



A review of the biology, fisheries and conservation of the whale shark *Rhincodon typus*

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Although the whale shark *Rhincodon typus* is the largest extant fish, it was not described until 1828 and by 1986 there were only 320 records of this species. Since then, growth in tourism and marine recreation globally has led to a significant increase in the number of sightings and several areas with annual occurrences have been identified, spurring a surge of research on the species. Simultaneously, there was a great expansion in targeted *R. typus* fisheries to supply the Asian restaurant trade, as well as a largely un-quantified by-catch of the species in purse-seine tuna fisheries. Currently *R. typus* is listed by the IUCN as vulnerable, due mainly to the effects of targeted fishing in two areas. Photo-identification has shown that *R. typus* form seasonal size and sex segregated feeding aggregations and that a large proportion of fish in these aggregations are philopatric in the broadest sense, tending to return to, or remain near, a particular site. Somewhat conversely, satellite tracking studies have shown that fish from these aggregations can migrate at ocean-basin scales and genetic studies have, to date, found little genetic differentiation globally. Conservation approaches are now informed by observational and environmental studies that have provided insight into the feeding habits of the species and its preferred habitats. Notwithstanding these advances, there remain notable gaps in the knowledge of this species particularly with respect to the life history of neonates and adults who are not found in the feeding aggregations.

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INTRODUCTION

The whale shark *Rhincodon typus* Smith 1828 has become an iconic shark in many respects; it is the world's largest living species of fish, but as a plankton feeder it is harmless to humans. It was first described to science in 1828 (Smith, 1828) but despite its status as the largest fish in the sea, by 1985, over 150 years later, there were only 320 records of this species (Wolfson, 1986). Similarly, while specimens had been dissected, much of its biology and habits remained uncertain, including its method of reproduction (Colman, 1997a; Stevens, 2007) prompting its description as enigmatic ('mysterious or difficult to understand' Oxford dictionary) by some researchers (Norman & Catlin, 2007; Schmidt *et al.*, 2010). In certain locations *R. typus* are known to occur on a predictable, seasonal basis (Anderson & Ahmed, 1993; Alava *et al.*, 1997a; Eckert & Stewart, 2001; Eckert *et al.*, 2002) and in some

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locations sizeable aggregations can be found (Taylor, 1989; Rowat, 1997; Heyman *et al.*, 2001; de la Parra Venegas *et al.*, 2011). The finding of these sites has significantly increased the number of sightings in recent years, especially as in many areas these aggregations have lent themselves to a lucrative and increasingly popular ecotourism industry (Colman, 1997a; Davis *et al.*, 1997; Graham, 2007; Quiros, 2007; Rowat & Engelhardt, 2007). Such predictability of occurrence, however, has in other areas rendered them vulnerable to exploitation and targeted fisheries since these giant fish attract a high price on the Asian markets for both their flesh as Tofu shark and also for their fins, to be used as trophy fins on display in shark-fin soup restaurants (Chen *et al.*, 1997; Hanfee, 2001; Chen & Phipps, 2002).

The reliable presence of *R. typus* at known seasonal aggregation sites and concern about the effect of the targeted fisheries, combined to accelerate research into the species and a significant amount has been accomplished since 1986. There have been two major reviews, an IUCN Red List assessment and a scoping study on the species during this period. This paper aims to provide a synthesis of previous significant findings, to highlight gaps in current knowledge and research, and to suggest how current or potential research initiatives can fill these gaps. This approach is taken firstly, with current information on *R. typus* biology, ecology and habits. Next population structure and behaviour are considered, before examining mortality and exploitation from both targeted fisheries and by-catch in non-targeted fisheries, as well as non-consumptive exploitation of *R. typus* in tourism activities and their perceived effects. The status of current conservation and management approaches at national and international scales will be discussed and finally, the core issues that need to be resolved for effective conservation are highlighted and in so doing it is decided whether or not *R. typus* can still be considered an enigma.

BIOLOGY, ECOLOGY AND HABITS

TAXONOMY

Rhincodon typus belongs to the monotypic family Rhincodontidae within the Order Orectolobiformes, which has 42 species including Stegostomidae (leopard sharks), Ginglymostomatidae (nurse sharks) and Orectolobidae (wobbegongs). Their association is based on several morphological and anatomical similarities to the other families in this order including skeletal anatomy, tooth and dermal denticle morphology, fin placement and barbel morphology (Compagno, 1973). For all these similarities however, *R. typus* is the only orectoloboid that is pelagic in habit. Although there is only one extant species, the fossil record indicates there were at least three ancestral species in the genus *Palaeorhincodon* dating from the Eocene period, 35–58 million years ago (Bourdon, 1999).

GENERAL DESCRIPTION

Rhincodon typus has a spindle shaped, fusiform body (widest in the middle and tapering to the ends) and is characterized by its large size, three conspicuous longitudinal ridges (carina) along its dorsal flanks, a large first dorsal fin and semi-lunate caudal fin. It has a broad, flattened head with a large terminal mouth and the dorsal

surfaces exhibit a marked pattern of light spots and stripes over a dark background, with a light ventral surface (Compagno, 2001). The characteristic body markings are a combination of two forms of camouflage; the spots and stripes being disruptive colouration, while the lighter ventral surface is termed counter-shading (Wilson & Martin, 2003). Both are probably used in a defensive manner and may be especially important during their early years to hide them from predators.

There has been little research into the anatomy of *R. typus* since the early days of research into the species (White, 1930; Dennison, 1937). As with all sharks, *R. typus* have a number of adaptations to make them more efficient; the skin is studded with dermal denticles which are hydrodynamic in form, reducing drag and surface-noise production. In *R. typus* these denticles have three longitudinal ridges, the central one forming a strong central keel with deep furrows on either side (Bigelow & Schroeder, 1948). They have a skeleton made of light-weight, flexible cartilage (Gudger, 1915). They also lack a rib-cage which saves weight and is compensated, to some extent, by a sub-dermal complex mesh corset of collagen fibres (Martin, 2005). This corset also functions as a flexible external skeleton, permitting the sub-dermal attachment of the locomotory muscles from the backbone in a light and mechanically efficient system. *Rhincodon typus* have a very high proportion of white myotomal locomotory muscle; this is muscle with a poor oxygen supply which functions by anaerobic glycolysis (Wilson & Martin, 2003). This allows the muscle to react very rapidly but builds up lactic acid; it is thought that such muscles are primarily used for short rapid bursts of speed. What advantage this has to *R. typus* is a matter of conjecture, but may have some bearing on their ability to perform very deep dives, currently recorded in excess of 1700 m (Tyminski *et al.*, 2008).

Very little research has been carried out on the physiology of *R. typus*, due largely to the difficulty of conducting such research on a fish of this size. Some haematology and clinical chemistry aspects have been derived from blood samples taken at the Georgia Aquarium (Dove *et al.*, 2010). Healthy captive individuals had typical elasmobranch erythrocytes similar to those of other orectolobiform sharks (Old & Huvneers, 2006) and white blood cell differentials similar to other elasmobranchs. Samples from two other individuals that later died both showed elevated white blood cell counts as their condition deteriorated. This is an area of research that offers much promise although some significant differences in haematology and clinical chemistry values were noted between samples taken from the caudal vein and dorsal posterior cardinal vein (Dove *et al.*, 2010) indicating standardization may be an issue. No hormonal studies have currently been completed on the species and this is an area with significant potential in terms of providing information on the reproductive state of individuals. Taking blood samples from free swimming *R. typus* may seem unlikely, but initial trials have indicated that this is possible (A. Dove pers. comm.).

Rhincodon typus is a filter feeder, specializing in feeding on a range of planktonic organisms, with the teeth themselves seeming to play little if any role in feeding (Gudger, 1915). Planktonic prey are captured by filtering the sea water through a filter-like apparatus comprising five sets of porous pads on each side of the pharyngeal cavity; the rear-most pair are almost triangular in shape and lead into a narrow oesophagus (Motta *et al.*, 2010). The pads are all interconnected by a connective tissue raphe so that water entering the pharyngeal cavity has to pass through the pads prior to passing over the gills and out through the external gill slits. While advances in knowledge of the structure and function of the feeding apparatus in sub-adult and

adult specimens have been made (Motta *et al.*, 2010), there has been little research into differences, if any, between these stages and the very young. The initial study by Garrick (1964) indicated that the filtration mechanism was very underdeveloped at the late embryo stage with only the rudimentary gill 'rakers'. Recent stable-isotope analysis of *R. typus* muscle tissue showed a positive relationship of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with the size of the fish, suggesting that as they increase in size, their diets change to include prey items of a larger size and higher trophic level (Borrell *et al.*, 2011). *Rhincodon typus* of <4 m total length (L_T) showed a lower $\delta^{13}\text{C}$ than larger individuals suggesting a transition from pelagic to more coastal foraging habitats. Further research in this area might provide clues as to the likely prey and thus habitat of very small juvenile *R. typus*.

REPRODUCTION AND LIFE HISTORY

Pregnant females and very small *R. typus* are very rarely encountered (Colman, 1997a; Fowler, 2000) with gravid females regularly reported from only one area, the south of Baja, in the eastern Pacific Ocean (Eckert & Stewart, 2001); large females are also present off Galapagos and the Philippines (M. Levine & J. Schmidt pers. comm.). The method of reproduction in this species was unclear until 1995, when a pregnant *R. typus* of 10.6 m L_T was landed at Chen-Kung fish market, Taiwan (Joung *et al.*, 1996). This fish had 304 embryos combined from the two uteri; many were in their egg cases and had external yolk sacs, but many were also not in egg cases and without a yolk sac. This proved conclusively that *R. typus* are aplacental viviparous. Three levels of embryo development were found giving L_T classes of 42–52, 52–58 and 58–64 cm; the largest being free of their egg cases, with no external yolk sacs, indicating they were ready to be released. This litter is the largest recorded from any shark species.

Currently only 19 *R. typus* specimens of <1.5 m have been reported (Table I), most of which have been captured in fishing gear. Of note, an embryo of 94 cm L_T was reported from India with an external yolk sac attached, indicating that it was not full term (Manojkumar, 2003), while in the Philippines a free swimming neonatal *R. typus* pup of 46 cm L_T was found (Aca & Schmidt, 2011). This latter specimen had a freshly healed vitelline scar on its abdomen, where the yolk sac had been recently adsorbed into the body, indicating that it was a full-term embryo (Duncan & Holland, 2006; Hussey *et al.*, 2010). These two findings suggest that *R. typus* pups may vary considerably in size at birth, compared to those found in the Taiwanese litter. The scarcity of these pups is a significant barrier to fully understanding the life history of *R. typus* and research into potential anatomical differences in these neonates may lead to the discovery of their habitat.

A total of 237 embryos from the Taiwanese litter were sexed, 114 were male and 123 were female indicating a normal 50:50 sex ratio at birth (Joung *et al.*, 1996; Leu *et al.*, 1997). Recent genetic analysis of 29 of the pups of various sizes, found that all had the same father (Schmidt *et al.*, 2010). This provides strong evidence that a single male sired the entire litter (monoandry), although probability analysis suggested it was feasible that another male might have sired <10% of these 300 pups.

This recent finding provides further insight into the reproductive strategy and habits of *R. typus*. The varied stages of embryo development recorded from this litter could easily have been reconciled by multiple paternity, but this now seems unlikely.

TABLE I. Records of neonatal *Rhincodon typus* (<1.5 m total length, L_T), area of discovery and source

Region	Numbers	L_T cm	Stage	Reference
Texas, Gulf of Mexico	1	35.5	Em	1
India, north Indian Ocean	1	94	Em	6
West Pacific Ocean	4	55–93	FS	2
West Atlantic Ocean	3	56, 56, 57	FS	2
Mauritius, south-west Indian Ocean	1	61	FS	4
Sierre Leone, west Atlantic Ocean	1	59	FS	3
Central Atlantic Ocean	1	55.7	FS	3
India, north Indian Ocean	1	95	FS	5
Bangladesh, north Indian Ocean	1	113	FS	7
Pakistan, north Indian Ocean	2	58	FS	7
Philippines, south-west Pacific Ocean	3	46, 64, 140	FS	8

Em, embryos with yolk sacs attached; FS, free-swimming individuals.

¹Garrick, 1964; ²Wolfson, 1983; ³Kukuyev, 1995; ⁴Colman, 1997a; ⁵Anon, 2002; ⁶Manojkumar, 2003; ⁷Rowat *et al.*, 2007a; ⁸Aca & Schmidt, 2011.

The same effect could be found if there was a long-term pairing with the same male, but pair-bonding has not been found in sharks (J. Schmidt pers. comm.). Potentially, this staged development could be the result of embryonic diapause where fertilized eggs are maintained in a state of dormancy prior to implantation as found in some elasmobranchs (Snelson *et al.*, 1989; Simpfendorfer, 1992; White *et al.*, 2002). In these cases, however, all the embryos implant at the same time and develop thereafter at the same rate, not in successive phases as seen in the Taiwanese *R. typus*. It thus seems likely that some form of sperm storage is being utilized with fertilization of the eggs staged over a period of time. Sperm storage has been recorded in other shark species, such as blue sharks *Prionace glauca* (L. 1758) and gummy sharks *Mustelus antarcticus* Günther 1870, where the oviducal gland is modified for long-term sperm storage (Pratt, 1993; Storrie *et al.*, 2008); this may be confirmed by future dissections of *R. typus* specimens.

Polyandry can be promoted by the sex ratios and population density at mating grounds, with high levels of polyandry expected if common mating grounds exist and monoandry if mating events are rare and with single individuals (Daly-Engel *et al.*, 2010). If the genetic make-up of the Taiwanese litter is typical for *R. typus*, it would thus seem likely that they mate rarely, with a single individual, and that breeding or mating areas with large numbers of adults are unlikely to be found in this species. Ongoing studies at sites where neonatal or very small juvenile *R. typus* are being found, such as in the Philippines (Aca & Schmidt, 2011) and Djibouti (Rowat *et al.*, 2007b), may provide further insight into the breeding behaviour of this species.

SIZE AND GROWTH

The largest *R. typus* individual reported to date was from the Taiwanese fishery in 1987 and was recorded as 20 m L_T and 34 t in mass (Chen *et al.*, 1997) while the next largest was 18.8 m L_T from the Indian fishery (Borrell *et al.*, 2011). Accurately

measuring large sharks, both in and out of the water, has proven difficult and complicates the question as to how large the *R. typus* may actually grow. Out of the water, fish >4 m L_T are difficult to handle to get accurate L_T measurements (Wintner, 2000). Similarly, the measurement method used affects L_T , i.e. tail stretched to the maximum length possible (stretched L_T) or placed at the angle normally found in a live fish (standard L_T) (Ecopacifico, 2010). In-water measurements using either comparison to an object of known size positioned next to the fish, or by using a tape measure or knotted rope alongside the fish, have been estimated to have errors of at least 50 cm (Meekan *et al.*, 2006; Graham & Roberts, 2007; Norman & Stevens, 2007; Bradshaw *et al.*, 2008; Holmberg *et al.*, 2009). New technology, based on digital photography or video is now being used to measure *R. typus* in water with much greater accuracy and precision. Stereo-photogrammetry produces a three-dimensional image of the subject from two angled cameras that can be accurately measured using specialized software (Klimley & Brown, 1983), while encouraging results on *R. typus* have been obtained through laser photogrammetry (Rohner *et al.*, 2011). The more widespread use of these types of measuring device should allow the accurate measurement of size and, over time, the estimation of growth rates in wild *R. typus* populations and should be encouraged at aggregation sites where individuals are known to return in successive years.

Growth rates measured in aquarium kept *R. typus* showed neonatal pups grew faster than larger juveniles (Table II) (Chang *et al.*, 1997; Leu *et al.*, 1997). Juveniles >3.5 m L_T showed variable rates with the females growing faster than males (Kitafuji & Yamamoto, 1998; Uchida *et al.*, 2000). Growth rates in wild populations, based on estimated L_T of live fish identified over several years, showed wide ranges (Table II) (Graham & Roberts, 2007; Riley *et al.*, 2010) that are confounded by the associated error margins of these methods (± 50 cm) (Holmberg *et al.*, 2009). Wintner (2000), using the number of growth rings in the vertebral column compared to L_T from 15 stranded *R. typus* specimens, estimated growth at the slower end of the aquarium-based growth rates (Table II).

TABLE II. Growth rates of *Rhincodon typus* of various total lengths (L_T) measured directly in aquaria, and growth estimates from vertebral rings and free-swimming length estimates

Sex	Habitat	Measurement method	Initial L_T (m)	End L_T (m)	Days measured	Rate cm year ⁻¹	Reference
?	Aquarium	Direct	0.6	1.4	120	240.3	1
M	Aquarium	Direct	0.6	3.7	1157	97.8	2
F	Aquarium	Direct	4.07	6.3	1825	45.2	3
F	Aquarium	Direct	3.65	5.3	2056	29.5	4
M	Aquarium	Direct	4.5	5.1	1040	21.6	4
M	Aquarium	Direct	4.85	5.2	458	25.5	4
F	Stranded	Vertebrae	—	—	—	20.7–27.8	5
M	Stranded	Vertebrae	—	—	—	21.1–33.5	5
?	Free swimming	Estimated	—	—	—	3–70	6
?	Free swimming	Estimated	—	—	—	8–82	7

?, unknown; M, male; F, female.

¹Chang *et al.*, 1997; ²Nishida, 2001; ³Kitafuji & Yamamoto, 1998; ⁴Uchida *et al.*, 2000; ⁵Wintner, 2000;

⁶Graham & Roberts, 2007; ⁷Riley *et al.*, 2010.

Growth rates and the age at first sexual maturity have a major bearing on the life history of a species and its role within its ecosystem. Based on information for many shark species, Pauly (1997) suggested a gradual slowing of growth to maturity; using these data the FishBase *R. typus* maturity table (<http://www.fishbase.org/Reproduction/MaturityList.php?ID=2081&GenusName=Rhincodon&SpeciesName=typus&fc=6>) calculated a length at first sexual maturity of 5.58 m L_T at an age of 8.9 years for *R. typus*. Fowler (2000) suggested an amendment to the maximum size using the 20 m L_T specimen reported by Chen *et al.* (1997); the amended table calculated a theoretical length at first maturity of 7.69 m L_T at an age of 21.4 years. Confirmation of size at first maturity has been limited: in stranded *R. typus* specimens from South Africa three males of 9.03, 9.22 and 9.45 m L_T were classed as mature, while other males of 8.66, 9.03 and 9.10 m L_T were found to be immature, as classified by the claspers being fully calcified with the outer clasper length noticeably longer than the pelvic fins (Wintner, 2000). No mature individuals were found from necropsies of another seven stranded female specimens of 4.8 to 8.7 m L_T in South Africa (Beckley *et al.*, 1997). This would suggest that males mature at ≥ 9 m L_T and that females are the same or perhaps larger than males at first maturity. Norman & Stevens (2007) found that at Ningaloo Reef 95% of male *R. typus* were mature at 9.1 m L_T , while 50% were mature at 8.1 m L_T based on clasper morphology. There is an urgent need to get accurate L_T measurements of *R. typus* combined with appropriate physiological evidence of their reproductive state, such as through hormone levels, to develop accurate life-history models. Such research at annual aggregation sites could go a long way to resolving key issues such as the L_T at first maturity of both sexes.

SENSES

Of all aspects of *R. typus* biology, the functioning of their senses is probably the least explored, due in no small part to the difficulties of working with a large pelagic vertebrate. Olfaction in sharks is well documented (Hueter *et al.*, 2004) and much research has been carried out in both open water (Sheldon, 1911; Parker & Sheldon, 1913) and laboratory conditions (Kleerekoper *et al.*, 1975; Kleerekoper, 1978). The role olfaction plays in *R. typus* is, however, largely unknown. The olfactory capsules in *R. typus* are spherical and moderately large (Dennison, 1937) which Martin (2007) suggested would have similar chemo-sensory detection abilities to those of the nurse shark *Ginglymostoma cirratum* (Bonnaterre 1788). While plankton *per se* may not have an identified scent, seabirds find areas of high plankton productivity by following dimethyl sulphide (DMS) given off when phytoplankton are grazed by herbivorous zooplankton (Nevitt *et al.*, 1995; Smythe-Wright *et al.*, 2005). As DMS is soluble in water, it could also be a good scent trail for *R. typus*; while no research has been undertaken in this field some correlational insights are available. Within commercial tuna fisheries, remotely sensed imagery of chlorophyll *a* concentration are used to locate potential target areas for fishing; chlorophyll *a* is the primary driver of the phytoplankton–zooplankton–baitfish food chain with tuna being attracted to baitfishes at dense chlorophyll patches after 5 days (Kumari *et al.*, 2009). Biophysical drivers have been shown to affect *R. typus* occurrence and abundance (Sleeman *et al.*, 2010; Sequeira *et al.*, 2011) and further research and sharing of occurrence

data at regional scales may allow further exploration of these techniques to predict other potential aggregation areas.

Rhincodon typus have relatively small circular eyes with a circular pupil, positioned laterally on the sides of the head and opposed to each other, giving the fish a wide field of vision. Binocular overlap in most shark species is small, resulting in blind spots directly in front of their noses and probably immediately behind their heads when stationary (Hueter *et al.*, 2004). Because of the broad, blunt shape of the head and the position of the eyes well back from the apex of the snout, this is almost certainly the case in this species, and it is suggested that vision may play a smaller part in feeding than olfaction (Clarke & Nelson, 1997). *Rhincodon typus* do not have a nictitating membrane that can be closed like an eyelid to protect the eye, but do have highly developed muscles that allow the whole eye to roll back into its socket (Norman, 1999; Martin, 2007). It is thought that shark vision is best adapted to short-range use and the eyes of *R. typus* certainly follow swimmers at distances of 3 to 5 m away, suggesting that they are capable of picking out objects and discerning movement at close range (Martin, 2007). No quantitative research has been done to date on *R. typus* vision, but this would certainly be feasible at seasonal aggregation sites and may be valuable in the development of interaction guidelines.

Rhincodon typus possess the largest known inner ear in the animal kingdom (much larger than those of whales) with the semicircular canals being close to the theoretical maximum size (Muller, 1999). In terms of sound detection this should make them most responsive to long wavelength, low-frequency sounds (Myrberg, 2001). The semicircular canals of sharks are highly sensitive to angular acceleration, though how the great size found in *R. typus* affects this or their perception of balance is not known. *Rhincodon typus* possess a mechano-sensory lateral line system similar to all sharks, but its capabilities in this species are largely unknown. The lateral line enables sharks to react to water currents (rheotaxis), as has been documented for a number of pelagic species (Hodgson & Mathewson, 1971; Kleerekoper, 1978) and in some bottom-dwelling sharks (Peach, 2002). A similar response to currents has been seen in *R. typus* tracked with satellite tags from the Seychelles (Rowat & Gore, 2007) and Taiwan (Hsu *et al.*, 2007), although it is not known to what extent this sense is developed. Given the plethora of tracking studies currently ongoing, there should be ample scope to explore this avenue and provide insight into the species' navigational abilities. Little work has been done on the cutaneous sensors in any sharks, let alone in *R. typus*; however, the rapid response of *R. typus* to being touched by swimmers tends to indicate that their tactile senses are acute (Quiros, 2005, 2007). Experimentation in this area could lead to undue disturbance of individuals, but the quantitative observation of incidents within tourism activities holds significant scope for data collection, and thus revision of management guidelines.

The ampullae of Lorenzini are pit-like organs which are clustered around the head of all sharks and rays that detect weak electric and magnetic fields (Bleckmann & Hofmann, 1999). These organs can detect the shark's movement across the lines of force of the earth's magnetic field and as such may be a navigational aid, as has been demonstrated in lemon sharks *Negaprion brevirostris* (Poey 1868) (Kalmijn, 1984), scalloped hammerhead sharks *Sphyrna lewini* (Griffith & Smith 1834) (Klimley, 1993) and *P. glauca* (Carey & Scharold, 1990). While *R. typus* certainly have the ampullae, their electro-magnetic sensing capability has yet to be demonstrated. The ampullae of Lorenzini have also been shown to be able to detect minute bio-electrical

fields and enable some shark species to detect hidden prey purely by this manner (Kalmijn, 1984). This sense has also been shown to be effective in the detection of planktonic prey in the Mississippi River paddlefish *Polyodon spathula* (Walbaum 1792) (Wilkens & Hofmann, 2007). While this ability has not been shown in *R. typus*, it is possible that this sense may play a major role in feeding and prey capture and might be a feasible area for experimental research.

Rhincodon typus has a small brain relative to its body mass with only the megamouth shark *Megachasma pelagios* Taylor, Compagno & Struhsaker 1983 brain being relatively smaller (Yopak & Frank, 2009). Comparison of the brain from a neonatal *R. typus* pup to those of 5 m juveniles showed that the pup had a relatively large brain compared to body size, almost filling the endocranial cavity. It appears, however, that neural tissue does not grow at the same rate as the rest of their body as the brain occupied only a portion of the cavity in the 5 m juveniles. *Rhincodon typus* shares several brain characteristics with three sharks of the Lamniformes order, the thresher sharks *Alopias superciliosus* Lowe 1841 and *Alopias vulpinus* (Bonnaterre 1788) and the basking shark *Cetorhinus maximus* (Gunnerus 1765). These characteristics include an exceptionally large cerebellum with the highest levels of foliation in the corpus, as found in the two *Alopias* spp. (Yopak & Frank, 2009). Although the exact function of a highly foliated cerebellum in this species is not clear, it has been linked to agile prey-capture abilities, high levels of habitat awareness and the ability to perform complex motor-skill tasks; this may be important in this species' extensive dives to depths in excess of 1700 m (Hueter *et al.*, 2008) and its long distance migrations of several thousand km (Eckert & Stewart, 2001; Wilson *et al.*, 2006; Rowat & Gore, 2007; Hueter *et al.*, 2008).

DISTRIBUTION

Rhincodon typus are circumglobal in all tropical and warm temperate seas from 30° N to 30° S (Compagno, 2001) (Fig. 1). They were thought to be absent in the Mediterranean Sea, but recent sightings have confirmed their presence there also (Jaffa & Taher, 2007). They are generally epipelagic and found in both oceanic and coastal waters, forming fairly predictable seasonal aggregations at some sites (Colman, 1997a; Compagno, 2001). They have also been recorded off South Africa between 30 and 35° S and off New Zealand between 34 and 38° S (Duffy, 2002; Compagno *et al.*, 2005). There are also reports of occasional *R. typus* sightings in latitudes with far cooler temperatures, as far as 41° N off the Scotian (Coad, 1995) and northern Californian coasts (Ebert *et al.*, 2004) and at 44° N in the Bay of Fundy, Canada (Turnbull & Randell, 2006). This increased geographic range into higher latitudes may be enabled by localized areas of warm water due to oceanic currents.

Recent research has shown that *R. typus* are predominantly found in warm temperatures: 27° C off Western Australia (Norman, 1999), 20–32° C in the Sea of Cortez, although temperatures as cold as 10° C were recorded (Eckert & Stewart, 2001), 25–35° C with limited periods at 6° C off Seychelles (Rowat & Gore, 2007). As such, short-term exposure to colder water would not seem to be a barrier to *R. typus* movements. Off Ningaloo Reef, Western Australia, the abundance of *R. typus* has been statistically correlated with the Southern Oscillation Index (SOI) and wind shear; during la Niña years a positive SOI causes warmer temperatures

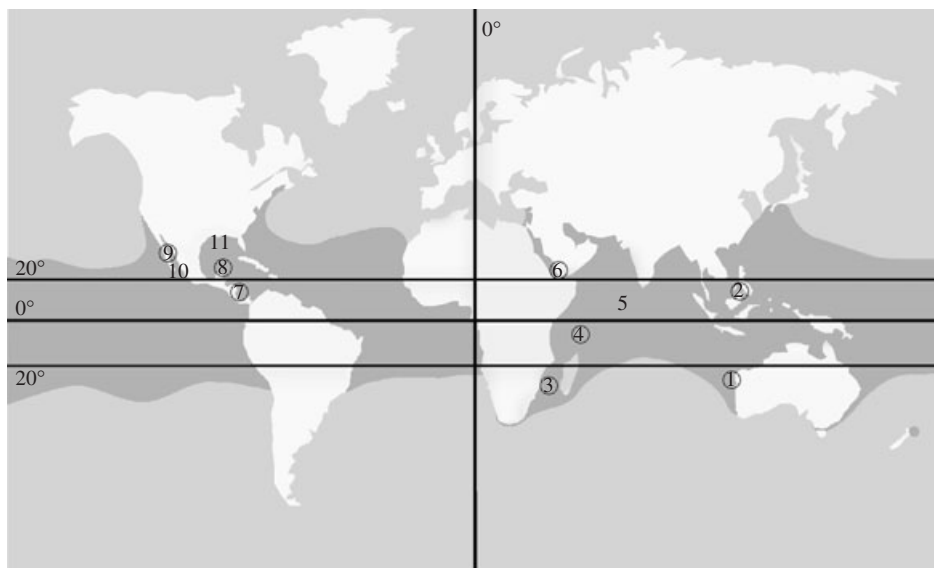


FIG. 1. Global range of *Rhincodon typus* distribution (■) with current known aggregation areas: 1, Ningaloo; 2, Philippines; 3, Mozambique; 4, Seychelles; 5, Maldives; 6, Djibouti; 7, Belize; 8, Holbox; 9, North Gulf of California; 10, South Gulf of California; 11, North Gulf of Mexico. Circled numbers indicate areas with dedicated *R. typus* tourism activities.

and is associated with more *R. typus* sightings (Wilson *et al.*, 2001; Sleeman *et al.*, 2009). With the increasing use of satellite tagging by a number of research groups the range and distribution of individuals tagged within seasonal aggregations will become clearer and should allow for wider comparison with biophysical factors and help define potential areas of occurrence and transitory pathways.

POPULATION STRUCTURE

PHYSICAL IDENTIFICATION

Determining the size, structure and distribution of wild animal populations is often difficult, especially when the species are marine and comparatively rare, as in *R. typus*. For many years, abundance has been estimated by surveying a portion of a population and using mark–recapture methodology (Petersen, 1896; Lincoln, 1930). The marking of individuals may be by the identification of natural marks and of scars, or can be by physically marking the individual such as with an identification tag. Such marking is generally thought of as an easy and fool-proof means of re-identification; however, marks wear off and tags can be lost, so such systems may only be effective in the short term (Stobo & Horne, 1994; Diefenbach & Alt, 1998).

The first attempt at identifying individual *R. typus* and estimating the numbers present was off Ningaloo Reef, in Western Australia. From the mid-1980s, Taylor (1989) collected photographs of *R. typus* individuals, and, using scarring patterns as a means of verification, found that the pattern of spots and stripes on their sides

was stable over the period of his study and could be used to identify the fish. The identification and subsequent resighting of several individuals in different years indicated that some displayed seasonal philopatry and had an affinity for the area. From 1992, using marker tags on the same aggregation, Taylor (1994), estimated the presence of around 200 individuals in 1993 and 220 in 1994 with tag loss of 40–50% (Colman, 1997a). Similar results confirming both philopatric behaviour and high rates of tag breakage and loss were reported from Belize (Graham & Roberts, 2007) and Seychelles (Rowat *et al.*, 2009).

Further studies from Ningaloo Reef (Norman, 2004) identified that the spot pattern of the lateral area behind the gill slits was apparently unique and could be used as a naturally occurring mark to identify *R. typus* individuals. In another study of images from Ningaloo Reef from 1992 to 2004, manual matching of the lateral area behind the gill slits of *R. typus* was carried out with a two-stage verification process (Meekan *et al.*, 2006). A total of 276 individuals were identified, 61 were seen multiple times with 25 seen between different years, re-confirming the philopatric nature of some individuals in this aggregation. One *R. typus* was identified over a period of 10 years and two fish over 12 years, confirming a moderately long-term stability of the lateral spot patterns. Using closed population models Meekan *et al.* (2006) estimated a super-population attending Ningaloo Reef of 278–589 individuals and with open (Jolly–Seber) models of 319–436 individuals. As the *R. typus* were predominantly juvenile and male, however, they concluded that this super-population was unlikely to constitute a complete sub-set of the Indian Ocean population (Meekan *et al.*, 2006). A proprietary computer programme based on the Groth algorithm for matching astronomical data (Groth, 1986), was developed to match *R. typus* spot patterns from the lateral area (Arzoumanian *et al.*, 2005) (See Appendix SI for further details; Marshall & Pierce, 2012). Resightings made through this programme, now known as the ECOCEAN programme, estimated the proportion of philopatric *R. typus* at Ningaloo Reef to be 0.65 (Holmberg *et al.*, 2008) and open population models on a slightly later data-set estimated 86–177 individuals present each year (Holmberg *et al.*, 2009).

Photo-identification studies in Seychelles using the free-ware I³S programme (www.reijns.com/i3s) (Van Tienhoven *et al.*, 2007) and carried out in parallel with marker tagging from 2001–2006, revealed a very high rate of tag loss after 300 days. Open population models based on I³S data gave an abundance estimate of 469–557 (95% C.I.) around the Seychelles from 2004 to 2009 (Brooks *et al.*, 2010) and showed the presence of a large proportion of transient *R. typus*, similar to the aggregations in Belize and Ningaloo Reef (Meekan *et al.*, 2006; Graham & Roberts, 2007) where the majority of *R. typus* were also male and immature. Consequently it was surmised that these transient aggregations of *R. typus* do not comprise the only or even the principle communities of this species (Brooks *et al.*, 2010). Comparing data with Djibouti and Mozambique found similar juvenile male-dominated aggregations, but from a total of 1069 identified *R. typus* no matches were found between these sites (Brooks *et al.*, 2010). A single individual identified from the Tanzanian aggregation was, however, recorded off Seychelles in 2010 (unpubl. data), which is supported by data from satellite tracking. While *R. typus* matches between Indian Ocean sites are still rare, several matches have been made between Mexico, Honduras, Belize, and the U.S. coast of the Gulf of Mexico (ECOCEAN, pers. comm.) which is also supported by satellite tracking data (Hueter *et al.*, 2008).

The estimations of *R. typus* population sizes are thus constrained by most sightings coming from the various aggregation sites, which are composed predominantly of juvenile male *R. typus* with very few females or adults. This is further complicated by variations in monitoring techniques, sighting effort and interpretation (Brooks *et al.*, 2010). As an example, there have been some indications that L_T and the numbers of *R. typus* present at Ningaloo Reef are decreasing (Bradshaw *et al.*, 2008); however, it is argued that the reduction of L_T is due to the recruitment of new, smaller individuals into the aggregation and that the aggregation size may be slightly increasing (Holmberg *et al.*, 2009). In the absence of data from the adults, the estimations derived from the aggregation sites should thus be considered only as a proxy for the overall status of regional *R. typus* populations.

Using identification data, the number of years that individuals remain associated with specific aggregations has been calculated and indicates that there may be variation between different sites (Rowat *et al.*, 2011). Continued monitoring of such sites and similar approaches at other aggregations can provide valuable information about the life history of this species. Some concerns have been raised on the reliance on photo-identification as the primary identification method, this is discussed in more detail in Appendix SI (Marshall & Pierce, 2012).

Another method employed to establish abundance is that of aerial surveys to census *R. typus* (Ligon, 1976; Taylor, 1994; Gifford, 2001; Hoffmayer *et al.*, 2005, 2007; Burks *et al.*, 2006; Cliff *et al.*, 2007; Gifford *et al.*, 2007a; Rowat *et al.*, 2008; de la Parra Venegas *et al.*, 2011). Just as with the use of photo-identification, however, there are limitations with the use of this method in establishing abundance in this species. The primary issue is that few of the surveys to date have accounted for the period of time that *R. typus* spend at depths where they are not visible, thus only those at the surface are counted which probably represent only a portion of the number present at any one time (Pollock *et al.*, 2006; Rowat *et al.*, 2008). Similarly, few such studies have accounted for the standard 'availability' and 'perception' errors associated with aerial surveys (Marsh & Sinclair, 1989; Pollock *et al.*, 2006). Another issue is the frequency of survey and movement patterns of *R. typus*, which being highly mobile can easily move into or out of the survey zone (Rowat *et al.*, 2008). As such, aerial monitoring can provide rapid surveys over large areas and synoptic estimates of abundance. It is particularly suited to aggregations of large numbers of individuals but it does have its own series of limitations that have to be considered.

MOLECULAR ECOLOGY

Efforts are ongoing to better understand how the individuals comprising the various *R. typus* aggregations in different localities are related. Analysis of mitochondrial control region DNA from 70 *R. typus* samples, from six areas around the world, identified 51 polymorphic sites in 44 haplotypes, but found no evidence of graphical clustering (Castro *et al.*, 2007). While there were statistically significant haplotype frequency differences between samples from the Atlantic and Indo-Pacific Ocean regions, haplotypes were shared between different areas with no significant genetic subdivision and the most common haplotypes were found globally. Similar analysis of *R. typus* mitochondrial control region polymorphism indicated that there was little likelihood of inter-region or inter-ocean genetic differences between *R. typus* from

the Gulf of California, Mexico, and from the North Pacific Ocean (Ramírez-Macías *et al.*, 2007). Their observations of *R. typus* sex and age segregation, when considered with the genetic data, led them to conclude that within this species females might exhibit natal-philopatry breeding and pupping in the same area as they were born, while males moved to other areas to mate.

Genetic analysis of 68 *R. typus* samples collected from sites around the world examined eight polymorphic microsatellite loci; the genetic make-up of the *R. typus* population in the Pacific Ocean was found to be very similar to that in the Indian Ocean and both were similar to that found off the Caribbean Atlantic Ocean (Schmidt *et al.*, 2009). They concluded that, although the sample size was small, it was likely that there was significant gene flow and thus segregated breeding populations were unlikely. In a further genetic study of a sample of the embryos from the Taiwanese female, Schmidt *et al.* (2010) also identified another haplotype from the mitochondrial control region bringing the current total identified for *R. typus* to 45.

The studies of Castro *et al.* (2007) and Schmidt *et al.* (2009) lean towards a worldwide panmictic *R. typus* population, however, the majority of the samples analysed in both studies were collected at aggregation sites. It may be that these sites attract individuals from reproductively segregated populations, which mix together at these aggregations, thus masking any geographic segregation when the sites are sampled. Bearing in mind the apparent regional segregation indicated by photo-identification (Taylor, 1996; Speed *et al.*, 2007; Rowat *et al.*, 2009), this is an area of research that requires further studies with substantially more samples needing to be collected globally.

Another issue relates to how many animals are needed to breed outside their natal populations to prevent differentiation between populations; opinions differ and range from as little as one migrant per generation (Wright, 1931). This is based, however, on many assumptions which may not be met in wild populations, where probably a greater number are needed to normalize the genetics (Mills & Allendorf, 1996). In juvenile aggregations of *R. typus*, the highest annual resighting levels are *c.* 50% (Rowat *et al.*, 2009; Brooks *et al.*, 2010) and while population segregation may not be the same in adult breeding populations, this level of emigration certainly supports that needed to prevent differentiation between sub-populations.

BEHAVIOUR

AGGREGATIONS

Little is known of *R. typus* behavioural ecology although in many areas their pattern of occurrence appears to be temporary and often linked to feeding on specific productivity events (Heyman *et al.*, 2001; Wilson *et al.*, 2001). In some of these areas these events seem to be on a longer, more diffuse scale and may be indicative of generally increased primary productivity over a wide area (Rowat *et al.*, 2009; de la Parra Venegas *et al.*, 2011).

Rhincodon typus are most often encountered singly and are not regarded as social animals; however, aggregations have been reported from several areas. The term aggregation has been used to describe areas with as few as two individuals present at one time, or even simply seasonal *R. typus* occurrence. Here the term is used to

describe sites with >10 individuals in an area <1 km². Most such reported aggregations are coastal. Off Ningaloo Reef, Western Australia the aggregation comprises individuals of 3–10 m L_T , but the majority were juveniles of 6–8 m L_T and predominantly males (82%) (Meekan *et al.*, 2006). Similarly structured *R. typus* aggregations are found in Belize (Heyman *et al.*, 2001), the Maldives (Riley *et al.*, 2010), Mozambique (Pierce *et al.*, 2008) and Seychelles (Brooks *et al.*, 2010), while in Djibouti the average sizes are smaller (Rowat *et al.*, 2007b). In the Gulf of California the *R. typus* aggregation in the north was juvenile male dominated, while further south individuals were solitary and mainly adult, and probably gravid females (Eckert & Stewart, 2001; Ramírez-Macías *et al.*, 2007). Another *R. typus* aggregation area was reported in the northern Gulf of Mexico in shelf-edge waters of 500–1000 m during the summer months (Hoffmayer *et al.*, 2005; Burks *et al.*, 2006), although smaller aggregations were also recorded closer to the coast during autumn. The aggregation of *R. typus* off Christmas Island was reported as being female biased (Hobbs *et al.*, 2009), but other reports indicated it was male dominated like most other aggregations (Meekan *et al.*, 2009). Probably the largest *R. typus* aggregation currently known is the ‘afuera’ aggregation off Isla Contoy, Caribbean Mexico, where aerial surveys have recorded 420 individuals in an area of 18 km² and aerial photographs have shown 68 *R. typus* in an area of *c.* 1 km² (de la Parra Venegas *et al.*, 2011), in-water identification revealed around 74% were males.

Segregation by size and sex are known from several shark species where females sharks occupy different habitats, grow faster, feed on different prey and are larger at first reproductive age than the males, such as in *S. lewini*, (Klimley, 1987). In *R. typus*, there is little evidence to support growth being a driver for the sexual segregation of aggregations, due in large part to the lack of females recorded. Stable-isotope analysis of *R. typus* of similar sizes has indicated, however, that females had lower values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than males (Borrell *et al.*, 2011) suggesting that they have a different, more pelagic diet. If this is the case and the females are feeding in different habitats and on different prey, research into as yet unstudied areas, such as their pelagic occurrence (Sequeira *et al.*, 2011) may provide information important for the species conservation. The social or behavioural role of aggregations may yet be found through ongoing studies in the areas where adults, in particular females, are reported, such as the Gulf of Mexico (Ramírez-Macías *et al.*, 2007) and Galapagos (Arnbom & Papastavrou, 1988).

One potential benefit of aggregating behaviour is the increased opportunity to find a mate. In *C. maximus*, targeted feeding aggregations have been recorded (Sims & Quayle, 1998) and recent studies have suggested that such aggregations may promote courtship behaviour (Harvey-Clark *et al.*, 1999; Sims *et al.*, 2000). While feeding behaviours have been reported from all of these *R. typus* aggregations, there is little support for any mating behaviour, although this would not be expected from predominantly juvenile individuals. Martin (2007) describes putative early courtship behaviour captured on video by aerial survey at Ningaloo Reef. This showed two *R. typus* performing close-following and parallel swimming behaviour, but no direct surface or in-water observation was available to confirm size or sex of the individuals. The studies in the Gulf of California (Eckert & Stewart, 2001; Ramírez-Macías *et al.*, 2007) indicate the presence of pregnant *R. typus* females, suggesting their proximity to breeding areas, but neither mating nor pupping has been recorded. These known *R. typus* aggregations thus appear to be the result of individuals’ foraging activities

drawing them coincidentally to the same location, rather than any behavioural or social need and as such *R. typus* could be regarded as being facultatively social (Martin, 2007) in that they do not necessarily have to form these aggregations.

Rhincodon typus do appear to learn, as individuals in captivity show changes of behaviour when their keepers appear with food, swimming in tight circles by the feeding point (Clarke & Nelson, 1997) waiting to be fed. They are also known to investigate the nets of local boats targeting anchovy-like fishes off Papua Province, eastern Indonesia (Harterink & Stijn, 2010), accepting hand-outs of the fishes from the fishermen. On a somewhat broader scale, *R. typus* were found in reasonable numbers at Ningaloo Reef two weeks before coral spawning and thus potentially in anticipation of the associated primary productivity event (Gunn *et al.*, 1999).

The existence of predictable *R. typus* aggregations has allowed studies of interaction with humans through ecotourism activities. Formal studies on the short-term effects of such interactions indicate that there may be subtle but definite changes in behaviour, with *R. typus* diving more frequently and spending less time at the surface (Quiros, 2007).

One of the issues about direct observation of *R. typus* behaviour has been that they are known to react to both boats and swimmers, and thus the presence of the observer influences the observations (Norman, 1999; Quiros, 2007). Focal animal monitoring from an observational platform that does not affect *R. typus* behaviour, a micro-light aircraft, has been ongoing in Seychelles since 2005. *Rhincodon typus* appear to be unaffected by the presence of the aircraft which has enabled the capture of >200 5 min observational records (Rowat, 2010). A total of 150 of these records have been without any external influence present, such as boats or swimmers and have enabled the development of specific baseline criteria; 50 records were in the presence of boats or swimmers and initial analysis has indicated a significant reduction in the time the fish spent swimming at the surface (unpubl. data). The combination of data from such aerial behavioural monitoring with short-term dead-reckoning tag deployments (Gleiss *et al.*, 2009) may provide valuable information both about the normal activities of *R. typus*, and also any changes in their behaviour. This type of approach also opens up areas of experimental research where, for instance, the different parameters of codes of conduct can be trialled and quantitatively assessed.

GEOGRAPHIC MOVEMENTS

Rhincodon typus movement patterns have been monitored by a number of means. Short-term active acoustic telemetry tracking of *R. typus* off Ningaloo Reef showed that individuals largely swam parallel to the reef edge at swimming speeds of *c.* 0.36–6.48 km h⁻¹ that varied between day and night (Gunn *et al.*, 1999). A reasonable number of *R. typus* movements have been tracked using buoyant satellite tags attached to the dorsal surface of free swimming *R. typus*, usually by means of long tethers, and a variety of attachment anchors, although only a limited number of studies have been published to date.

Early satellite tracking studies showed that the *R. typus* could travel very long distances (>13 000 km in 37 months) and achieve speeds of up to 3.9 km h⁻¹ (Eckert & Stewart, 2001). Several subsequent studies have confirmed the species' ability to travel long distances, off Asia (Eckert *et al.*, 2002), South Africa and Utila, Honduras (Gifford *et al.*, 2007b), Seychelles (Rowat & Gore, 2007) and Taiwan (Hsu *et al.*,

2007). All of these studies showed movements through waters under different jurisdictions and all had issues, to some extent, with short tag attachment periods. Some attempts have been made to dorsal-fin mount satellite tags in *R. typus* allowing transmission when the fish are at the surface and avoiding the premature detachment issues inherent with tether based systems (Bonfil *et al.*, 2005; Hammerschlag *et al.*, 2011). *Rhincodon typus*' tracks have been shown to be influenced by prevailing geo strophic currents (Rowat & Gore, 2007) and by boundary currents and local bathymetry (Hsu *et al.*, 2007). To date, however, there have been few attempts to correlate *R. typus* movements with oceanographic features such as thermal fronts, geo strophic currents or magnetic fields. This is an area that requires detailed research and the development of tags that can detect and record magnetic fields may open up new areas of research into movement patterns.

The deployment of arrays of acoustic listening stations enables the long-term monitoring of movements of multiple individuals using coded acoustic tags; off Belize 53% of tags deployed on *R. typus* were recorded the following year (Graham & Roberts, 2007). While the range at which listening stations can detect acoustic tags varies depending on several factors (Voegeli *et al.*, 1998; Heupel *et al.*, 2006), their widespread use in fisheries research has increased the number and extent of arrays regionally and globally. This has led to their utility in larger scale co-operative tracking projects such as the Ocean Tracking Network (O'Dor, 2010) and prompted several *R. typus* acoustic tagging initiatives as in the Gulf of Mexico (Hueter *et al.*, 2008) as well as the Marine Megamnet (Graham *et al.*, 2008).

At the moment, although satellite-tracked *R. typus* have been shown to make some very long journeys, none of the reports published to date have indicated whether any of these individuals were sighted again in the locations where they were tagged, thus showing true migration. This seems to be at odds with the data from the identification studies in the same areas that have recorded the apparent return of individual fish over many years.

One study off Belize, did recover a pop-up archival tag (PAT) tag from an *R. typus* at the same location where it was tagged after nearly a year; this tag did record deep dives, but no indication was given as to its probable track or distance covered during deployment (Graham *et al.*, 2006). In another study off Seychelles, one PAT indicated a maximum distance of travel from the tagging location of 879 km, before being released 20 km from the original tagging location 101 days later, while a second PAT indicated a journey of 1045 km in 97 days. Both individuals were identified at the same site after 4 and 3 y respectively (unpubl. data). Thus, there are some indications that *R. typus* may indeed undertake true migrations, returning to specific areas after long distance journeys. Due to the relatively short periods of tag retention, tagging and tracking alone are unlikely to resolve the issue of true migration, but, used in conjunction with long-term photographic identification (photo ID), such information can be reliably developed.

VERTICAL MOVEMENTS AND DIVING BEHAVIOUR

The first information about *R. typus* vertical movement habits was revealed by a data storage tag (DST) and acoustic tracking studies at Ningaloo Reef (Gunn *et al.*, 1999). Tag data showed the individual spent 60% of daytime in the top 10 m, while during the night most of the time was spent at depths down to 90 m. These data

were corroborated by two *R. typus* tracked by acoustic tags which spent 52–53% of daytime in water <10 m, however, the findings were confounded by one *R. typus* tracked during the night which spent 73% of the time at this depth. These conflicting data show that individual *R. typus* in the same area may not necessarily behave in the same way.

Since this study technology has improved and archival tags with transmitting capacities have become the preferred tool for *R. typus* researchers eliminating the need for the tag to be either retrieved or actively followed to recover data. These PATs have revealed *R. typus* diving behaviour in epipelagic (0–200 m), mesopelagic (200–1000 m) and bathypelagic (>1000 m) zones and changes in behaviour in relation to time, location and bathymetry.

Off Belize, *R. typus* were shown to make mesopelagic dives to 980 m (the limit of the tags used) with ascents significantly faster than descents, but the majority of time was spent at 50–250 m. The data also indicated the influence of lunar phases on the depth range which corresponded to the timing of local snapper [*Lutjanus cyanopterus* (Cuvier 1828) and *Lutjanus jocu* (Bloch & Schneider 1801)] spawning events (Graham *et al.*, 2006). Similar results were found in Seychelles, with mesopelagic dives of 750–1000 m overall however, 96% of the time was spent at epipelagic depths <100 (Rowat & Gore, 2007). Mesopelagic diving behaviour was recorded from *R. typus* off Ningaloo Reef with depths of 980 m, the limit of the tags used; however, >40% of the time was <15 m and >50% at <30 m. (Wilson *et al.*, 2006). In all of the above studies temperature data retrieved reflected the dive depths with *R. typus* spending very little time at minimum temperature, but tolerating temperatures as low as 2.2° C. Wilson *et al.* (2006) also found that dive depths during daytime were generally greater than at night; however, in coastal waters one *R. typus* spent daylight hours near the surface and nights at depths of 30–80 m but reversed that pattern in deep water. Their data also indicated that deep dives were often crepuscular, occurring around dawn and dusk. Off Holbox, south-east Gulf of Mexico, an area with a depth of 10–20 m, data from retrieved PAT tags showed 43.9% of the time was spent at the surface during the day, compared to only 16.0% at night (Motta *et al.*, 2010), which supports aerial survey findings (de la Parra Venegas *et al.*, 2011). This is similar to the behaviour found coastally by Wilson *et al.* (2006).

Further evidence of *R. typus*' ability to change their diving pattern in relation to bathymetry was recorded by PATs deployed off Mozambique (Brunnschweiler *et al.*, 2009). Similar to the findings of Wilson *et al.* (2006), one individual stayed in shallow depths during the day and deeper depths at the night in coastal waters, but reversed this behaviour in oceanic waters. On 10 separate days bathypelagic dives to 1286 m were recorded, the maximum depth these tags could record, but similar to previous studies, most of the time (79.6%) was spent at <100 m in the epipelagic zone. During the night 79.1% of epipelagic dives were >50 m compared to 14.7% during the day; in comparison most of the deepest meso and bathypelagic dives were made during the day (Brunnschweiler & Sims, 2011). The *R. typus* apparently dived to bathypelagic depths directly from the epipelagic zone, but spent little time at the maximum depth and quickly returned to mesopelagic depths.

The deepest dive recorded so far for *R. typus* was 1720 m recorded by a PAT deployed off Holbox, (Tyminski *et al.*, 2008). Five individuals recorded bathypelagic dives >1350 m, with one individual moving 7213 km, from Holbox to off Rio de

Janeiro, Brazil. Bathypelagic dives (>1000 m) were initiated from shallow depths, with steep descents and steep ascents, and little time spent at the maximum depth. This is similar to bathymetric dives recorded by Brunnschweiler & Sims (2011) but appears to be in contrast to those from Belize, where ascents were significantly faster than descents (Graham *et al.*, 2006). There was also evidence from these data that in coastal, bathymetrically constrained waters, more time was spent in shallow waters during the day, while at night deeper depths were preferred (Tyminski *et al.*, 2008); however, there was no obvious reversal of this in offshore waters. These data also indicated crepuscular diving activity as found in Belize (Graham *et al.*, 2006), but unlike that study there was no correlation with the lunar phase.

The reasons *R. typus* make dives to meso and bathypelagic depths is unclear, but may be indicative of foraging behaviour, especially when crossing comparatively less productive oceanic surface waters (Sleeman *et al.*, 2010; Brunnschweiler & Sims, 2011). In *C. maximus*, it has been suggested that deep diving behaviour in stratified oceanic waters may be to allow multiple layers of water to be sampled for scent trails (Sims & Quayle, 1998) which might also hold true for *R. typus*.

Data from dead-reckoning data-logger tags, known as daily diary tags, has suggested that *R. Typus* pattern of diving behaviour can be adapted for different situations (Gleiss *et al.*, 2009). The initial studies indicate that by using their negative buoyancy to glide at very shallow angles during descents, *R. Typus* minimized the energetic costs of horizontal movement. Further studies in this area may provide interesting information as to the energetic costs of long distance migrations and the foraging strategy of this species.

The information gained from satellite tagging *R. typus* has given insights into both their capacity for ocean-scale movements as well as their ability to make deep dives and change their diving patterns relative to environmental or bathymetric conditions. The combination of these data with information from ancillary sources, such as photo-identification and environmental monitoring will help to place these movements within an ecological context, but more diverse variables need to be incorporated. One recent advance is that of fine-scale location data available from GPS data captured by the tags and relayed through the satellite system. This technology has found favour in tracking marine turtles (Witt *et al.*, 2010) but, due largely to the constraints of the horizontal flat-plate GPS antennae, has not found much take-up with fish researchers thus far. One approach has been to package this technology into a towed PAT-type tag which has been tried with great promise on swordfish *Xiphias gladius* L. 1758 (Evans *et al.*, 2011), a species with noted crepuscular diving behaviours and thus very difficult to obtain good geo locations by using light levels. The use of this technology to provide fine-scale position information along with vertical depth and temperature data would enable a substantial increase in the knowledge of behaviours of *R. typus* in their open-ocean environments as well as information on these environments themselves.

FEEDING AND PREY ITEMS

The pad-like filtering apparatus of the *R. typus* is unlike that of the other filter feeding sharks, *C. maximus* and *M. pelagios*, whose filters comprise stiff bristle-like gill rakers. *Rhincodon typus* are able to feed by suction, which may allow them to target more mobile prey and so they are better suited to dense prey aggregations,

while *C. maximus* and *M. pelagios* are apparently better adapted to feeding on lower densities of prey organisms, filtering large volumes of water (Taylor *et al.*, 1983). Three feeding techniques have been observed in *R. typus*: ram-feeding, suction feeding and active surface ram-feeding. Ram-feeding is reported most often, where the fish swims forward at a steady speed with its mouth partly or fully open, straining prey particles from water by forward locomotion. This has also been termed 'passive feeding' as there is little, if any, pumping of the gills (Taylor, 2007). This type of feeding occurs in low prey densities (Nelson & Eckert, 2007), while at Ningaloo Reef this behaviour was associated with the presence of copepods and chaetognaths (Taylor, 2007). Suction feeding is the active gulping of water and food by *R. typus*, often while stationary in a vertical or horizontal position; this behaviour has been associated with medium prey densities (Nelson & Eckert, 2007). Active surface ram-feeding occurs where *R. typus* is at the surface with the top of its mouth clear of the water, often with most of its back out of the water, swimming strongly often in a circular path. This behaviour was noted in the densest plankton conditions (Nelson & Eckert, 2007), and off Ningaloo Reef, this active behaviour was associated with surface swarming euphausiids (Taylor, 2007). In all methods of feeding, the filtration pads will at some time become blocked with particulate matter and *R. typus* apparently clear them by back-flushing in a manoeuvre where the fish appears to cough underwater, ejecting a stream of debris (Hoffmayer *et al.*, 2007; Nelson & Eckert, 2007; Taylor, 2007; Motta *et al.*, 2010). How *R. typus* tracks its prey during these feeding events is largely unknown and is an area of research that could be explored at the reliable seasonal feeding aggregations.

There has been some research on *R. typus* food preferences, most of which are pelagic invertebrates. They have been recorded feeding on masses of the copepod *Acartia clausi* off La Paz, southern Gulf of California (Clarke & Nelson, 1997) and take advantage of localized productivity events off Western Australia feeding on tropical krill *Pseudeuphausia latifrons* (Gunn *et al.*, 1999; Wilson *et al.*, 2001; Taylor, 2007). They have also been reported feeding on thimble jellyfish *Linuche unguiculata* (Schwartz 1788) off Belize, where they also feed on eggs released by spawning *L. cyanopterus* and *L. jocu* (Heyman *et al.*, 2001). *Rhincodon typus* are also recorded feeding on eggs of little tunny *Euthynnus alletteratus* (Rafinesque 1810) off the Yucatan Peninsula, eastern Mexico (de la Parra Venegas *et al.*, 2011), and possibly from blackfin *Thunnus atlanticus* Lesson 1831 and skipjack tuna *Katsuwonus pelamis* (L. 1758) off the Mississippi Delta, U.S. coast of the Gulf of Mexico (Hoffmayer *et al.*, 2007), and on the megalopa larvae of the endemic red land-crabs *Gecarcoidea natalis* off Christmas Island (Norman, 1999; Davies, 2007; Meekan *et al.*, 2009).

Rhincodon typus have also been recorded feeding on small schooling fishes, such as on Australian anchovy *Engraulis australis* (White 1790) off New Zealand (Duffy, 2002). This has been corroborated in some of the very few examinations of the stomach contents such as in the Taiwanese *R. typus* fishery, where small fishes, shrimp and plankton were found (Chen *et al.*, 1997). Similar contents and a small amount of algae were found in two Indian *R. typus* (Rao, 1986). In Seychelles, gut contents of two *R. typus* were full of algae, but this was thought to have been incidentally ingested during feeding around floating sea-weed (Wright, 1877). In 2010, examinations on three stranded *R. typus* in South Africa revealed the stomachs were filled with a virtual monoculture of the mysid shrimp *Gastrosaccus gordonae*

(G. Cliff & A. Connell, pers. comm.). While mysids are a component of plankton rich areas visited by *R. typus* (Gunn *et al.*, 1999), this is the first indication of *R. typus* directly targeting them. Microscopic and DNA examination of faeces from three *R. typus* confirmed their liking for *P. latifrons* (Jarman & Wilson, 2004), megalopa larvae of *G. natalis* (Hobbs *et al.*, 2009; Meekan *et al.*, 2009), while faeces from two *R. typus* off Djibouti revealed copepods, chaetognaths and large numbers of brachyuran crab zoea (unpubl. data).

While great strides have been made in the understanding of the filtration mechanism of *R. typus*, there is little hard evidence regarding their foraging behaviour, how they locate their prey or what they feed on away from the shallow-water feeding sites. Muscle stable-isotope studies suggest that there may be differences in diet between young *R. typus* and their older conspecifics and also between sexes (Borrell *et al.*, 2011), albeit that sample sizes were small. Analysis and comparison of stable-isotope levels from skin biopsy samples may allow a significant increase in sample quantity and provide a clearer insight to this aspect. Advances in technology may allow the instrumentation of *R. typus* with long-term video or particle capture facilities that could also provide some answers to these questions.

ASSOCIATIONS WITH OTHER FAUNA

Many of the earliest records describe a variety of other animals associated with *R. typus*. Parasitic copepods are common on fish of this size (Yamaguti, 1963), and several have been identified on *R. typus* (Norman *et al.*, 2000), but two species appear to be unique to them. The siphonostomatoid copepod *Prosaetes rhinodontis* (originally *Stasiotes rhinodontis*) was found on the surface of the filtration pads of *R. typus* (Wright, 1877) and thought to be parasitic, while another siphonostomatoid copepod *Pandarus rhincodonicus* was thought to be commensal, feeding on bacteria on the surface of the fish's skin (Norman *et al.*, 2000).

Several species of fishes are also commonly found with *R. typus* ranging from the so-called pilot fishes, such as the black-banded pilot *Naucrates ductor* (L. 1758) (Colman, 1997a; Rowat, 2010) and the golden pilot *Gnathanodon speciosus* (Forsskål 1775) (Taylor, 1994; Clarke & Nelson, 1997) to the live-sharksucker *Echenei naucrates* L. 1758 and the common remora *Remora remora* (L. 1758) (Colman, 1997a). Smaller varieties of sharksucker are also found often living in the mouth and peribrachial cavity, as well as in the spiracle such as the white suckerfish *Remora albescens* (Temminck & Schlegel 1850). In some areas *R. typus* are often accompanied by cobia *Rachycentron canadum* (L. 1766), which in some popular reports have been variously mistaken as baby whale sharks or real sharks. In reality *R. typus* are seldom seen with other sharks, with very few records in the literature: with *S. lewini* off Baja California, Mexico (Wolfson, 1987) and tiger sharks *Galeocerdo cuvieri* Péron & LeSueur 1822 off the Galapagos (Arnbom & Papastavrou, 1988). Due to the temperature separation between habitats of *R. typus* and *C. maximus*, they are seldom recorded together except in areas where a warm current is deflected into cold water, such as Monterey Bay, California (Ebert *et al.*, 2004) and off southern Brazil (Gadig, 2007).

As *R. typus* tend to aggregate in areas of high productivity, they are often reported with other species that are similarly attracted to such food sources. They have been recorded with plankton feeding species of mobulids such as the giant manta

Manta birostris (Walbaum 1792) (Wolfson, 1987), the reef manta *Manta alfredi* (Krefft 1868), the shortfin devilray *Mobula kuhlii* (Müller & Henle 1841) and pygmy devilray *Mobula eregoodootenkee* (Bleeker 1859) (unpubl. data). They have long been associated with schooling tuna *K. pelamis* enabling fishers to target these schools effectively (Springer, 1957; Iwasaki, 1970; Rao, 1986; Silas, 1986; Matsunaga *et al.*, 2003). This has helped both artisanal fishers as well industrialized fleets of purse seiners with the United Nations Food and Agriculture Organisation stating that between 1976 and 1982 ‘Globally, 8% of purse-seine sets are carried out in the presence of a whale shark’ (FAO, 2011). *Rhincodon typus* have also been associated with several other commercially valuable fish species including *E. australis* (Duffy, 2002) and giant herring *Elops hawaiiensis* Regan 1909 (Wilson, 2002).

MORTALITY AND EXPLOITATION

NATURAL MORTALITY

Natural mortality in *R. typus* is probably highest in the early juvenile stages; while there is little hard evidence to support this, the large number of pups found in the Taiwanese female (Joung *et al.*, 1996) are indicative of potential high mortality. Also, juvenile *R. typus* have been recovered from the gut of a blue marlin *Makaira nigricans* Lacépède 1802 (Colman, 1997a) and a *P. glauca* (Kukuyev, 1995), confirming that *R. typus* pups will be taken by larger predators. Similarly, reports from many of the *R. typus* photo-identification studies have revealed a high incidence of bite marks and scars suggesting that the species is subject to attacks from various other predators through their juvenile stages, although they apparently survive a number of such incidents (Taylor, 1989; Norman, 2002; Arzoumanian *et al.*, 2005; Meekan *et al.*, 2006; Rowat *et al.*, 2007b; Speed *et al.*, 2008a). Larger *R. typus* are also subject to attack by predators such as killer whales *Orcinus orca* (O’Sullivan & Mitchell, 2000) and other large sharks (Fitzpatrick *et al.*, 2006) although it is not known how frequently this occurs.

Rhincodon typus are known to become stranded in very few areas, such as along the Indian Ocean coast of South Africa (Beckley *et al.*, 1997) and off both Indian Ocean and Pacific coasts of Australia (Speed *et al.*, 2008b). The cause of these strandings is not clear, but in South Africa it is thought that it might be a function of the local topography and swell patterns or a sudden change in water temperature causing metabolic problems (Beckley *et al.*, 1997). Off Australia there were no indications of any injuries and no other cause was proposed (Speed *et al.*, 2008b).

ANTHROPOGENIC MORTALITY AND FISHERIES

The surface swimming habits of *R. typus* make them open to injuries caused by collisions with boats and many of the earliest reports on the species were gathered from such incidents (Gudger, 1927, 1937a, b, c, 1938). Mortalities from boat strikes are seldom reported in scientific literature now, but certainly continue (Rowat, 2010) and injuries from boat and propeller strikes are commonly recorded in monitoring programmes (Taylor, 1989; 1994; Norman, 2002; Arzoumanian *et al.*, 2005; Meekan *et al.*, 2006; Rowat *et al.*, 2007b; Speed *et al.*, 2008a).

The effects of hunting or fisheries on any slow maturing species are liable to have significant effects on their populations unless this is carefully controlled (Jackson *et al.*, 2001; Estes *et al.*, 2006). *Rhincodon typus* are slow growing and late maturing (Fowler, 2000; Wintner, 2000) and so potentially at risk from targeted fishing practices. In general, before 1990, there was little market for *R. typus* products; oil was used to waterproof boats (Anderson & Ahmed, 1993) and for manufacturing shoe polish (Rao, 1986). Small scale artisanal fisheries for *R. typus* existed in several countries such as India, Iran, Maldives, Pakistan and the Philippines (Anderson & Ahmed, 1993; Alava *et al.* 1997b; Hanfee 1997; Fowler, 2000). Although even this level of exploitation was thought to affect local abundance in the Maldives and the fishery was banned in 1995, as recommended by Anderson & Ahmed (1993). Off Taiwan, pre-1990, there was no dedicated fishery and *R. typus* were caught as by-catch in set-net fisheries (Chen *et al.*, 1997). In the early 1990s there was a rapid increase in demand for *R. typus* once the flesh, known as tofu shark, was found to be a delicacy by the Taiwanese restaurant trade (Chen *et al.*, 1997). As the cartilage fibres in the fins were apparently not good for making soup, however, they were either discarded or sold as display or trophy fins for shark-fin soup restaurants (Chen & Phipps, 2002). The demand for tofu shark led to the consequent expansion of the Indian, Philippine and Taiwanese fisheries, all of which would prove to be short-lived.

In the mid 1990s, the Philippines processed between 450 and 799 *R. typus* per year (Alava *et al.*, 1997b), while the Indian fishery recorded up to around 430 (Hanfee, 2001) although other sources have claimed substantially higher catches (Norman, 2002). The *R. typus* fishery in Taiwan was landing 250–270 individuals per year in the late 1990s which were all juveniles <7 m, while the catch from India comprised generally larger individuals >7 m (Hanfee, 2001; Chen & Phipps, 2002).

The catch from the major Philippine grounds declined by 27% in 1997 and following the setting up of an *R. typus* sanctuary around Donsol (12° 54' N 123° 36' E) in 1998, a complete ban on fishing *R. typus* and Mobulidae was imposed (Pine *et al.*, 2007). Similar declines were seen in India where only 160 *R. typus* were landed in 2000 and the species was then protected under national legislation (Hanfee, 2007). In Taiwan, the 2001–2002 total catch declined to just 113 despite increased demand and value; however, imports of *R. typus* rose to meet the demand with 7000 t imported in 2001 with a similar amount exported, the largest markets being South Korea and the U.S.A. (Chen & Phipps, 2002). Surprisingly, the following year only 2 t were recorded as exported (Chen & Phipps, 2002) and Taiwan prohibited the killing of the *R. typus* as well as the sale of its meat and other products in 2008 (RoC, 2007). The perceived value of *R. typus* fins for display purposes, however, appears to have increased over the years and there are recent reports of live individuals being finned in the Maldives (Riley *et al.*, 2009) and Philippines (David, 2010).

Rhincodon typus are also taken in other areas as by-catch in net fisheries targeting other species. The greatest effect is from fisheries targeting species such as *K. pelamis*, with which *R. typus* are regularly found. The largest mortality is probably that from the purse-seine fisheries use of *R. typus* as an indicator of tuna presence and setting nets around them (Iwasaki, 1970; Rao, 1986). Records from purse-seine fleets have shown that while there are many *R. typus* associated sets, in some fisheries the individuals are released from the nets alive most times (Chassot *et al.*, 2009; Amandè *et al.*, 2010). There is a perceived level of under-reporting of *R. typus* sets

in this fishery, due in part to *R. typus* being found in the catch although, because the *R. typus* were not seen at the surface, the set was not recorded as a *R. typus* set (SPC-OFP, 2010). Records show a range of *R. typus* mortality from two animals in the Russian Indian Ocean fleet (Romanov, 2002), to an estimated 60 individuals from 2007–2009 in the Pacific fleets (SPC-OFP, 2010). The high mortality in this latter fishery prompted a proposal to ban the setting of nets around *R. typus* to the 2010 annual session of the Western and Central Pacific Fisheries Commission; however, this ban was not supported (WCPFC, 2011).

NON-CONSUMPTIVE EXPLOITATION

The use of *R. typus* as a tourism feature has increased dramatically since c. 1990 from the fledgling industry started at Ningaloo Reef in Western Australia (Taylor, 1994). Here, the development and control of *R. typus* interaction activities was guided by a code of conduct (Colman, 1997b) and by legislative controls on the numbers of operators and licences (Mau & Wilson, 2008) to minimize negative interactions with the fish. This code has become a best-practic model for many other areas, but its implementation elsewhere has met varying degrees of success. In Belize, the number of operators grew from one in 1996 to 26 in 2005 (Carne, 2007). Despite iterative revisions of management, the numbers of *R. typus* present at the aggregation declined as did the chances of seeing one (Quiros, 2005; Carne, 2007). More management changes were introduced and tourism continued to increase with a peak of >2000 visitors in 2006 (Carne, 2008).

In Donsol, *R. typus* tourist numbers rose from 850 in 1998, to 3299 in 2004 (Pine *et al.*, 2007). By 2005, visitors had risen to 7100, but lack of enforcement of the code of conduct was having measurable effects on the sharks' behaviours (Quiros, 2007) prompting tighter interaction controls. Off the Yucatan Peninsula, Caribbean Sea, *R. typus* tourism started in 2002 and immediately flourished (Remolina Suárez *et al.*, 2007), but raised concerns with respect to negative effects on *R. typus*. By 2007, visitors increased to >16 000 with 140 tour operators, however, compliance with the codes of conduct was still an issue (Remolina Suárez, 2008).

The deleterious effects of such interactions on *R. typus* may be both short and long-term (Norman, 2002). Short-term effects include eye-rolling, banking, rapid diving and avoidance behaviour, all of which may disturb and stop *R. typus* from feeding effectively. Long-term effects may include disruption of normal feeding activities, avoidance of or displacement from these areas, stress, injury and even mortality, due to boat strikes (Norman, 2002).

Globally, *R. typus* tourism activities are the most prominent form of shark-based activities (Gallagher & Hammerschlag, 2011), due in no small part to their massive size and perceived human-friendly nature (see Fig. 1 for tourism sites). At Ningaloo Reef, the oldest of these *R. typus* tourism sites, the activities have become more of a mainstream tourism product, appealing to a wider participant age base with a broader general wildlife interest (Catlin & Jones, 2010). The popularity of *R. typus* tourism has given the live fish a real economic value in many areas. In turn these areas have also supported a significant number of research activities, as shown throughout this review, and in some areas the tourism activities directly fund the ongoing monitoring and research programme (Rowat & Engelhardt, 2007). There is significant scope for tourism operators to become more involved in supporting research activities and in

collecting routine data on sightings and interactions, as is done in some areas (Mau & Wilson, 2008). Collation of these data on a regional basis, as has been done for photo identities in the Indian Ocean (Brooks *et al.*, 2010), might go some way to fill gaps in knowledge of their behavioural ecology.

CONSERVATION AND MANAGEMENT

Several countries have developed national conservation measures for *R. typus* including Australia, Belize, Djibouti, Honduras, India, Maldives, Mexico, Philippines, Seychelles, Taiwan, Thailand and the U.S.A. (Rowat, 2010).

The first international initiative for the management of marine resources was the United Nations Convention on the Law of the Sea (UNCLOS, 1982); this provides a framework for the conservation and management of fisheries and other uses of the seas, but to date no management initiatives under this convention has included *R. typus*. Under the aegis of this convention, the United Nations Agreement on Straddling and Highly Migratory Fish Stocks was introduced in 1995, which has potential for direct actions to be taken in relation to species such as *R. typus* (UNCSSHMF, 1995). As yet, however, no action plans for *R. typus* have been drawn up under this agreement. Also in 1995, the FAO finalized a Code of Conduct for Responsible Fisheries and then in 1998 the International Plan of Action for Conservation and Management of Sharks (FAO, 1999); this should have benefits to *R. typus* populations, but unfortunately as of July 2011 only 13 National Plans Of Action had been published (<http://www.fao.org/fishery/ipoa-sharks/npoa/en>).

In 2000, *R. typus* was classified by the International Union for the Conservation of Nature as vulnerable in the Red List of Threatened Animals (IUCN, 2010). This was based on falling populations as shown by declining landings and actual levels of exploitation; also, population decline was projected or suspected in the future, based on potential levels of exploitation deemed likely to occur if directed fisheries remain unmanaged, and as a result of by-catch (Norman, 2000). This classification was largely supported by the data from the Indian and Philippine fisheries (Alava *et al.*, 1997a; Hanfee, 1997). These data also led to the inclusion of the species on Appendix II of the Convention of Migratory Species of Wild Animals (CMS) in 1999 (CMS, 1999) and to Appendix II of CITES, the Convention of Trade in Endangered Species, in 2002 (CITES, 2002). The inclusion on CITES was based on the criteria that 'it is known, inferred or projected that harvesting of specimens from the wild for international trade has, or may have, a detrimental impact on the species by exceeding, over an extended period, the level that can be continued in perpetuity'. While neither listing provides for direct conservation or management, CITES does require that international trade in any whole or part of the animal is monitored and in so doing assists in global conservation. The CMS has provided a forum for the development of more direct conservation approaches with the subsequent adoption, in 2010, of a memorandum of understanding on migratory sharks listed on the convention's appendices, which includes the *R. typus* (CMS, 2010) and as such provides a viable route to develop international conservation actions. There were 17 signatory countries to this memorandum as of May 2011 and technical meetings are progressing to finalize the conservation and management plan.

CONCLUSIONS AND FUTURE DIRECTIONS

This review has emphasized that significant steps have been made by numerous researchers and monitoring programmes to elucidate the biology and ecology of *R. typus*; however, there are still some very important questions which remain unanswered about the life of the world's largest extant fish, which have been raised here within the various sections along with suggestions as to potential avenues to resolve them.

Some data that might help to provide answers come from an unlikely source, the oceanic purse-seine tuna fleets. Most regional fishery management organizations require that the vessel captains maintain detailed log books recording the sets made and catches therein, which also includes sets made on *R. typus* (Iwasaki, 1970; Rao, 1986; Amandè *et al.*, 2010). These data are now being analysed to provide information on the hitherto largely unknown patterns of pelagic occurrence of *R. typus* in the Indian Ocean (Sequeira *et al.*, 2011) and similar studies of Atlantic purse-seine fishery data are ongoing. This information, when combined with the data from coastal monitoring programmes, might provide an indication of how these groups interact. The presence of trained scientific observers aboard a large number of the purse-seiners may also enable more detailed data to be collected to identify if the individuals seen are the elusive adult *R. typus*. If data generated from studies of this nature do shed light on adult populations of *R. typus*, they might also answer some of the still existing questions about the age of first maturity of *R. typus* and where, when and how often they reproduce, which are significant issues in the development of appropriate national and regional conservation and management plans.

One of the unanswered questions regarding the juvenile *R. typus* found at the seasonal aggregations is where they go to when they disappear from these areas. The results of satellite tagging suggest that they can and do move large distances from these sites (Eckert & Stewart, 2001; Wilson *et al.*, 2006; Rowat & Gore, 2007; Hueter *et al.*, 2008), but some sites have shown high numbers of individuals returning in successive years (Speed *et al.*, 2007; Brooks *et al.*, 2010; Riley *et al.*, 2010). It is currently unclear, however, whether the apparently philopatric fish actually leave their aggregation area or are simply not visible to observers because they have moved a little further offshore, or deeper, or that the number of observations are less due to poor sea conditions or changes in survey effort. The relative ease of identifying the philopatric *R. typus* using photo ID should enable targeted satellite studies on this particular group of *R. typus* in several aggregations. The high rate of resightings also makes these philopatric individuals good candidates for long-term archival-tag studies. Similarly, comparison of satellite tracking data with the predicted pelagic occurrence within ocean basins may tie together different pieces of the global jig-saw.

While information from the targeted *R. typus* fisheries, in addition to information from industrialized high seas fisheries for other species and the continued research at the known aggregation sites may shed some light onto these issues, it is likely they will raise further specific research questions. Continued long-term monitoring effort at the known aggregations, may yet confirm inter-aggregation movements suggested by a few satellite tracks and should also provide more detailed information relative to the biophysical characteristics of these environments. The location and habits of adult *R. typus*, where they mate and give birth, and where the pups live are fundamental ecological issues, yet despite hundreds of *R. typus* being sighted each

year, the answers to these questions are still elusive. The world's largest shark thus remains an enigma 183 years after first being described.

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SUPPORTING INFORMATION

Supporting Information may be found in the online version of this paper:

APPENDIX SI. Photo identification using computer programmes.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

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