	0.44	1		
Habitat	0.18	0.19	0.80	0.06	0.03	0.11	0.15	0.12	0.04	1	
ENSO	0.20	0.20	0.12	0.15	0.56	0.45	0.33	0.85	0.20	0.11	1
Coral Bay											
Variable	Encounter	Daily Enc	Depth	Distance	SOI	Vessel	Month	Year	Sex	Habitat	ENSO
Encounter	1										
Daily Enc	0.12	1									
Depth	-0.01	-0.09	1								
Distance	0.17	0.06	-0.02	1							
SOI	0.04	0.09	-0.04	-0.03	1						
Vessel	0.14	0.12	0.14	0.07	0.19	1					
Month	0.18	0.25	0.08	0.45	0.27	0.20	1				
Year	0.36	0.44	0.10	0.20	0.66	0.38	0.38	1			
Sex	0.13	0.12	0.01	0.08	0.10	0.17	0.14	0.40	1		
Habitat	0.07	0.19	0.86	0.10	0.11	0.11	0.13	0.17	0.11	1	
ENSO	0.17	0.27	0.08	0.31	0.58	0.22	0.43	0.88	0.17	0.11	1

in one day. A recent study investigating the short-term effects of tourism on the whale sharks in NMP also highlighted that a cumulative whale shark encounter duration exceeded the time limit permitted (Reynolds et al., 2024a). The cumulative whale shark encounter duration is not addressed in the current whale shark management plan for NMP, rather, encounter durations are managed only at the individual vessel-whale shark encounter level.

Cumulative encounters have been highlighted in other marine fauna such as bottlenose dolphins that were subject to consecutive approaches by numerous vessels in Port Stephens, Australia (Allen et al., 2007) and spinner dolphins that were exposed to high levels of repeated human activities in Hawaii (Tyne et al., 2018). The concern from these repeated and cumulative encounters is a fitness cost from the disruption of a significant portion of the whale shark's daily behaviour patterns. This could result in less time spent foraging and feeding, and increased stress from the presence of vessels and people. To help understand how often the whale sharks are engaged in cumulative encounter durations that exceed the 90-minute contact

zone time limit and the 60 minute in-water time limit, adding the identity of the vessel receiving the handball of the whale shark, could be included in the NMP EMS database. Moreover, a restriction on the number of whale shark transfers permitted between vessels could also be considered as an approach to reduce the cumulative duration of whale shark encounters in NMP. Another alternative to restrict the cumulative total duration of encounters would be to maintain the commercially licensed standard of one tour operating per day per licenced vessel. Although the effects of cumulative whale shark encounters have not been investigated in detail in NMP or at other aggregation sites with tourism activity, individual encounter duration has been analysed for Mozambique and the Philippines. In Mozambique in-water observations were used during swim-with encounters with tourists and found no change in whale shark encounter duration or frequency of whale sharks displaying avoidance behaviours (Haskell et al., 2014). The duration of encounters with whale sharks in the Philippines, also using in-water observations, was found to decrease when motorised

TABLE 4 Generalised Additive Mixed Models (GAMMs) for predicting whale shark encounter duration from commercial tour operations in Tantabiddi and Coral Bay from 1st March – 31st July between 2011 and 2019 in the Ningaloo Marine Park (NMP), Western Australia from a full-subset theoretical information analysis approach.

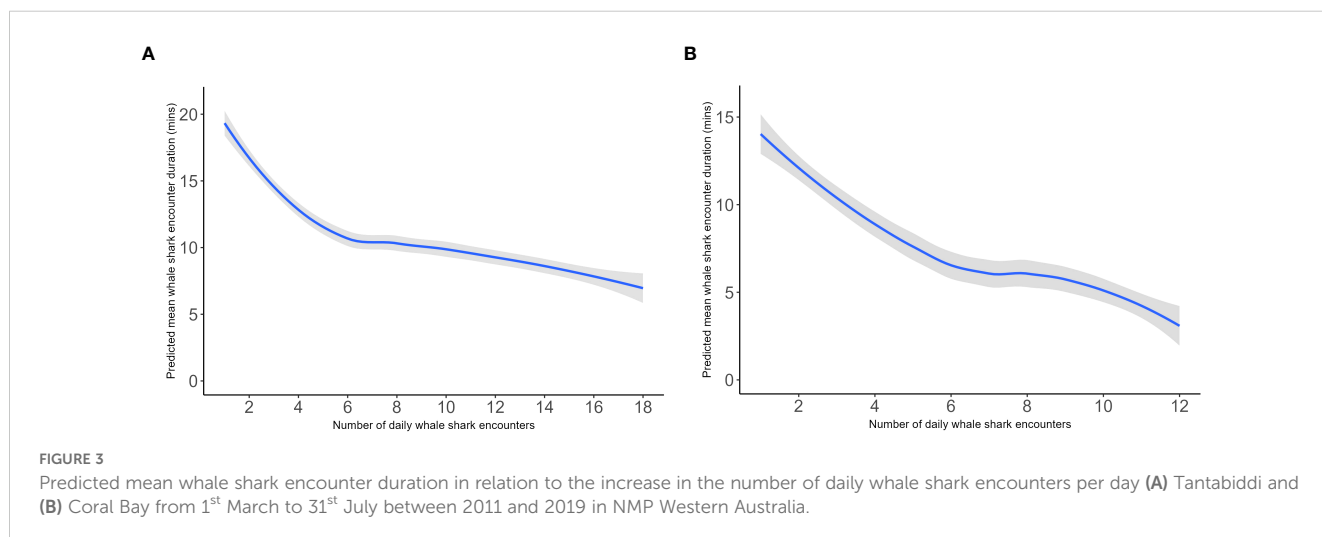
Tantabiddi	ΔAIC_c	ωAIC_c	R^2	EDF
Daily Encounters + Distance + SOI + Habitat + Vessel	0	0.806	0.21	179.34
Daily Encounters + Distance + Depth + SOI+ Vessel	2.931	0.186	0.20	176.98
Daily Encounters + Habitat + Distance + Month + Vessel	10.494	0.004	0.20	183.11
Coral Bay	ΔAIC_c	ωAIC_c	R^2	EDF
Daily Encounters + Encounter + Sex + SOI + Vessel	0	0.129	0.35	172.57
Daily Encounters + Encounter + Month + Sex + SOI + Vessel	0.052	0.126	0.35	181.04
Daily Encounters + Encounter + ENSO + Sex + Vessel	0.899	0.082	0.35	179.63
Daily Encounters + Month + Sex + SOI + Vessel	1.62	0.057	0.35	177.58
Daily Encounters + Encounter + Month + Depth + Sex + SOI + Vessel	1.958	0.049	0.35	181.36
Daily Encounters + Encounter + Depth + Sex + SOI + Vessel	2.064	0.046	0.35	173.19
Daily Encounters + ENSO + Sex + Vessel	2.264	0.042	0.35	175.5
Daily Encounters + Encounter + Habitat + Sex + SOI + Vessel	2.275	0.041	0.35	175.74
Daily Encounters + Encounter + Distance + Sex + SOI + Vessel	2.45	0.038	0.35	173.11

Models ordered by parsimony. Akaike Information Criterion (ΔAIC_c), AIC weights (ωAIC_c), variance (R^2), and effective degrees of freedom (EDF).

vesselstbcstrwere in close proximity and when the encounters occurred in deep water and behavioural changes were also observed (Araujo et al., 2017). Blanchard et al. (2020) used controlled approaches to whale sharks in the Gulf of Baja California and found that whale sharks displayed short term behavioural changes in the presence of vessels and swimmers including change of direction, diving, and acceleration. The cumulative whale shark encounter durations require further investigation, particularly their effect on the whale sharks involved.

We investigated the spatial density distribution of the encounters with whale sharks in 1 km² grid cells from commercial tours that operate from Tantabiddi and Coral Bay using all whale shark encounter data from March to July between 2010 and 2023 to identify areas of higher concentrations that could

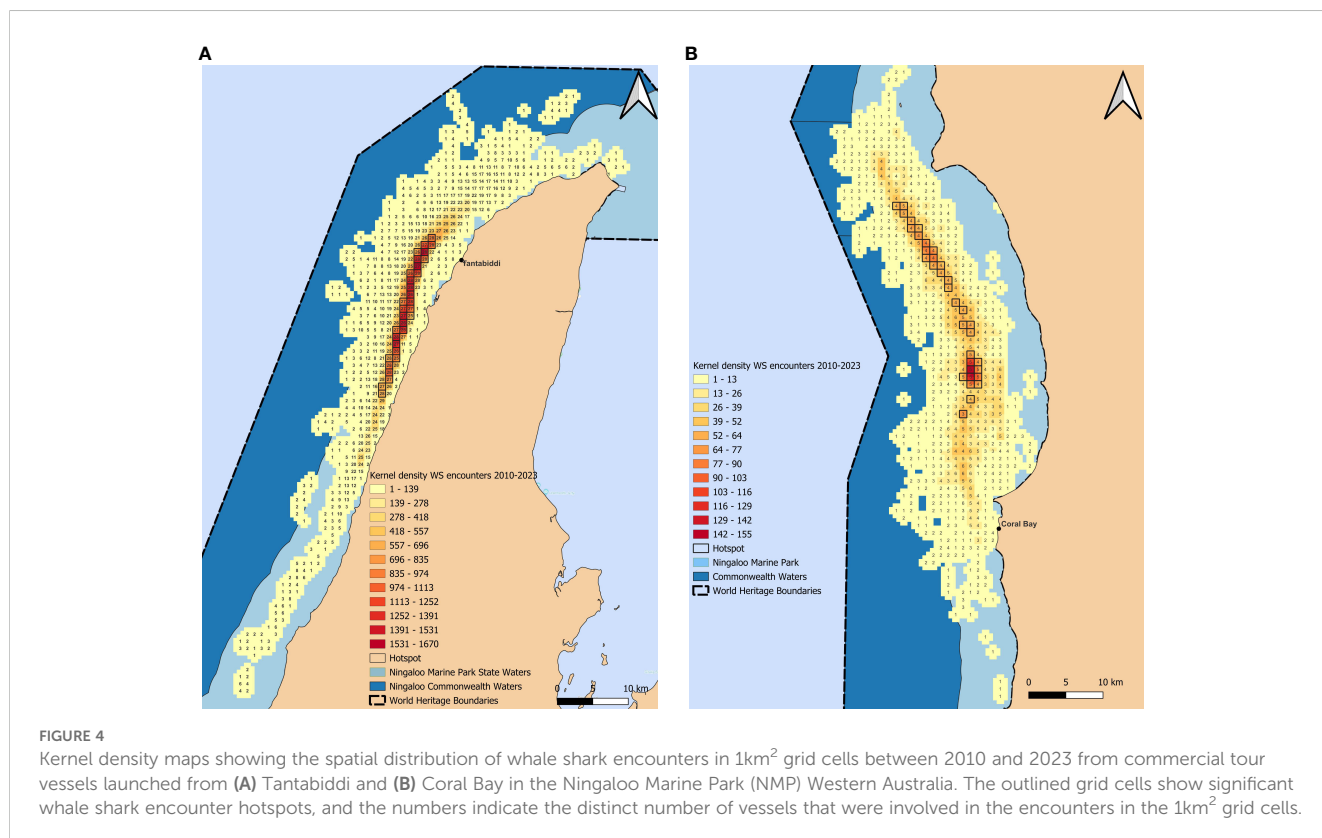
be considered hotspots. We found significant hotspots in both areas. In Tantabiddi hotspots were of a higher concentration of encounters and vessels than those identified in Coral Bay as there are much fewer commercial tours launched from Coral Bay than Tantabiddi. The density distribution of these hotspots of whale shark encounters were uniformly distributed from the operations that worked from Tantabiddi and Coral Bay. Identifying hotspots of human-wildlife encounters can help inform management agencies of areas that may require different management approaches, and if so, measures can be developed to identify and mitigate potential negative impacts on the focal animals and the people engaging in wildlife encounters in those areas. Spatial density distribution patterns of whale shark encounters in this study for Tantabiddi were consistent with patterns shown in previous studies on whale



shark encounters in NMP (Anderson et al., 2014) also showing that distribution in the Tantabiddi area is uniform. Anderson et al. (2014) also suggested that the distance from the reef crest and passages were important in predicting the presence/absence of whale shark encounters. However, conversely to Anderson et al. (2014), we show that the density distribution is uniform in Coral Bay, which could be the result of a larger dataset over a longer temporal scale. Furthermore, whale sharks have recently been shown to follow high prey density areas that are associated with a complex topography, particularly along the reef edge in NMP (D'antonio et al., 2024), which could affect the whale sharks distribution. Ningaloo is a fringing reef, and all whale shark tours are conducted outside of the fringing reef area. Further investigation is required to understand what could be influencing the uniform nature of the density distribution of the whale shark encounter hotspots in Tantabiddi and Coral Bay. Monitoring the spatial density distribution of whale shark encounters in NMP can help identify changes in the spatial density distribution. This can help identify potential indicators such as the effects of climate change (Sequeira et al., 2012, 2014; Reynolds et al., 2024b) and water temperature changes from more frequent and extreme El Niño and La Niña events and changes in prey distribution. Although it has been suggested that climate change could affect the density distribution of whale sharks on a global scale (Sequeira et al., 2014), regional models suggest in some areas, under the predicted increase in SST, NMP included, whale shark habitat suitability under a warming climate may remain relatively stable (Reynolds et al., 2024b). However, it is possible that whale sharks may

experience water temperatures above those predicted, which could affect their thermal tolerance limits (Reynolds et al., 2024b) and their resulting density and distribution.

A La Niña event occurred in March 2011, and El Niño events occurred during May and June 2012, May to July 2015, and March to June 2019 during the whale shark tourism season but no significant difference in the whale shark encounter duration in relation to the SOI at Tantabiddi or Coral Bay was detected. SOI has been linked to the Leeuwin Current and consequently to productivity in NMP (Wilson et al., 2001; Feng et al., 2009), which in turn has influenced the number of whale sharks observed in NMP (Wilson et al., 2001). During a La Niña year, the strength of the Leeuwin Current increases, driving patterns of higher productivity along the central WA coast. Conversely, current strength and productivity declines in El Niño years. Although we didn't observe it during this study, it has been suggested that these changes in productivity associated with the El Niño Southern Oscillation (ENSO) phenomenon could drive changes in the abundance and residency patterns of whale sharks along the WA coast including at NMP (Sleeman et al., 2010a, b). Chlorophyll a, and sea surface temperature (SST) are influenced by the SOI and are important influences on trends of within-season whale shark encounters at NMP. There is a well-established link between chlorophyll a, and zooplankton biomass in marine ecosystems which, combined with evidence that whale sharks aggregate at NMP to feed on zooplankton helps explain the link between chlorophyll a, and whale shark distribution. Both chlorophyll a, and SST are thought to influence the distribution of planktivorous and secondary carnivores that feed on species at lower



trophic levels such as zooplankton, krill and small bait fishes (Sanzogni et al., 2015; Lester et al., 2022). Although climate change cannot be addressed at a marine park level alone, it is important to recognise that NMP will be under pressure from climate change. Strong La Niña influenced the increase in water temperature and the number of cyclones in the region (Moore et al., 2012) and these events caused coral bleaching and a change in the spatial heterogeneity of coral cover in the region including NMP (Moore et al., 2012, Depczynski et al., 2013). As the whale sharks that frequent the NMP are closely linked to the ecology of the area, climate change has implications for the whale shark aggregations in NMP and potentially the whale shark tourism industry that relies on the predictable, seasonal annual aggregation of whale sharks in the area.

Several studies have investigated the impacts of commercial in-water interactions on whale sharks in NMP (Sanzogni et al., 2015; Raudino et al., 2016; Lester et al., 2019; Reynolds et al., 2024a). There has been little evidence to suggest that tourist encounters with whale sharks have affected the likelihood of repeat encounters (Sanzogni et al., 2015; Lester et al., 2019). This suggests that long-term impacts of tourism on the whale sharks at NMP are not apparent, at current levels of tourism up to 2019. However, here we did find that as the number of daily whale shark encounters increased the duration of those encounters decreased, suggesting that cumulative daily whale shark encounter durations may be having short term effects on the focal animal within a day. Aerial surveys in NMP, have shown that whale sharks changed direction more frequently (Raudino et al., 2016), which could be interpreted as an avoidance strategy and have potential short-term fitness costs, but investigating long term effects were beyond the scope of the study and dataset (Raudino et al., 2016). From data collected from tags, Reynolds et al., 2024a, used direction of travel to investigate potential impacts of tourism interactions on short term changes in whale shark behaviour. It was found that the whale sharks' mean direction of travel changed in the presence of tourism encounters, however their direction of travel was still in relatively straight paths and not very erratic suggesting little change in overall direction of travel (Reynolds et al., 2024a). The increase in energy expenditure for this change in direction was unquantifiable (Reynolds et al., 2024a) and therefore the fitness costs of such changes in direction remains unknown. Other studies elsewhere have noted increased avoidance behaviours and changes in the direction of travel (Quiros, 2007; Pierce et al., 2010; Haskell et al., 2014; Blanchard et al., 2020; Gayford et al., 2023) and decreases in encounter duration with closer proximity to vessels (Pierce et al., 2010; Araujo et al., 2017). In the Bay of La Paz, Mexico, it has been suggested that tourism increases the probability of whale sharks being in a disturbed behavioural state when in an encounter with a swimmer (Gayford et al., 2023). Unlike in NMP, the whale sharks in La Paz particularly display relatively angular and rapid movements (Gayford et al.,

2023). However, individual whale sharks were not identified in the Bay of La Paz and therefore repeated encounters of the same individuals were not taken into consideration during the study (Gayford et al., 2023).

Even though there is evidence to suggest that there are behavioural impacts on whale sharks in the presence of swimmers elsewhere, there is little evidence to suggest that the whale sharks in NMP are negatively impacted by tourism. However, it is important to continue to assess the effectiveness of the management program as pressures increase and to be able to adapt accordingly when evidence of impacts arise. The number of whale shark tours and numbers of people swimming with whale sharks as measures of pressure on whale sharks have steadily increased. Cumulative whale shark encounters are not addressed in the current whale shark management plan for NMP and should be investigated further. Here we found that the increase in the number of whale shark encounters per day decreases the duration of a whale shark encounter, suggesting a possible effect on the whale sharks experiencing multiple encounters per day. If these repeated and cumulative whale shark encounters have the potential to impact whale shark behaviour and the visitor experience, then 'handballing' of a whale shark to another tour operator will need to be managed. Tourism is one of the only pressures we can effectively manage for the whale shark aggregation in NMP. If the whale shark encounter duration becomes shorter, visitor satisfaction may be impacted and given that many are international tourists that have travelled great distances and paid a considerable amount to swim with whale sharks in NMP. One of the strengths of the whale shark management program which has led to it being considered world best practice (Ziegler and Dearden, 2022; Reynolds et al., 2024a) is that the effectiveness of the program to manage impacts on whale sharks has been tested at changing levels of tourism/people pressure. Taking precautionary approaches and testing the effectiveness of the management program must continue under changing pressures and a changing environment for it to be considered best practice.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because Data were collected as a licence obligation of the whale shark tour operators.

Author contributions

JT: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. HR: Conceptualization, Data curation, Writing – original draft, Writing – review & editing. EL: Conceptualization, Data curation, Writing – review & editing. GF: Data curation, Writing – review & editing. PB: Data curation, Writing – review & editing. KW: Conceptualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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