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Population structure and residency of whale sharks *Rhincodon typus* at Utila, Bay Islands, Honduras

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There were 479 reported whale shark *Rhincodon typus* encounters between 1999 and 2011 at the island of Utila, which forms part of the Meso-American Barrier Reef System (MBRS) in the western Caribbean Sea. The majority of *R. typus* were found to feed on small bait fish associated with various tuna species. Ninety-five individual *R. typus*, ranging from 2 to 11 m total length (L_T), were identified through their unique spot patterns. A significant male bias (65%) was present. There was no significant difference between the mean \pm s.d. L_T of female (6.66 ± 1.65 m) and male (6.25 ± 1.60 m) *R. typus*. Most *R. typus* were transient to Utila, with 78% sighted only within a single calendar year, although some individuals were sighted in up to 5 years. Mean residency time was modelled to be 11.76 days using maximum likelihood methods.

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Key words: Atlantic; movement; philopatry; sexual segregation; site fidelity.

INTRODUCTION

The whale shark *Rhincodon typus* Smith 1828 is a very large, highly mobile species found in tropical and subtropical seas worldwide (Rowat & Brooks, 2012). Despite their broad distribution, there are only a small number of locations in which they are predictably found on an interannual basis. *Rhincodon typus* are thought to feed primarily on zooplankton and small fishes, and they are most frequently observed during ephemeral bursts of high biological productivity such as fish spawning events (Heyman *et al.*, 2001; Hoffmayer *et al.*, 2007; de la Parra Venegas *et al.*, 2011; Robinson *et al.*, 2013) or major zooplankton blooms (Motta *et al.*, 2010; Ramírez-Macías *et al.*, 2012a).

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At least some *R. typus* show fidelity to specific locations, often on an annual or semi-annual basis (Graham & Roberts, 2007; Holmberg *et al.*, 2008, 2009; Rowat *et al.*, 2011), which can render them relatively susceptible to even small-scale fisheries. *Rhincodon typus* were classified as Vulnerable on the IUCN Red List of Threatened Species following their regional depletion in the Indian and western Pacific Oceans by targeted fisheries in India, Taiwan and the Philippines until the late 1990s and 2000s (Norman, 2005). Although a contemporary fishery may be active off mainland China (Li *et al.*, 2012), many countries have recognized the value of live specimens as a draw for marine tourists (Davis *et al.*, 1997; Pierce *et al.*, 2010; Gallagher & Hammerschlag, 2011).

Rhincodon typus tourism is a popular activity along the Meso-American Barrier Reef system (MBRS), which extends to the west and north for c. 1000 km along the coasts of Guatemala, Belize and México within the western Caribbean Sea. Utila, Roatán and Guanaja comprise the Bay Islands of Honduras, which form the southern section of the MBRS. The oceanography of this area is highly dynamic, with variation in the major Caribbean Current and the propagation of eddies affecting local-scale currents and temperature along the MBRS (Ezer *et al.*, 2005; Lin *et al.*, 2011). There is high oceanographic and ecological connectivity within the MBRS, with larval dispersal (Paris *et al.*, 2007) and river plumes (Chérubin *et al.*, 2008; Soto *et al.*, 2009) noted to move through the entire area. *Rhincodon typus* are found throughout the MBRS. Major feeding areas have been described in Belize at Gladden Spit, where *R. typus* aggregate around full moon periods within the months of March to May to feed on lutjanid spawn (Heyman *et al.*, 2001; Graham & Roberts, 2007), and off the state of Quintana Roo on the Yucatan Peninsula of México where *R. typus* aggregate inshore to feed on zooplankton blooms (Motta *et al.*, 2010; Ramírez-Macías *et al.*, 2012a) and offshore to feed on tuna eggs (de la Parra Venegas *et al.*, 2011). Large *R. typus* aggregations have also been noted to occur in the northern Gulf of México (Hoffmayer *et al.*, 2005, 2007; McKinney *et al.*, 2012).

The island of Utila is a popular scuba diving destination, with *R. typus* as one of its major attractions. While the regular presence of *R. typus* at the island is well known (Gifford *et al.*, 2007; Graham, 2007), and they are specifically protected by national legislation (Graham, 2007), little focused work has been conducted on the species in Honduran waters. Two *R. typus* were tracked using tethered tags in 1999, both of which travelled away from Utila to Belizean waters and the Gulf of México, respectively (Gifford *et al.*, 2007). The characteristic spots on *R. typus* lend themselves to photographic identification, as they are individually distinct and long lasting (Marshall & Pierce, 2012), providing an opportunity for collaboration with tourism.

Present data are analysed from contributed *R. typus* photograph submissions from citizen scientists visiting Utila to the ECOCEAN Global Whale Shark Library (www.whaleshark.org) and a dedicated photo-identification programme (www.utilawhalesharkresearch.com) aiming to describe the population structure of *R. typus* sighted from the island. A modified maximum likelihood approach (Whitehead, 2001) was used to compare these data against residency models to investigate the dynamics of *R. typus* movement patterns. These statistical models have been used previously for *R. typus* (Ramírez-Macías *et al.*, 2012b), reef manta rays *Manta alfredi* (Krefft 1868) (Deakos *et al.*, 2011) and a number of marine mammal species (Whitehead, 2001; Wimmer & Whitehead, 2005; Parra *et al.*, 2006;

Dulau-Drouot *et al.* 2012). This approach is particularly valuable for opportunistic sighting data, such as photographic mark–recapture, as it uses re-identification data itself to determine the spatial and temporal distribution of effort. This is useful for this type of dataset, where only positive sighting data have been reported by contributors working in conjunction with the tourism industry.

MATERIALS AND METHODS

STUDY SITE AND DATA COLLECTION

The island of Utila, Honduras, is located 30 km north of the mainland near the edge of the continental shelf, with depths increasing steeply to 1000 m *c.* 6 km from the north coast (Fig. 1). Fringing coral-reef systems ring the island, which is 13 km in length. Dedicated vessel-based surveys, conducted from March 2001 to April 2011, circuted the island between *c.* 100 and 2000 m from shore while observers searched visually for *R. typus* swimming near the surface or other evidence of marine animal activity.

Once located, each *R. typus* position was recorded with either global positioning system (GPS) equipment or through visual reference to features on the island. Snorkelers entered the water to estimate *R. typus* total length (L_T), either visually or by calculating it through reference to a measuring stick. As there is a known error associated with visual estimates (Rohner *et al.*, 2011), mean L_T was used when multiple encounters were recorded from a single *R. typus*. In a small number of cases these estimates showed considerable variation between observers. Where there was a difference of ≥ 3 m between two L_T estimates, the L_T of those individuals ($n = 2$) were not included in results or further analysis. Where more than two estimates were available, any measurement differing by ≥ 3 m was treated as an outlier and was not included in the calculation of mean L_T . The sex of each *R. typus*, and maturity in males, were determined through the presence (and calcification) or absence of claspers (Norman & Stevens, 2007). Obvious external scars were noted and photographed, and behavioural observations on the *R. typus* and associated fauna were recorded.

Identification photographs were taken for submission to the ECOCEAN Whale Shark Library, from which an individual identity was obtained. Individuals were first identified from a high-quality photograph of the left flank only, to avoid the possibility of double-counting *R. typus*, although right-side photographs were also obtained from the same *R. typus* where possible (Arzoumanian *et al.*, 2005; Holmberg *et al.*, 2008). Re-identifications could then be made from either left or right-side photographs when the latter were associated with a known individual. There were no obvious behavioural responses by *R. typus* to observers that would compromise collection of in-water data. Additional encounter and photographic data were made available to the study through public and researcher submissions to the library dating from January 1999. These external sighting data were similar in terms of information collected and were combined with data collected by the authors.

DATA ANALYSIS

Sex bias among identified *R. typus* was evaluated using a χ^2 -test to assess deviation from an assumed 1:1 male to female ratio ($n = 63$), and a *t*-test was used to compare the mean L_T between the sexes ($n = 60$). The seasonality of *R. typus* presence was assessed using only sightings of identified *R. typus* to avoid the inclusion of repeated encounters with the same individual.

Sighting data from identified *R. typus* were also used to assess the lagged identification rate (R_{LI}), the probability of re-identifying *R. typus* over increasing time periods, here measured in days (Whitehead, 2001). A plot of R_{LI} through time was produced for all identified *R. typus* to provide insight into the residency characteristics of individual *R. typus* around Utila over the duration of the study. A R_{LI} plot showing a steep decline after a certain time lag, then levelling off above zero for a longer time lag, as noted in previous elasmobranch studies (Deakos *et al.*, 2011; Ramírez-Macías *et al.*, 2012b), would suggest that: (1) many *R. typus* leave Utila

after residing in the area for a certain time, while (2) some *R. typus* remain resident and (3) some *R. typus* return to the study area (Whitehead, 2001). Exponential models, representing a closed population and populations where various combinations of emigration, re-immigration and mortality (including permanent emigration) were present, were fitted to empirical R_{LI} data as in Whitehead (2001). Data were bootstrapped 100 times to generate s.e. for both R_{LI} results and parameter estimates for fitted models. These analyses were conducted using the movement module in SOCPROG 2.4 (Whitehead, 2009) and compared using the quasi-Akaike information criterion (QAIC) to account for over-dispersion of data (Whitehead, 2007).

RESULTS

RHINCODON TYPUS SIGHTINGS AND SEASONALITY

All Honduran *R. typus* sightings reported to the ECOCEAN database, with the exception of three from Roatán (one with GPS location data) and one from half-way between Roatán and Utila, were from Utila. A total of 479 *R. typus* sightings were recorded from Utila between January 1999 and April 2011, most of which were from the northern side of Utila which is close to the edge of the continental shelf. There were associated GPS data for 118 sightings (Fig. 1). Including those with text descriptions of locations, more than half (55%) of the sightings were reported from the north-eastern corner of the island. A total of 211 encounters were identifiable to individual *R. typus*. Following removal of repeated encounters with the same *R. typus* within a single calendar month, data were summarized to present the number of unique monthly sightings of each individual ($n = 148$, encounters of 95 individual *R. typus*; Fig. 2). Sightings were recorded in all months, with the peak number of unique encounters in March and April (47.3% of the total), although a positive bias in sighting reports (*i.e.* non-sightings were not recorded) meant that standardizing for effort was not possible.

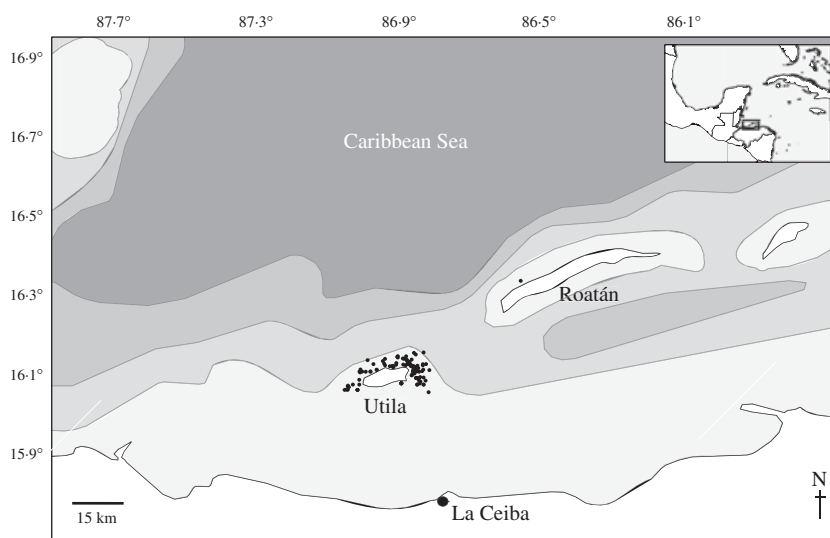


FIG. 1. The Utila study site, with all recorded GPS locations for *Rhincodon typus* sightings (●). □, 0–199 m; ■, 200–999 m; ■, 1000–1999 m; ■, >2000 m.

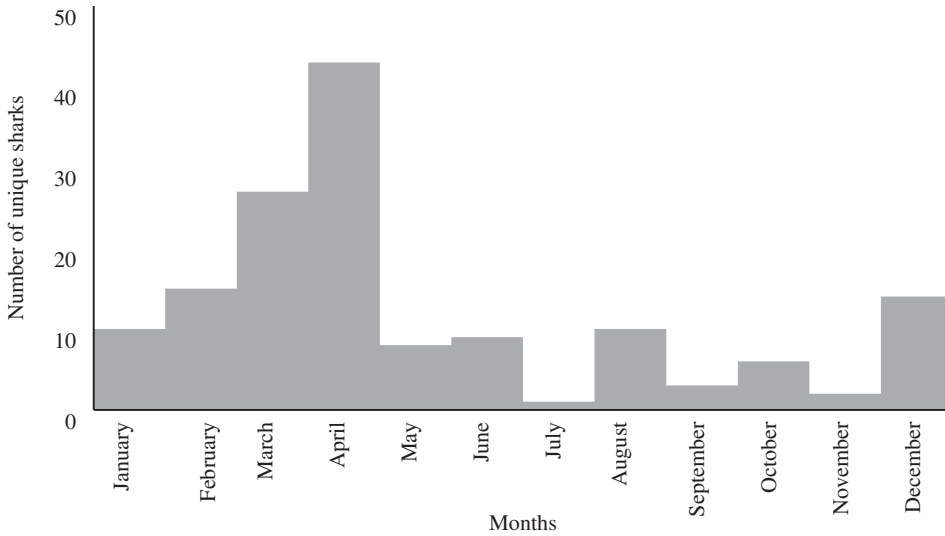


FIG. 2. *Rhincodon typus* sightings at Utila by month (2001–2011).

Rhincodon typus were found free-swimming at the surface on a small number of occasions, but were most regularly encountered while feeding alongside or among actively feeding schools of tuna (Fig. 3). These boils of intense surface disturbance were located by observing tunas jumping and birds flying in tight circles over patches of water. *Rhincodon typus* were usually present at boils dominated by blackfin tuna *Thunnus atlanticus* (Lesson 1831) and occasionally by little tunny *Euthynnus alletteratus* (Rafinesque 1810) and skipjack tuna *Katsuwonus pelamis* (L. 1758). *Rhincodon typus* were observed feeding on larval fishes and bait fishes at these events, either vertical suction-feeding at stationary boils or surface ram-feeding at mobile boils. Bait fishes were often observed to congregate around the feeding *R. typus* in an apparent attempt to avoid predators, with the *R. typus* then becoming the focal point of the feeding activity. Up to three *R. typus* were reported within single boils. These boils were also generally attended by white terns *Gygis alba* and often brown boobies *Sula leucogaster*. Silky sharks *Carcharhinus falciformis* (Müller & Henle 1839), *Mobula* rays, bottlenose dolphins *Tursiops truncatus*, spinner dolphins *Stenella longirostris*, pilot whales *Globicephala macrorhynchus*, killer whales *Orcinus orca* and billfishes (Istiophoridae) were also present on occasion.

POPULATION STRUCTURE

Ninety-five individual *R. typus* were identified between February 2001 and April 2011. Twenty-two were female, 41 male (including at least four mature individuals) and 32 were of unknown sex. There was a significant male bias within *R. typus* of known sex ($\chi^2 = 2.93$, $P < 0.05$). Estimated L_T of these *R. typus* ranged from 2.0 m to 11.0 m overall, with females ranging from 3.6 m to 9.6 m L_T (mean \pm s.d. 6.66 ± 1.65 m, $n = 22$) and males from 2.0 m to 10.6 m L_T (mean \pm s.d. $6.66 \pm 6.25 \pm 1.60$ m, $n = 38$) (Fig. 4). There was no significant



FIG. 3. (a) Tuna boil with feeding *Rhincodon typus* at surface (in circle) and (b) underwater view of vertically suction-feeding *R. typus* at a boil.

difference between the estimated mean L_T of females and males ($t = 0.933$, 58 d.f., $P > 0.05$). Large propeller scars were noted on three *R. typus* (Fig. 5).

SITE RESIDENCY AND LAGGED IDENTIFICATION RATE

Seventy-four *R. typus* (78%) were sighted only within a single calendar year, while four were seen in two consecutive years. The number of new *R. typus* identified per year showed no asymptote (Fig. 6), indicating an open population within the study period. Several *R. typus*, however, were sighted in 2 ($n = 12$), 3 ($n = 5$), 4 ($n = 2$) or 5 years ($n = 2$) over the duration of the study (12 years), indicating some fidelity to Utila. The longest time between re-sightings of an individual *R. typus* was 2597 days, between 24 February 2004 and 5 April 2011, for a 7 m male.

There was a rapid decrease in R_{LI} between 1 and 16–31 (mean 22.6) days, after which the rate levelled out at slightly above zero for the remainder of the study. There was a slight increase between 256 and 511 (mean 374.8) days, suggesting a near-annual periodicity in some *R. typus* (Fig. 7). Of eight models fitted to the data (Table I), QAIC results indicated that H (emigration + re-immigration + mortality)

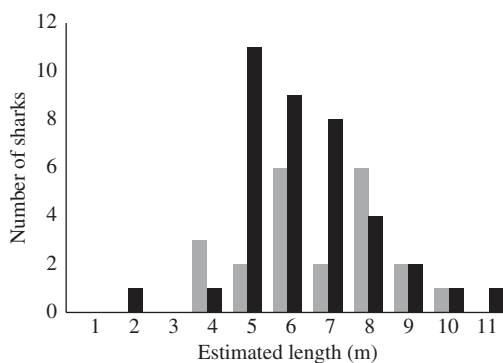


FIG. 4. Total length (L_T) frequency of individually identified *Rhincodon typus* at Utila (■, female; ■, male).

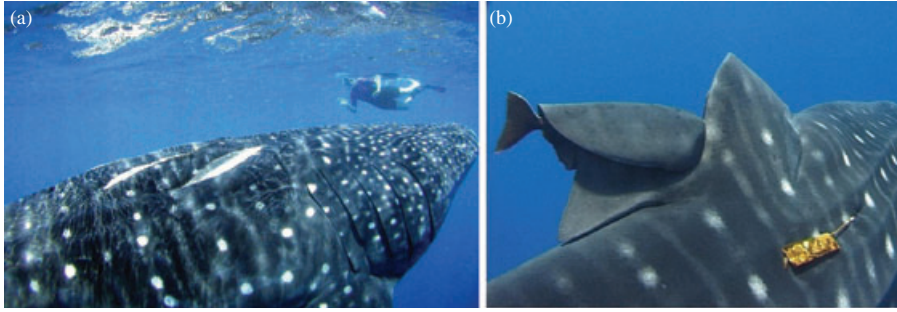


FIG. 5. Examples of propeller damage to *Rhincodon typus* from Utila: (a) large parallel lacerations on dorsal surface and (b) cuts on first dorsal fin.

provided the best representation of reality. Estimates of mean population size and residence times from this model indicate that $\text{mean} \pm \text{s.e.} = 4.63 \pm 1.07$ (95% C.I. 3.62–7.55) *R. typus* were in the study area at any one time, residing within the area for $\text{mean} \pm \text{s.e.} = 11.76 \pm 4.54$ (95% C.I. 5.82–23.68) days. They were then absent from the study area for 86.00 ± 141.16 (95% C.I. 32.89–495.82) days with a $\text{mean} \pm \text{s.e.}$ mortality and permanent emigration rate of 0.0008 ± 0.0003 (95% C.I. -1.80×10^{-5} to 0.001).

DISCUSSION

The northern coast of Utila is a hotspot for *R. typus* sightings within the southern MBRS. Ninety-five individual *R. typus* were identified over the 12 years from 1999 to 2011, with a significant bias towards juvenile males. Few very small (<3 m) or large (>10 m) individuals were present. On the basis of these photographic re-sightings,

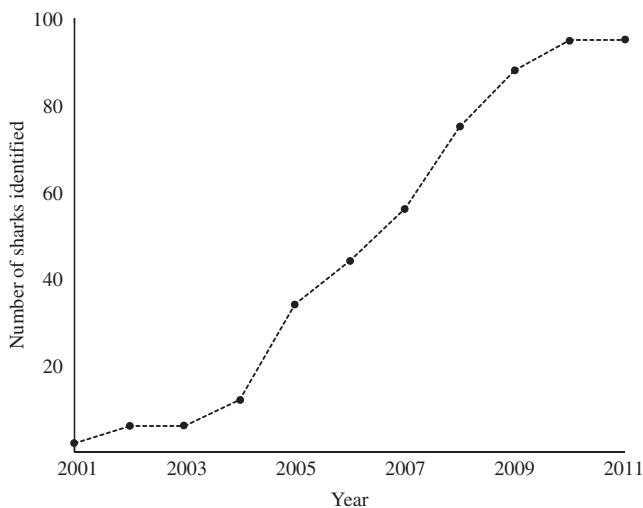


FIG. 6. Discovery curve for newly identified *Rhincodon typus* at Utila (2001–2011).

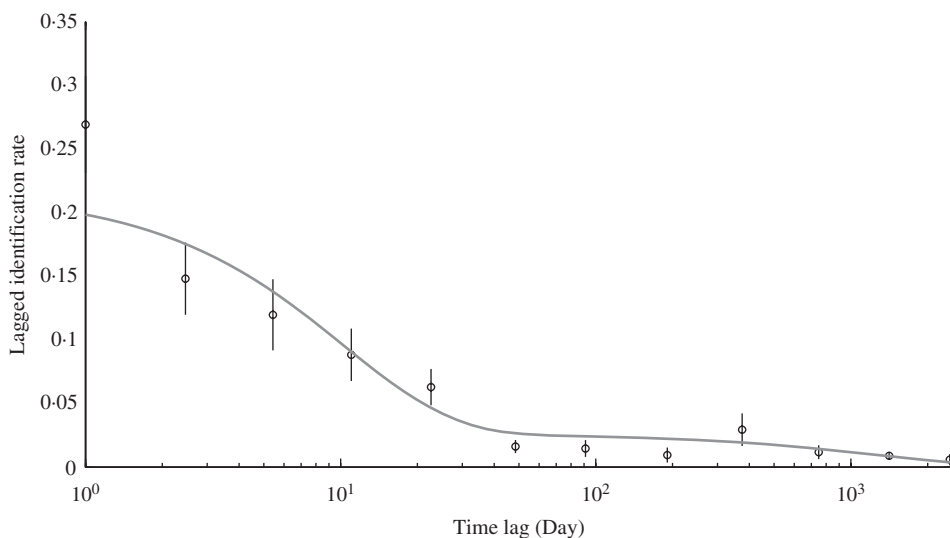


FIG. 7. Mean \pm s.e. lagged identification rate, the probability of re-identifying *Rhincodon typus* over increasing time periods, for *R. typus* at Utila, with fitted emigration + re-immigration + mortality model (—).

most *R. typus* are transient or short-term residents of the Utila coast, with a modelled mean residency time of *c.* 12 days. A smaller number of individuals did, however, demonstrate longer-term fidelity to the island, with re-sightings taking place up to 7 years apart. Given the importance of marine tourism to the local economy, adherence to an effective code of practice to mitigate any negative impacts on swimmer

TABLE I. Model comparisons for lagged identification rate of *Rhincodon typus*

Model	Scenario	Δ QAIC
A	Closed ($a1^{-1} = N$)	77.58
B	Closed ($a1 = N$)	77.58
C	Emigration and mortality ($a1$ = emigration rate; $a2^{-1} = N$)	30.29
D	Emigration and mortality ($a1 = N$; $a2$ = mean residence time)	8.45
E	Emigration + re-immigration ($a1$ = emigration rate; $a2(a2 + a3)^{-1}$ = proportion of population in study area at any time)	30.29
F	Emigration + re-immigration ($a1 = N$; $a2$ = mean time in study area; $a3$ = mean time out of study area)	12.17
G	Emigration + re-immigration + mortality	8.45
H	Emigration + re-immigration + mortality ($a1 = N$; $a2$ = mean time in study area; $a3$ = mean time out of study area; $a4$ = mortality rate)	0.00

QAIC, quasi-Akaike information criterion; N , population size within the study area.

and boat interactions with *R. typus* is likely to benefit future encounters with these returning individuals (Quiros, 2007; Pierce *et al.*, 2010).

In contrast to other *R. typus* hotspots on or adjacent to the MBRS, Utila is characterized by a lack of well-defined seasonality and pronounced year-to-year variation in peak *R. typus* abundance. Instead, *R. typus* sightings at Utila are closely linked to the presence of feeding *T. atlanticus*. The same association has been noted off the coast of Belize (Baughman, 1955; Graham & Roberts, 2007). Anecdotal reports from skippers and dive operators indicate that the presence of tuna schools off Utila is similarly aperiodic. The oceanographic environment of the western Caribbean is dynamic, being influenced by meanderings of the Caribbean Current and the propagation of eddies (Ezer *et al.*, 2005; Paris *et al.*, 2007) that have been suggested to affect *R. typus* sightings in other locations (Rohner *et al.*, 2013). The pronounced difference in sighting frequency between Utila and Roatán, which have a high oceanographic connectivity (Soto *et al.*, 2009), suggest that other factors may also influence local abundance as happens in Western Australia (Sleeman *et al.*, 2010) and the Seychelles (Rowat *et al.*, 2009). Further exploration of the drivers of regional *R. typus* abundance, coupled with regular sampling to standardize sightings per unit effort, is likely to be informative.

Rhincodon typus feeding behaviour is plastic and varies depending on the type and behaviour of prey species. In Utila, the majority of encounters were of *R. typus* feeding on the surface among tuna schools, utilizing either vertical suction-feeding or ram filter-feeding while moving with the tuna school. Few encounters with non-feeding *R. typus* were reported, although *R. typus* swimming near the surface should have been readily visible during boat-based searches if they were present due to the normally calm, sunny conditions. While most tagging studies have shown that *R. typus* spend a significant proportion of their time at the surface (Rowat & Brooks, 2012), individual *R. typus* change their behaviours in different habitats (Brunnschweiler *et al.*, 2009; Brunnschweiler & Sims, 2011). Satellite-tagged *R. typus* from Utila were shown to repeatedly dive to 320 m depth (Gifford *et al.*, 2007), and *R. typus* tagged at Gladden Spit, Belize, spent the greatest proportion of their time in 50–250 m depths (Graham *et al.*, 2006). It is possible that the noise produced by feeding *T. atlanticus*, which regularly jump while they prey on zooplankton, attracts the *R. typus* to the surface. *Rhincodon typus* have the largest known inner ear of any animal, theoretically optimized for long wavelength, low-frequency sounds (Myrberg, 2001; Rowat & Brooks, 2012). Some of the larger boils are >100 m in diameter and created by thousands of feeding *T. atlanticus*, which create significant noise underwater. *Rhincodon typus* were less regularly associated with boils of other tuna species, which do not jump as regularly.

The size structure and sex ratio of *R. typus* identified at Utila were similar to those observed in Belize, México and northern Gulf of Mexico waters (Hoffmayer *et al.*, 2005; Graham & Roberts, 2007; de la Parra Venegas *et al.*, 2011; Ramírez-Macías *et al.*, 2012a), in that juvenile males make up the majority of individuals. Although some mature males are present, most *R. typus* are below 7–8 m L_T size at male maturity for *R. typus* in the region (Ramírez-Macías *et al.*, 2012a). Few large females were sighted, with the largest being estimated at 9.6 m L_T . No *R. typus* of <2 m L_T were reported. Pronounced sex and size-based segregations appear to be present in the Caribbean. Although recently-mated male *R. typus* have been reported from Belize and México (Graham, 2007), and an egg case has been recovered from

the northern Gulf of Mexico (Baughman, 1955; Garrick, 1964), there have been no free-swimming <2 m L_T *R. typus* recorded from the region (Graham, 2007; Ramírez-Macías *et al.*, 2012a). Three <2 m L_T *R. typus* have been reported from the Saint Peter and Saint Paul Archipelago ($00^\circ 55' N$; $29^\circ 20' W$) in the central tropical Atlantic Ocean, along with several >10 m L_T *R. typus* (Hazin *et al.*, 2008), raising the possibility that *R. typus* may move into the Atlantic Ocean to breed at larger sizes.

Large scars from boat propellers were found on three *R. typus*. *Rhincodon typus* movements along the MBRS coincide with an important shipping lane linking the U.S.A. with Central American countries (Graham, 2007), and boat or propeller scars have also been noted from Belize (Graham & Roberts, 2007) and in 25% of *R. typus* identified near Isla Holbox, Mexico (Ramírez-Macías *et al.*, 2012a). Although the presence of scarring may not affect the survivorship of these individuals in itself (Speed *et al.*, 2008), mortality or significant impairment is likely to occur in badly damaged *R. typus* (Knowlton & Kraus, 2001; Carrillo & Ritter, 2010), which will obviously lessen re-sighting probabilities. While the incidence of scarring is therefore not necessarily representative of the number of boat strikes, it does indicate that *R. typus* are being injured by large boats in the region. It may be appropriate to limit large vessel access or speed within high-use areas for *R. typus*.

The majority of *R. typus* (78%) identified from Utila were only seen within a single calendar year, suggesting that most are relatively transient to the island. This was supported by the discovery curve of newly identified *R. typus*, which showed no asymptote over the 10 year study period. The percentage of returning individuals in Utila (22%) was similar to that observed in other locations including Holbox Island, Mexico (13%; Ramírez-Macías *et al.*, 2012a), Djibouti (23%), the Seychelles (28%; Rowat *et al.*, 2011) and Western Australia (35%; Holmberg *et al.*, 2009). Although the high degree of transience precluded the application of standard mark–recapture models, as have been successfully used to model *R. typus* population ecology in other locations (Rowat & Brooks, 2012), this type of opportunistic photo-identification data is well suited to using lagged identification rate to assess population-level site fidelity (Whitehead, 2001). A mean of 4.63 *R. typus* was estimated to be present off Utila at any given time over the study period. The short residence time of most *R. typus* was shown by a rapid decrease in R_{LI} between 1 and 16–31 days, with a modelled mean residency time of 11.76 days. Few direct comparative data are available from other locations for *R. typus*. Lagged identification rates have been modelled for *R. typus* within the Gulf of California using the same maximum likelihood techniques as in the present study. Although no mean values were provided, *R. typus* identified from Bahía de Los Ángeles had R_{LI} dropping between 3 and 30 days, while *R. typus* from Bahía de La Paz had R_{LI} falling over 3–60 days (Ramírez-Macías *et al.*, 2012b). Residency in both areas was best approximated to emigration, re-immigration and mortality models. Using mark–recapture modelling, *R. typus* at Ningaloo Reef, Western Australia were estimated to be resident for a mean of 33 days (Holmberg *et al.*, 2009). While estimates of short-term residency from photographic sightings are inherently biased towards observable *R. typus*, and as such are partially dependent on sampling effort, the maximum likelihood technique used here is designed to allow for this as a source of bias. Since a population-level analysis does not, however, capture the details of individual variation, it would be useful to compare photo-identification results

with estimates derived from direct monitoring of electronically-tagged *R. typus* in future.

Some *R. typus* showed a degree of fidelity to Utila, with 22% sighted over multiple calendar years with a maximum observed re-sighting duration of slightly over 7 years. The slight increase in R_{LI} observed between 256 and 511 (mean 374.8) days is suggestive of near-annual visitation in some individuals. Site fidelity was best represented as a rapid emigration, followed by re-immigration in some individuals (after a mean of 86 days), with a proportion of *R. typus* permanently leaving the area (due to emigration or death). This behavioural heterogeneity, with regard to transience or site fidelity, seems to be common across sites in *R. typus*. In Utila, 78% of *R. typus* were transient, here defined as those *R. typus* sighted solely within a single calendar year. Longer-term studies from elsewhere include a 14 year dataset from Western Australia, where 65% of *R. typus* ($n = 386$) were transient (Holmberg *et al.*, 2009), the Seychelles, where 72% of *R. typus* ($n = 398$) were transient over 8 years (Rowat *et al.*, 2011) and Djibouti where 77% of *R. typus* ($n = 257$) were transient over 8 years (Rowat *et al.*, 2011). Population structure, in terms of juvenile male bias, was similar in the four locations, with Djibouti the only area with a significant mean \pm s.d. L_T difference (3.7 ± 0.6 m in that location; Rowat *et al.*, 2011). Taken together, the short intra-annual residence time and relatively high level of transience within the study period support a hypothesis that oceanographic conditions, rather than specific biological phenomena, are the primary influence on *R. typus* sightings at Utila.

Although satellite-tracking studies of *R. typus* have regularly documented international movements (Rowat & Brooks, 2012), photo-identification studies at aggregation sites in the Indian Ocean have shown little population-level connectivity (Holmberg *et al.*, 2009; Brooks *et al.*, 2010). Although the movements of *R. typus* away from Utila are not yet understood, studies using placard and tethered satellite tags on the species within the MBRS region have shown movements between Belize, México and Utila (Gifford *et al.*, 2007; Graham & Roberts, 2007). The similar size and sex structures noted within *R. typus* feeding areas in Honduras, Belize and México, coupled with the geographical proximity and oceanographic linkages within the MBRS, raise the possibility that this area should be regarded as a single unit for management purposes.

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