REVIEW PAPER
Inferred global connectivity of whale shark *Rhincodon typus* populations

A. M. M. Sequeira*†, C. Mellin*‡, M. G. Meekan‡, D. W. Sims§
and C. J. A. Bradshaw*‖

The Environment Institute and School of Earth and Environmental Sciences, The University of Adelaide, Adelaide, SA 5005, Australia, ‡Australian Institute of Marine Science, UWA Oceans Institute (MO96), 35 Stirling Highway, Crawley, Western Australia 6009, Australia, §Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2 PB, U.K. and ‖South Australian Research and Development Institute, P. O. Box 120, Henley Beach, SA 5022, Australia

Ten years have passed since the last synopsis of whale shark *Rhincodon typus* biogeography. While a recent review of the species' biology and ecology summarized the vast data collected since then, it is clear that information on population geographic connectivity, migration and demography of *R. typus* is still limited and scattered. Understanding *R. typus* migratory behaviour is central to its conservation management considering the genetic evidence suggesting local aggregations are connected at the generational scale over entire ocean basins. By collating available data on sightings, tracked movements and distribution information, this review provides evidence for the hypothesis of broad-scale connectivity among populations, and generates a model describing how the world's *R. typus* are part of a single, global meta-population. *Rhincodon typus* occurrence timings and distribution patterns make possible a connection between several aggregation sites in the Indian Ocean. The present conceptual model and validating data lend support to the hypothesis that *R. typus* are able to move among the three largest ocean basins with a minimum total travelling time of around 2–4 years. The model provides a worldwide perspective of possible *R. typus* migration routes, and suggests a modified focus for additional research to test its predictions. The framework can be used to trim the hypotheses for *R. typus* movements and aggregation timings, thereby isolating possible mating and breeding areas that are currently unknown. This will assist endeavours to predict the longer-term response of the species to ocean warming and changing patterns of human-induced mortality.   © 2013 The Authors

Journal of Fish Biology © 2013 The Fisheries Society of the British Isles

Key words: meta-population; migration; movement; sea surface temperature.

INTRODUCTION

The whale shark *Rhincodon typus* Smith 1828 is a filter-feeding chondrichthyan that can reach over 18 m in total length (L_T) (Chen *et al*., 1997; Compagno, 2001; Borrell *et al*., 2011), making it the largest extant fish species. Being large and docile,

its geographic range is known across most tropical and warm temperate waters (Compagno, 2001; Last & Stevens, 2009), especially around sites where individuals aggregate seasonally. Little is known, however, about how these aggregations are connected *via* migration, apart from preliminary population genetic evidence suggesting connectivity at the generational scale (Castro *et al.*, 2007; Schmidt *et al.*, 2009). Furthermore, their pelagic distribution is poorly described, as is the true extent of their range. Rising concerns about how warming seas will affect *R. typus* distributions are potentially being manifested already; for example, occasionally individuals are sighted at latitudes higher than their nominal 30°, namely in the Bay of Fundy, Canada 44° N (Turnbull & Randell, 2006), in the southern Azores, Portugal 41° N (Sa, 2008) or to the north-east of New Zealand >35° S (Duffy, 2002). This lack of understanding of their distribution, connectivity and migration pathways therefore severely limits the capacity to broker international conservation plans for the species.

Rhincodon typus sightings are most often reported nearshore because they often aggregate in specific locations along the coast within warm and temperate waters at approximately the same time every year (Rowat, 2007). The incentive for aggregating is not yet fully understood, but most studies suggest that such occurrences are related to food blooms, currents or temperature variation (Colman, 1997; Wilson, 2002; Meekan *et al.*, 2009; Cárdenas-Palomo *et al.*, 2010; Kumari & Raman, 2010; Sleeman *et al.*, 2010a). In contrast, *R. typus* are rarely recorded on the high seas, largely because of the challenges of sampling the oceans (Richardson & Poloczanska, 2008). Following the drive to chase ever-more-elusive commercial fish species, the fishing industry appears to be the only sector capable of recording marine species regularly in the open ocean (Sequeira *et al.*, 2012). *Rhincodon typus* targeted fisheries ran mainly in South-East Asia and India prior to the turn of the last century (Joung *et al.*, 1996; Pravin, 2000; Stevens, 2007; White & Cavanagh, 2007). As a consequence of declining landings, the species was classified as vulnerable in 2000 in the IUCN Red List (Norman, 2012) and the fisheries were eventually banned; the last bans occurred in India in 2001 (Indian Wildlife Protection Act, Schedule I, amended in 2001) and in Taiwan in 2007 (COA, 2007). Although most of the bans happened more than a decade ago, a recent review of this classification resulted in no change of status (Norman, 2012). Together with the Taiwanese commercial catch lasting until 2007, the persistent high threat risk of the migratory *R. typus* (UNCLOS, 1982; UN FSA, 1995) might be due to a low scrutiny of the ban's implementation (Stewart & Wilson, 2005), and continued illegal fishing in areas such as eastern Indonesia (White & Cavanagh, 2007) and the Maldives (Riley *et al.*, 2009). Unintentional catch of *R. typus* also occurs in other fisheries of large ocean coverage (*e.g.* purse seiners; Romanov, 2002).

Rhincodon typus based tourism has proven the worth of live sharks (Anderson & Waheed, 2001), with related incomes replacing those once provided by targeted fisheries (Quiros, 2007). Established tourism operations continue to expand throughout the world at known *R. typus* aggregation sites, such as in the Seychelles (Rowat & Engelhardt, 2007), Australia (Catlin & Jones, 2009) and Mexico (Venegas *et al.*, 2011), and they play an important conservation role because of the positive example of economic benefits from renewable tourism. Tourism also assists *R. typus* research because photographs taken during diving operations are used to identify returning

individuals (Speed *et al*., 2007), which provides data essential for estimating abundance, vital rates and persistence probability (Meekan *et al*., 2006; Bradshaw, 2007; Rowat *et al*., 2009). By collating tourism-derived photographic data from different locations, research is currently pursuing evidence of inter-aggregation migration hypothesized to occur given the finding of ocean-scale genetic connectivity (Castro *et al*., 2007; Schmidt *et al*., 2009); however, none has yet been found (Brooks *et al*., 2010).

Examining *R. typus* at the scale of single aggregations cannot adequately describe the species' life history because it encapsulates only a small proportion of the life cycle. Collecting data outside aggregation areas is therefore essential. Continual developments in tagging technology to improve estimates of home range size, movement patterns and habitat use (Hammerschlag *et al*., 2011) have been partially successful in this regard, although despite >3000 *R. typus* tagged to date (www.whaleshark.org), trajectories have not revealed reliable evidence for inter-aggregation connection. This is not entirely surprising given the low probability of resighting migratory individuals in widely spaced aggregations. The lack of bio-logging efficiency is mostly due to premature detachment and limited spatial coverage of acquired data (Brunnschweiler *et al*., 2009), tag removal and damage (Fitzpatrick *et al*., 2006; Hays *et al*., 2007) which might result in part from attacks from other sharks or killer whales *Orcinus orca* (Fitzpatrick *et al*., 2006; Speed *et al*., 2008), and the accumulation of bio-fouling organisms causing tag malfunction (Hays *et al*., 2007). Moreover, although tracking methods can provide some insight into the movement behaviour of *R. typus*, they are still unlikely to encompass the full range of the population's distribution.

Mitochondrial and microsatellite DNA studies performed to investigate putative links among *R. typus* aggregations have revealed that the three major ocean basins have low genetic differentiation (Schmidt *et al*., 2009), albeit in the Atlantic Ocean they had moderately different mitochondrial haplotype frequencies from those in the Indian and Pacific Oceans (Castro *et al*., 2007). These results partially validate the prediction that *R. typus* have at least generational-scale migrations that connect populations among the world's oceans. According to Hartl & Clark (1989), population differentiation can be prevented with only a few breeding migrants per generation, and panmixia can occur even with only about four breeding migrants per generation (Hartl & Clark, 1989; Morjan & Rieseberg, 2004). Given the species' long generation time (ranging from 15 to 37 years; Bradshaw *et al*., 2007), only rare dispersal would be required to demonstrate equivalent gene flow. This suggests that current bottom–up approaches based on collecting difficult-to-obtain tagging data to estimate vital rates and life-history traits have a low probability of characterizing broad-scale migratory patterns. Since Smith first described the species in 1828, little is known about their physiology (*e.g*. growth rates) or reproduction (*e.g*. mating areas, variation in pup production and breeding frequency). The only clue that *R. typus* are ovoviviparous was provided by a single pregnant female specimen carrying 300 embryos in different stages of development (Joung *et al*., 1996).

In this overview and analysis, a top–down approach is proposed to infer *R. typus* occurrence probability and global patterns of movement. The primary focus of research should be shifted to broader-scale approaches that generate hypotheses based on conceptual models of migration. Testing these hypotheses indirectly through modelling approaches, or directly *via* improved technologies that provide higher-quality

and longer-term migration data, will ultimately produce a more realistic picture of the species' distribution throughout its life cycle. This will assist in making predictions on population viability and redistribution resulting from warming oceans and changing patterns of human-induced mortality.

KNOWLEDGE BASE

The understanding of *R. typus* ecology and biology has accelerated from an average of less than three papers per year between 1992 and 2005 to a mean of 15·7 per year over the following 6 years [Thomson-Reuters ISI Web of Knowledge (http://wokinfo.com/) on 23 March 2011 using 'whale shark' and '*Rhincodon typus*' as key words]. A peak in the number of papers occurred following the first international whale shark conference in Perth, WA, Australia (Irvine & Keesing, 2007).

Since *R. typus* were first identified in Table Bay, South Africa (Smith, 1828), Gudger (1934) has published the highest number of peer-reviewed papers on the species, mainly describing occurrences in Florida, the Gulf of California (Sea of Cortés), Seychelles, Galapagos, Hawaii, The Bahamas and the Caribbean Sea. Gudger (1932, 1934) was also the first to attempt to portray *R. typus* migratory behaviour partially as a function of ocean current patterns. Iwasaki (1970) attempted to surmise the distribution of *R. typus* based on data collected by Japanese tuna fishing vessels, from which he concluded that their occurrence around Japan was seasonal and depended mainly on the behaviour of the Kuroshio Current, temperature and prevailing winds. Uchida (1984) suggested that *R. typus* are regular in their annual appearance on the east coast of Taiwan, but that seasonality in presence on the west coast depended on temperature. Later, Taylor (1996) published the first paper describing the regular autumn aggregation of *R. typus* at Ningaloo Reef, Australia, and associated it with possible zooplankton blooms following the coral spawn. Since then, Ningaloo Reef has been the site of the most targeted studies (Fig. 1), even if much research has been done elsewhere relating mainly to occurrence, movement, tourism, mortality and feeding behaviour (Fig. 1; Table SI, Supporting Information). Few data are available on *R. typus* life-history traits such as reproduction (Joung *et al*., 1996; Chang *et al*., 1997; Schmidt *et al*., 2010) and growth (Pauly, 1997; Wintner, 2000) or morphology and physiology (Wilson & Martin, 2001; Yopak & Frank, 2009; Dove *et al*., 2010), which reflects the difficulty in obtaining specimens for detailed examination and measurement. From the summary of recent studies per site (Fig. 1; Table SI, Supporting Information), the following trends emerge: (1) knowledge of *R. typus* ecology is most advanced in the Indian Ocean, and (2) similar work has been done in different locations worldwide, but (3) mostly at the scale of individual aggregations.

Recent genetic studies (Castro *et al*., 2007; Schmidt *et al*., 2009) provide the only clue so far that the world's *R. typus* populations are connected *via* dispersal occurring during some stage of the life cycle. There has been no effort so far, however, to synthesize all the disparate information available into a conceptual model of dispersal and population connectivity, even after the conservation of *R. typus* was highlighted as requiring both 'regional cooperation and conservation initiatives' (Rowat, 2007).
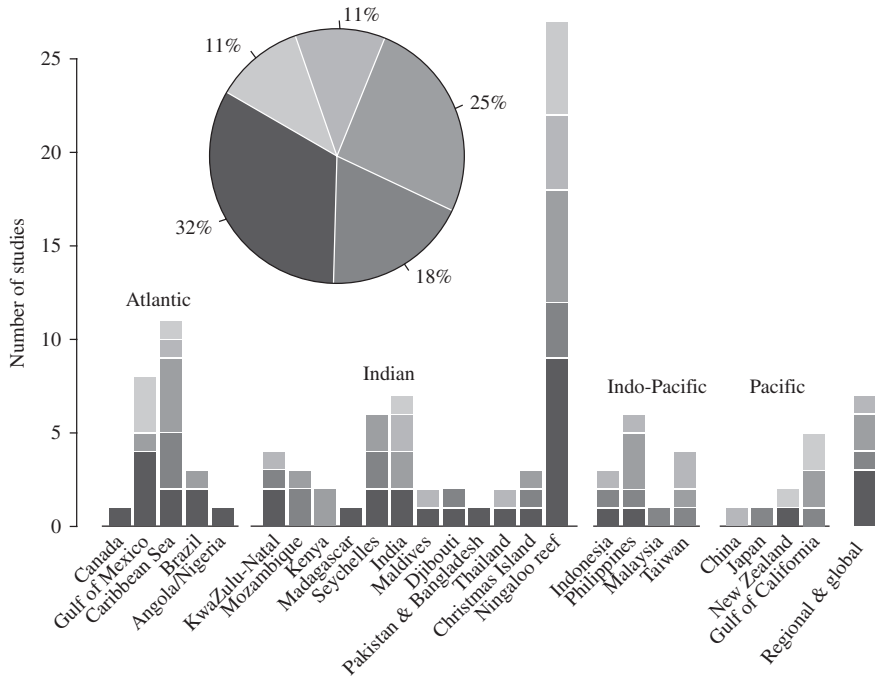
FIG. 1. Graphical illustration of the number of representative *Rhincodon typus* studies (since 1997) grouped by occurrence, population and correlates for occurrence (■), movement (■), tourism and conservation (■), mortality (■) and foraging (■), in different locations worldwide (see Table I, Supporting Information).

GLOBAL OCCURRENCES

The first 76 recorded *R. typus* occurrences worldwide were compiled in the early 1930s by Gudger (1932). He suggested the Sulu Sea (between southern Philippines and northern Borneo) as the single location from which all *R. typus* originate, dispersing from there depending on environmental conditions (Gudger, 1934). Subsequently, Wolfson & Notarbartolo-di-Sciara (1981) counted 345 records worldwide (including repeat sightings) until 1980. Currently, *R. typus* have been recorded in the three major oceans spanning the Equator and have been seen, even if only occasionally, near the shore of more than 100 countries in five continents (Fig. 2; Compagno, 2001; Martin, 2007; Rowat, 2007; Stacey *et al*., 2008).

Although existing photo-identification libraries have yet to report a match from *R. typus* seen at distant locations, there is some evidence for short-distance movements. This is the case for resighting of the same fish in Gladden Spit (Belize), Isla Contoy (Mexico) and Utila (Honduras) (Graham & Roberts, 2007), and a resighting in Mozambique of a *R. typus* tagged in the Seychelles 11 months earlier (Rowat & Gore, 2007).

Peaks in *R. typus* occurrence appear to happen synchronously in different locations around the world (Table I). For example, in January they occur off KwaZulu-Natal (South Africa), Djibouti and Christmas Island (Australia); in March to May, they occur at Gladden Spit (Belize), Gujarat (India), Ningaloo (Australia) and around the Philippines; in August to October, *R. typus* have been reported in Portugal (around the
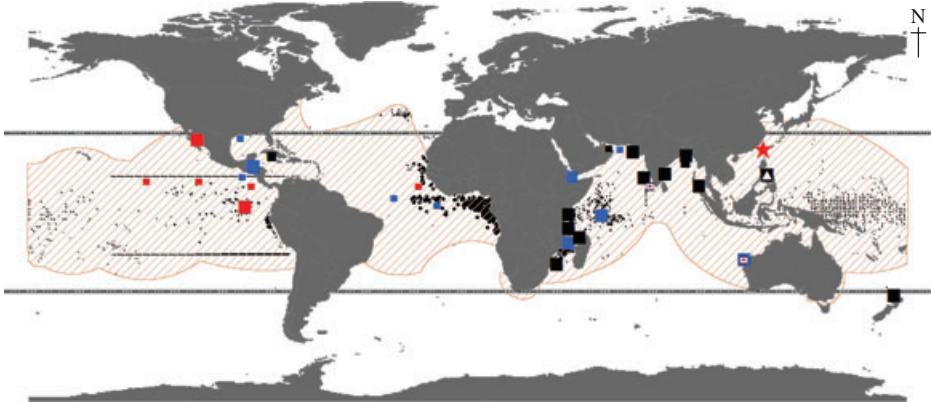
FIG. 2. Compilation of worldwide *Rhincodon typus* occurrences from Compagno (2001), Martin (2007), Stacey *et al*. (2008) and Rowat (2007) showing latitudinal range (▭) overlaid with the IUCN (Norman, 2012) distribution (▨). ▪, <1 m total length (L_T) sex not specified; ▪, <1 m L_T males; ▪, 1 m L_T females; ▪, 1–3 m L_T sex not specified; ■, *c*. 5 m L_T males (Djibouti); ■, *c*. 7 m L_T sex not specified; ■, *c*. 7 m L_T males; ■, *c*. 7 m L_T females (mostly; square size increases with increase in L_T); ▲, 46 cm L_T (smallest *R. typus*); ◉, groups of juveniles (≥ 10 individuals); ★, the sighting of pregnant female >10 m L_T with 300 embryos (Joung *et al*., 1996); •, long-term (1980–2010) *R. typus* sightings from tuna fisheries.

Azores), Mozambique, Seychelles and Gulf of California, Mexico. When examining the timings over several years, however, a pattern of sequential monthly peaks at neighbouring locations emerges (Table I).

A highly skewed sex ratio is common in certain aggregations (*e.g*. Ningaloo, Seychelles, Mozambique and Belize) where mostly immature males are found (Meekan *et al*., 2006; Graham & Roberts, 2007; Rowat *et al*., 2011). Rowat *et al*. (2011) provided some evidence for size segregation, stating that individuals observed in the Djibouti aggregation (mainly immature males) are smaller than those from the Seychelles (and other locations in the Indian Ocean). They suggested that the Djibouti population might be a 'staging' group for other regional aggregations (*i.e*. segregation might therefore be another feature contributing to migration among sites). In the Gulf of California (Mexico), *R. typus* can be segregated both by sex (Eckert & Stewart, 2001) and size, with larger adult females mainly seen in the southern part of the Sea of Cortés (Ramírez-Macías *et al*., 2007).

Smaller *R. typus* (<2·5–3 m L_T) have been observed only rarely (Colman, 1997) and almost all neonates reported so far have been caught as by-catch in purse-seine fisheries (Wolfson, 1983). The smallest neonate ever recorded (46 cm L_T) was recently found swimming freely in Sorsogon, Philippines (Aca & Schmidt, 2011), and the only fertility data available for the species are derived from a single, 10·6 m L_T female caught off Taiwan containing 300 'ready-to-be-born' embryos measuring 58–64 cm (Joung *et al*., 1996).

TRACKING STUDIES

Gunn *et al*. (1999) and Eckert & Stewart (2001) published the first *R. typus* tracking results derived from satellite tags deployed at Ningaloo Reef (Western

TABLE I. Global sequence of *Rhincodon typus* monthly appearance timings (3 years presented) in different locations worldwide. Locations are ordered geographically from the North Atlantic Ocean, through the Indian Ocean to the east and west Pacific Ocean

Ocean	Country	Location	References
Atlantic Ocean	Portugal	Azores islands	Machete & P. Afonso, pers. comm.
	Mexico	Yucatan Penisula	Motta et al. (2010)
	Belize	Gladden Spit	Heyman (2001); Graham & Roberts (2007)
	Honduras	Off Bay Islands	Harborne et al. (2001)
	Brazil	St Peter St Paul Archipelago	Hazin et al. (2008)
Indian Ocean	South Africa	KwaZulu-Natal	Beckley et al. (1997); Cliff et al. (2007) Rowat (2007)
	Mozambique		Pierce et al. (2010); Gifford et al. (2007)
	Madagascar		Jonahson & Harding (2007)
	Seychelles		Rowat & Engelhard (2007) Rowat et al. (2011); Rowat (2007)
	Tanzania	Zanzibar	Rowat (2007)
	Kenya	Shimoni	Rowat (2007)
	Kenya	Mombassa	Rowat (2007)
	Djibouti		Rowat et al. (2011); Rowat et al. (2007) (anecdotal reports)
	India	Gujarat	Pravin (2000)
	India	South	Rowat (2007)
	Maldives	West	Anderson & Ahmed (1993)
	Maldives	East	Anderson & Ahmed (1993)
	India	Tamil Nadu	Pravin (2000)
	Bangladesh		Rowat (2007)
	Thailand	Andaman sea	Rowat (2007)
	Australia	Christmas Island	Hobbs et al. (2009)
	Australia	Ningaloo	Taylor (1996)
Pacific Ocean	Phillipines		Quiros (2007)
	Taiwan	West	Chang et al. (1997)
	Taiwan	East	Chang et al. (1997)
	Japan	Okinawa Islands	Iwasaki (1970)
	Japan	Main island	Iwasaki (1970)
	Japan	Ogasawara Islands	Iwasaki (1970)
	Australia	Coral sea	Gunn et al. (1992) in Colman (1997)
	New Zealand		Duffy (2002)
	Gulf of California	Bahia de Los Angeles	Nelson & Eckert (2007); Cárdenas-Torres et al. (2007)
	Galapagos		Green (2011)

■, seasonal peaks; ■, full season; ■, occasional sightings; ▨, large distances between the locations above and below the grey cells.

Australia) and the Sea of Cortés (Gulf of California), respectively. Despite the >3000 data-logging and satellite tags deployed to date (www.whaleshark.org, consulted 5 August 2011), only 109 *R. typus* tracks are publicly available (Tables II–IV), with only 75 published in peer-reviewed papers.

Most of the tracking results available are from the Indian Ocean (47 tracks), with Ningaloo being the main tagging location. Next was the Pacific Ocean from where 30 tracks have been published (16 starting at the Sea of Cortés and 14 from the Galapagos Islands), followed by 22 in the Atlantic Ocean deployed mostly in Belize, and finally 10 in the Indo-Pacific Ocean area (from the Philippines, Malaysia and Taiwan). The sex ratio of these tracked individuals is 33 females, 31 males and 45 unknown (Tables II–IV). Average track duration is *c*. 90 days, although they range from only a few hours (Gunn *et al*., 1999) to >3 years (Eckert & Stewart, 2001), with *c*. 30% of the tracks lasting <1 month and only two lasting >9 months. Distances travelled ranged from 4 to 12 620 km (mean *c*. 1545 km), with only 10 *R. typus* travelling >2000 km.

Compiling all published tracks at a global scale (Fig. 3) shows that the current information on *R. typus* movement range and habitat use is still highly scattered. In the Atlantic Ocean, for example, there are tracks in the area of the Gulf of Mexico (Gifford *et al*., 2007) that confirm the link between Honduras, Belize and Mexico suggested by Graham & Roberts (2007). There is also a >7000 km track from a tag deployed at Quintana Roo (Mexico) finishing in the central Atlantic Ocean south of the Saint Peter and Saint Paul Archipelago, Brazil, *c*. 5 months later (Hueter *et al*., 2008). There are no tracks available, however, from locations in the eastern Atlantic Ocean where *R. typus* have been reported (*e.g*. Portugal or the west coast of Africa; Fig. 2). In the Indian Ocean, existing tracks link different aggregations. This is the case for South Africa and Mozambique (Gifford *et al*., 2007), Mozambique and Madagascar (Brunnschweiler *et al*., 2009), United Arab Emirates and Qatar (MML, 2010) and Ningaloo with Timor, Indonesia and Christmas Island (CSIRO, 2005; Wilson *et al*., 2006; Wilson *et al*., 2007). There is also a 60 day track suggesting a connection between Seychelles and Sri Lanka (Rowat & Gore, 2007), although it was inferred on the basis of only one transmission obtained after an inactive period of 1·5 months (represented as a straight line in Fig. 3). Likewise, the tags deployed in western Philippines (Eckert *et al*., 2002) show a possible connection with Malaysia and south Vietnam, while *R. typus* tagged in Taiwan (Hsu *et al*., 2007) reached waters off east Philippines.

Several tags deployed in the Gulf of California (Eckert & Stewart, 2001) showed that most *R. typus* remain in the Sea of Cortés; however, four left the gulf and one was reported to have travelled almost 13 000 km from the east to the west Pacific Ocean in 1144 days (<37 months). Eckert & Stewart (2001) asserted that due to data-storage limitations, *R. typus* with longer tracks (and not surfacing regularly enough to transmit stored data) were located less frequently. *Rhincodon typus*, however, spend most of their time at the surface (Wilson *et al*., 2006; Sleeman *et al*., 2010a, b), so such long periods without surfacing for satellite position acquisition are unlikely. For this reason, the 37 month track with an atypically straight trajectory, lack of surface intervals and unprecedented rate and magnitude of travel should be deemed biologically unrealistic (*e.g*. it is more likely that the satellite tag had detached and was floating passively with the currents). Recently, some tags deployed near the Galapagos (Table III and Fig. 3) have revealed that most *R. typus* head west after

TABLE II. List of published *Rhincodon typus* tracks from the Indian Ocean

Tag	L_T (m)	Sex	Tagging date	Pop-up date	Duration (days)	Distance (km)	Mean speed (km day^{-1})
South Africa – Cape Vidal (Gifford *et al*., 2007)							
1*	7	F	08.03.1998	25.03.1998	17	199	–
2*	7	M	25.10.1998	01.11.1998	7	90	–
3*	8	M	23.01.1999	25.01.1999	<3	65	–
Mozambique – Tofo (Brunnschweiler *et al*., 2009)							
4*	6–7	F	18.02.2006	16.5.2006	87	1200	31·2
Madagascar – Nosy Be (Graham *et al*., 2008)							
5	–	–	5–12.12.2005	15.04.2006	–	–	–
6	–	–	5–12.12.2005	07.02.2006	–	–	–
7	4	M	5–12.12.2005	24.11.2005	–	–	–
8	8	F	5–12.12.2005	19.12.2005	–	–	–
9	–	–	5–12.12.2005	15.03.2006	–	–	–
Djibouti – Arta Beach (Rowat *et al*., 2007)							
10	3	M	22.01.2006	31.01.2006	9	–	10·1
The Gulf (MML, 2010)							
11*	4·2	F	18.03.2010	20.04.2010	33	–	–
Seychelles – Mahe (Rowat & Gore, 2007)							
12*	5·0	–	02.09.2001	17.10.2001	46	1422·74	33·1 (max)
13*	7·0	–	25.10.2001	12.11.2001	19	502·10	23·8 (max)
14*	6·5	M	25.10.2001	23.12.2001	60	3382·62	56·9 (max)
Australia – Ningaloo							
15[a]	–	–	28.03.1994	–	<1	–	60·5
16[a]	–	–	29.03.1994	–	<2	–	51·3
17[a]	–	–	06.04.1997	–	<2	–	64·8
18[a]	–	–	10.04.1997	–	<1	–	73·5
19*,[b]	7·0	F	22.04.2002	17.07.2002	85	3130	36·0
20*,[b]	4·2	M	05.05.2005	29.09.2005	147	–	–
21*,[b]	4·0	F	06.05.2005	19.09.2005	136	–	–
22*,[b]	7·5	–	05.05.2005	30.08.2005	118	–	–
23*,[b]	4·2	M	07.05.2005	10.06.2005	34	–	–
24*,[b]	–	–	02.05.2005	10.06.2005	39	–	–
25*,[b]	4·2	–	06.05.2005	04.06.2005	29	–	–
26*,[b]	7·3	M	28.06.2005	31.07.2005	33	1740	52·8
27[c]	8·0–10·0	F	02.05.2003	10.05.2003	8	85	–
28[c]	6·0	F	03.05.2003	04.05.2003	1	16	–
29[c]	4·5	F	05.05.2003	–	–	–	–
30*,[c]	6·0–8·0	–	05.05.2003	11.11.2003	191	942	–
31[c]	4·5	M	03.05.2004	03.05.2004	0	4	–
32[c]	8·5	F	03.05.2004	03.05.2004	0	7	–
33[c]	7·5	F	03.05.2004	07.05.2004	4	93	–
34[c]	4·7	F	04.05.2004	–	–	–	–
35[c]	4·5	F	04.05.2004	–	–	–	–
36*,[c]	11·0	F	04.05.2004	31.08.2004	119	1302	–
37[c]	7·3	F	04.05.2004	–	–	–	–
38*,[c]	4·7	–	05.05.2004	24.11.2004	203	673	-
39[c]	7·6	F	05.05.2004	–	–	–	–
40[c]	5·6	F	07.05.2004	–	–	–	–

TABLE II. Continued

Number	L_T (m)	Sex	Tagging date	Pop-up date	Duration (days)	Distance (km)	Mean speed (km day^{-1})
41[c]	7·6	F	07.05.2004	10.05.2004	3	16	–
42*,[c]	6·2	F	08.05.2004	06.09.2004	119	738	–
43*,[c]	7·2	M	08.05.2004	04.07.2004	57	1501	–
44[c]	7·0	F	08.05.2004	–	–	–	–
45*,[c]	5·3	F	09.05.2004	11.12.2004	216	443	–
46[d]	4–5	M	05.05.2005	29.09.2005	147	–	–
Christmas Island (Australian Institute of Marine Sciences†)							
47*	5	M	17.01.2008	14.04.2008	88	–	–

L_T, total length; F, female; M, male. *Tracks recreated and displayed in Fig. 3. †Whale shark tagged by M. G. Meekan (unpubl.). Superscript letters indicate the reference for each track where there are multiple references for the same tagging location: [a]Gunn *et al*. (1999). [b]CSIRO (2005). [c]Wilson *et al*. (2006). [d]Wilson *et al*. (2007).

congregating at this location, although the information available is still incomplete (www.galapagoswhaleshark.com).

THE BIG PICTURE: FORMULATING GLOBAL HYPOTHESES

After collating all available *R. typus* occurrences and tracking data, the question of whether *R. typus* are migrating across or within oceans remains unanswered. It must be concluded therefore that such conventional methods to study *R. typus* movement are still of insufficient temporal and spatial coverage to provide useful conclusions at the ocean-basin scale. A different approach by shifting research from a local to a global perspective is proposed.

The Indian Ocean is the region from which most *R. typus* data have been collected; therefore, it is the best region in which to begin formulating hypotheses regarding *R. typus* movement patterns. Some locations are known to be linked *via* direct observation such as Mozambique and Seychelles (Rowat & Gore, 2007) or Ningaloo and Christmas Island (Fig. 3). It is clear that appearance timings occur sequentially (Table I). Therefore, it is hypothesized that at least some *R. typus* move in a general clockwise pattern from the south-west (KwaZulu-Natal) in January, to the south-east Indian Ocean (Ningaloo) in March over *c*. 2 years. According to Eckert & Stewart (2001), the mean pace at which *R. typus* travel varies from *c*. 2 to 30 km day^{-1}, with greater horizontal distance covered when closer to the surface. Average speeds of around 30 km day^{-1} have also been reported by others (Eckert *et al*., 2002; Hsu *et al*., 2007; Rowat & Gore, 2007; Hueter *et al*., 2008; Brunnschweiler *et al*., 2009), while faster speeds have been reported for short-term movements (Gunn *et al*., 1999). Assuming constant travel speeds, a dominance of surface swimming and otherwise ideal conditions, a *R. typus* moving at *c*. 30 km day^{-1} would be able to travel >10 000 km year^{-1}, approximately the distance between South Africa and south-western Australia. Using this logic, 2 years to complete the longer clockwise migration from South Africa to Ningaloo is biologically plausible.

TABLE III. List of published *Rhincodon typus* tracks from the Pacific Ocean and Indo-Pacific Ocean area

Number	L_T (m)	Sex	Tagging date	Pop-up date	Duration (days)	Distance (km)	Mean speed (km day^{-1})
China−Hainan (MCSS, 2009)							
1*	–	M	28.06.2009	31.07.2009	33	–	–
Taiwan (Hsu *et al.*, 2007)							
2*	4·5	M	08.04.2002	01.11.2002	208	5896	28·3
3	4·2	F	17.04.2002	–	–	–	–
4*	4·2	M	13.11.2002	28.02.2003	108	3732	34·6
5*	4·0	M	09.04.2004	01.08.2004	114	3121	28·4
Philippines – Salay (Eckert *et al.*, 2002)							
6	7	–	05.02.1997	–	10	900	18·9
7*	3	–	18.02.1997	02.05.1997	73	1567	31·9
Philippines – Donsol (Eckert *et al.*, 2002)							
8*	5	–	23.02.1997	03.03.1997	8	54	13·7
Malaysia – Usukan Island (Eckert *et al.*, 2002)							
9*	7	–	03.02.1997	9.02.1997	6	220	6·9
10*	7	–	05.02.1997	12.06.1997	127	8025	23·3
11*	7	–	05.02.1997	15.02.1997	10	900	18·9
Gulf of California – Sea of Cortez (Eckert and Stewart, 2001)							
12*	3·7	F	06.10.1994	07.10.1994	1	57·5	–
13*	4·6	–	22.09.1994	14.10.1994	22	–	–
14*	3·0	F	19.09.1994	06.10.1994	17	320·3	21·7
15	4·6	–	20.09.1994	–	17	31·7	3·2
16*	4·3	–	20.09.1994	29.10.1994	39	818·3	23·5
17	4·0	–	23.09.1994	–	5-7	23·3	8·4
18	4·0	–	07.10.1994	–	1	11·2	–
19*	6·1	F	10.09.1995	22.09.1995	12	404·6	23·6
20*	3·7	–	10.09.1995	13.09.1995	3	8·5	11·1
21*	7·1	–	12.09.1995	26.11.1998	1144	12 620·0	17·1
22*	3·7	F	10.09.1995	28.09.1995	18	46·3	2·0
23*	–	–	09.09.1995	07.10.1995	28	199·6	–
24	15·0	F	20.06.1996	–	111	2863·6	28·8
25*	18·0	F	19.06.1996	20.07.1996	30	206·8	18·2
26*	–	F	19.06.1996	15.04.1998	665	7762	23·3
Galapagos – Total of 14 tracks (Green, 2011)							
27*	–	–	07.2011	–	–	–	–

L_T, total length; F, female; M, male.*Tracks displayed in Fig. 3.

Once in Ningaloo, although the strength of the southward-flowing Leeuwin Current along the western coast of Australia might influence the degree to which they penetrate southward, previous tagging results show that the predominant movements are northward towards Indonesia, and then either westward or eastward (Fig. 3; CSIRO, 2005). Tagging data show that *R. typus* take *c*. 5 months to return to the central Indian Ocean (passing near Christmas Island much earlier than the seasonal peak in abundance) and *c*. 4 months to travel east as far as East Timor. Although peaks of occurrence are not published for the southern areas of the Malay Archipelago and

TABLE IV. List of published *Rhincodon typus* tracks from the Atlantic Ocean (Gulf of Mexico)

Number	L_T (m)	Sex	Tagging date	Pop-up date	Duration (days)	Distance (km)	Mean speed (km day^{-1})
Belize–Gladden Spit (Graham *et al*, 2006)							
1	5·5	M	23.04.2000	07.05.2000	14	–	–
2	3·6	M	23.04.2000	02.06.2000	40	–	–
3	9·7	M	11.04.2001	15.10.2001	188	–	–
4	6·7	M	11.04.2001	Removed	248	–	–
5	6·7	M	21.04.2000	06.05.2000	14	–	–
6	5·5	–	25.04.2000	08.08.2000	105	–	–
7	5·5	–	25.04.2000	15.06.2000	40	–	–
8	5·2	M	16.03.2001	31.07.2001	127	–	–
9	6·7	M	11.04.2001	30.06.2001	187	–	–
10	5·2	M	11.04.2001	–	163	–	–
11	5·5	–	10.05.2001	03.07.2001	249	–	–
Honduras–Utila (Gifford *et al*., 2007)							
12*	8·0	M	18.02.1999	29.06.1999	132	–	–
13*	8·0	M	31.12.1999	31.01.2000	31	–	–
U.S.A.–Florida (MML, 2010)							
14*	7·5	F	28.05.2010	20.08.2010	84	–	–
15*	7·5	M	18.06.2010	04.10.2010	108	–	–
Mexico–Quitana Roo (Hueter *et al*, 2008)							
16*	6·0	M	31.08.2005	01.10.2005	31	889	28·7
17*	5·5	M	02.09.2005	01.10.2005	29	260	9·0
18*	7·0	M	23.07.2006	27.12.2006	157	970	6·2
19*	8·0	M	13.09.2006	22.10.2006	39	712	18·3
20*	7·0	F	13.09.2006	25.11.2006	73	1027	14·1
21*	8·0	F	14.09.2006	10.01.2007	118	371	3·14
22*	7·5	F	31.08.2007	24.01.2008	150	7213	48·1

L_T, total length; F, female; M, male. *Tracks displayed in Fig. 3.

Timor, *R. typus* are found occasionally in the Coral Sea, *c*. 4–5 months after the Ningaloo peak (Table I). From the Coral Sea, environmental conditions are probably influential on the patterns of subsequent movement. Either they (1) move farther south towards the north coast of New Zealand (surpassing 35° S) where their occurrence peaks in February (Duffy, 2002), (2) return to the Indian Ocean or (3) migrate eastward [*R. typus* are occasionally seen around the islands of the south-west and central Pacific Ocean (Compagno, 2001; and data collected by purse-seine fisheries; Fig. 2)].

In the central Indo-Pacific Ocean, *R. typus* tracked from Taiwan travelled close to the Philippines even outside the peak abundance season (March and June). Eckert *et al*. (2002) tracked *R. typus* from the Philippines in February, from where they travelled west passing Malaysia and South Vietnam towards the Gulf of Thailand in *c*. 4·5 months. There are many routes that potentially link the Pacific and Indian Oceans in the Malay Archipelago (*e.g*. Andaman and Java Seas), such that *R. typus* can cross over to the Indian Ocean towards Christmas Island or the north of Australia.
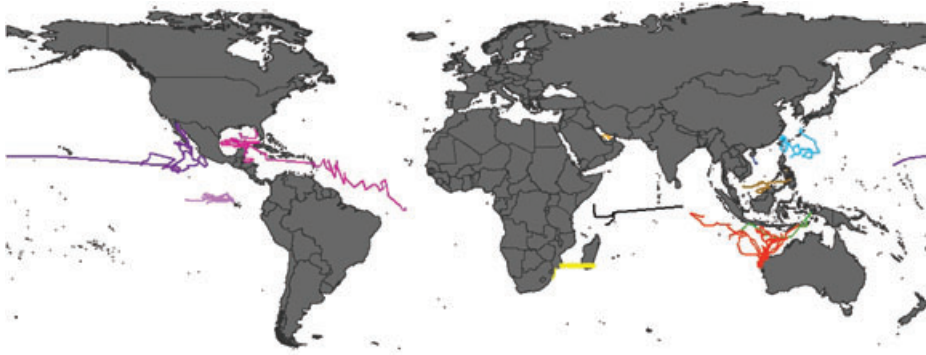
FIG. 3. Global overview of published *Rhincodon typus* tracks (——, Gulf of California; ——, Galapagos; ——, Gulf of Mexico; ——, The Arabian Gulf; ——, Seychelles; ——, South Africa–Mozambique; ——, Ningaloo (Western Australia); ——, Christmas Island; ——, Hainan (China); ——, Taiwan; ——, Philippines–Malaysia). Colour code indicates area of tag deployment. Tracks adapted from original sources as detailed in Tables II–IV.

From a temporal perspective (Table I), there are no obvious paths from eastern locations in the Indian Ocean to the west through to Bangladesh. This leads to the hypothesis that *R. typus* could swim straight towards the Maldives (as was the case for a *R. typus* tagged off Ningaloo moving far into the central Indian Ocean). This would also be consistent with the lower numbers of *R. typus* sighted on the eastern coast of India compared to the western coast (Pravin, 2000). Additionally, *R. typus* could also move from the Maldives through to the Seychelles and then to South Africa based on observed temporal patterns of occurrence (Table I).

For population connectivity to be available between the Indo-Pacific and Atlantic Oceans, *R. typus* would need to travel through the Cape of Good Hope, South Africa. Beckley *et al.* (1997) suggested that *R. typus* strandings on the east coast of South Africa might be associated with the changes in temperature associated with the Agulhas Current from the Indian Ocean mixing with the cold water upwelled by the Benguela Current in the south-east Atlantic Ocean. Beckley *et al.* (1997) also stated that stranded animals were generally small, which suggests that only larger animals would survive the crossing from the Indian to the Atlantic Oceans. The greater thermal inertia of larger *R. typus* might allow them to move in the southern Atlantic Ocean until they reach the warmer waters of, for example, Gabon (peak of occurrences registered by purse-seine fisheries in the Atlantic; Fig. 2), or the region around the Brazilian Saint Peter and Saint Paul Archipelago where *R. typus* are observed year-round, but mainly during the first semester with a peak in June (Hazin *et al.*, 2008), 6 months after the peak in South Africa.

Within the entire Atlantic Ocean, there are tracks available mostly for the areas of the Gulf of Mexico and Caribbean Sea that show some linkages between the aggregations of Central America (Fig. 3). This suggests that there is a single meta-population here. The odd long track starting from Mexico in August and finishing south of the Saint Peter and Saint Paul Archipelago in January suggests that *R. typus* from this Central American population can travel great distances within the Atlantic Ocean. Year-round sightings of *R. typus* in the archipelago outside of peak months (Hazin *et al.*, 2008) hint at the possibility of a trans-Atlantic Ocean thoroughfare.

Because the occurrence of *R. typus* in the Azores in the eastern Atlantic Ocean is seasonal (mostly at the end of August and September) and does not occur every year (M. Machete & P. Afonso, pers. comm.), it is possible that *R. typus* travel there only when environmental conditions (especially water temperature) are most suitable (Sa, 2008). The Azores Current, flowing south of the Azores Archipelago (where most *R. typus* are spotted by tuna fisheries), originates from the Gulf Stream (Klein & Siedler, 1989). When the Gulf Stream is strong, the warmer-than-usual waters near the Azores might encourage more northerly forays (Sa, 2008). It is therefore hypothesized that individuals travelling to the Azores might originate from the Gulf of Mexico. *Rhincodon typus* are also occasionally seen in the Madeira Islands (Portugal) to the south-east of the Azores (Wirtz *et al.*, 2008). Because water temperatures in these parts of the Atlantic Ocean are generally cooler, movements towards the warmer southerly waters closer to the Equator near the Saint Peter and Saint Paul Archipelago and West Africa would be more typical, a prediction supported by observation from fishing fleets in those areas.

Breeding within the Atlantic Ocean is supported by the discovery of a single neonate (58 cm L_T) specimen inside the stomach of a captured blue shark *Prionace glauca* (L. 1758) (Kukuyev, 1996; Martin, 2007). Other neonates have been caught near the Equator in this ocean (Wolfson, 1983) and an egg case was found in the Gulf of Mexico in the early 1950s (Baughman, 1955). Neonates have also been found in the eastern Pacific Ocean (Wolfson, 1983), where large adult females are often observed (Eckert & Stewart, 2001). Although more is known about *R. typus* inhabiting the Indian Ocean, only two neonates (<1 m) have ever been reported there (Rowat *et al.*, 2008). Despite young juveniles (*c*. 1 m L_T) occasionally observed swimming with larger individuals (Pillai, 1998), most of the Indian Ocean aggregations comprise mainly of immature males, which makes it unlikely that the region includes a permanent breeding area. If there is a nursery in the Indo-Pacific Ocean area (*e.g.* around the Philippines), and if *R. typus* are able to cross to the Indian Ocean, small juveniles could potentially occur in the latter even in the absence of a nursery.

Notwithstanding these hypothetical linkages, *R. typus* is known to often return to the same aggregation at least semi-annually (*e.g.* Maldives and Ningaloo; Meekan *et al.*, 2006) based on photographic matching (Speed *et al.*, 2007). Such repeat sightings do not support the notion that all individuals regularly travel around ocean basins over 2–4 year cycles. It is hypothesized instead that although *R. typus* can travel over entire or even between ocean basins, many (perhaps most) remain close to single aggregation sites for several months or years. For example in the Maldives, *R. typus* might remain in the general area, travelling west (December to April) to east (May to November) of the islands over one or more years (Table I), or extend the travelling farther from Gujarat (north-west side of India) to west of the Maldives in the first half of the year, and then east of the Maldives and Tamil Nadu (east of India) in the second. From here, they would have the option to move east (*e.g.* to Bangladesh in December) or back to the west of the Maldives, south India and Gujarat (Table I). This back-and-forth movement around India and the Maldives accords with the higher resighting rate in the Maldives relative to other nearby locations (Riley *et al.*, 2010). Other examples of these hypothesized shorter migration routes and possible populations are depicted in Fig. 4.
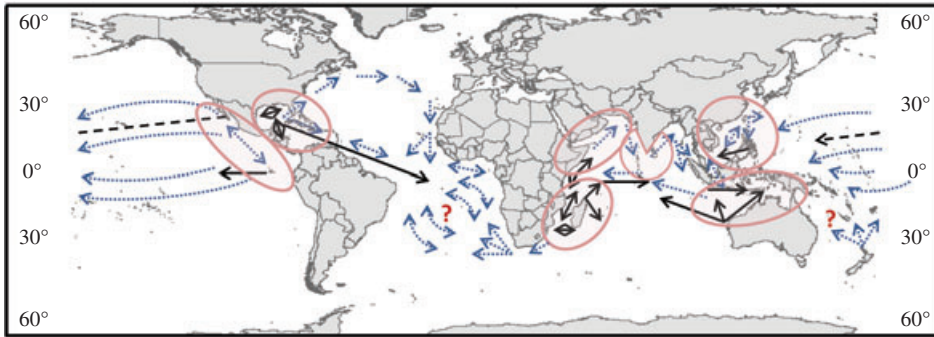
FIG. 4. *Rhincodon typus* migration patterns depicting probable sub-populations (○), possible links between sub-populations (aggregations; ··➤), movements revealed from tagging data (⟶) and no current evidence for a migratory pathway (dashed arrows), except the questionable 13 000 km track across the Pacific Ocean from Eckert & Stewart (2001). ?, No information available on timings of occurrences or tracked *R. typus* to assist in formulating hypotheses about movement patterns in the area.

FORESEEING CHANGE

The global distribution of *R. typus* lies predominantly within tropical and warm temperate waters between *c*. 30° N and 30° S (Compagno, 2001; Last & Stevens, 2009). Since the late 1980s, however, individual *R. typus* have been observed at even higher latitudes. Indeed, Wolfson (1986) recorded *R. typus* at latitudes of 41° N and 36·5° S, and more recently, Duffy (2002) reported them off New Zealand south of 35° S. One *R. typus* has even been sighted as far north as 44° N in the Bay of Fundy, Canada (Turnbull & Randell, 2006). *Rhincodon typus* are also occasionally sighted south of the Azores (*c*. 41° N), mainly by tuna fishermen (M. Machete & P. Afonso, pers. comm.) and recently, many sightings (>400) have been made mainly around the island of Santa Maria, Azores from June to September, probably in response to an unusual pulse of warm water (Sa, 2008).

Rhincodon typus mainly stay within a narrow range of sea surface temperatures. In the Sea of Cortés, most tracked individuals were in waters between 28 and 32° C (Eckert & Stewart, 2001); in the Seychelles, most were between 25 and 35° C (Rowat & Gore, 2007); in the north-western Pacific Ocean, most were between 23 and 32° C (Hsu *et al*., 2007) and for pelagic sightings derived from fisheries records, >90% of 1185 records were in surface waters between 26·5 and 30·0° C (Sequeira *et al*., 2012). If water temperature plays an important role in modifying *R. typus* distribution, the rapid warming of the world's oceans arising from anthropogenic climate change (Hegerl & Bindoff, 2005) will probably affect their future distribution. Because *R. typus* seem to avoid higher temperatures (*e.g*. around the Equator; Sequeira *et al*., 2012), poleward shifts are more probable than an overall expansion of their current distribution. In addition to these expected distributional changes, shifts in both abundance and distribution are expected from previous (Romanov, 2002; Bradshaw *et al*., 2007) and ongoing (White & Cavanagh, 2007; Riley *et al*., 2009) commercial fishing, potentially from excessive disturbance arising from ecotourism at aggregation sites (Cárdenas-Torres *et al*., 2007; Quiros, 2007; Rowat & Engelhardt, 2007; Pierce *et al*., 2010) and other human-related disturbances (Haetrakul *et al*., 2007; WWF, 2012).

CONCLUSIONS

Despite ample evidence that *R. typus* are capable of long-distance travel, confirmed by genetic evidence that the world's populations are connected at least at the generational scale, it is known that many individuals spend long periods within the immediate environs of particular locations. A conceptual model has thus been provided based on known movement patterns, aggregation timings and oceanic structure, demonstrating how intra and inter-ocean movements might occur, even if they do so rarely, and without non-genetic evidence yet to test the hypotheses. This lack of evidence, however, does not counter the model. It mostly derives from the thousands (i.e., not millions or tens of millions) of photographs used in photo-identification studies. Photo-matching is only semi-automated (*e.g.* I3S; Van Tienhoven *et al.*, 2007), thus limiting the probability of photographing migrating individuals, and making the probability of resighting these individuals in other aggregations even smaller. Moreover, flank mismatch (right or left side only) can also limit the number of individuals that can be compared.

Viewing *R. typus* ecology from a global perspective therefore engenders many related hypotheses that can be tested as technology improves and genetic evidence is refined, and it isolates the most important questions to determine the long-term conservation status of this species. A natural progression of the global movement model is the construction of a broad-scale population model that connects sub-populations on the basis of inferred demographic and movement rate data. Application and continual refinement of biologically plausible rates will further hone the global model and its predictions, thereby unfolding key aspects of the species' cryptic life history so that research can target the most relevant aspects. It is clear that more data are required from locations close to key aggregation sites where hypothesized connections can be validated. Tagging and photographic identification data within these regions should be prioritized on the basis of their putative connections predicted under the global model. For example, areas such as Madagascar, the Seychelles and Tanzania, or the Philippines, Malaysia and Gulf of Thailand require much broader research coverage to validate the existing hypotheses of connectivity.

Tagging studies should also target many *R. typus* within the same aggregation to chronicle the highest number of potential movement patterns (Eckert & Stewart, 2001; Wilson *et al.*, 2006), and tags should be deployed as close to the end of the peak aggregation season as possible to maximize the potential for measuring long-distance trajectories, especially given the short monitoring periods characteristic of such studies (Hammerschlag *et al.*, 2011). Other improvements to maximize monitoring time include the application of anti-fouling paint to tracking equipment (Hammerschlag *et al.*, 2011), using Fastloc GPS technology (Hays *et al.*, 2007) and switching from steel to copper saltwater switches used to improve the efficiency of duty cycling (Hays *et al.*, 2007). Improvements in tag attachment methods are also needed to prevent premature detachment (Brunnschweiler *et al.*, 2009).

Another important consideration when describing migratory patterns is that longer migrations might reflect sex and age-specific behaviour. Indeed, three of the five *R. typus* tracks exceeding 3000 km (excluding the longer track from the Pacific Ocean and the juveniles tracked off Taiwan) were large females (*c*. 7 m) (Fig. 3). As suggested previously, female natal philopatry might result in long migrations only for the purposes of occasional breeding (Ramírez-Macías *et al.*, 2007). This

sort of sex-specific behaviour would also explain the high resighting rates in some aggregations dominated by immature males. While a similar number of males and females tracks have been published to date, different size classes (≤ 6 or > 6 m) have different average track lengths (250 and 1240 km, respectively where information on sex is available). Of course, there are exceptions to this trend; some juveniles tagged in Taiwan had tracks > 3000 km although they remained resident (Hsu *et al*., 2007). More tracking studies of longer duration will assist in describing these stage-specific movement trends and capacities.

Given the large distances between some of the known aggregations, another way to refine knowledge of this species is to profit from the opportunities provided by certain pelagic fisheries. Expansive commercial fisheries (*e.g*. tuna purse seiners) do release *R. typus* that are accidentally captured or encircled by their nets. Tagging endeavours associated with these releases could potentially provide the data necessary to estimate vital rates and a better description of pelagic movement patterns. Further, focussing tag deployments and tissue collections near potential thoroughfares, such as those hypothesized under the present model like the Saint Peter and Saint Paul Archipelago and Christmas Island, would probably increase the probability of capturing pan or trans-oceanic movements.

Supporting Information

Supporting Information may be found in the online version of this paper:
 TABLE SI. Summary of representative *Rhincodon typus* studies (since 1996) included in Fig. 1, grouped by (1) occurrence, population and correlates for occurrence, (2) movement, (3) tourism and conservation, (4) mortality and (5) foraging, in different locations worldwide

References

Aca, E. Q. & Schmidt, J. V. (2011). Revised size limit for viability in the wild: neonatal and young of the year whale sharks identified in the Philippines. *Asia Life Sciences* **20**, 361–367.
Anderson, R. C. & Ahmed, H. (1993). *The Shark Fisheries in the Maldives*. Malé: Ministry of Fisheries and Agriculture, Republic of the Maldives (Bay of Bengal Programme).
Anderson, R. C. & Waheed, A. (2001). The economics of shark and ray watching in the Maldives. *Shark News - Newsletter of the IUCN Shark Specialist Group* **13**, 1–4. http://www.iucnssg.org/tl_files/Assets/pdf/SN/SN13%20LOW%20RES.pdf
Baughman, J. L. (1955). The oviparity of the whale shark, *Rhincodon typus*, with records of this and other fishes in Texas waters. *Copeia* **1955**, 54–55.

Beckley, L. E., Cliff, G., Smale, M. J. & Compagno, L. J. V. (1997). Recent strandings and sightings of whale sharks in South Africa. *Environmental Biology of Fishes* **50**, 343–348.

Borrell, A., Aguilar, A., Gazo, M., Kumarran, R. P. & Cardona, L. (2011). Stable isotope profiles in whale shark (*Rhincodon typus*) suggest segregation and dissimilarities in the diet depending on sex and size. *Environmental Biology of Fishes* **92**, 559–567.

Bradshaw, C. J. A. (2007). Swimming in the deep end of the gene pool: global population structure of an oceanic giant. *Molecular Ecology* **16**, 5111–5114.

Bradshaw, C. J. A., Mollet, H. F. & Meekan, M. G. (2007). Inferring population trends for the world's largest fish from mark–recapture estimates of survival. *Journal of Animal Ecology* **76**, 480–489.

Brooks, K., Rowat, D., Pierce, S. J., Jouannet, D. & Vely, M. (2010). Seeing spots: photo-identification as a regional tool for whale shark identification. *Western Indian Ocean Journal of Marine Sciences* **9**, 185–194.

Brunnschweiler, J. M., Baensch, H., Pierce, S. J. & Sims, D. W. (2009). Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean. *Journal of Fish Biology* **74**, 706–714.

Cárdenas-Palomo, N., Herrera-Silveira, J. & Reyes, Ó. (2010). Spatial and temporal distribution of physicochemical features in the habitat of whale shark *Rhincodon typus* (Orectolobiformes: Rhincodontidae) in the north of Mexican Caribbean. *Revista de Biología Tropical* **58**, 399–412.

Cárdenas-Torres, N., Enríquez-Andrade, R. & Rodríguez-Dowdell, N. (2007). Community-based management through ecotourism in Bahia de Los Angeles, Mexico. *Fisheries Research* **84**, 114–118.

Castro, A. L. F., Stewart, B. S., Wilson, S. G., Hueter, R. E., Meekan, M. G., Motta, P. J., Bowen, B. W. & Karl, S. A. (2007). Population genetic structure of Earth's largest fish, the whale shark (*Rhincodon typus*). *Molecular Ecology* **16**, 5183–5192.

Catlin, J. & Jones, R. (2009). Whale shark tourism at Ningaloo Marine Park: a longitudinal study of wildlife tourism. *Tourism Management* **31**, 1–9.

Chang, W.-B., Ley, M.-Y. & Fang, L.-S. (1997). Embryos of the whale shark, *Rhincodon typus*: early growth and size distribution. *Copeia* **1997**, 444–446.

Chen, C.-T., Liu, K.-M. & Joung, S.-J. (1997). Preliminary report on Taiwan's whale shark fishery. *Traffic Bulletin* **17**, 53–57.

Cliff, G., Anderson-Reade, M. D., Aitken, A. P., Charter, G. E. & Peddemors, V. M. (2007). Aerial census of whale sharks (*Rhincodon typus*) on the northern KwaZulu-Natal coast, South Africa. *Fisheries Research* **84**, 41–46.

Colman, J. G. (1997). A review of the biology and ecology of the whale shark. *Journal of Fish Biology* **51**, 1219–1234.

Compagno, L. J. V. (2001). *Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date*, Vol. **2**. Rome: FAO.

Dove, A. D. M., Arnold, J. & Clauss, T. M. (2010). Blood cells and serum chemistry in the world's largest fish: the whale shark *Rhincodon typus*. *Aquatic Biology* **9**, 177–183.

Duffy, C. A. J. (2002). Distribution, seasonality, lengths, and feeding behaviour of whale sharks (*Rhincodon typus*) observed in New Zealand waters. *New Zealand Journal of Marine and Freshwater Research* **36**, 565–570.

Eckert, S. A. & Stewart, B. S. (2001). Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez (Mexico) and the north Pacific Ocean. *Environmental Biology of Fishes* **60**, 299–308.

Eckert, S. A., Dolar, L. L., Kooyman, G. L., Perrin, W. & Rahman, R. A. (2002). Movements of whale sharks (*Rhincodon typus*) in South-east Asian waters as determined by satellite telemetry. *Zoological Society of London* **257**, 111–115.

Fitzpatrick, B., Meekan, M. & Richards, A. (2006). Shark attacks on a whale shark (*Rhincodon typus*) at Ningaloo reef, Western Australia. *Bulletin of Marine Science* **78**, 397–402.

Gifford, A., Compagno, L. J. V., Levine, M. & Antoniou, A. (2007). Satellite tracking of whale sharks using tethered tags. *Fisheries Research* **84**, 17–24.

Graham, R. T. & Roberts, C. M. (2007). Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. *Fisheries Research* **84**, 71–80.

Gudger, E. W. (1932). The whale shark, *Rhincodon typus*, among the Seychelles islands. *Nature* **130**, 169.

Gudger, E. W. (1934). The geographical distribution of the whale shark (*Rhincodon typus*). *American Museum of Natural History* , 863–893.

Gunn, J. S., Whitelaw, A. W., Davis, T. L. O., Bailey, K. & Itano, D. G. (1992). Tuna tagging in the Coral Sea. *Australian Fisheries* **51**, 22–24.

Gunn, J. S., Stevens, J. D., Davis, T. L. O. & Norman, B. M. (1999). Observations on the short-term movements and behaviour of whale sharks (*Rhincodon typus*) at Ningaloo Reef (Western Australia). *Marine Biology* **135**, 553–559.

Hammerschlag, N., Gallagher, A. J. & Lazarre, D. M. (2011). A review of shark satellite tagging studies. *Journal of Experimental Marine Biology and Ecology* **398**, 1–8.

Harborne, A. R., Afzal, D. C. & Andrews, M. J. (2001). Honduras: Caribbean coast. *Marine Pollution Bulletin* **42**, 1221–1235.

Hartl, D. L. & Clark, A. G. (1989). *Principles of Population Genetics*, 2nd edn. Sunderland, MA: Sinauer Associates Inc..

Hays, G. C., Bradshaw, C. J. A., James, M. C., Lovell, P. & Sims, D. W. (2007). Why do Argos satellite tags deployed on marine animals stop transmitting? *Journal of Experimental Marine Biology and Ecology* **349**, 52–60.

Hazin, F. H. V., Vaske Júnior, T., Oliveira, P. G., Macena, B. C. L. & Carvalho, F. (2008). Occurrences of whale shark (*Rhincodon typus* Smith, 1828) in the Saint Peter and Saint Paul archipelago, Brazil. *Brazilian Journal of Biology* **68**, 385–389.

Hegerl, G. C. & Bindoff, N. L. (2005). Warming the world's oceans. *Science* **309**, 254–255.

Heyman, W. D., Graham, R. T., Kjerfve, B. & Johannes, R. E. (2001). Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series* **215**, 275–282.

Hsu, H.-H., Joung, S.-J., Liao, Y.-Y. & Liu, K.-M. (2007). Satellite tracking of juvenile whale sharks, *Rhincodon typus*, in the Northwestern Pacific. *Fisheries Research* **84**, 25–31.

Irvine, T. R. & Keesing, J. K. E. (Eds) (2007). Whale sharks: science, conservation and management. In: Proceedings of the First International Whale Shark Conference. *Fisheries Research* **84**.

Iwasaki, Y. (1970). On the distribution and environment of the whale shark, *Rhincodon typus*, in Skipjack fishing grounds in the Western Pacific Ocean. *Journal of the College of Marine Science and Technology, Tokai University* **4**, 37–51.

Jonahson, M. & Harding, S. (2007). Occurrence of whale sharks (*Rhincodon typus*) in Madagascar. *Fisheries Research* **84**, 132–135.

Joung, S.-J., Chen, C.-T., Clark, E., Uchida, S. & Huang, W. Y. P. (1996). The whale shark (*Rhincodon typus)* is a livebearer: 300 embryos found in one 'megamamma' supreme. *Environmental Biology of Fishes* **46**, 219–223.

Klein, B. & Siedler, G. (1989). On the origin of the Azores current. *Journal of Geophysical Research* **94**, 6159–6168.

Kukuyev, E. I. (1996). The new finds in recently born individuals of the whaleshark *Rhincodon typus* (Rhiniodontidae) in the Atlantic Ocean. *Journal of Ichthyology* **36**, 203–205.

Kumari, B. & Raman, M. (2010). Whale shark habitat assessments in the northeastern Arabian Sea using satellite remote sensing. *International Journal of Remote Sensing* **31**, 379–389.

Last, P. R. & Stevens, J. D. (2009). *Sharks and Rays of Australia*, 2nd edn. Collingwood: CSIRO.

Martin, R. A. (2007). A review of behavioural ecology of whale sharks (*Rhincodon typus*). *Fisheries Research* **84**, 10–16.

Meekan, M. G., Bradshaw, C. J. A., Press, M., McLean, C., Richards, A., Quasnichka, S. & Taylor, J. G. (2006). Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. *Marine Ecology Progress Series* **319**, 275–285.

Meekan, M. G., Jarman, S. N., McLean, C. & Schultz, M. B. (2009). DNA evidence of whale sharks (*Rhincodon typus*) feeding on red crab (*Gecarcoidea natalis*) larvae at Christmas Island, Australia. *Marine and Freshwater Research* **60**, 607–609.

Morjan, C. L. & Rieseberg, L. H. (2004). How species evolve collectively: implications of gene flow and selection for the spread of advantageous alleles. *Molecular Ecology* **13**, 1341–1356.

Motta, P. J., Maslanka, M., Hueter, R. E., Davis, R. L., Parra, R. d. l., Mulvany, S. L., Habegger, M. L., Strother, J. A., Mara, K. R., Gardiner, J. M., Tyminski, J. P. & Zeigler, L. D. (2010). Feeding anatomy, filter-feeding rate, and diet of whale sharks *Rhincodon typus* during surface ram filter feeding off the Yucatan Peninsula, Mexico. *Zoology* **113**, 190–212.

Nelson, J. D. & Eckert, S. A. (2007). Foraging ecology of whale sharks (*Rhincodon typus*) within Bahía de Los Angeles, Baja California Norte, México. *Fisheries Research* **84**, 47–64.

Pauly, D. (1997). Growth and mortality of the basking shark *Cetorhinus maximus* and their implications for management of whale sharks *Rhincodon typus*. In *Elasmobranch Biodiversity, Conservation and Management, International Seminar and Workshop, Sabah, Malaysia* (Fowler, S. L., Reed, T. M. & Dipper, F. A., eds), pp. 199–208. Gland: IUCN SSC Shark Specialist Group. http://data.iucn.org/dbtw-wpd/edocs/ssc-op-025.pdf

Pierce, S. J., Méndez-Jiménez, A., Collins, K., Rosero-Caicedo, R. & Monadjem, A. (2010). Developing a code of conduct for whale shark interactions in Mozambique. *Aquatic Conservation: Marine and Freshwater Eecosystems* **20**, 782–788.

Pillai, S. K. (1998). On a whale shark *Rhincodon typus* found accompanied by its young ones. *Marine Fisheries Information Service Technical and Extension Series* **152**, 15.

Pravin, P. (2000). Whale shark in the Indian coast – need for conservation. *Current Science* **79**, 310–315.

Quiros, A. L. (2007). Tourist compliance to a code of conduct and the resulting effects on whale shark (*Rhincodon typus*) behavior in Donsol, Philippines. *Fisheries Research* **84**, 102–108.

Ramírez-Macías, D., Vázquez-Juárez, R., Galván-Magaña, F. & Munguía-Vega, A. (2007). Variations of the mitochondrial control region sequence in whale sharks (*Rhincodon typus*) from the Gulf of California, Mexico. *Fisheries Research* **84**, 87–95.

Richardson, A. J. & Poloczanska, E. S. (2008). Under-resourced, under threat. *Science* **320**, 1294–1295.

Riley, M. J., Harman, A. & Rees, R. G. (2009). Evidence of continued hunting of whale sharks *Rhincodon typus* in the Maldives. *Environmental Biology of Fishes* **86**, 371–374.

Riley, M. J., Hale, M. S., Harman, A. & Rees, R. G. (2010). Analysis of whale shark *Rhincodon typus* aggregations near South Ari atoll, Maldives Archipelago. *Aquatic Biology* **8**, 145–150.

Romanov, E. V. (2002). Bycatch in the tuna purse-seine fisheries of the western Indian Ocean. *Fishery Bulletin* **100**, 90–105.

Rowat, D. (2007). Occurrence of whale shark (*Rhincodon typus*) in the Indian Ocean: a case for regional conservation. *Fisheries Research* **84**, 96–101.

Rowat, D. & Engelhardt, U. (2007). Seychelles: a case study of community involvement in the development of whale shark ecotourism and its socio-economic impact. *Fisheries Research* **84**, 109–113.

Rowat, D. & Gore, M. (2007). Regional scale horizontal and local scale vertical movements of whale sharks in the Indian Ocean off Seychelles. *Fisheries Research* **84**, 32–40.

Rowat, D., Meekan, M. G., Engelhardt, U., Pardigon, B. & Vely, M. (2007). Aggregations of juvenile whale sharks (*Rhincodon typus*) in the Gulf of Tadjoura, Djibouti. *Environmental Biology of Fishes* **80**, 465–472.

Rowat, D., Gore, M. A., Baloch, B. B., Islam, Z., Ahmad, E., Ali, Q. M., Culloch, R. M., Hameed, S., Hasnain, S. A., Hussain, B., Kiani, S., Siddiqui, J., Ormond, R. F., Henn, N. & Khan, M. (2008). New records of neonatal and juvenile whale sharks (*Rhincodon typus*) from the Indian Ocean. *Environmental Biology of Fishes* **82**, 215–219.

Rowat, D., Gore, M., Meekan, M. G., Lawler, I. R. & Bradshaw, C. J. A. (2009). Aerial survey as a tool to estimate whale shark abundance trends. *Journal of Experimental Marine Biology and Ecology* **368**, 1–8.

Rowat, D., Brooks, K., March, A., McCarten, C., Jouannet, D., Riley, L., Jeffreys, G., Perri, M., Vely, M. & Pardigon, B. (2011). Long-term membership of whale sharks (*Rhincodon typus*) in coastal aggregations in Seychelles and Djibouti. *Marine and Freshwater Research* **62**, 621–627.

Schmidt, J. V., Schmidt, C. L., Ozer, F., Ernst, R. E., Feldheim, K. A., Ashley, M. V. & Levine, M. (2009). Low genetic differentiation across three major ocean populations of the whale shark, *Rhincodon typus*. *PLoS One* **4**, e4988. doi: 4910.1371/journal.pone.0004988

Schmidt, J. V., Chen, C.-C., Sheikh, S. I., Meekan, M. G., Norman, B. M. & Joung, S.-J. (2010). Paternity analysis in a litter of whale shark embryos. *Endangered Species Research* **12**, 117–124.

Sequeira, A., Mellin, C., Rowat, D., Meekan, M. G. & Bradshaw, C. J. A. (2012). Ocean-scale prediction of whale shark distribution. *Diversity and Distributions* **18**, 504–518.

Sleeman, J. C., Meekan, M. G., Wilson, S. G., Polovina, J. J., Stevens, J. D., Boggs, G. S. & Bradshaw, C. J. A. (2010*a*). To go or not to go with the flow: environmental influences on whale shark movement patterns. *Journal of Experimental Marine Biology and Ecology* **390**, 84–98.

Sleeman, J. C., Meekan, M. G., Fitzpatrick, B. J., Steinberg, C. R., Ancel, R. & Bradshaw, C. J. A. (2010*b*). Oceanographic and atmospheric phenomena influence the abundance of whale sharks at Ningaloo Reef, Western Australia. *Journal of Experimental Marine Biology and Ecology* **382**, 77–81.

Smith, A. (1828). Descriptions of new, or imperfectly known objects of the animal kingdom, found in South Africa. *South African Commercial Advertiser* **145**, 2.

Speed, C. W., Meekan, M. G. & Bradshaw, C. J. A. (2007). Spot the match – wildlife photo-identification using information theory. *Frontiers in Zoology* **4**, 2. doi: 10.1186/1742-9994-1184-1182

Speed, C. W., Meekan, M. G., Rowat, D., Pierce, S. J., Marshall, A. D. & Bradshaw, C. J. A. (2008). Scarring patterns and relative mortality rates of Indian Ocean whale sharks. *Journal of Fish Biology* **72**, 1488–1503.

Stevens, J. D. (2007). Whale shark (*Rhincodon typus*) biology and ecology: a review of the primary literature. *Fisheries Research* **84**, 4–9.

Stewart, B. S. & Wilson, S. G. (2005). Threatened fishes of the world: *Rhincodon typus* (Smith 1828) (Rhincodontidae). *Environmental Biology of Fishes* **74**, 184–185.

Taylor, J. G. (1996). Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research* **47**, 637–642.

Turnbull, S. D. & Randell, J. E. (2006). Rare occurrence of a *Rhincodon typus* (whale shark) in the Bay of Fundy, Canada. *Northeastern Naturalist* **13**, 57–58.

Uchida, S. (1984). Investigations of whale shark in Taiwan and Philippines. *Report of Japanese Group for Elasmobranch Studies* [Itaera rui kenkyu renrakukai ho]. Tokyo: Ocean Research Institute, University of Tokyo (in Japanese with English abstract).

Van Tienhoven, A. M., Den Hartog, J. E., Reijns, R. A. & Peddemors, V. M. (2007). A computer-aided program for pattern-matching of natural marks on the spotted ragged tooth shark *Carcharias taurus*. *Journal of Applied Ecology* **44**, 273–280.

Venegas, R. d. l. P., Hueter, R., Cano, J. G., Tyminski, J., Remolina, J. G., Maslanka, M., Ormos, A., Weigt, L., Carlson, B. & Dove, A. (2011). An unprecedented aggregation of whale sharks, *Rhincodon typus*, in Mexican coastal waters of the Caribbean Sea. *PLoS One* **6**, e18994. doi: 18910.11371/journal.pone.0018994

White, W. T. & Cavanagh, R. D. (2007). Whale shark landings in Indonesian artisanal shark and ray fisheries. *Fisheries Research* **84**, 128–131.

Wilson, S. G. (2002). A whale shark feeding in association with a school of giant herring at Ningaloo Reef, Western Australia. *Journal of the Royal Society of Western Australia* **85**, 43–44.

Wilson, S. G. & Martin, R. A. (2001). Body markings of the whale shark: vestigial or functional? *Western Australian naturalist* **24**, 115–134.

Wilson, S. G., Polovina, J. J., Stewart, B. S. & Meekan, M. G. (2006). Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology* **148**, 1157–1166.

Wilson, S. G., Stewart, B. S., Polovina, J. J., Meekan, M. G., Stevens, J. D. & Galuardi, B. (2007). Accuracy and precision of archival tag data: a multiple-tagging study conducted on a whale shark (*Rhincodon typus*) in the Indian Ocean. *Fisheries Oceanography* **16**, 547–554.

Wintner, S. P. (2000). Preliminary study of vertebral growth rings in the whale shark, *Rhincodon typus*, from the east coast of South Africa. *Environmental Biology of Fishes* **59**, 441–451.

Wirtz, P., Fricke, R. & Biscoito, M. J. (2008). The coastal fishes of Madeira Island - new records and an annotated check-list. *Zootaxa* **1715**, 1–26.

Wolfson, F. H. (1983). Records of seven juveniles of the whale shark, *Rhincodon typus*. *Journal of Fish Biology* **22**, 647–655.

Wolfson, F. H. (1986). Occurrences of whale shark, *Rhincodon typus* Smith. In *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes* (Ureno, T., Arai, R., Taniuchi, T. & Matsuura, K., eds), pp. 208–226. Tokyo: Ichthyological Society of Japan.

Wolfson, F. H. & Notarbartolo-di-Sciara, G. (1981). The whale shark bibliography. *Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **122**, 171–203.

Yopak, K. E. & Frank, L. R. (2009). Brain size and brain organization of the whale shark, *Rhincodon typus*, using magnetic resonance imaging. *Brain, Behaviour and Evolution* **74**, 121–142.

Electronic References

CSIRO (2005). Whale Sharks: six whale sharks tagged at Ningaloo Reef. Hobart, TAS: Commonwealth Science and Industrial Research Organization–Marine and Atmospheric Research. Available at http://www.cmar.csiro.au/tagging/whale/ningaloo.html

COA (2007). COA bans fishing for whale sharks. In *Taipei Times*. **27/05/07**, 4. Available at http://www.taipeitimes.com/News/taiwan/archives/2007/05/27/ 2003362648/

Graham, R. T., Jacquin, S., Bakary, G., Witt, M. & Randriamahazo, H. (2008). Characteristics of whale shark seasonality and abundance in NW Madagascar and dispersal in the Western Indian Ocean. *Second International Whale Shark Symposium, Holbox*, Quinta Roo, Mexico (PowerPoint display only). Available at http://www.domino.conanp.gob.mx/presentaciones.html/ (accessed 26 October 2012).

Green, J. R. (2011). Tracks of all 14 tagged animals. *Galapagos Whale Shark Project – Researching for Knowledge*. Available at http://www.galapagoswhaleshark.com/index. php?option=com_content&view=article&id=2:track-of-all-tagged-animals&catid=1:last est&Itemid=22

Haetrakul, T., Munanansup, S., Assawawongkasem, N. & Chansue, N. (2007). A case report: stomach foreign object in whale shark (*Rhincodon typus*) stranded in Thailand. In *4th International Symposium on SEASTAR2000 and Asian Biologging Science*, pp. 83–85. Kyoto: Kyoto University Research Information Repository 2009-03-12T05:56:49Z. Available at http://repository.kulib.kyoto-u.ac. jp/dspace/bitstream/2433/71015/1/8thSEASTAR_83.pdf (accessed 26 October 2012).

Hueter, R., Tyminski, J. & de la Parra, R. (2008). The geographical movements of whale sharks tagged with pop-up archival satellite tags off Quintana Roo, Mexico. *Second International Whale Shark Symposium, Holbox*, Quinta Roo, Mexico (PowerPoint display only). Available at http://www.domino.conanp.gob.mx/doc_conf/Bob.pdf

MCSS (2009). *China Splash Tag starts to transmit*! Mont Fleuri: Marine Conservation Society Seychelles. Available at http://seychelles-whale-sharks.blogspot.co.uk/2009/07/ china-splash-tag-starts-to-transmit.html

MML (2010) *Dubai whale shark's movements mapped: whale shark released from Atlantis, The Palm is the first tracked in Arabian Gulf*. Sarasota, FL: Mote Marine Laboratory. Available at http://www.mote.org/index.php?src=news&refno=379&category=News room

Norman, B. 2012. *Rhincodon typus*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. Available at http://www.iucnredlist.org/details/19488/0

Sa, N. (2008). Gigantes na ilha de Santa Maria. *National Geographic*. (November, 2008). Available at http://www.nationalgeographic.pt/sumario.jsp?id=1744887/ (accessed 26 October 2012).

Stacey, N., Karam, J., Dwyer, D., Speed, C. & Meekan, M. (2008). Assessing traditional ecological knowledge of whale sharks (*Rhincodon typus*) in eastern Indonesia: a pilot study with fishing communities in Nusa Tenggara Timur. *Report Prepared for the Department of the Environment, Water, Heritage and the Arts, Canberra*. Darwin: School for Environmental Research, Charles Darwin University. Available at http://www.environment.gov.au/coasts/publications/assessing-whale-sharks.html/ (accessed 26 October 2012).

UNCLOS (1982). *United Nations Convention on the Law of the Sea. Division for Ocean Affairs and the Law of the Sea*. New York, NY: United Nations. Available at http://www.un.org/Depts/los/convention_agreements/convention_overview_convention.htm/

UNFSA (1995). Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 Relating to the Conservation and Management of Straddling Stock and Highly Migratory Fish Stocks. In *Sixth Session of the United Nations Conference on Straddling Fish Stocks and Highly Mirgratory Fish Stocks*. **A/CONF.164/37**. New York, NY: United Nations General Assembly. Available at http://daccess-dds-ny.un.org/doc/UNDOC/GEN/N95/274/67/PDF/N9527467.pdf?OpenElement

WWF (2012). Dead whale shark found off Manila Bay. *WWF, Newsroom*. Manilla: World Wildlife Foundation. Available at http://www.wwf.org.ph/newsfacts.php?pg=det&id=169/