

# Movement patterns of whale sharks in Cenderawasih Bay, Indonesia, revealed through long-term satellite tagging

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**Abstract.** Whale sharks, *Rhincodon typus*, are found circumglobally in tropical and warm temperate seas, exhibiting a range of residency and movement patterns. To determine spatio-temporal habitat use by juvenile male whale sharks in Cenderawasih Bay, Indonesia, we collected data from June 2015 to November 2016 using 16 fin-mounted satellite tags that provided exceptionally long track durations. Fifteen tags transmitted for 48–534 days (mean =  $321 \pm 33$ , s.e.), with 13 tags transmitting for  $\geq 220$  days. Four sharks remained within the bay for the duration of the study, while of the 11 sharks that travelled outside the bay, eight left between March and May 2016. They ranged throughout coastal and offshore waters, travelling up to 5144 km away from Cenderawasih Bay, with a mean horizontal speed of only  $3.3 \text{ km day}^{-1} \pm 0.70$ , s.e. A switching state space model was fitted to satellite fix data to identify behavioural states. It revealed that sharks spent an average of 81% of their time in foraging-related behaviours, mostly in shallow waters (median depth = 35 m), with travelling observed mainly over deeper waters (median depth = 1284 m). The movement patterns reveal variable periods of residency, with individual patterns of horizontal movement most likely in response to different abiotic and biotic factors, including food availability, which may trigger seasonal dispersal.

**Additional keywords:** telemetry, spatial distribution, West Papua, elasmobranch, Bird's Head Seascape.

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## Introduction

The world's largest fish, the whale shark, *Rhincodon typus*, is a highly mobile species that occurs in tropical and warm temperate seas worldwide (Rowat and Brooks 2012). Due to its K-selected life history, high value in international trade, highly migratory movement patterns, low abundance, and docile nature, whale sharks are protected in several countries (Stewart and Wilson 2005). In order to effectively manage and conserve this species, an understanding of its temporal and spatial movement patterns, in addition to the abiotic and biotic factors that may influence the shark's aggregation behaviour and movements, is essential (Rowat and Brooks 2012; Berumen *et al.* 2014; Prebble *et al.* 2018).

Globally, 20 whale shark aggregation hotspots have been identified (Norman *et al.* 2017). Most of these are associated with periods of high food availability due to plankton blooms or fish and coral spawning events (Taylor 1994, 1996; Heyman *et al.* 2001; Maguire 2006). Whale shark diets vary geographically and seasonally, but their main food sources include nektonic prey such as small fishes and cephalopods, along with

a variety of zooplankton (Taylor 1994; Norman 1999; Stevens 2007; Motta *et al.* 2010; Borrell *et al.* 2011; Rohner *et al.* 2013b). Whale sharks feed passively (swimming with their mouth agape) and actively (chasing prey such as small fishes and sergestid shrimps through the water column) (Motta *et al.* 2010; Fox *et al.* 2013; Rohner *et al.* 2015). Additionally, they hang vertically in the water and use their mouths to actively suck in water to filter through their gills. Although some filter-feeding sharks (such as basking sharks, *Cetorhinus maximus*) are dependent on a forward swimming motion to operate their filtration and breathing mechanisms, whale sharks use buccal pumping, a method of suction filter-feeding, which allows them to draw water into their mouth at higher velocities than swimming-dependent filter-feeders (Compagno 2001). This enables them to capture larger nektonic prey in addition to zooplankton aggregations. However, due to this, they filter a far smaller volume of water, resulting in a less efficient means of concentrating diffuse planktonic prey whilst still incurring the high cost of increased drag from their open mouth (Cade *et al.* 2020). Therefore, whale sharks may be more reliant

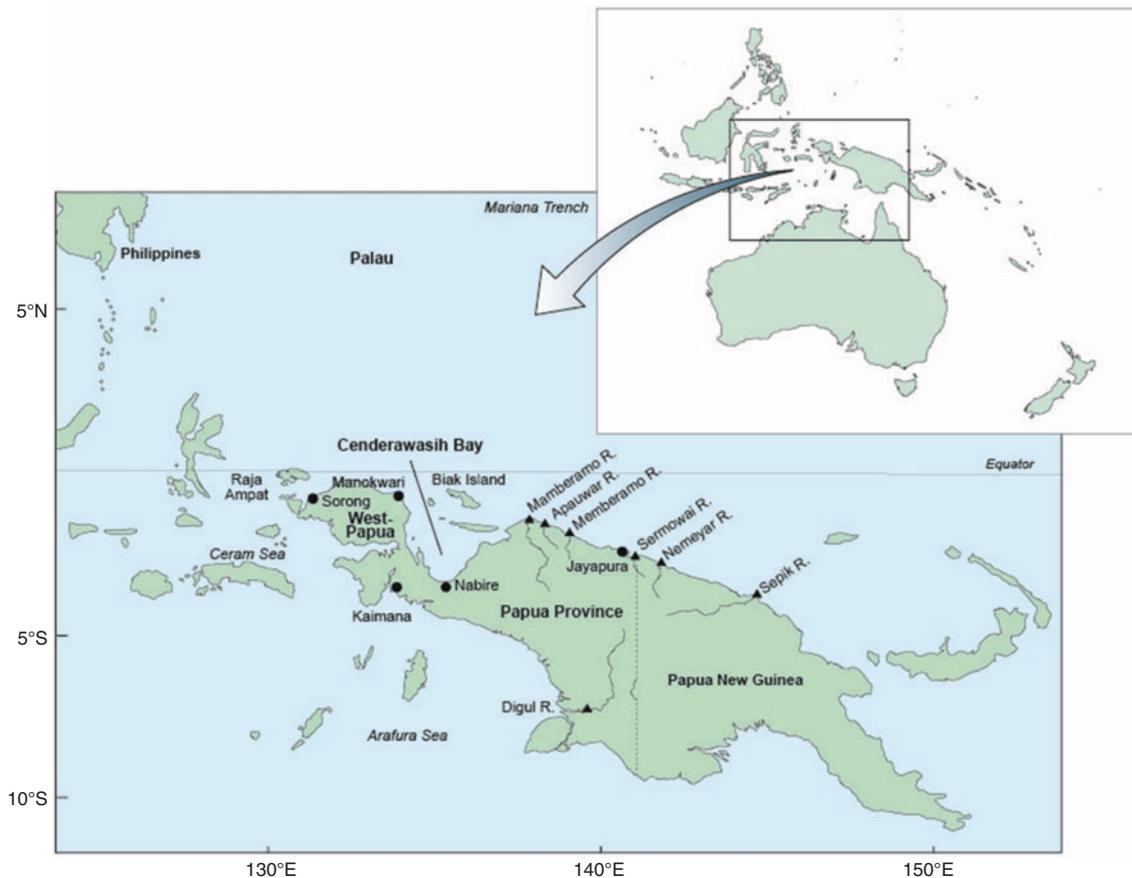


Fig. 1. Map of the study region centred upon Cenderawasih Bay, West Papua, Indonesia.

on dense aggregations of prey than other filter-feeding fish (Rohner *et al.* 2015).

Gene flow between whale sharks inhabiting different ocean basins is limited (Castro *et al.* 2007; Schmidt *et al.* 2010; Sequeira *et al.* 2013); however, a comprehensive understanding of whale shark migratory routes and movement patterns globally has yet to be fully resolved (Rowat and Brooks 2012). Over recent decades, satellite tracking using the Argos system has become a popular means of studying the movement patterns of marine vertebrates (Hays *et al.* 2007). This technique has elicited a wealth of information on distribution patterns as well as habitat use (Block *et al.* 2005; Diamant *et al.* 2018), foraging ecology (Sale *et al.* 2006; Rohner *et al.* 2018) and migratory patterns (Block *et al.* 2001; Hearn *et al.* 2016). By combining tag data and modern statistical methods, we can examine the biological and statistical complexity within data (Jonsen *et al.* 2005), allowing estimation of other processes that may be intractable by other methods. One of these methods, switching state space modelling (SSSM), uses remotely sensed location data to identify foraging and travelling patterns when direct observation is not possible (Jonsen *et al.* 2007).

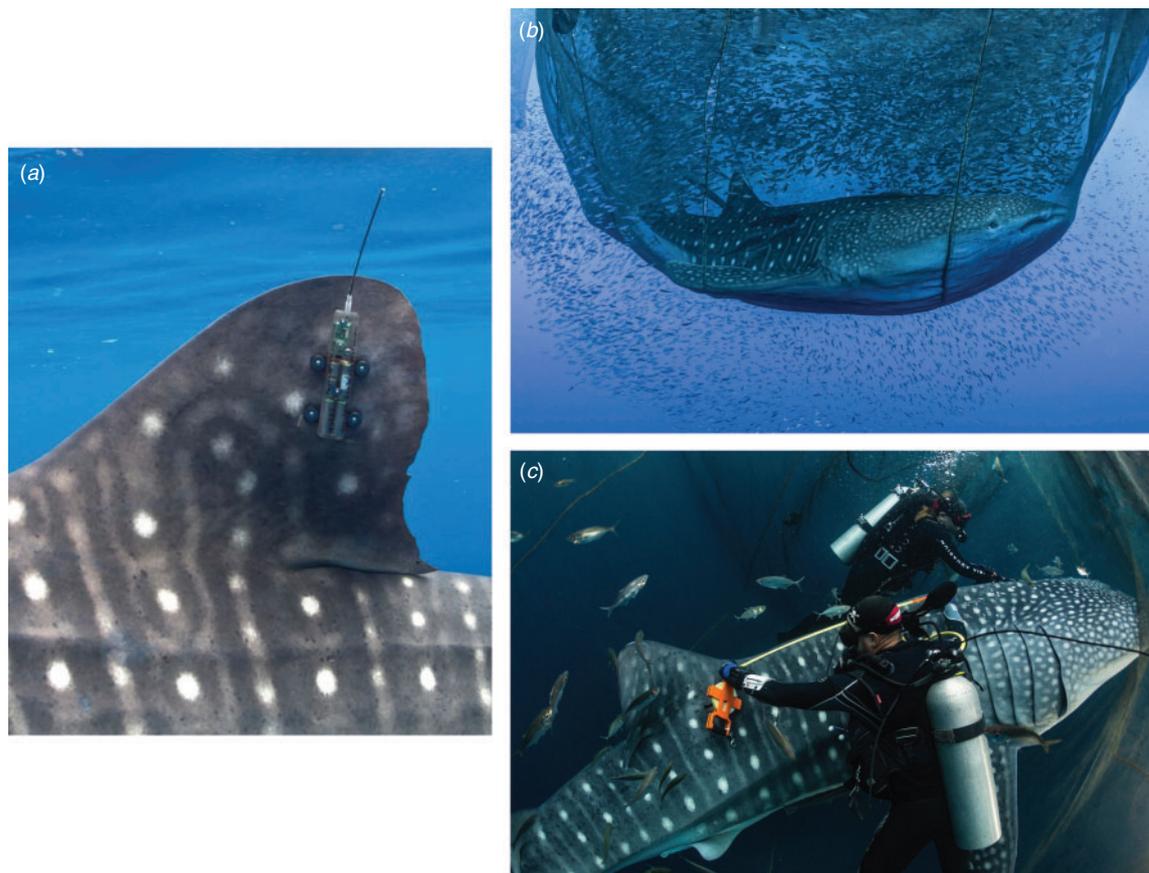
Whale sharks exist throughout the Indonesian archipelago, though perhaps the most consistent aggregation is in Cenderawasih Bay in West Papua (Fig. 1). Despite growing scientific and tourism interest in the whale sharks of Cenderawasih Bay,

little is known about this population (Stewart 2011; Himawan *et al.* 2015). Here, we report the development of a novel fin-mounting technique for whale shark satellite tags which produces much longer tag retention than normally achieved with whale sharks. We use satellite telemetry data from the successful tag deployments, and SSSM to determine the temporal and spatial movement patterns of whale sharks over an 18-month period in Cenderawasih Bay.

## Methods

### Study area and tagging procedures

Cenderawasih Bay (2.5°S, 135.3°E) in north-eastern Indonesia (spanning the provinces of Papua and West Papua) is ~430 km at its widest point and ~240 km across at the middle, with a maximum depth of 1630 m (Fig. 1). Approximately 50% of the bay is included within the Cenderawasih Bay National Marine Park, including the main whale shark aggregation area near Nabire. As Cenderawasih Bay and surrounding areas of the Bird's Head Seascape are close to the equator, the main seasonal influences are the monsoon weather patterns that are driven by the annual movement of the intertropical convergence zone (Mangubhai *et al.* 2012). The movement of this zone results in two monsoon seasons: (1) the north-west monsoon, from November to March, characterised by warmer sea surface



**Fig. 2.** (a) SPLASH10-346A tag mounted on the dorsal fin of a whale shark; (b) shark in the bagan net before fin-mounted tag attachment and (c) measuring a shark before conducting fin-mounted operation in Cenderawasih Bay, Indonesia.

temperatures (SST), increased rainfall, intermittent strong winds, and swell in the north and, (2) the south-east monsoon, from May to October with cooler SSTs, decreased precipitation, persistent wind, and a strong swell in the south (Prentice and Hope 2007). Cenderawasih Bay's SST stays relatively constant (29–30°C) throughout the year.

Village elders report that whale sharks have targeted large schools of clupeid and atherinid fish in the bay since at least the 1940s, occasionally beaching themselves in the process. Importantly, whale sharks in Cenderawasih today are most frequently observed close to lift-net fishing vessels (locally called 'bagans': Himawan *et al.* 2015) which have operated in nearshore coastal waters of the bay since 2003 and target the same small clupeid and atherinid fishes that the whale sharks appear to preferentially feed upon (Stewart 2011). Whale sharks are commonly observed swimming beneath the bagans feeding upon the aggregated fish, and are occasionally caught in the nets when they are lifted. As the net is large (~20 m × 20 m × 12 m), whale sharks that are accidentally captured are free-swimming in the net until the fishermen collect the fish. This is done by isolating the whale shark in a small (~8 m × 8 m) section of net while the rest of the catch is collected. The sharks are then released unharmed by lowering the net. Though fishers attempt to avoid this accidental capture when possible, the phenomenon provides a unique

opportunity to deploy fin-mounted satellite tags on the whale sharks, as described below.

Between June 2015 and May 2016, dorsal fin-mounted SPLASH tags (model SPLASH10-346A, Wildlife Computers, Redmond, WA, USA, with a two-year battery life) (Fig. 2a) were deployed on 16 juvenile (3.0–7.0 m) male whale sharks in Cenderawasih Bay. The tags were equipped with a wet-dry switch that enabled transmission to an Argos satellite when the shark's dorsal fin broke the surface of the water. The number of days a tag was active was calculated as the first transmission date to the last Argos uplink date. The tags collected ambient temperature, light level, and pressure (depth) data that were summarised and compressed for transmission to Argos satellites. These variables were measured every 10 s and summarised into 12-h periods to facilitate data transmission.

Tags were deployed on sharks that were accidentally caught in the lift-nets, using the following standardised procedure. Most of the lift-net was pulled from the water, isolating the captured shark in a small (typically 8 × 8 m) 'pocket' of the net. Once the shark settled to the bottom of the net (Fig. 2b), it was measured for total length (TL) (Fig. 2c) from the tip of the mouth to the top lobe of the caudal fin, after which its sex and maturity (for males only) were assessed based on clasper size and morphology (Norman and Stevens 2007).

Photographs of the shark were taken for identification purposes and the deployment location recorded via GPS. A pneumatic drill attached to a modified SCUBA regulator and dedicated tank was used to drill four holes, spaced to fit the tag, through the shark's dorsal fin using a 9-mm masonry drill bit. A hypoallergenic nylon sleeve was custom cut underwater and threaded through the tag and dorsal fin. Compressible rubber washers were threaded around each nylon sleeve (on the opposite side of the fin from the tag) to allow for fin growth during the deployment period. Stainless steel screws (with washers) were screwed into the nylon sleeves from both sides to secure the tag in place. The net was lowered and the shark released, in all cases swimming away from the net rapidly (though frequently returning to the vicinity of the net to feed within 1–3 h). The entire process was completed in 25–50 min. All sharks left the net unharmed and their tags transmitted within 72 h after release, though one tag subsequently appeared to suffer damage to the antenna and did not transmit useable data for this study. As whale sharks are able to buccal pump water over their gills while immobilised in the net, they did not require a long period of recovery or monitoring after tagging (Compagno 2001; Escalle *et al.* 2016).

Satellite tagging was conducted under the following three permits issued to AS by the Cenderawasih Bay National Park Authority (BBTNTC): SIMAKSI SI.18/BBTNTC-2/TEK/2015, SIMAKSI SI.46/BBTNTC-2/TEK/2015, and SIMAKSI SI.05/BBTNTC-2/TEK/2016. All tagging was conducted according to the ethical guidelines for care and use of animals of the Ministry of Environment and Forestry as approved within these three permit applications.

### Tracking and analysis

Although the tags were programmed to transmit up to 250 times per day, actual transmission rates varied depending on the amount of time the shark spent at the surface. Sharks provided, on average, 0.4–1.5 (mean = 0.86) fixes per day (calculated across the entire tracks), which was sufficient to ascertain surface movements remotely. All tracks were analysed using *R* (R Core Development 2016) code in the integrated development environment RStudio 3.2.1 and 3.3.1, adapted from a previous study (Francis *et al.* 2015).

Improbable Argos fixes were filtered out using the *argosfilter* package (Freitas *et al.* 2008) in *R*. This removed positions requiring speeds between fixes of greater than a given threshold (we used  $2 \text{ m s}^{-1}$  or  $173 \text{ km day}^{-1}$ ) unless they were within 5 km of the previous position. This constraint prevents removal of locations that generate artificially high speed estimates as a result of two fixes being obtained within a short time (Freitas *et al.* 2008). Selecting an appropriate speed threshold for the filter was difficult, because maximum swimming speeds have rarely been reported for whale sharks. Average swimming speeds are typically less than  $0.85 \text{ m s}^{-1}$ , but may be as high as  $1.6 \text{ m s}^{-1}$  (Eckert *et al.* 2002; Rowat *et al.* 2007; Motta *et al.* 2010; Hueter *et al.* 2013). Maximum swimming speeds of  $3.1\text{--}3.8 \text{ m s}^{-1}$  reported by Hsu *et al.* (2007) are probably unreliable given the short time gaps between their fixes (3, 17, 20 and 101 min) and the effect of location errors on the estimates (an obvious location error can be seen in one track shown by

Hsu *et al.* 2007, fig. 7A). Our threshold of  $2 \text{ m s}^{-1}$  retained 96.0% of fixes, and increasing it would have had little effect (thresholds of  $3 \text{ m s}^{-1}$  and  $4 \text{ m s}^{-1}$  would have increased the retention rate to 96.9% and 97.5% respectively).

Movement tracks were subjectively divided into three categories: bay (occurring exclusively within or just outside the boundary of Cenderawasih Bay) (Fig. 1), coastal (outside the bay, but always within 5 km of the mainland), and offshore (tracks that moved well beyond the continental shelf) movements. Data used in this study spanned the period 9 June 2015 to 30 November 2016, although 14 tags continued transmitting beyond that period.

### Switching State Space Models

A key assumption of SSSM is that, given enough time, animal movements are an integration of more than one behavioural mode (Jonsen *et al.* 2007). The resulting time-series of positions may be non-linear and is best analysed using a switching model (Morales *et al.* 2004; Jonsen *et al.* 2005). State-space models are time-series methods that allow unobserved states and biological parameters to be estimated from data observed with error (Jonsen *et al.* 2005). Here, SSSMs were used to identify two contrasting behavioural states: (1) sharks typically travelled slowly over short distances, made frequent changes of direction, and remained within the same general area (referred to as area-restricted searching, likely indicating foraging or feeding-related behaviour and hereafter referred to as foraging), and (2) sharks travelled rapidly over long distances with few angle changes (often associated with travelling between regions) (Turchin 1991; Jonsen *et al.* 2007). Transitional values are those that could not be confidently classified as either foraging or travelling, showing characteristics between these two states.

A SSSM was fitted to the whale shark data using the *bsam* package in *R*, which in turn used JAGS 4.2.0 software to perform the Bayesian analyses (<https://sourceforge.net/projects/mcmc-jags/files/JAGS/4.x/Windows/>). This modelling approach was specifically developed and adapted for use with satellite tracking data (Jonsen *et al.* 2005, 2007). A hierarchical, switching, first-difference, correlated random walk model (hDCRWS) was simultaneously fitted to data from the 15 sharks with tag transmissions (see Table 1). First-difference models operate on the difference between location fixes, rather than the locations themselves, as the random walk is associated with the movements between locations (Jonsen *et al.* 2005). Hierarchical models estimate a single set of movement parameters simultaneously across all sharks, rather than separately for each shark, as this provides improved behavioural state estimation through reduction of uncertainty (Jonsen 2016). Errors were modelled with *t*-distributions because Argos errors are non-normal, and different error distributions were allowed for each of the Argos location classes, thus accounting for the variable location accuracy from Argos positions (Jonsen *et al.* 2005, 2007). The model was fitted with a two-day time step because of the irregular nature of the fixes and frequent presence of gaps of more than one day between fixes. Attempts to use a one-day time step failed to converge. A total of 90 000 Markov Chain Monte Carlo (MCMC) samples was used, with the first 60 000 being discarded as the adaptation and burn-in phase. The remaining

**Table 1. Summary of 16 SPLASH tags deployed on juvenile male whale sharks in Cenderawasih Bay, Indonesia**

Asterisks indicate estimated total length (TL) to the nearest 0.5 m; otherwise TL was measured directly as described in Methods section. Last Argos uplink date reported in table is maximally 30 Nov. 2016 (end of study), though most of the tags continued to transmit after this date. Tag 144882 did not transmit data during the study period

PTT Argos no.	Total length (m) at time of tagging	Tag deployment date	Latitude (N)	Longitude (E)	Last Argos uplink date
144881	4.0*	29 Oct. 2015	-3.242	134.992	30 Nov. 2016
144882	4.5*	9 Jun. 2015	-3.211	134.948	n.a.
144883	4.5*	9 Jun. 2015	-3.211	134.948	24 Nov. 2016
144884	4.5*	9 Jun. 2015	-3.211	134.948	15 Aug. 2016
144885	5.6*	10 Jun. 2015	-3.211	134.948	20 May 2016
144886	7.0*	11 Jun. 2015	-3.211	134.960	24 Jun. 2016
151097	3.0*	29 Oct. 2015	-3.242	134.993	30 Nov. 2016
153664	6.0*	29 Oct. 2015	-3.225	135.018	29 Nov. 2016
153665	4.95	29 Oct. 2015	-3.242	134.993	29 Nov. 2016
153666	4.51	5 Nov. 2015	-3.242	134.993	30 Nov. 2016
158579	5.93	19 May 2016	-3.303	135.060	17 Sep. 2016
158580	4.0*	17 Feb. 2016	-3.206	134.947	30 Nov. 2016
158581	5.8	17 Feb. 2016	-3.206	134.947	30 Nov. 2016
158582	5.97	21 Feb. 2016	-3.192	134.908	02 Oct. 2016
158583	3.6	21 Feb. 2016	-3.192	134.908	21 Apr. 2016
158584	3.98	22 Feb. 2016	-3.262	135.032	30 Nov. 2016

30 000 samples were thinned to 1000 (every 30th sample) to minimise within-chain sample autocorrelation (Jonsen *et al.* 2007). Inspection of standard diagnostics plots (produced by the *bsam* function *diag\_ssm*) showed that one MCMC chain failed to converge, so the model was refitted using 130 000 MCMC samples with the first 100 000 samples being discarded. Diagnostics for the new model showed satisfactory convergence of both chains.

Values of the behavioural mode parameter *b* were used to infer which behavioural state applied to each shark at each fitted track location; *b* values range from 1 (which indicates a travelling state with high certainty) to 2 (which indicates a foraging state with high certainty). In this study, *b* values less than 1.3 were interpreted as travelling and *b* values greater than 1.7 were interpreted as foraging. Intermediate values of *b*, which suggest an uncertain behavioural state, were treated as transitional. Although these classification criteria are subjective, and the time step of the fitted model averages the movement signal across a two-day period, the *b* values were used to indicate where and when important foraging and travelling activities, and the transitions between them, occurred.

## Results

### *Movement, speed and distance*

This is the first study to analyse tracks from whale sharks satellite-tagged using a fin-mounting technique, which allows long-term deployments of 1–2 years (Hammerschlag *et al.* 2011), considerably longer than achieved in most whale shark satellite tagging studies (McKinney *et al.* 2017). Fifteen of the 16 satellite tags deployed between June 2015 and May 2016 successfully transmitted data (Table 1). The time between first and last transmissions ranged from 48 to 534 days (mean = 321 ± 33, s.e.), with a range of 0–14 transmissions per day (mean = 0.86 transmissions day<sup>-1</sup> ± 0.08, s.e.). Whale

sharks in Cenderawasih Bay are almost exclusively males (93.6%; Meyers 2017), and all tagged individuals were juvenile males (mean TL = 4.89 m ± 0.3, s.e.; range = 3–7 m) (Table 1). The tags transmitted from an area covering ~2170 km in latitude (9.14°S to 10.4°N) and ~1880 km in longitude (126.2°E to 143.1°E).

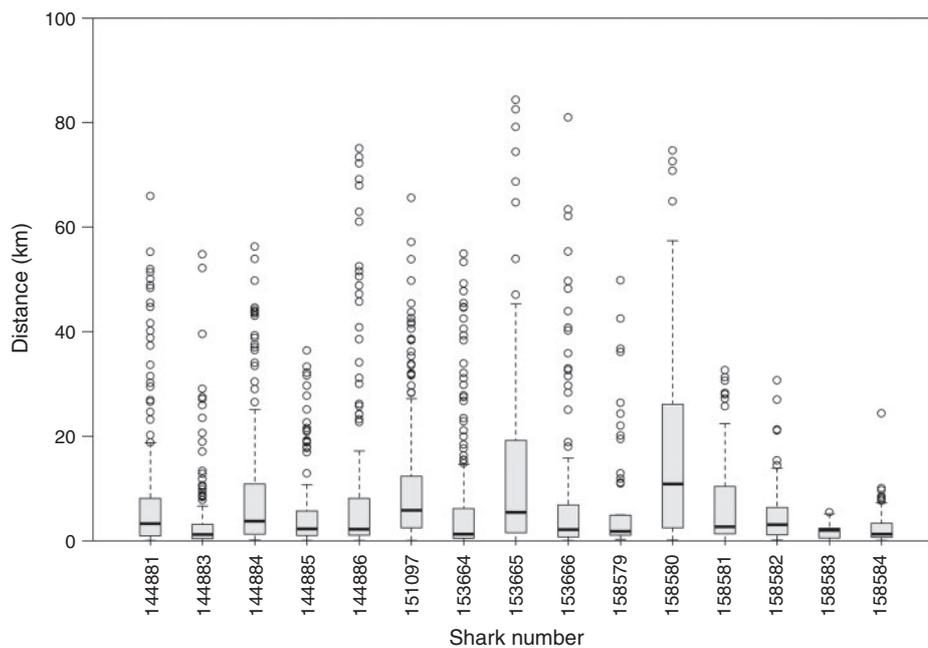
Speed and distance estimates were based on the SSSM fitted to all 15 transmitting sharks using a two-day time step (Table 2). Estimates were smoothed and interpolated, leading to an underestimation of the true values. The mean total distance covered by each shark was 2503 km (±402, s.e.; range = 100–5144 km) with median daily speeds ranging from 1.2 to 10.9 km day<sup>-1</sup> (mean = 3.3 km day<sup>-1</sup> ± 0.7, s.e.) (Fig. 3), equivalent to 0.05 to 0.45 km h<sup>-1</sup> (mean = 0.14 km h<sup>-1</sup> ± 0.03, s.e.). Most daily speeds (79%, *n* = 1897) were between 0 and 10 km day<sup>-1</sup> (see Supplementary Fig. S1 online). The displacement between tagging location and final transmission ranged from 3 to 719 km (mean = 167 ± 65, s.e.), and maximum displacements from the tagging location were 19–1636 km (mean = 597 ± 124, s.e.). Faster and more variable swimming speeds were observed outside the bay than inside the bay (Fig. 4). As movements were likely not in a straight line and our analysis only computed point to point distances, these are conservative values.

### *Movement patterns*

Sharks displayed three classes of movement patterns: staying within Cenderawasih Bay, travelling outside the bay but remaining within adjacent coastal regions, and travelling outside the bay and into deep offshore waters. Shorter tracks were restricted to Cenderawasih Bay (Fig. 5a), east of the bay hugging the Papuan coastline, and slightly north of the bay out and around Biak Island (Fig. 5b). Longer tracks moved north to Palau and the Philippines and west to Raja Ampat and continuing south into the Ceram and Arafura Seas (Fig. 5c; see Fig. 1 for locations).

**Table 2.** Summary of modelled SSSM track data for 15 male whale sharks tagged in Cenderawasih Bay, Indonesia

Tag no.	Track duration (days)	Displacement from tagging location (last position; km)	Maximum distance from tagging location (km)	Cumulative distance travelled (km)	Median daily speed (km day <sup>-1</sup> )
144881	396	7	800	3268	3.3
144883	534	25	362	1727	1.2
144884	432	719	731	3718	3.8
144885	340	13	186	1713	2.3
144886	378	103	666	3561	2.2
151097	398	534	604	4176	5.9
153664	380	14	896	2602	1.3
153665	394	36	1543	5144	5.4
153666	390	31	419	2652	2.2
158579	118	425	425	845	1.9
158580	286	553	1636	4741	10.9
158581	224	18	428	1527	2.7
158582	222	19	178	1099	3.1
158583	48	5	19	100	2.1
158584	278	3	64	676	1.3
<b>Mean</b>	321	167	597	2503	3.3
s.e.	± 33	± 65	± 124	± 402	± 0.7



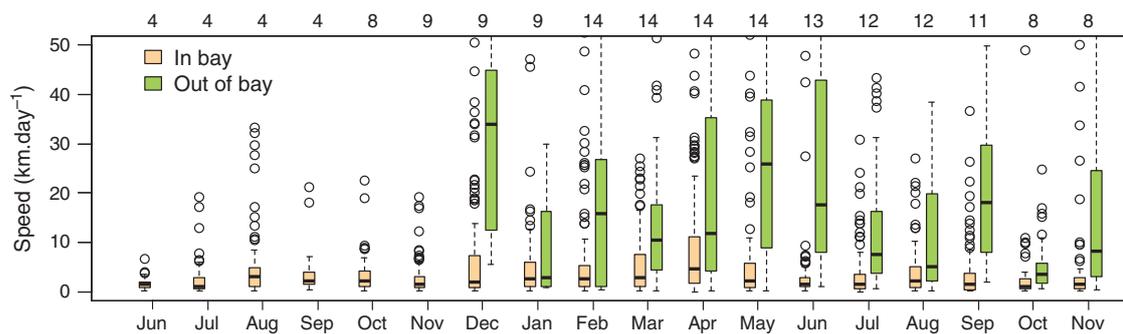
**Fig. 3.** Daily distance travelled by 15 male whale sharks in Cenderawasih Bay, Indonesia. The central black bar indicates the median, the box spans the first and third quartiles, and the whiskers extend to the most extreme data point (no more than 1.5 times the interquartile range from the box). Circles indicate outliers.

*Within and near Cenderawasih Bay*

Of the 15 tagged sharks, seven remained within Cenderawasih Bay, or moved only slightly outside it (Fig. 5a). Four remained completely within the bay for the duration of the study, travelling a mean distance of 897 km (±340, s.e.), with a mean median speed (hereafter referred to as mean speed) of 2.2 km day<sup>-1</sup> (±0.38, s.e.). The shortest movement was by shark 158584, which remained within the bay throughout its 278-day

transmission time (travelling only 676 km). One shark, tag 158583, had a short transmitting time of 48 days; when eliminated from distance calculations, the remaining three sharks travelled a mean distance of 1162 km (±259, s.e.) with a mean speed of 2.3 km day<sup>-1</sup> (±0.45, s.e.).

The remaining three sharks stayed within the bay for most of the study but took brief forays outside the bay boundaries (mean percentage of time spent out of bay = 8.3 ± 4.0%, s.e., mean



**Fig. 4.** Speed estimates for 15 male whale sharks inside and outside of Cenderawasih Bay, Indonesia, from June 2015 to November 2016. Some data are truncated at the top of the plot. Numbers on the top axis are the total number of sharks tracked each month. See Fig. 3 caption for key to boxplots.

number of days spent out of bay =  $9.3 \pm 4.4$ , s.e.) and travelled a mean distance of 1366 km ( $\pm 267$ , s.e.).

#### Coastal

Two sharks (144886 and 153664) moved south-east along the coast and one shark (153666) travelled west along the coast of West Papua towards Raja Ampat (Fig. 5b). These three sharks travelled a mean distance of 2938 km ( $\pm 312$  km, s.e.) and a mean travel speed of  $1.9 \text{ km day}^{-1}$  ( $\pm 0.3$ , s.e.).

#### Offshore

Five of 15 sharks embarked on long-distance movements (Fig. 5c); three (144884, 151097, and 158580) travelled north-west (one as far north as Mindanao in the Philippines, Fig. 1), then south into the Ceram and Arafura Seas; the other two (144881 and 153665) travelled north into Palauan waters before returning to Cenderawasih. The horizontal distances travelled by these sharks ranged from 3268 km to 5144 km (mean = 4209 km  $\pm$  436, s.e.) with mean speeds ranging from  $3.3 \text{ km day}^{-1}$  to  $10.9 \text{ km day}^{-1}$  (mean =  $5.9 \text{ km day}^{-1} \pm 1.7$ , s.e.). The longest track was 5144 km (tag 153665, 5 m TL) over 394 days (Fig. 5c). This shark travelled north to near the southern end of the Mariana Trench and west towards Raja Ampat before ending back in Cenderawasih Bay.

#### Movements in and out of Cenderawasih Bay

Over the course of this study, 11 sharks travelled outside the bay; eight departed the bay between late March and early May 2016; two of the remaining three departed in December 2015, and one left in September 2016 (see Supplementary Fig. S2 online). Three of these 11 sharks (27%; tag numbers: 144884, 151097, 158580) did not return to the bay by the time this study concluded in November 2016. For all 15 sharks,  $\sim 78\%$  of the time was spent in the bay. Mean times spent inside and out of the bay were  $125 \pm 16$  (s.e.) days (range = 25–262 days) and  $36 \pm 11$  (s.e.) days (0–114 days), respectively. Mean displacement from tagging position was highest April through July, with a peak in May of  $\sim 350$  km (Supplementary Fig. S2). Departure date did not appear to be related to the size of the shark (Pearson's correlation coefficient  $r = -0.37$ ,  $P = 0.21$ ); however, smaller sharks returned to the bay later than larger sharks ( $r = -0.83$ ,  $P = 0.005$ ).

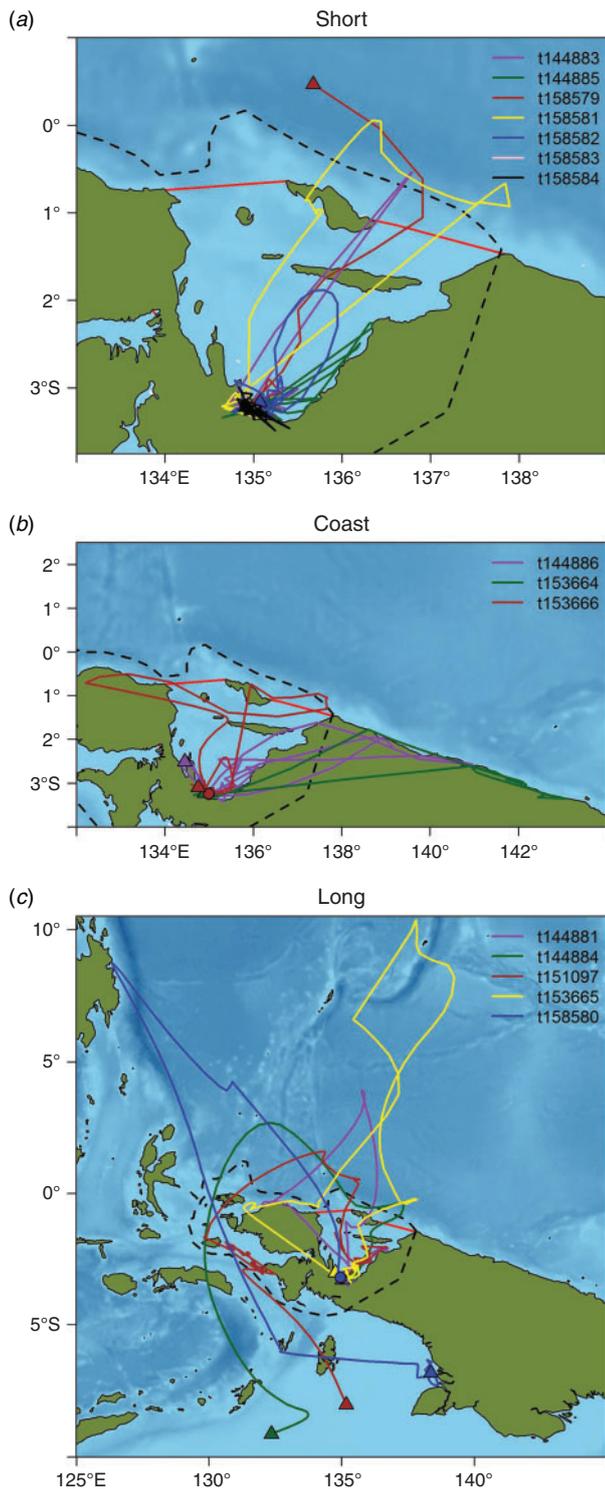
#### Behavioural states

Area-restricted searching (ARS, indicative of feeding-related or foraging behaviour, noting the aforementioned limitations of this classification) (mean = 80.7%; range = 49.3–100%) and travelling (mean = 11.0%; range = 0–24.2%) were the predominant behavioural states in Cenderawasih Bay and in coastal areas located around West Papua and Papua New Guinea, though 8.7% of data points were classified as transitional (Fig. 6). Foraging occurred in waters between  $11^\circ\text{N}$  and  $8^\circ\text{S}$ , with a band of concentrated activity between  $1^\circ\text{N}$  and  $3^\circ\text{S}$ . Travelling occurred over approximately the same areas with a concentration between  $4^\circ\text{N}$  and  $3^\circ\text{S}$ . Foraging occurred mainly in shallow water over the continental shelf, while travelling occurred over deeper water beyond the edge of the continental shelf. The interquartile ranges of seabed depths for foraging and travelling states were 10–118 m and 212–4011 m respectively (see Supplementary Fig. S3 online). Transitional values were spread across the full depth range for both foraging and travelling locations but were generally intermediate between the two.

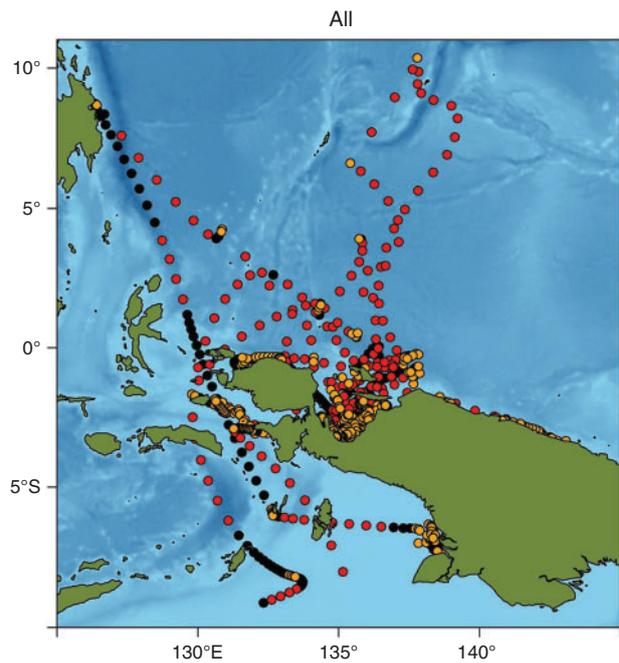
Median chlorophyll-*a* concentrations were highest for foraging locations ( $0.43 \text{ mg m}^{-3}$ ), intermediate for transitional locations ( $0.31 \text{ mg m}^{-3}$ ) and lowest for travelling locations ( $0.21 \text{ mg m}^{-3}$ ), although the interquartile ranges overlapped considerably (see Supplementary Fig. S4 online). This suggests that the whale sharks spent more time foraging in more productive areas.

#### Discussion

Previously, whale sharks in Cenderawasih Bay were suggested to be highly mobile and transient (Tania *et al.* 2016). Our long-term tag deployments reveal that while some whale sharks travel outside the bay, others remain within the bay year-round. Furthermore, the majority (67%) had their last position within the bay and close to their original tagging positions. As all of the sharks in this study were tagged within the bay, there is an unavoidable bias as these individuals may favour remaining in or returning to the bay. It is tempting to suggest that movements out of the bay may relate to reproduction or mate searching as they near maturation (Hueter *et al.* 2013); however, several of the smaller, clearly immature sharks also made movements outside the bay. Our largest shark, a 7-m male (tag 144886), and presumably the closest to maturation (males have been reported as mature at  $>8$  m TL: Norman and Stevens 2007) remained



**Fig. 5.** SSSM tracks of 15 whale sharks tagged in Cenderawasih Bay, Indonesia showing: (a) tracks that remained in and near Cenderawasih Bay ( $n = 7$  sharks), (b) coastal tracks ( $n = 3$ ) and (c) offshore tracks ( $n = 5$ ). Red line (grey dotted line in the print version) indicates bay boundary; dashed black line indicates Bird's Head Seascape boundary; circles are tagging locations (all in southern Cenderawasih Bay); triangles are last known positions (as of 30 November 2016). Tracks are drawn using straight lines between modelled locations and, as such, occasionally appear to indicate movement over land.



**Fig. 6.** Behavioural state estimates for all tagged whale sharks red (grey in the print version), travelling; black, transitional; orange (white in the print version), foraging obtained from the SSSM for all whale sharks tagged in Cenderawasih Bay, Indonesia. Data range from June 2015 to November 2016.  $n = 2424$  data points.

within the bay for most of the study period. In other locations, sharks aggregate seasonally, usually in response to a predictable food source (Colman 1997; Heyman *et al.* 2001; Stewart and Wilson 2005). The higher food availability near river mouths along the northern New Guinea coastline and especially within Cenderawasih Bay may be a primary factor influencing whale shark movements in this area.

With foraging opportunities outside of the bay, the choice to remain may indicate more favourable prey availability within the bay. Indeed, the year-round presence of a large fleet of bagan fishing vessels in this region is a clear indication of the dense schools of baitfish that are consistently found in this area. These baitfish in turn seem to be drawn to this area by the rich organic inputs from a large number of mangrove-lined rivers and streams that form estuaries along this coastline. The whale sharks in Cenderawasih Bay seem to be targeting these same year-round aggregations of small fish as the bagan fishing boats do, and older fishermen interviewed recall whale sharks beaching themselves chasing shoals of fish as early as the 1940s. Site fidelity in whale sharks has been similarly reported in other areas with abundant foraging opportunities (Araujo *et al.* 2014; Rohner *et al.* 2015; Cagua *et al.* 2015; Thomson *et al.* 2017; McCoy *et al.* 2018). Immature or non-breeding animals' movements are typically driven by food availability or habitat stability (Baker 1978), and thus if these sharks have a relatively constant food source available (as evidenced by high levels of ARS-foraging), staying in the bay and not expending energy on travel may be the best option for optimal growth and/or survival.

Three sharks exhibited an interesting pattern of nearshore movement along the Papuan coastline, with extended periods

spent close to river mouths. We presume they were feeding in seasonally productive waters associated with these estuaries. Seasonal feeding aggregations of whale sharks near river mouths have also been reported elsewhere; the largest known whale shark aggregation in South-east Asia is at Donsol, Philippines, where sharks aggregate near two large river mouths (McCoy *et al.* 2018). Similarly, whale sharks have been observed in feeding aggregations near the Mississippi River mouth, USA, in association with recently spawned little tunny, *Euthynnus alletteratus*, eggs (Hoffmayer *et al.* 2005), and in nearshore coastal areas in Madagascar (Diamant *et al.* 2018) and Mozambique (Rohner *et al.* 2018).

West Papuan sharks foraged near the mouths of the Mamberamo, Apauwar, Memberamo, Sermowai, Nemeyar, Digul, and Sepik Rivers (Fig. 1) along the coastline of New Guinea. During the wet season, outflow from these rivers dramatically increases, driving an increase in suspended nutrients (primarily phosphates and nitrates) at the coast (Mughtar 2004). Strong currents from the east push these nutrients farther west and closer to the opening of Cenderawasih Bay, where whale sharks forage. Most of the fish schools in this area are found near the continental slope and east of the Mamberamo river mouth (Genisa 2000), which again may explain why the whale sharks are frequenting this area.

It is commonly observed that when river outflow volume increases (e.g. during the monsoon season and other heavy rainfall events), a clear frontal boundary develops between a river plume and nearby marine waters (Le Fevre 1987) supporting increased planktonic and nektonic organisms, including larval fishes (Grimes and Finucane 1991; Olson *et al.* 1994). Frontal boundaries and river plumes are recurrent and often spatially predictable, potentially providing a reliable food source for plankton-consuming species. Approximately 70 fish species are found in the Mamberamo River plume, which likely indicates a high level of productivity (Mughtar 2004). Whale sharks feed elsewhere in high-productivity areas such as at fish- and coral-spawning grounds (Colman 1997; Taylor and Pearce 1999; Heyman *et al.* 2001), and plankton blooms (Motta *et al.* 2010; Rohner *et al.* 2013a, 2018), and they may be targeting these river plumes for feeding. Basking sharks, another filter-feeding shark, are not indiscriminate planktivores, but often choose the richest plankton patches associated with thermal fronts (Sims and Quayle 1998) and hotspots of productivity (Sims *et al.* 2003; Sims 2008). We suggest that whale sharks are likely behaving in a similar manner, travelling to river mouths during productive times to take advantage of rich prey patches.

One-third of the tagged sharks embarked on long-distance, offshore movements, with four out of five doing so during March–May (the boreal spring). The New Guinea Coastal Undercurrent (NGCUC) begins flowing in April and extends westward in the summer, similar to the near-surface monsoon-controlled South Equatorial Current also observed at this time (Prentice and Hope 2007; Wijeratne *et al.* 2018). During this time of year, a major current reversal occurs north of Cenderawasih Bay, potentially influencing whale shark movements. The sharks' oceanic movements suggest the influence of boundary currents (Rowat and Gore 2007) and bathymetry (Hsu *et al.* 2007), which may be correlated with the NGCUC current, bringing nutrient-rich, biologically productive water farther

offshore during this period of current reversal (Wijeratne *et al.* 2018). Whale sharks tagged at Ningaloo Reef, Australia, seem to respond to the Southern Oscillation Index (El Niño and La Niña), wind shear (Sleeman *et al.* 2010) and the along-shelf currents that resuspend nutrients and create a pulse of productivity that the sharks feed on. Additional work is needed in West Papua to determine the role of currents in whale shark seasonal distribution.

Three out of five sharks that exited the bay were observed on the south coast of the island of New Guinea near the Arafura Sea at the conclusion of our study in November. Cold water upwelling occurs near Raja Ampat and Kaimana year-round; however, the upwelling is most intense during the south-east monsoon (May–October) when the strong southerly winds bring significantly cooler water than in Cenderawasih Bay (Mangubhai *et al.* 2012). This combination of lower SSTs and nutrient-rich upwelling may explain why these sharks had not returned to the bay by November 2016. Future work analysing multi-year tag data may reveal whether similar movement patterns are observed over longer periods, and identify the environmental variables that are most important in driving whale shark movements.

Whale sharks in this study travelled more slowly ( $\sim 3.2$  km day<sup>-1</sup>) than reported from other locations, where movement rates ranged from  $\sim 2$  to 38 km day<sup>-1</sup> (Eckert *et al.* 2002; Wilson *et al.* 2006; Hueter *et al.* 2013; Hearn *et al.* 2016; Diamant *et al.* 2018; Rohner *et al.* 2018). Sharks that remained within the bay for the duration of the study travelled shorter distances and at slower speeds than sharks that left the bay, with foraging the predominant behaviour in the bay and most travelling taking place outside of the bay and in deeper waters. Despite the apparent differences, direct comparisons of travelling speeds among studies should be made cautiously due to differences in tag technologies, and whether a study used raw or modelled locations (Hueter *et al.* 2013).

Although whale sharks are capable of travelling across ocean basins over two- to four-year cycles, many appear to remain at an aggregation site for several months to years (Sequeira *et al.* 2012). This pattern of high site fidelity (at least over several years) involving periodic return to aggregation areas has been reported from several regions (Riley *et al.* 2010; Berumen *et al.* 2014; Rohner *et al.* 2015, 2018; Norman *et al.* 2017; McKinney *et al.* 2017; Prebble *et al.* 2018). Male whale sharks tagged in Cenderawasih Bay also followed this pattern, with many returning to the bay after having made trips farther off-shore or along the shelf.

Search theory predicts that animals will switch their behavioural mode depending on the type of abiotic and biotic factors they encounter as they move throughout their range (Turchin 1991). We used filters to eliminate Argos-derived position errors (Jonsen *et al.* 2005) and a SSSM to generate smoothed, regularised tracks. SSSM classification of behavioural states indicated that the juvenile male sharks were primarily engaged in foraging or feeding-related activity (81% of their time, on average). Our definition of foraging locations and dates was based on the modelled speed of movement and changes in direction at a relatively coarse temporal scale (two-day time step). Whale sharks incur high costs associated with drag from their open-mouth feeding behaviour, and individual feeding

bouts can last several hours, adding to the energetic cost. In Yucatan, Mexico, bouts lasted up to 11 h and it was estimated that 20% of the time budget of whale sharks was spent feeding (Cade *et al.* 2020). Further work at a finer temporal scale would be required to determine what proportion of the time classified as foraging at Cenderawasih Bay was actually spent feeding, but it would likely be considerably less than 81%, even for juvenile males with higher energetic needs for growth. Despite this, sharks in this area are undoubtedly spending most of their time searching for food. In contrast, at Ningaloo Reef, Western Australia, where predictable high-density patches of krill aggregate at sunset, whale sharks had short, intense feeding periods, with their movement patterns linked to these prey patches (Gleiss *et al.* 2013). Unlike baleen whales that migrate vast distances to feed on densely aggregated prey in high latitudes, large tropical filter-feeding fish like whale sharks are unable to forage in polar waters due to their ectothermic metabolisms (Rohner *et al.* 2015) and hence face challenges in finding sufficient prey in comparatively nutrient-poor, warmer waters. This likely explains the large percentage of their time that whale sharks dedicate to foraging in Cenderawasih Bay and elsewhere (Rohner *et al.* 2015).

Fifty percent of travelling was observed over seabed depths between 212 and 4011 m, while 50% of foraging behaviour took place in shallower waters, between 10 and 118 m depth, with a clear depth-related separation between these two behaviours. Food resources in the open ocean are often more scarce and less predictable than in coastal and bay habitats (Moore *et al.* 2013), and it seems likely that whale sharks travel quickly through (deeper) areas of lower food availability and focus their foraging in more productive (shallow) locations.

Although some sharks travelled out of the bay, most were transmitting from within the bay at the conclusion of our study, highlighting Cenderawasih Bay (and the national marine park it encompasses) as a vital habitat for these sharks and a region where conservation efforts should be intensified. Though whale sharks are capable of long-distance migrations, a range of recent studies report that whale shark subpopulations appear to show strong site fidelity and limited exchange of individuals between aggregation sites that are several hundred kilometres apart (Jonsen *et al.* 2005; Norman *et al.* 2017; Diamant *et al.* 2018; Rohner *et al.* 2018), suggesting that whale shark conservation and management initiatives should be regionally focussed for maximum effectiveness (Prebble *et al.* 2018). Although we do not yet fully understand whale shark movements and the factors influencing them in this region, our analysis of 15 tagged sharks has allowed us to identify three primary movement types within the Cenderawasih Bay aggregation: within and near bay, coastal, and offshore movements. However, even within these primary categories, a considerable amount of individual variability was observed; a similar pattern of variability was also recently reported for whale sharks tagged off western Madagascar (Diamant *et al.* 2018). This suggests that although environmental factors and especially food availability may be primarily responsible for these movements, they may not be the only factors driving whale shark movement behaviour and spatial distribution. Since completing this study, an additional 38 whale sharks have been fin-mount tagged in eastern Indonesian waters. Our ongoing analyses of the rich dataset provided

by these 53 tagged whale sharks will further elucidate broad-scale movement patterns in the region and the individual movement variability among sharks. This will undoubtedly provide a wealth of conservation and management recommendations to marine resource managers in West Papua, Papua New Guinea, Palau, the Philippines and potentially other nearby countries.

### Conflicts of interest

The authors declare no conflicts of interest.

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