Potential distribution and marine reserve use by an endangered migratory giant

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Running title: Distribution and reserve use by whale sharks

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Abstract word count: 294

Word count: 5738

Number of references: 72

(A) ABSTRACT

(B) Aim

Understanding the spatial and temporal variation in the distribution of highly migratory species is critical for management and conservation efforts. However, challenges in observing mobile marine species throughout their migratory pathways can impede the identification of critical habitat, linkages between these habitats and threat-mitigation strategies. This study aimed to gain insight into the long-term residency and movement patterns of the whale shark (*Rhincodon typus*), and to reveal important habitat in the context of *R. typus* usage of existing Marine Protected Areas (MPAs).

(B) Location

South-eastern Indian Ocean.

(B) Methods

Satellite telemetry was used to remotely track the long-term movements 29 *R. typus*, and to quantify shark usage of the existing MPA network. From the tracking data and environmental predictors, non-linear models were developed to predict suitable *R. typus* habitat throughout the south-eastern Indian Ocean.

(B) Results

This study includes the first documented complete return migrations by *R. typus* to Ningaloo Marine Park, which was found to be an important area for the species all year round. We found that while existing MPAs along Australia's west coast do afford some protection to *R. typus*, telemetry-based habitat models revealed large areas of suitable habitat not currently protected, particularly along the Western Australian coast, in the Timor Sea, and in Indonesian and international waters.

(B) Main conclusions

Animal-borne telemetric devices allowed the gathering of long term spatial information from the elusive and highly mobile *R. typus,* revealing the spatial scale of their migration in the south-eastern Indian Ocean. Suitable habitat was predicted to occur inside conservation areas, but our

findings indicate that the current MPA network may not sufficiently protect *R. typus* throughout the year. We suggest that telemetry-based habitat models can be an important tool to inform conservation planning and spatial management efforts for migratory species.

(B) Keywords biotelemetry, generalised additive model, habitat suitability model, Marine Protected Areas, migration, potential distribution, satellite remote sensing, species distribution model, whale shark, *Rhincodon typus*

(A) INTRODUCTION

Knowledge of the broad-scale movements of migratory species is essential for conservation and management (Costa *et al.*, 2012; Berumen *et al.*, 2014; Ferreira *et al.*, 2015). However, movement patterns and migration paths of marine species are often poorly understood, due to the logistical challenges of surveying these highly mobile and often elusive animals throughout such extensive and complex environments (Heupel *et al.*, 2015; Hussey *et al.*, 2015). This paucity of data can lead to gaps in the protection of critical habitats for species along entire migratory routes or throughout entire life cycles (Beger *et al.*, 2010; Block *et al.*, 2011; Runge *et al.*, 2014; Beger *et al.*, 2015; Mazor *et al.*, 2016; McGowan *et al*., 2016).

One migratory marine species whose distribution and movement patterns are poorly understood is the world's largest extant fish, the whale shark (*Rhincodon typus*). In 2016 the conservation status of *R. typus* was updated from 'Vulnerable' to 'Endangered' on the International Union for the Conservation of Nature's (IUCN) Red List (Pierce & Norman, 2016), because of anthropogenic threats including targeted fishing (Li et al., 2012; Pierce & Norman, 2016), by-catch (Lascelles et al., 2014; Pierce & Norman, 2016), pollution (such as oil spills and plastics) (Lascelles et al., 2014), ship strike (Graham, 2007; Berumen et al., 2014; Pierce & Norman, 2016), and activities associated with oil and gas exploitation (Graham, 2007). Effective conservation of *R. typus* requires accurate information on their movements and distribution in order to understand their spatial and temporal exposure to these threats (Berumen et al., 2014). Whale sharks are known to aggregate at various coastal locations in the tropics in response to seasonal increases in productivity (Colman, 1997; Heyman *et al.*, 2001; Nelson & Eckert, 2007; Motta *et al.*, 2010). However, sighting records of *R. typus* are generally limited to coastal areas during aggregation periods, because of improved access to animals (Rowat & Brooks, 2012). Sightings outside these periods and in pelagic waters are relatively rare (Rowat & Brooks, 2012; Sequeira *et al.*, 2013). This paucity of information on long term movements and distributions of *R. typus* is hampering conservation efforts (Sequeira *et al.*, 2013; Berumen *et al.*, 2014).

In the Indian Ocean, *R. typus* aggregate in some coastal areas, including Ningaloo Reef in Western Australia (WA) during the austral autumn/winter (Colman, 1997; Wilson *et al.*, 2001; Norman & Stevens, 2007; Anderson *et al.*, 2014; Norman *et al.*, 2016). This aggregation supports a lucrative tourism industry (Catlin *et al.*, 2010), and most sightings records come from the northern area of Ningaloo Reef in which the industry operates (Anderson *et al.*, 2014; Norman *et al.*, 2016). Although *R. typus* exhibit long distance movements away from this region (Wilson *et al.*, 2005; Sleeman *et al.*, 2010b; Norman *et al.*, 2016), and genetic studies suggest that some degree of broad scale mixing of Indo-Pacific populations is occurring (Vignaud *et al.*, 2014), movements outside this recognised aggregation period are relatively unknown (Norman *et al.*, 2016).

While at Ningaloo Reef, *R. typus* are protected by a network of State and Commonwealth marine preserves. Although Marine Protected Areas (MPAs) are widely recognised as a key tool in the conservation of marine biodiversity (Lester *et al.*, 2009; Klein *et al.*, 2015), their effectiveness in conserving migratory species has been questioned (Hays *et al.*, 2014), and there is a lack of understanding of the extent to which existing protected areas cover the distributions of migratory species (Runge *et al.*, 2015). The use of Australia's network of MPAs by *R. typus* has never before been quantified, and it is unclear how much of their preferred or suitable habitat is protected. This is because other areas in the Indian Ocean that could be important habitat for *R. typus* have yet to be identified (Norman *et al.*, 2016).

Biotelemetry is a valuable tool for gathering spatial information, particularly for mobile marine species (Hussey *et al.*, 2015). However, there has been a long-standing disconnect between animal migration ecology, and spatial conservation and management decision making (McGowan *et al.*, 2016; Beger *et al*., 2015). Migratory animals tend to be ignored when planning MPAs, because large-scale migration data are difficult and expensive to obtain, may far exceed the spatial scale of planning, and spatial planning tools to incorporate animal telemetry are in their infancy (McGowan *et al.*, 2016). In addition, telemetry data are presence-only, limited by the number of animals tagged to adequately represent population patterns (Block *et al.*, 2011; Mazor *et al.*, 2016). Spatial planning requires ecological information from the entire planning area to avoid biasing prioritisations towards areas where data exist. Species distribution models (SDMs) serve to overcome this challenge by predicting suitable habitat for species for which distributions are unclear (Torres *et al.*, 2015), and can give useful ecological insights (Elith & Leathwick, 2009). These models predict the potential distribution of a species based on statistical relationships between recorded occurrences and environmental predictor variables (Torres *et al.*, 2015). Habitat selectivity models do this by identifying physical and environmental characteristics that influence known distributions of a species and finding other areas that share these characteristics (Raymond *et al.*, 2015).

This study aims to identify important areas for, and understand the movement ecology of *R. typus* through biotelemetry. The evaluation of the use of existing MPAs off Australia's west coast by tagged *R. typus* will provide insight into how the species is protected by the existing network of Australia's MPAs. Habitat selectivity modelling based on satellite-tracked movement data will help to reveal the potential distribution of *R. typus* throughout the south-eastern Indian Ocean. The techniques used could be applied to *R. typus* populations worldwide, as well as other mobile marine species, and to inform future management and conservation efforts.

(A) METHODS

(B) Study Area

Ningaloo Reef is located on the west coast of the Cape Range Peninsula, WA (Fig. 1). It is entirely encompassed by the Ningaloo Marine Park, which lies within state waters and covers approximately 2633 km^2. Adjacent to this is the Ningaloo Commonwealth Marine Reserve, which lies within Commonwealth waters and covers an area of 2435 km^2 (Australian Government Department of the Environment and Energy, 2016) (Fig. 1b). For the purposes of this study, the "Ningaloo Marine Park (NMP)" was considered to include both the Ningaloo Commonwealth Marine Reserve and the Ningaloo Marine Park.

The whale shark ecotourism industry at Ningaloo Reef operates during the austral autumn and winter, generally between March and July (Holmberg *et al.*, 2009; Anderson *et al.*, 2014; Government of Western Australia Department of Parks and Wildlife, 2014), sometimes extending into August and September (Government of Western Australia Department of Parks and Wildlife, 2014).

To investigate *R. typus* distribution patterns throughout the south-eastern Indian Ocean, the area of interest was defined by an area spanning 100° E - 130° E longitude, and from 0° (the equator) to

35° S latitude. This was based on areas utilised by tagged sharks in previous studies (Wilson *et al.*, 2005; Wilson *et al.*, 2007; Sleeman *et al.*, 2010b; Norman *et al.*, 2016), and areas hypothesised as important feeding habitats for *R. typus* (Norman *et al.*, 2016). A number of MPAs exist in this area, including Commonwealth marine reserves, in Commonwealth waters (between 3 nautical miles (nm) and 200 nm offshore), and those administered by the Western Australian State Government (between the coast and 3 nm offshore) (see Figure S1 in Supporting Information).

(B) Tagging and Tracking

Spatial and temporal data were collected as part of an ongoing *R. typus* tagging programme coordinated by ECOCEAN at Ningaloo Reef. In 2010, one Wildlife Computers' SPOT tag (Wildlife Computers Inc., WA, USA) and one Wildlife Computers' SPLASH tag encased in a positively buoyant syntactic foam body tethered to a stainless steel dart by a 2 m wire were deployed on two sharks. The dart was inserted into the flank of the shark just below the first dorsal fin using a Woodie 1000 speargun (Undersee Australia Pty. Ltd., Sydney, NSW). Tags deployed in 2012, 2013, 2014, and 2015 were mounted on a negatively buoyant clamp and deployed on the upper leading edge of the shark's first dorsal fin (see Norman *et al.*, 2016). The one tag deployed in 2012 employed a galvanic time release mechanism on the clamp (Gleiss *et al.*, 2009). Tags deployed in 2013 (n = 8), 2014 (n = 2) and 2015 (n = 12) included a corrodible section of dissimilar metals on the clamp arm. To minimise impact, all tags were designed to release approximately six to twelve months from deployment. Before tagging, each shark was photographed according to standardised protocol and later identified in the Wildbook for Whale Sharks (Arzoumanian *et al.*, 2005; Wildbook, 2016) (Table 1 and see www.whaleshark.org).

Positional information for each tagged shark was obtained via the Argos CLS satellite network (Argos, 2016). This system calculates the location of the tag by using Doppler effect measurements from consecutive transmissions received by the satellites from the tag. Each location estimate is assigned a "location class", indicating the degree of accuracy to which they are calculated. The detections of tagged sharks through time were mapped in ZoaTrack (www.zoatrack.org) (Dwyer *et al.*, 2015) and erroneous detections (i.e. those occurring on land or those too distant from earlier or later more accurate detections to be biologically possible) were identified and excluded from further analyses. Estimates of the minimum distance travelled by each shark were generated using the Great Circle distance algorithm in ZoaTrack.

(B) Use of Existing MPAs

To evaluate the use of existing MPAs by *R. typus,* boundary data of MPAs in the region were downloaded as shapefile objects from the Australian Government Department of the Environment and Energy website (https://www.environment.gov.au/land/nrs/science/capad). The number and proportion of detections from within each MPA and the Great Circle distance of each detection to the border of the closest MPA was calculated using the rgdal (Bivand *et al.*, 2016), sp (Pebesma & Bivand, 2005; Bivand *et al.*, 2013), rgeos (Bivand & Rundel, 2016) and geosphere (Hijams, 2016a) packages in R (R Core Team, 2016). Usage of these areas during "whale shark season" (defined herein as March to August, i.e. the austral autumn and winter), and other times of year, "non-whale shark season" (September to February, i.e. the austral spring and summer) were compared to assess temporal variability in the occupancy of the MPAs.

(B) Habitat Selectivity Modelling

The detections of the tagged sharks in this study represent presence information, but true absences (i.e. locations where animals could have visited but did not) were unknown. To generate absence data, randomised tracks were simulated following methods outlined by Wakefield *et al.* (2011) and Raymond *et al.* (2015). Here, the actual tracks were filtered, allowing the prediction of the simulated tracks back to a common time step of 24 hours. The error between the fixes was considered using the correlated random walk (rwalc) function in the RWalc package (Wotherspoon & Raymond, 2016) in R. Simulated tracks began at the same point as the actual track on which they were based, but proceeded randomly throughout the available marine environment (constrained by actual trip duration and travel speed), as if the animals were displaying no preference for any particular environmental conditions (Aarts *et al.*, 2008; Raymond *et al.*, 2015). From the track of each tagged shark, 10 simulated tracks were generated. The physical and environmental conditions at the detections along the actual tracks represent habitat used by the tagged sharks (utilised habitat), and those along the simulated tracks represent habitat that could potentially have been used by the tagged sharks but was not (available habitat) (Raymond *et al.*, 2015).

In order to model the habitat preference of *R. typus*, physical and environmental information known to influence the abundance and distribution of *R. typus* (Sleeman *et al.*, 2007; Rohner, 2012; Sequeira *et al.*, 2012; Sequeira *et al.*, 2014) and other marine megafauna (Sleeman *et al.*, 2007; Raymond *et al.*, 2015) were matched to the locations of detections on the actual and random tracks. Sea surface temperature (SST) and chlorophyll-a concentration (Chl) were sourced from the National Oceanographic and Atmospheric Administration's (NOAA) Environmental Research Division Data Access Program (ERDDAP) website. The xtractomatic package (Mendelssohn, 2015) in R was used to extract SST and Chl eight day composite data from the Polar Orbiting Environmental Satellites' (POES) Advanced Very High Resolution Radiometer (AVHRR) and from the Aqua satellite's Moderate Resolution Imaging Spectroradiometer (MODIS) respectively. The bathymetry values (i.e. the elevation of the sea floor) at the location of each detection were determined from the GEBCO_2014 30 arc-second grid (downloaded from The General Bathymetric Chart of the Oceans' (GEBCO) website) using the raster package (Hijams, 2016b) in R.

To explore non-linear relationships between the variables and the presence of *R. typus,* binomial generalised additive mixed-effects models (GAMMs) with the logistic link function were constructed using the mgcv package (Wood, 2011) in R. These models describe habitat use relative to habitat availability and are known as presence-background or habitat selectivity models (Wakefield *et al.*, 2011; Raymond *et al.*, 2015). This framework was chosen to account for the serial correlation of repeated detections from the same individuals and the covariation of environmental variables (Aarts *et al.*, 2008; Raymond *et al.*, 2015). The optimal amount of smoothing was determined by modelling the covariates with varying numbers of spline points (k) and comparing the Akaike information criterion (AIC) of each of the models. The model with the lowest AIC value (k = 3) was used. Individual identity ("*ANIMALID*") was used as the random intercept. The following model was used, with some covariates log or square root transformed to meet model assumptions of homoscedasticity:

$$logit(\pi) = \alpha + f\left(\sqrt{Bathymetry}\right) + f(SST) + f(log_{10}Chl) + ANIMALID$$

$$ANIMALID \sim N(0, \sigma^2_{ANIMALID})$$

This assumes that *ANIMALID* is normally distributed, with a mean 0 and variance $\sigma^2_{ANIMALID}$. The full model is presented, without any prior model selection, because of the small number of non-collinear covariates, as advocated by Zuur *et al.* (2012).

Once constructed, models allowed the suitability of the habitat for *R. typus* to be predicted throughout the broader area of interest (i.e. the south-eastern Indian Ocean). Therefore, the physical and environmental variables were also extracted for the broader study area using the xtractomatic and raster packages in R (see Figure S2 in Supporting Information). Models were run with data on SST and Chl covering the full temporal extent of the actual tracking data (May 2010 to May 2016), averaged by month, and then divided into whale shark season and non-whale shark season. The relative suitability of the habitat in each raster cell was plotted to create distribution maps, showing areas in which *R. typus* could occur across the broader study area for the two time periods.

Data from an additional four sharks tagged at Ningaloo Reef in April and August 2016 (using the methods described above for the 2015 tags) (Table 1) were used as an independent dataset to assess the model predictions using area under the curve (AUC) cross-validation statistics. AUC statistics were calculated from receiver operating characteristic (ROC) curves, using the inflection point to maximize the true positive rate while minimizing the false-positive rate (DeLong *et al.*, 1988). ROC curves and AUC statistics were calculated using the PresenceAbsence package in R (Freeman, 2008). The mean and standard deviation of the AUC values for each time period are reported. Boundaries of existing MPAs in the region and the locations of the detections from this independent dataset were overlayed on the distribution maps to determine spatial overlap.

(A) RESULTS

Tagged sharks (n = 25) were tracked for an average of 90.9 ± 13.7 days (mean ± SE), with the longest tag deployment lasting 261 days (Shark A-546) (Table 1). The average number of detections received from each shark was 103.4 ± 23.0 (mean ± SE), with 1.1 ± 0.2 (mean ± SE) detections per day. Tagged animals travelled an average total minimum (Great Circle) distance of 2349.0 ± 310.1 km (mean ± SE) and an average minimum distance per day of 28.7 ± 2.7 km (mean ± SE). The greatest distance travelled by one of the tagged sharks (Shark A-958) was 6157 km, which it covered in 260 days. The directions of the sharks' movements were mostly to the north and north-east of NMP, however sharks also moved north-west and south, with one (A-633) travelling as far south as the Rottnest Trench (Fig. 1a). While being tracked, nine of the tagged sharks returned to NMP after travelling at least 300 km away from their tagging locations, at the northern end of Ningaloo Reef. These represent the first satellite-tracked homing movements of *R. typus* to NMP (Fig. 1a). Many sharks travelled considerable distances from NMP, with seven of the tagged sharks detected further than 1000 km away (Table 1). The maximum distance of any shark detection was from A-1041 (tagged on 29 July 2015), which travelled at least 1567.4 km from NMP to the south coast of Java, Indonesia (Fig. 1a and Table 1). Transmissions from A-1041 ceased in December 2015, while it was still in that area. However, photo-identification confirmed that A-1041 was back at Ningaloo Reef on 21 April 2016 (Wildbook, 2016).

(B) Use of Existing MPAs

Of the total number of detections received from all sharks (n = 2586), 41 % were from inside the boundaries of NMP. During non-whale shark season, 33 % of all detections were from inside NMP, with this figure rising to 50 % during whale shark season. The number of tagged sharks detected inside NMP and the distances individuals travelled away from the area varied throughout the year (Fig. 2). Of the total number of detections received from within NMP (n = 1061), those obtained during whale shark season (55 %) were concentrated throughout the northern extent of NMP (Fig. 1b). Detections obtained during non-whale shark season were concentrated further south, in an area between Point Cloates and Coral Bay (Fig. 1b). Detections from this southern area of NMP were received from 12 out of the total 25 tagged sharks, with eight of these sharks utilising the area during September and/or October (Fig. 2a). All nine sharks that displayed homing movements to NMP returned to this southern area, with seven individuals first detected back in the area during September and October, one in November and one in January (Fig. 2b).

Other MPAs distributed along Australia's west coast were rarely used by tagged sharks, with only 3 % of all detections transmitted from inside other MPAs (see Table S1 in Supporting Information). These detections were found in five out of a possible 15 MPAs in the region traversed by the tagged sharks. In total, 56 % of all detections from the 25 tagged sharks were from regions not currently protected by any existing MPA.

(B) Habitat Preference

GAMMs revealed non-linear relationships between the physical and environmental variables used in the models (bathymetry, SST, Chl), and the occurrence of *R. typus* (Fig. 3). All variables were found to be significant predictors of *R. typus* occurrence ($p < 0.05$). In contrast to the simulated tracks, tagged sharks preferred shallow, coastal waters, but were also found in very deep waters far from shore (Fig. 3a). Although tagged sharks travelled long distances and were detected in waters with depths of up to 6563 metres below sea level (mbsl), 56 % of all detections were from locations in coastal waters with depths of ≤ 200 mbsl. This apparent preference for shallow waters was even more marked in whale shark season, with 70 % of all detections during this period coming from locations where water depth was ≤ 200 mbsl. Tagged sharks also preferred warmer SSTs (Fig. 3b) and mid-range Chl concentrations, although most of the Chl concentrations at the detection points were low or mid-range, with few very high concentrations (Fig. 3c). Tagged sharks were found in waters where SSTs ranged from 20°C to 31°C, with most detections (72 %) occurring where SSTs were between 23°C and 28°C. The average SST at all detection locations was 25.3 ± 0.03°C (mean ± SE).

(B) Species Distribution Predictions

The results from the habitat selectivity model were used to generate maps showing the relative suitability of habitat for *R. typus* across the area of interest in the south-eastern Indian Ocean (Fig. 4). Areas of habitat with higher suitability were found in continental shelf waters along the Western Australian coast; close to the coastlines of the islands of Indonesia; and in coastal shelf waters in the Timor Sea. Model validation confirmed a strong predictive capacity of the GAMM. The average AUC values of the four additional sharks from the independent dataset used to assess the model predictions were 0.80 ± 0.11 (mean ± SD) during whale shark season and 0.87 ± 0.13 (mean ± SD) during non-whale shark season.

When the boundaries of existing MPAs were overlayed on the maps of predicted habitat suitability (Fig. 4), an area of high suitability was encapsulated by NMP during both whale shark and non-whale shark seasons. Some areas of higher habitat suitability along the WA coast and in the Timor Sea are also covered by existing MPAs, such as the Dampier Commonwealth Marine Reserve, the Eighty Mile Beach Commonwealth Marine Reserve and the Kimberley Commonwealth Marine Reserve (see Fig. S1). However, there are other areas of higher suitability for *R. typus* along the WA coast that are not protected by any existing MPAs, such as around Dirk Hartog Island and to the east of Bernier and Dorre Islands, just north of Shark Bay, and the coastline around Port Hedland and between Onslow and Karratha. Areas around the Indonesian islands and in international waters that are predicted to have higher suitability for *R. typus* are likewise unprotected by any existing MPAs.

(A) DISCUSSION

The satellite tracks of 29 *R. typus* tagged in this study provide the first recorded homing movements of *R. typus* to NMP, revealing that some sharks migrated long distances away from NMP before returning to the area intra-annually. Using detection data from tagged sharks and habitat selectivity modelling, this study revealed NMP as an area of important habitat for *R. typus*, not only during the recognised whale shark season, but throughout the year. The southward shift in concentration of the detections within NMP during non-whale shark season discovered a pattern of previously unreported use of this area at this time of year. Whale sharks displayed a preference for warmer, shallower waters, and moved across national boundaries into Indonesian and international waters, as well as along the WA coastline, into areas that are not covered by any existing MPAs.

(B) Movement and Habitat Preference of Whale Sharks

This study, the most extensive satellite telemetry study on *R. typus* conducted in Australia, has shown that sharks generally made relatively short forays away from Ningaloo Reef before returning to the area intra-annually (Fig. 1). Previous studies have suggested that sharks exhibit high individual fidelity to the Ningaloo Reef area during the austral autumn/winter, with individuals often resighted in the area over consecutive years (Holmberg *et al.*, 2008; Holmberg *et al.*, 2009; Anderson *et al.*, 2014; Norman & Morgan, 2016; Norman *et al.*, 2016). While these observations documented the usage by *R. typus* of areas accessed by tourism operators during the whale shark season, the movements and whereabouts of sharks between these resighting events remained unclear. Previous satellite tracking studies of *R. typus* showed movements of sharks to the north, north-east and north-west of Ningaloo Reef, however, no sharks were tracked returning to Ningaloo Reef (Wilson *et al.*, 2005; Wilson *et al.*, 2007; Sleeman *et al.*, 2010b). Furthermore, as individuals in these studies were not recorded in the Wildbook for Whale Sharks, it remains unknown whether these individuals returned to the area. Although bi-annual circumnavigation of the Indian Ocean by *R. typus* has been suggested, based primarily on the timings of sightings at coastal locations around the ocean basin (Sequeira *et al.*, 2013), our results do not support this. Indeed, despite over 7000 photo-identification records of individual sharks from 54 countries in the Wildbook for Whale Sharks, there have been no records that confirm long, ocean-basin scale migrations (Wildbook, 2016; Norman *et al.*, in review). The results presented here add to the mounting evidence from around the world that *R. typus* display high site fidelity to coastal aggregation locations (Holmberg *et al.*, 2009; Hueter *et al.*, 2013; Berumen *et al.*, 2014; Cagua *et al.*, 2015; Norman *et al.*, in review), and support the hypothesis that Ningaloo Reef is acting as a post-nursery conditioning area, a coastal location where juvenile *R. typus* gather to feed and mature (Norman *et al.*, in review).

Detections from tagged sharks in this study were received from within NMP throughout the year and the suitability of habitat in NMP for *R. typus* was relatively high in both whale shark and non-whale shark season (Fig. 4). It has previously been suggested that *R. typus* could be year-round residents at coastal aggregation sites, with changes in behaviour, habitat use or poor observational conditions/changes in survey effort making this residency cryptic outside the recognised aggregation period (Eckert & Stewart, 2001; Rowat & Brooks, 2012; Cagua *et al.*, 2015). Whale sharks have been reported anecdotally and in the Wildbook for Whale Sharks at Ningaloo Reef outside the whale shark season (Norman *et al.*, 2016; Wildbook, 2016), and the tracked sharks provide further evidence of this year-round use. This study found that, outside the whale shark season, the range of the sharks shifted southward within NMP (Fig. 1b). The evidence that *R. typus* are using NMP all year and using certain areas of it at different times of the year is important for the tourism industry and its management agency, the Western Australian Department of Parks and Wildlife. "Whale shark season" at Ningaloo Reef may reflect the lack of search effort by the tourism industry in the summer (because of reduced tourist numbers), rather than a lack of whale sharks. These findings also suggest that there is potential for tourism operators to extend their working season.

Tagged sharks displayed a preference for shallower, warmer waters, but could also be found in very deep waters distant from any coastline (Fig. 3). While this and other studies (Wilson *et al.*, 2001; Sleeman *et al.*, 2007; Sleeman *et al.*, 2010a; Rohner, 2012; Sequeira *et al.*, 2012) suggest that *R. typus* prefer certain habitat characteristics, it remains unclear what drives large scale migratory movements of *R. typus*. It has been shown that *R. typus* move independently of surface ocean currents (Sleeman *et al.*, 2010b), perhaps responding to ephemeral changes in prey availability (Norman *et al.*, 2016). As the tagging hardware is only able to acquire a location fix through air (and not through sea water), shark detections in this study were limited to occasions when the dorsal fin of the shark breaks the water surface and exposes the attached tag. As *R. typus* are usually observed swimming just below the ocean surface, it is generally rare for the dorsal fin to break the surface except during active surface feeding (Gleiss *et al.*, 2013). It is therefore possible that many of the detections recorded from the tagged sharks represent such feeding events, and the environments at these locations are producing favourable feeding conditions. Whale sharks feed on zooplankton and Chl is often used as a proxy for this (because of the ease of Chl data collection via remote sensing and the lack of available zooplankton data) even though zooplankton biomass is only moderately related to Chl (Rohner, 2012). Despite this, Chl was still a significant predictor of *R. typus* presence in our model and our model performed well when assessed with an independent dataset.

Whale sharks may also come to the surface to thermoregulate, i.e. to bask in warm surface waters after time at depth in cooler waters (Thums *et al.*, 2013). The sharks tagged in this study displayed a preference for mid-range SSTs, from 23°C to 28°C, consistent with findings from other studies that *R. typus* prefer a narrow thermal range (Sequeira *et al.*, 2012; Acuna-Marrero *et al.*, 2014; Afonso *et al.*, 2014). To better understand what is driving the movements of *R. typus*, behavioural data loggers (Gleiss *et al.*, 2009) could be deployed in conjunction with satellite tracking, to elucidate the behaviour of sharks at specific locations.

(B) Threats and Conservation

In Australian waters, *R. typus* are protected from targeted fishing under state and federal legislation (Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act); Conservation and Land Management Act 1984; and Wildlife Conservation Act 1950). Marine Protected Areas theoretically provide higher levels of protection, from anthropogenic threats such as shipping traffic. However, some zones of MPAs still allow commercial activities including fishing operations and mining exploration and leases (Australian Government Department of the Environment and Energy, 2016). Tagged sharks were rarely detected inside existing MPAs, apart from NMP, and there are large areas along the WA coast and in the Timor Sea in which *R. typus* were predicted to occur that are not covered by these existing MPAs (Fig. 4). The waters of north-western Australia are the focus of extensive petroleum and natural gas extraction industries, with increases in shipping associated with these activities (Bejder *et al.*, 2012; Pendoley *et al.*, 2014). Recreational boating and fishing activities are also increasing, as north-western Australia and Ningaloo Reef draw increasing numbers of tourists (Pendoley *et al.*, 2014; Tourism Western Australia, 2016). As *R. typus* tend to spend extended periods swimming just below the surface, they are highly vulnerable to ship and propeller strike (Rowat & Brooks, 2012). In order to ensure the protection of *R. typus* from such activities, there is a need for accurate knowledge of their occurrence and distribution. The areas traversed by the tagged sharks and predicted to be highly suitable for *R. typus* by the habitat selectivity model could be used to inform management of shipping lanes (Sequeira *et al.*, 2012) and decision-making on mining leases and other commercial and recreational activities, in and outside of MPAs. While it is naïve to suggest that protection of *R. typus* should be the only consideration in planning MPAs, techniques used in this study could be applied to movement data from other migratory species that traverse the south-eastern Indian Ocean, to identify areas of important habitat for multiple species and inform future conservation priorities. While our study used data from animals tagged in only one location, existing movement data from *R. typus* tracking studies, and future tagging of *R. typus* in other locations around the south-eastern Indian Ocean and throughout their known range could be used to produce less biased and more extensive predictions of the species' distribution. The predicted suitable habitat for *R. typus* in Indonesian and international waters, and the visitation by some of the tracked sharks to such areas, also highlights the need for international co-operation in the protection of this endangered species.

(B) Conclusion

The application of biotelemetry has provided insights into the movements of *R. typus* from Ningaloo Reef, and extended the spatial and temporal reach of our knowledge of *R. typus* occurrence throughout the south-eastern Indian Ocean. The techniques used in this study could be applied to other *R. typus* populations, other migratory marine species, and in multi-species studies, in order to better inform management and conservation. The findings of this study have improved the understanding of *R. typus* movements and potential distribution in the south-eastern Indian Ocean and have implications for the ongoing conservation and management of this species.

(A) ACKNOWLEDGEMENTS

Tagging was conducted under permits issued by Murdoch University Animal Ethics Committee (permit numbers W2058/07 and W2402/11), the Western Australian Department of Environment and Conservation (permit numbers SF007471, SF008572 and SF009184) and The Western Australian Department of Parks and Wildlife (permit numbers SF009879 and SF010414).

This research made use of data and software tools provided by Wildbook for Whale Sharks, an online mark-recapture database operated by the non-profit scientific organization Wild Me, as well as ZoaTrack, an online platform for displaying and analysing movement data, supported by The Atlas of Living Australia (ALA).

Thanks to the staff and volunteers of ECOCEAN, as well as the many funders, donors, supporters and collaborators who made the satellite tracking programme possible. Tags deployed in 2015 were sponsored by 16 schools in WA as part of a joint ECOCEAN – Western Australian Department of Education programme, designed to engage students in Science, Technology, Engineering and Maths (STEM) learning. The Director General of Education, Sharyn O'Neill, Professor Lyn Beazley and Hester Bushell were instrumental in building the programme. Their support and the participation of all the schools, teachers and students are greatly appreciated.

(A) LIST OF BRIEF TITLES OF ITEMS IN THE SUPPLEMENTARY MATERIAL

Additional supporting Information may be found in the online version of this article:

Table S1 Information on Marine Protected Areas around the Western Australian coast utilised by 25 satellite-tracked whale sharks (*Rhincodon typus*).

Figure S1 Map of existing Commonwealth and State Marine Protected Areas around the Western Australian Coast.

Figure S2 The background raster layers of physical/environmental variables over the study area in the south-eastern Indian Ocean used as inputs in the habitat suitability modelling.

(A) BIOSKETCH

This work is a collaboration between researchers from ECOCEAN, a not-for profit research organisation (www.whaleshark.org.au) and The University of Queensland’s Franklin Eco-lab (www.uq.edu.au/eco-lab/) and Centre of Excellence for Environmental Decisions (CEED) (www.ceed.edu.au/), focused on using spatial ecology in the prioritisation of conservation decisions. Author contributions: All authors contributed to the conception of ideas and the writing; S.R. and R.D. led the writing and analysed the data; B.N. and S.R. conducted field work and collected the data.

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(A) TABLES

Table 1. Information from deployments of satellite-linked tags on whale sharks (*Rhincodon typus*), at Ningaloo Reef, Western Australia from 2010 – 2016.

Shark ID	Estimated length (m)	Sex	Date of tag deployment	Date of last detection	No. of days tracked	Minimum distance travelled (km)	No. of detections	Maximum detected distance from NMP (km)
A-958	5.0	Male	24/07/2015	9/04/2016	260	6156.99	226	1312.99
A-1095	7.5	Male	24/07/2015	7/11/2015	106	5703.97	457	1248.26
A-1041	4.5	NA	29/07/2015	14/12/2015	138	3690.05	162	1567.40
A-1135	7.5	Female	18/07/2015	21/12/2015	156	3635.39	106	1289.38
A-788	9.0	Female	28/07/2015	10/12/2015	135	3633.51	248	669.24
A-1019	5.0	Female	24/07/2015	22/11/2015	121	3379.98	78	788.31
A-919	5.5	Male	29/07/2015	1/11/2015	95	3278.13	163	1180.56
A-633	5.0	Male	24/08/2013	14/03/2014	203	3213.95	77	845.99
A-546*	7.0	Male	9/04/2013	25/12/2013	261	3159.90	403	312.78
A-349	9.0	Female	3/08/2013	15/10/2013	74	3122.74	77	1349.65
A-660ǂ	6.0	Male	16/07/2010	20/09/2010	67	2571.28	37	985.47
A-666*	6.5	Female	18/07/2015	29/09/2015	73	2247.80	57	880.79
A-666*	5.5	Female	20/07/2013	5/10/2013	78	2226.72	51	612.04
A-957	5.0	Male	22/07/2015	22/08/2015	31	2153.52	21	780.67
A-683ǂ	6.0	Male	16/07/2010	29/08/2010	45	1906.40	7	1282.34
A-481	6.5	Female	7/07/2013	6/10/2013	92	1653.16	73	264.74
A-013	9.0	Male	30/07/2015	12/10/2015	74	1621.16	63	462.22

Table 1. Continued

Shark ID	Estimated length (m)	Sex	Date of tag deployment	Date of last detection	No. of days tracked	Minimum distance travelled (km)	No. of detections	Maximum detected distance from NMP (km)
A-720	5.5	Male	21/08/2013	7/11/2013	79	1327.08	47	202.80
A-843	8.0	NA	9/09/2012	21/10/2012	43	1181.62	33	210.46
A-546*	7.5	Male	24/07/2015	10/09/2015	48	1065.97	89	377.13
A-302	5.0	Male	21/06/2014	27/07/2014	37	576.63	38	218.53
A-707	6.0	Male	24/07/2015	8/08/2015	15	522.79	19	331.83
A-088	7.5	Female	21/06/2014	29/06/2014	9	357.86	19	70.17
A-883	3.0	Male	10/04/2013	22/04/2013	13	227.84	22	#
A-534	6.5	Male	16/06/2013	4/07/2013	19	110.36	13	#
A-1249~	10.0	Male	28/04/2016	7/09/2016	133	2877.28	210	NA
A-1310~	7.5	Male	05/08/2016	29/10/2016	86	1641.84	93	NA
A-907~	7.5	Male	05/08/2016	05/11/2016	93	1306.93	105	NA
A-1312~	5.0	Male	09/08/2016	14/11/2016	98	847.32	74	NA

All tags deployed were satellite-linked SPOT tags (Wildlife Computers Inc., WA, USA), except for that deployed on A-683, which was a SPLASH tag (Wildlife Computers Inc., WA, USA). ɨ indicates tags encased in positively buoyant foam and attached to the shark with a tether and dart into the flank. All other tags were attached to a negatively buoyant clamp and mounted on the first dorsal fin. Shark IDs were determined by photo-identification in the Wildbook for Whale Sharks (Wildbook, 2016). * indicates sharks that were tagged in two different years. ~ indicates sharks that were tagged in 2016 and used as an independent dataset to validate the habitat suitability model predictions. Estimated lengths in metres are total body lengths of the sharks estimated by an experienced researcher. Sex was determined from visual examination of the presence (male) or absence (female) of claspers. NA indicates information is not available. Date of last detection is the date on which the last reliable transmission was received from the tag. Minimum distance travelled is the Great Circle Distance of the straight line distance between successive detections. No. of detections is the number of reliable positional fixes received from each tag. Maximum detected distance from NMP is the distance of the furthest detection received from each tag from the closest point on the outer border of the Ningaloo Marine Park. # indicates that the shark was not detected outside Ningaloo Marine Park over the tracking period.

(A) FIGURE LEGENDS

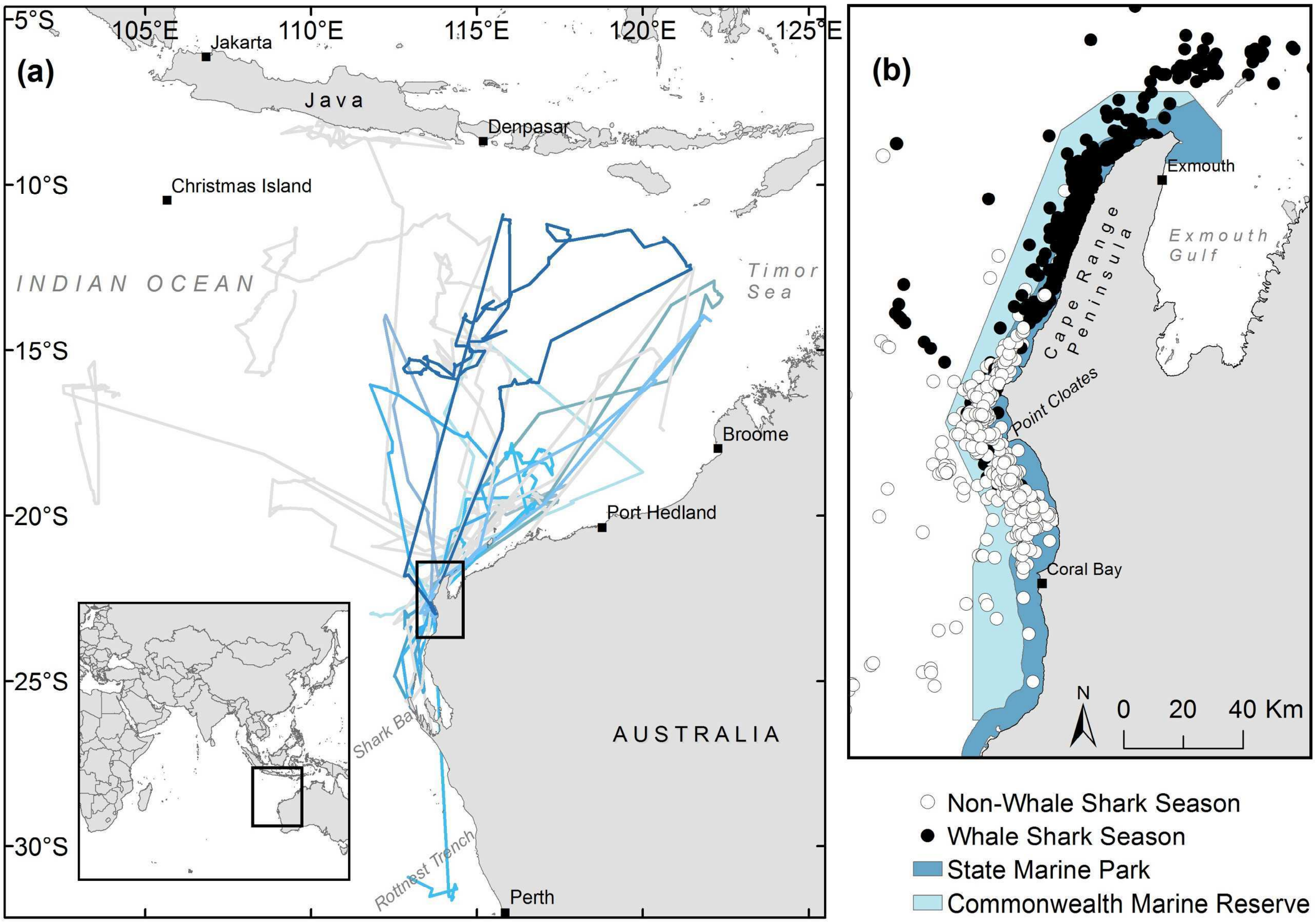
Figure 1 (a) The tracks of 25 whale sharks (*Rhincodon typus*) tagged with satellite-linked transmitters at Ningaloo Reef from 2010 – 2015. Each line represents the movement of an individual animal. Coloured lines represent the tracks of nine tagged sharks that returned to Ningaloo Reef after moving at least 300 km away from their tagging locations. Tracks represent the shortest route between successive detections from the tags. **(b)** The location of the Commonwealth Marine Reserve and State Marine Park at Ningaloo Reef, along the west coast of the Cape Range Peninsula, Western Australia. Circles represent detections of the 25 tagged sharks, separated according to season.

Figure 2 (a) The total number of whale sharks (*Rhincodon typus*) that were detected via transmissions from satellite tags each month and, of those, the number that were detected from at least one location within the boundaries of Ningaloo Marine Park (NMP). **(b)** The distance of tagged *R. typus* from the closest point on the outer border of NMP over time. The sharks (n = 25) were tagged between 2010 and 2015, however distances are plotted by calendar month to show movements during whale shark season (WSS, March – August) and non-whale shark season (Non-WSS, September – February). Lines represent individual sharks.

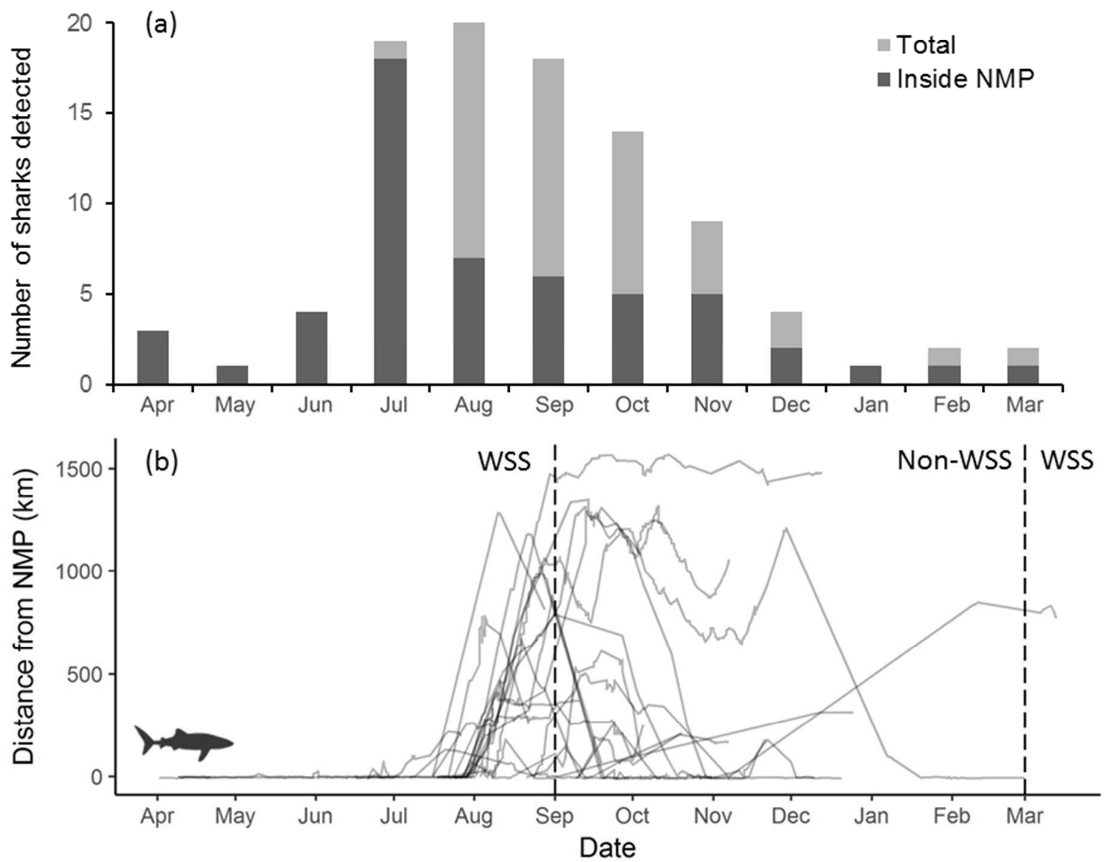
Figure 3 The generalised additive mixed-effects model (GAMM) outputs, showing the effects of the covariates **(a)** bathymetry (bathy), **(b)** sea surface temperature (sst) and **(c)** Chlorophyll-a concentration (chl), on the scale of the link-function (y-axes). Dotted lines represent 95% confidence limits and the black lines show the mean population responses (i.e. the fixed effect).

Figure 4 Maps showing the relative suitability of habitat for whale sharks (*Rhincodon typus*) in the south-eastern Indian Ocean during (**a - b**) whale shark season (March – August) and **(c - d)** non-whale shark season (September – February). Existing Marine Protected Areas (State and Commonwealth) are outlined in black. Yellow circles represent locations from four whale sharks tracked via satellite telemetry during 2016 that were used to validate the habitat suitability model.

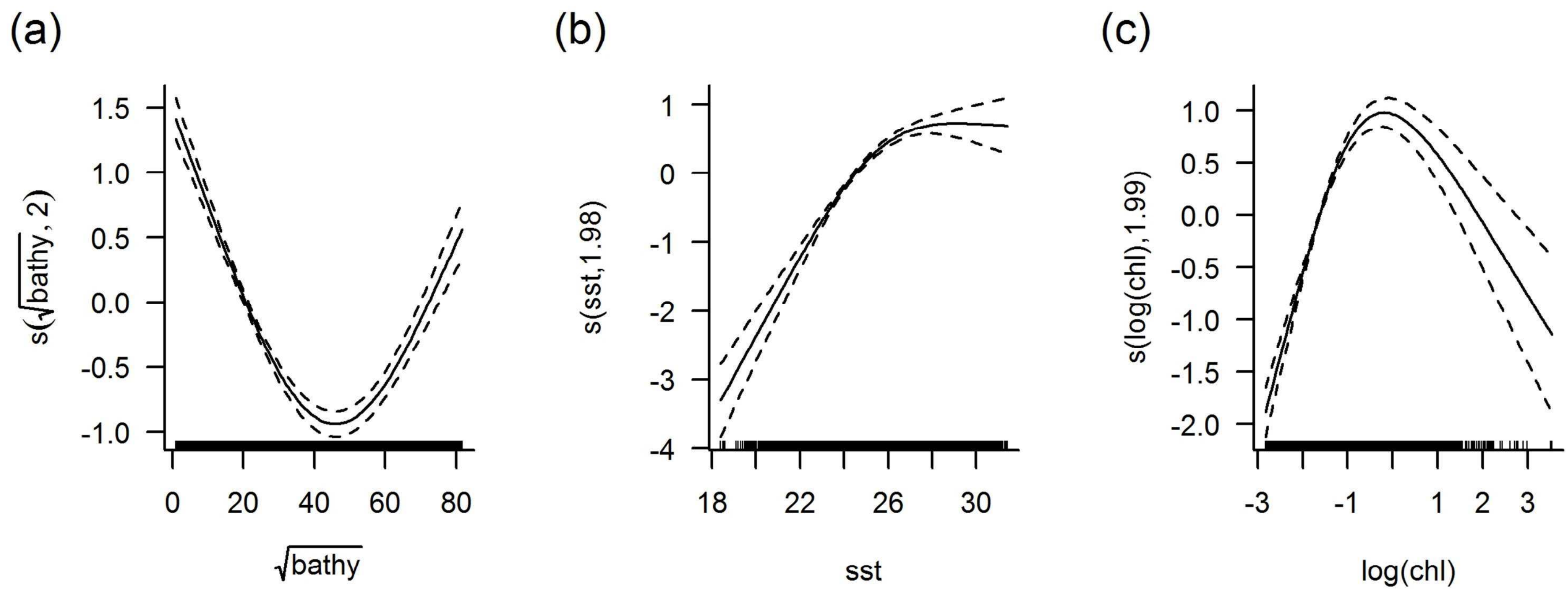
(A) FIGURES



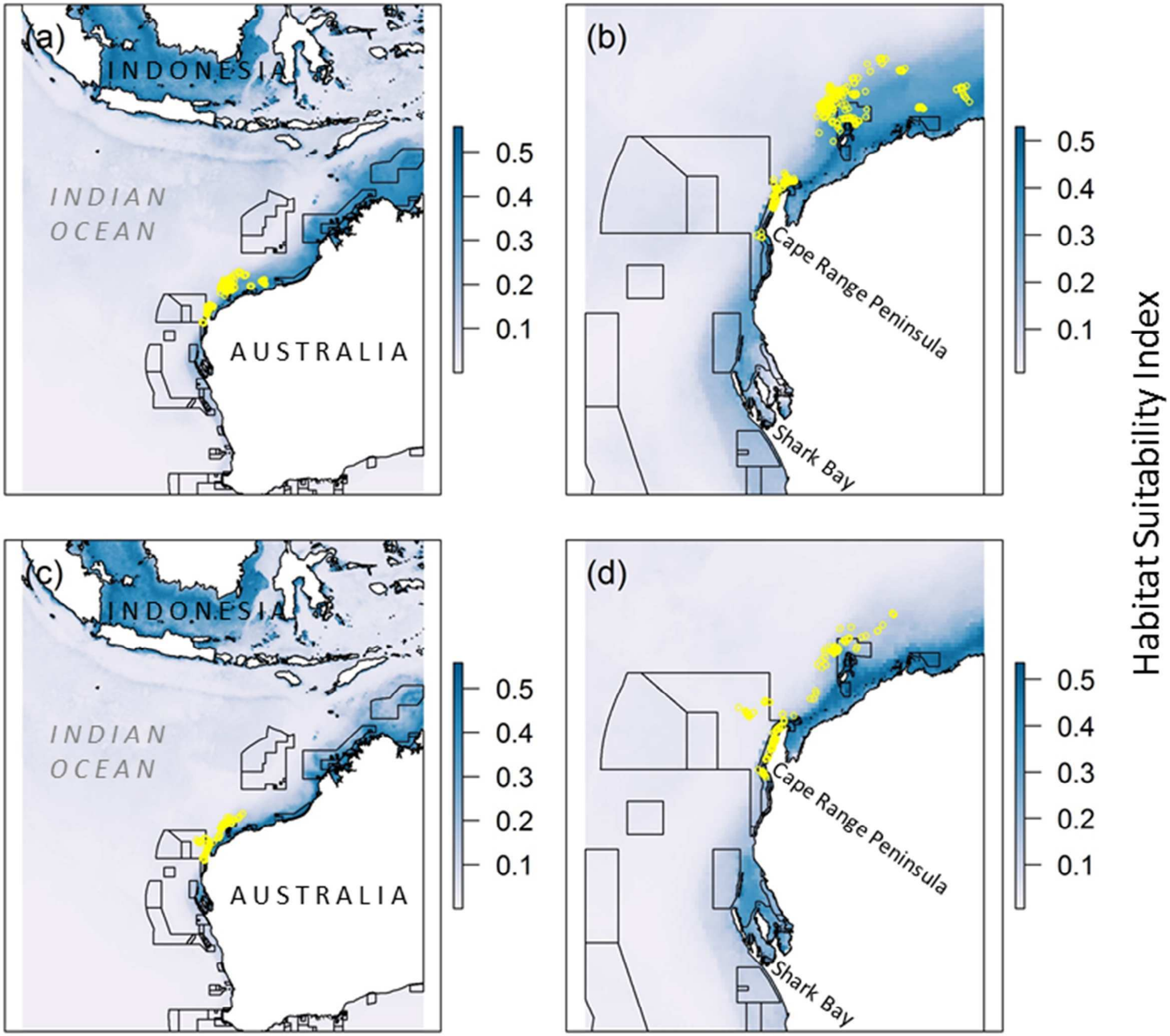
(a)
5°S
105°E
110°E
115°E
120°E
125°E
Jakarta
Java
Denpasar
10°S
Christmas Island
INDIAN OCEAN
Timor Sea
15°S
Broome
20°S
Port Hedland
25°S
AUSTRALIA
Shark Bay
30°S
Rottnest Trench
Perth
(b)
Exmouth
Exmouth Gulf
Cape Range Peninsula
Point Cloates
Coral Bay
N
0 20 40 Km
Non-Whale Shark Season
Whale Shark Season
State Marine Park
Commonwealth Marine Reserve



(a)
Number of sharks detected
20
15
10
5
0
Total
Inside NMP
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
(b)
Distance from NMP (km)
1500
1000
500
0
WSS
Non-WSS
WSS
Date



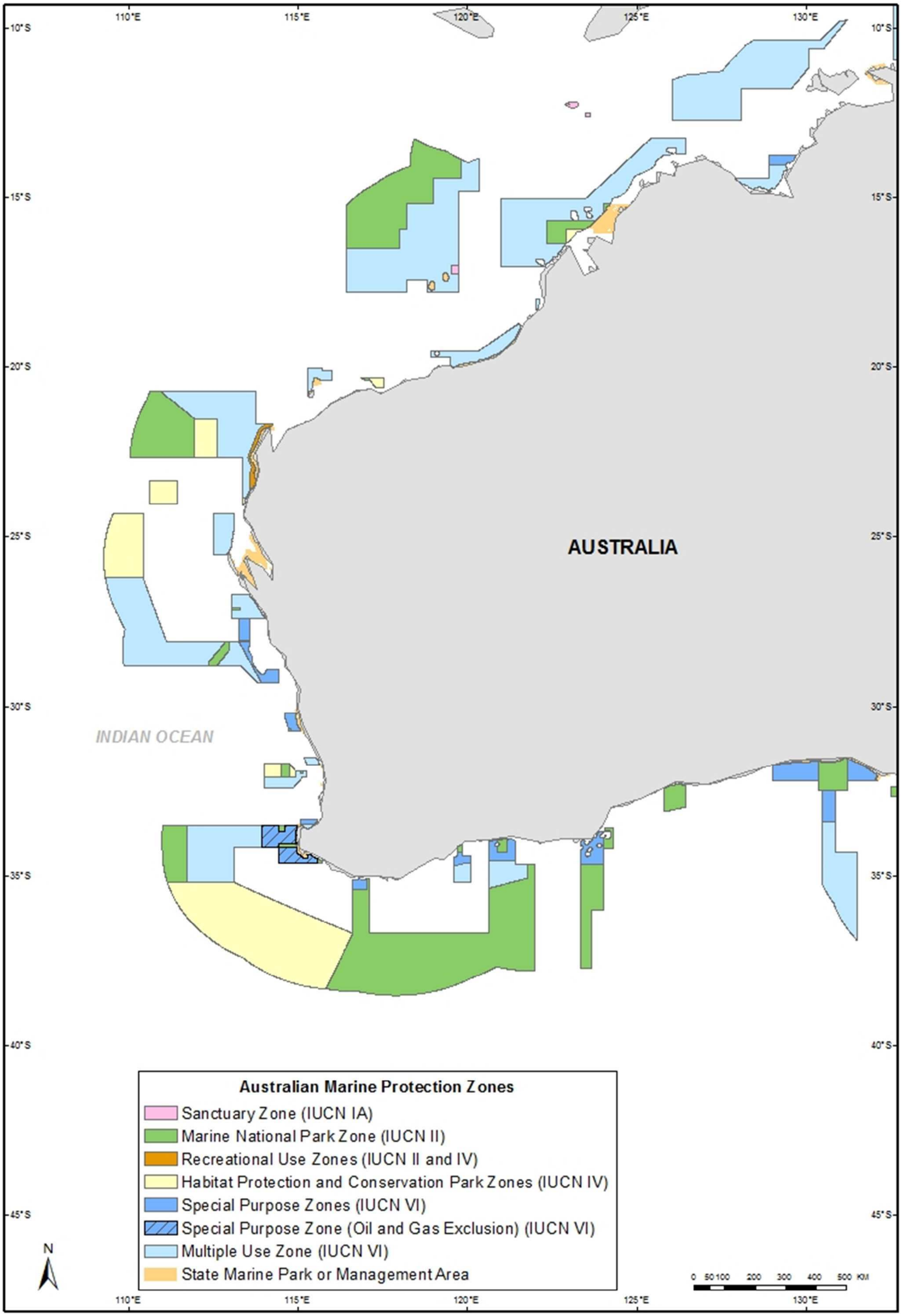
(a)
s(√bathy, 2)
1.5
1.0
0.5
0.0
-0.5
-1.0
0
20
40
60
80
√bathy
(b)
s(sst,1.98)
1
0
-1
-2
-3
-4
18
22
26
30
sst
(c)
s(log(chl),1.99)
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-3
-1
1
2
3
log(chl)


(a)
INDONESIA
INDIAN
OCEAN
AUSTRALIA
0.5
0.4
0.3
0.2
0.1
(b)
Cape Range Peninsula
Shark Bay
0.5
0.4
0.3
0.2
0.1
Habitat Suitability Index
(c)
INDONESIA
INDIAN
OCEAN
AUSTRALIA
0.5
0.4
0.3
0.2
0.1
(d)
Cape Range Peninsula
Shark Bay
0.5
0.4
0.3
0.2
0.1

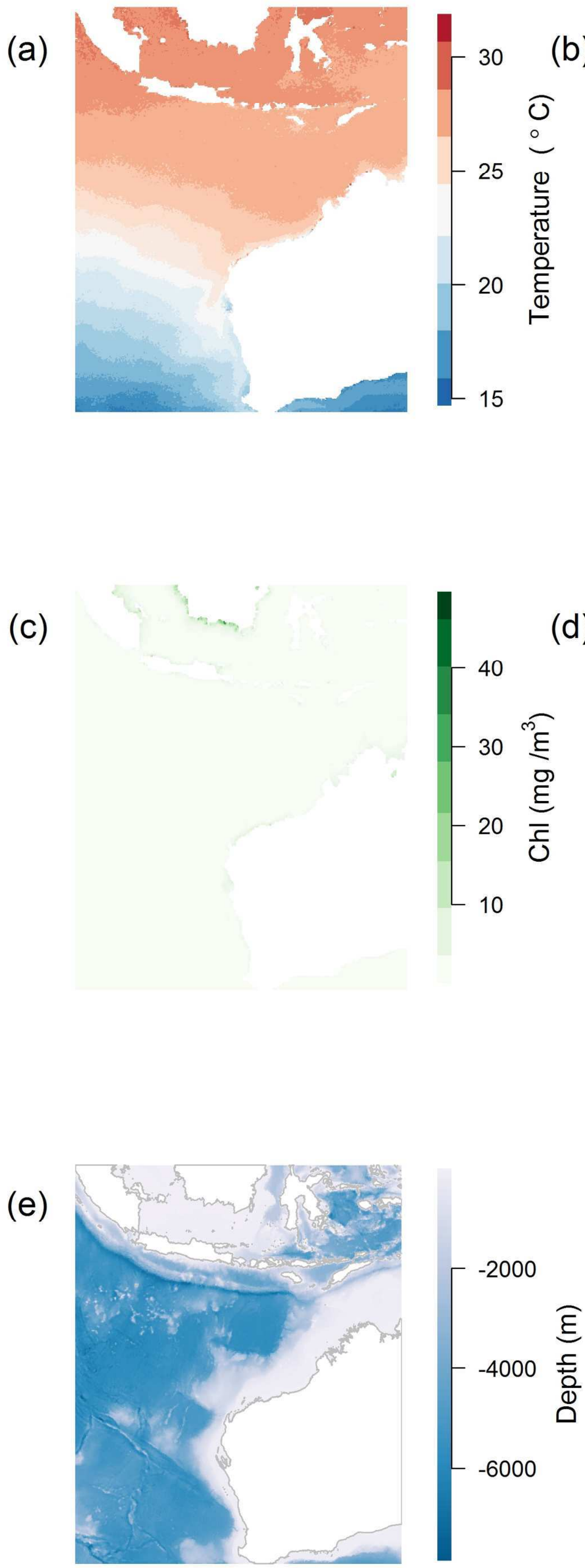
(A) SUPPORTING INFORMATION

Table S1 Information on Marine Protected Areas utilised by 25 satellite-tracked whale sharks (*Rhincodon typus*), in the south-eastern Indian Ocean.

Marine Protected Area	Zone utilised	Number of detections	Number of sharks
Gascoyne, Commonwealth Marine Reserve	Multiple-use zone (IUCN code VI)	57	11
	Marine National Park zone (IUCN code II)	1	1
Shark Bay, Commonwealth Marine Reserve	Multiple-use zone (IUCN code VI)	4	2
Montebello, Commonwealth Marine Reserve	Multiple-use zone (IUCN code VI)	2	2
Argo-Rowley Terrace, Commonwealth Marine Reserve	Multiple-use zone (IUCN code VI)	5	2
	Marine National Park zone (IUCN code II)	9	1
Muiron Islands Marine Management Area (State Waters)	Marine Management Area (IUCN code VI)	1	1
Ningaloo Commonwealth Marine Reserve and Western Australian Ningaloo Marine Park (State Waters)	Recreational use zones (IUCN codes II and IV) All zones	1061	25



110°E
115°E
120°E
125°E
130°E
10°S
15°S
20°S
25°S
30°S
35°S
40°S
45°S
AUSTRALIA
INDIAN OCEAN
Australian Marine Protection Zones
Sanctuary Zone (IUCN IA)
Marine National Park Zone (IUCN II)
Recreational Use Zones (IUCN II and IV)
Habitat Protection and Conservation Park Zones (IUCN IV)
Special Purpose Zones (IUCN VI)
Special Purpose Zone (Oil and Gas Exclusion) (IUCN VI)
Multiple Use Zone (IUCN VI)
State Marine Park or Management Area
N
0 50 100 200 300 400 500 KM


(a)
30
25
20
15
Temperature (° C)
(b)
30
25
20
15
Temperature (° C)
(c)
40
30
20
10
Chl (mg /m3)
(d)
40
30
20
10
Chl (mg /m3)
(e)
-2000
-4000
-6000
Depth (m)