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Scarring patterns and relative mortality rates of Indian Ocean whale sharks

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This study recorded the scarring rate and severity for whale sharks *Rhincodon typus* from three Indian Ocean aggregations (Australia, Seychelles and Mozambique), and examined whether scarring (mostly attributed to boat strikes and predator attacks) influences apparent survival rates using photo-identification libraries. Identifications were based on spot-and-stripe patterns that are unique to individual whale sharks. Scarring was most prevalent in the Seychelles aggregation (67% of individuals). Predator bites were the most frequent source of scarring (aside from minor nicks and abrasions) and 27% of individuals had scars consistent with predator attacks. A similar proportion of whale sharks had blunt trauma, laceration and amputation scars, the majority of which appeared to be caused by ship collisions. Predator bites were more common (44% of individuals) and scars from ship collisions were less common at Ningaloo Reef than at the other two locations (probability of among-site differences occurring randomly = 0·0007 based on a randomized multinomial contingency analysis). In all aggregations, scars occurred most often on the caudal fin, which may result from the fin being the body part closest to the surface when boats pass over, or they may provide a large target for predator attack. No evidence was found for an effect of scarring on apparent survival (ϕ; mean ± S.E.) for the Ningaloo (not scarred $\phi = 0{\cdot}858 \pm 0{\cdot}033$; scarred $\phi = 0{\cdot}929 \pm 0{\cdot}033$) or Seychelles populations (not scarred $\phi = 0{\cdot}502 \pm 0{\cdot}060$; scarred $\phi = 0{\cdot}538 \pm 0{\cdot}070$). The lower apparent survival of the Seychelles population may be attributed to a high number of transient whale sharks in this aggregation that might bias estimates. This study indicates that while scarring from natural predators and smaller vessels appears to be unrelated to whale shark survival, the effect of deaths related to ship strike need to be quantified to assist in future management of this species.

Key words: boat strike; mark–recapture; photo-identification; *Rhincodon typus*; scarring; survival rates.

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INTRODUCTION

'*...Rhineodon* [sic] *typus, fears not shark, man nor ship*' Gudger, 1941.

Declines in populations of whale sharks *Rhincodon typus* Smith have been observed and predicted in many regions (CITES, 2002; IUCN, 2005; Theberge & Dearden, 2006; Bradshaw *et al.*, 2007). This species, the world's largest fish and one of the most wide-ranging marine vertebrates (Wilson *et al.*, 2006; Bradshaw, 2007; Castro *et al.*, 2007), is known to be susceptible to a variety of threats including direct harvest, ecosystem modification and collisions with ocean-going vessels (Bradshaw *et al.*, 2007) that may be the cause of these declines. The prospect of losing such a large and iconic species is of both conservation and economic concern. For example, the disappearance of the species could precipitate large annual losses generated from whale shark tourism globally (Graham, 2004).

Although potential sources of population decline have been recognized for many years (Colman, 1997), their relative importance remains largely unquantified. The large size (>12 m total length, L_T), slow swimming speeds (between 1 and 3 km h^{-1}) (Gunn *et al.*, 1999; Eckert & Stewart, 2001; Eckert *et al.*, 2002; Hsu *et al.*, 2007) and tendency to spend a large proportion of their time at the surface (Wilson *et al.*, 2006) renders this species particularly vulnerable to ramming by vessels (Gudger, 1940), artisanal and commercial fishing (Colman, 1997) and predation by large sharks and some cetaceans (Fitzpatrick *et al.*, 2006). Additionally, these animals make annual long-distance migrations through international and national waters (Wilson *et al.*, 2006). This means that whale sharks may experience protection by legislation and management in some areas, while being exploited in other parts of their range (Bradshaw, 2007), a problem common to other wide-ranging marine species such as North Atlantic right whales *Eubalaena glacialis* Muller (Ward-Geiger *et al.*, 2005). Thus, identifying mortality sources and areas where these pose a risk to whale sharks are important steps in formulating global initiatives for conservation.

Legal and illegal fishing of whale sharks is often suggested to be a major factor causing population declines (Chen & Phipps, 2002; CITES, 2002; Bradshaw *et al.*, 2007). This mortality is relatively easy to quantify because animals are brought to shore by fishermen and sold in markets. Other factors such as predation and boat strike, however, may be equally important, but are far more difficult to estimate reliably because they are thought to occur principally in the open ocean. Despite the lack of direct observation, where whale sharks survive predatory attacks or collisions with ships, some evidence of these events may be left in the form of scars or injuries on the body. Analysis of scarring patterns may thus provide an insight into the relative importance and source of mortality afflicting whale sharks, as is the case for other large marine species such as manta rays (Mobulinae), manatees, whales, dolphins and seals (Kraus, 1990; Hiruki *et al.*, 1993; Angliss & DeMaster, 1997; Visser, 1999; Heithaus, 2001*a*; Laist *et al.*, 2001; Naessig & Lanyon, 2004; Rommel *et al.*, 2007).

Each whale shark has a unique pattern of spots and stripes (Meekan *et al.*, 2006) that can be used to identify individuals (Speed *et al.*, 2007). Photographic databases are now used worldwide in mark–recapture studies to document population trends and estimate demographic rates (Fujiwara & Caswell, 2001;

Stevick *et al.*, 2001; Bradshaw *et al.*, 2003; Meekan *et al.*, 2006; Speed *et al.*, 2007). A combination of information on rates and source of scarring in conjunction with mark–recapture data may provide a means to quantify relative mortality rates among whale shark populations experiencing different direct and indirect human impacts. Similar analyses of the survival implications of scarring and injuries have been made in other taxa, *e.g.* Iberian lynx *Lynx pardinus* Temminck, North Atlantic right whales and Hawaiian monk seals *Monachus schauinslandi* Matschie (Kraus, 1990; Garcia-Perea, 2000); however, no study to date has combined photo-identification with scarring to test the hypothesis that scarring is indicative of higher mortality rates.

This study documents the severity, positioning and likely causes of scars observed on whale sharks participating in three Indian Ocean aggregations: (1) Ningaloo Reef, Western Australia, (2) Mahe, Seychelles and (3) southern Mozambique. Using capture–mark–recapture (CMR) models and quantified scarring patterns, relative apparent survival rates were estimated between two of the study sites (Ningaloo and Seychelles) and compared to shipping traffic rates to estimate the potential high-risk boat-strike areas for this species.

MATERIALS AND METHODS

SCARRING DATABASES AND IMAGE MATCHING

Scarring image libraries were constructed from larger whale shark photo-identification databases for Ningaloo Reef, Western Australia (22°50′ S; 113°40′ E), Mahe, Seychelles (4°36′ S; 55°26′ E) and southern Mozambique (23°52′ S; 35°33′ E). (Fig. 1). The Ningaloo scarring library consisted of images of individuals with scars taken over 10 capture sessions (years) between 1992 and 2006 (not including 1997–2000 and 2002). The Seychelles library consisted of images taken over six capture sessions between 2001 and 2006 and also included scarring information obtained from a tagging database. The Mozambique scarring library consisted of images taken during one capture session over the 2004–2005 season.

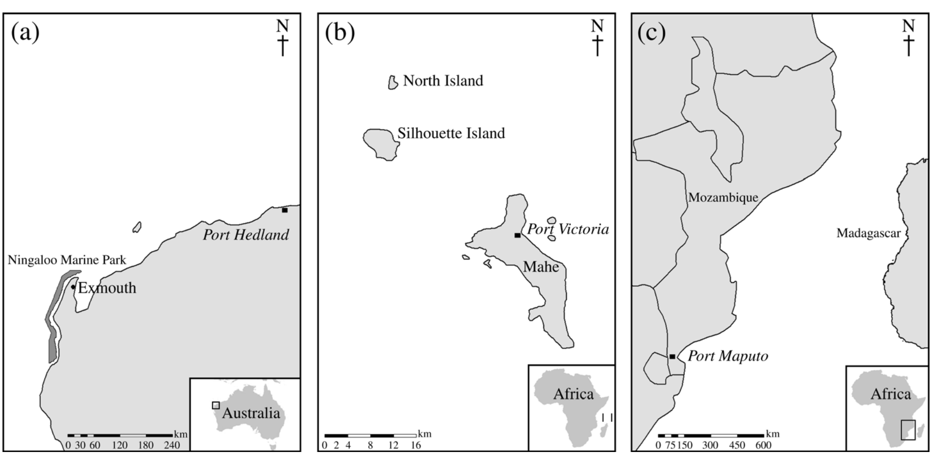

FIG. 1. Indian Ocean whale shark aggregation sites: (a) Ningaloo Reef (Western Australia), (b) Seychelles and (c) Mozambique.

Images were matched using the software I^3S (Van Tienhoven *et al.*, 2007) and visual confirmation following guidelines for use on whale sharks outlined in Speed *et al.* (2007). Where images did not lend themselves to the fingerprinting process required for I^3S, images were matched manually by an experienced photo-archivalist (Meekan *et al.*, 2006) using not only the pattern of natural pigmentation, but also other individually unique identifiers such as scars and tags.

SCARRING CATEGORIES

Seven scarring categories were created based on images present in the libraries for each region: (1) abrasions, (2) lacerations, (3) nicks, (4) bites, (5) blunt trauma, (6) amputations and (7) 'other' (Appendix). Each image was assigned to one or more of the seven categories by visual inspection. The severity of scarring was classified into two groups: 'major' or 'minor'. Major scars were considered to be potentially life-threatening and included complete or near-complete amputation of the first dorsal, pectoral or caudal fins, lacerations penetrating the sub-dermal layer, blunt trauma around the head or gills and large shark bites (>300 mm in length) [Fig. 2(a)–(c)]. Minor scars were considered to be superficial and included abrasions, partial amputations, small bites, nicks and 'other' [Fig. 2(d)–(f)].

DATABASE COMPARISONS

The frequency of individuals with scars per capture session was initially calculated for each database and then combined to give total numbers of scarred individuals per aggregation. Due to differing numbers of sample periods among databases, estimates were standardized for cross-database comparisons by dividing the number of scarred individuals by the total number of individuals photographed for each aggregation. The total number of whale sharks scarred per database was also recalculated with the scarring categories 'nicks' and 'abrasion' omitted for two reasons: (1) the scar categories are unlikely to affect survival rates given that they are by definition superficial wounds and (2) minor scars were often not photographed on individuals at Ningaloo Reef. The proportion of individuals with differing scar types were calculated for each

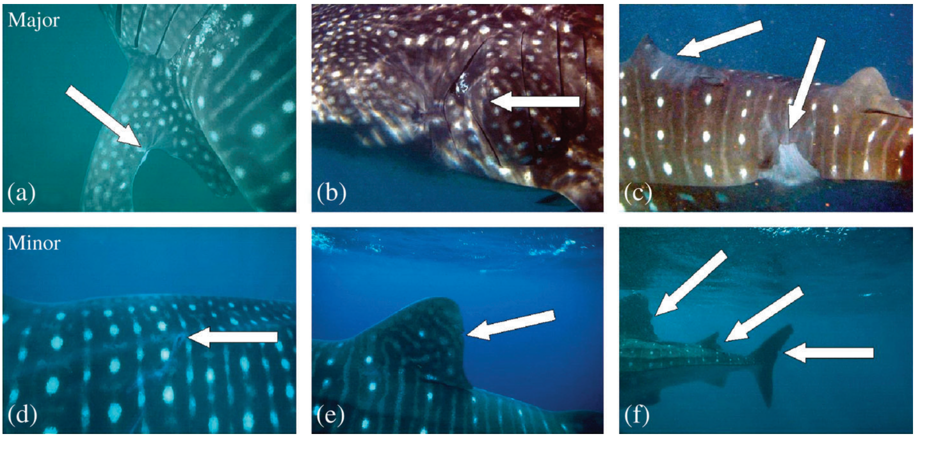

FIG. 2. Classification of scar severity (⟹). (a)–(c) examples of 'major' scarring: (a) a large bite taken out of the left pectoral fin, (b) blunt trauma to the left side of head and (c) bites taken out of dorsal fin and left flank. (d)–(f) examples of 'minor' scarring: (d) abrasion on the right flank, (e) small nick taken out of the trailing edge of the dorsal fin and (f) nicks and small bites taken out of the first and second dorsal fins and caudal fin.

aggregation (with minor scars omitted). A randomized multinomial contingency analysis (10 000 iterations) was constructed to test the hypothesis that the distribution of animals in each scar category differed among aggregations. Scar categories were combined into three main classes to avoid low-frequency classes dominating results: bites, blunt trauma and lacerations or amputation (ignoring other categories). Scar positions on the body of each whale shark were also recorded to compare among aggregations and to determine the most commonly scarred areas of the body.

EFFECTS OF SCARRING ON APPARENT SURVIVAL

Capture histories consisting of inter-season resights from Ningaloo and Seychelles were initially constructed using matches identified by I^3S as well as tags deployed in Seychelles. The capture history for the Mozambique aggregation was unable to be included because there were too few sample sessions. To avoid double-counting, individuals with only the left side photographed were removed from the Ningaloo capture history (because there were fewer left-side photographs than right-side), while individuals with only the right side photographed were removed from the Seychelles capture history (fewer right-side photographs there) (Meekan *et al.*, 2006). Capture histories included (1) whether the individual was scarred or not (three categories: major, minor and none), (2) the putative source of scarring (anthropogenic, bite, unknown or none) and (3) the body position of the scar (fin, body or none). Cormack-Jolly-Seber (CJS) CMR models were used and executed in the programme MARK (White & Burnham, 1999) to model apparent survival of (ϕ) and resighting probability (p) (Bradshaw *et al.*, 2007). The major focus of this analysis was to assess whether the apparent survival rate for whale sharks with scars differed from whale sharks without scars.

The initial analysis examined whether there was evidence for time variance in ϕ or p over the study period (1992–2006) at Ningaloo, which was analogous to the approach adopted by Bradshaw *et al.* (2007), although the current analysis included two additional capture sessions (2005 and 2006). This process was then repeated for the Seychelles aggregation. The second analysis included scarring as an additional group effect on ϕ or p. Scar type and severity were examined to assess whether they influenced ϕ or p. Models were compared using Akaike's information criterion (AIC) corrected for small sample sizes (AIC_c) (Burnham & Anderson, 2002) and goodness-of-fit was estimated using the bootstrap GOF function in the programme MARK (White & Burnham, 1999).

SHIPPING ACTIVITY AROUND AGGREGATIONS

Due to limited availability of spatial shipping data for the east coast of Africa, shipping density was unable to be modelled around the three whale shark aggregations. Consequently, the number of commercial ships (*i.e.* container ships and bulk carriers) calling in at the largest and nearest port to each aggregation was obtained through associated port authorities as a proxy for shipping intensity. Where available, statistics on smaller vessel traffic were also noted. Ship-calling data were obtained for the fiscal year from 01 July 2005 through to 30 June 2006 from Port Hedland (Australia), Port Victoria (Seychelles) and Port Maputo (Mozambique) authorities.

RESULTS

The Seychelles aggregation had the highest percentage of scarred individuals (67%, 534 of 797), followed by Mozambique (37·2%, 67 of 180) and Ningaloo (27%, 84 of 311). After the removal of minor scars (nicks and abrasions), the total percentages of scarred individuals per aggregation dropped to 45·3% (361 of 797) for Seychelles, 22·7% (41 of 180) for Mozambique, and 20% (62 of 311) for Ningaloo Reef. Nicks were the most abundant scar category in all

TABLE I. Percentage of individual whale sharks within scar type and body location category among three Indian Ocean aggregations observed. Number of sightings are given in parenthesis

	Aggregation		
	Ningaloo	Seychelles	Mozambique
Scar type (%)			
Abrasions	21·4 (18)	14·6 (77)	40·3 (27)
Lacerations	8·3 (7)	34·5 (182)	7·5 (5)
Nicks	11·9 (10)	48·6 (256)	14·9 (10)
Bites	44·0 (37)	21·4 (113)	14·9 (10)
Blunt trauma	8·3 (7)	5·1 (27)	7·5 (5)
Amputations	15·5 (13)	21·4 (113)	26·9 (18)
Other	2·4 (2)	4·4 (23)	10·4 (7)
Scar location (%)			
Head	9·5 (8)	11·6 (61)	30·0 (20)
Dorsal fin	30·0 (25)	38·5 (203)	20·9 (14)
Caudal fin	25·0 (21)	62·2 (349)	31·3 (21)
Pectoral fin	22·6 (19)	14·4 (76)	22·4 (15)
Flank	25 (21)	25·2 (133)	34·3 (23)

n = number of sightings.

aggregations (Table I). After the removal of these minor scars (nicks and abrasions), bites were the most common scars (Table I and Fig. 3). The randomized contingency analysis demonstrated that the probability of generating the same among-site differences in the distribution of individuals within the three major scar categories (bites, blunt trauma and lacerations or amputations) was = 0·0007 (based on 10 000 iterations). Observed and expected frequencies were similar for Seychelles and Mozambique animals, but Ningaloo had more bites and fewer amputations and lacerations than expected (Fig. 4).

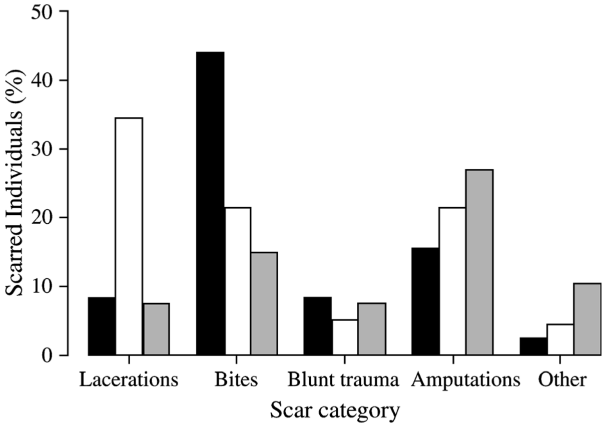

FIG. 3. Percentage occurrence of individuals within scar categories by location: Ningaloo (■) Seychelles (□) and Mozambique (▩).

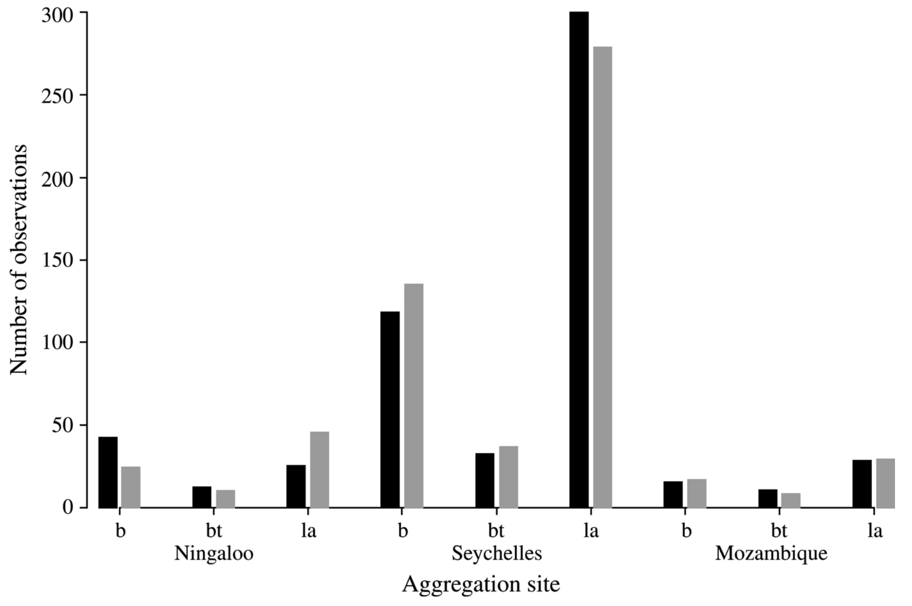

FIG. 4. Observed (■) and expected (■) numbers of whale sharks in each scarring category among aggregation sites (b, bites; bt, blunt trauma; la, lacerations and amputations).

Caudal fins were the most commonly scarred body part [Fig. 5(a)] at all locations [Fig. 5(b)].

The saturated Cormack–Jolly–Seber capture–mark–recapture model [ϕ (*ts*) p (*ts*)] relating time (t) and scarring (s) to apparent survival (ϕ) and resight probability (p) for the 221 individual whale sharks seen at Ningaloo fit the data reasonably well (probability of observing the model deviance as large = 0·134 based on 1000 iterations). Therefore, no adjustment to AIC_c was made for overdispersion (White & Burnham, 1999). Most parameters were inestimable using the *ts* interaction for ϕ and p, so these group factors were considered separately in all subsequent model comparisons. The most highly ranked model ($wAIC_c$ = 0·84) had scar effects on apparent survival and time-variant resighting probability [ϕ (s) p (t)] (Table II); however, 95% CI for scarred and not-scarred individuals overlapped substantially (Table III).

There was no overdispersion detected for the Seychelles dataset, and the most highly ranked model ($wAIC_c$ = 0·99) demonstrated time variance in ϕ and p (Table II). Many of the interval estimates of ϕ were inestimable, however, so the second-most highly ranked model was used to test for scarring effects. Again, there was considerable overlap in the 95% CI between scarred and non-scarred individuals (Table III), suggesting little evidence for an effect on apparent survival. Apparent survival rates were considerably lower in the Seychelles (*c.* 0·50) compared to Ningaloo Reef (*c.* 0·90).

The number of commercial ships that called in to Port Hedland during the fiscal year of 2005–2006 was 925 (excluding fishing vessels). The intended destinations after departure for the majority of these ships were Asia. The number

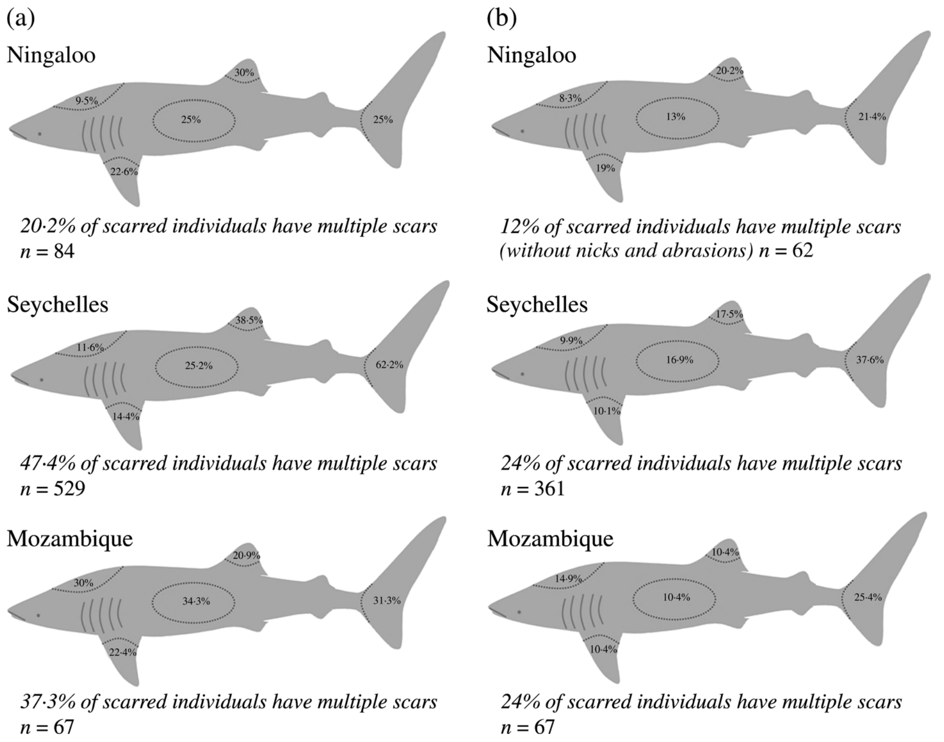

FIG. 5. (a) Position of scars and (b) position of scars on body with nicks and abrasions omitted by aggregation site (n = number of scarred individuals).

of commercial vessels calling in to Port Victoria during the same period was 510; however, there was also a notably high number of fishing vessels (628), both purse-seine and longline, whose next destination was the high seas. For commercial vessels, the next port of call was largely south-east African and Indian Ocean island ports or European or Asian ports. The number of commercial ships that docked at Port Maputo during this period was 674, with the final destination of most of these vessels also being Asia.

DISCUSSION

The prevalence and origin of large scars on whale sharks leads to the hypothesis that activities other than direct overexploitation from fishing may also contribute to observed and modelled population declines of whale sharks in the Indian Ocean. Of the 1288 individuals identified in this study, 36% bore prominent scars (*i.e.* excluding nicks and abrasions). Bite marks were the most common form of major scar (27% of scarred individuals) followed by lacerations and amputations (19%) and blunt trauma (7%). Bite scars were probably the result of attacks by large predators such as sharks and killer whales. Non-lethal attacks by a large (>4 m) predatory shark on a whale shark have been recorded at Ningaloo Reef (Fitzpatrick *et al.*, 2006) and a fatal attack on an 8 m whale shark by killer whales *Orcinus orca* L. was observed in the Gulf

TABLE II. Five most highly ranked Cormack–Jolly–Seber models testing the effects of scarring (s) and time (t) on apparent survival (Φ) and resight probability (p) of whale sharks participating in the Ningaloo Reef aggregation between 1992 and 2006, and at Seychelles between 2001 and 2006. Shown are the difference in Akaike's information criterion corrected for small sample sizes between the current and top-ranked model (ΔAIC_c), AIC_c weight ($wAIC_c$), the number of model parameters (k), and model deviance [(.), a constant parameter]

Model	ΔAIC_c	$wAIC_c$	k	Deviance
Ningaloo Reef				
Φ (s) p (t)	0·000	0·842	10	133·021
Φ (.) p (t)	3·381	0·155	10	136·402
Φ (.) p (.)	58·406	0·000	2	208·329
Φ (t) p (.)	58·114	0·000	10	191·135
Φ (t) p (t)	12·535	0·000	17	129·777
Seychelles				
Φ (t) p (t)	0·000	0·999	8	31·894
Φ (s) p (t)	25·201	0·000	7	61·233
Φ (.) p (t)	23·491	0·000	6	61·580
Φ (.) p (.)	57·842	0·000	2	104·074
Φ (t) p (.)	28·918	0·000	6	67·006

of California (J. B. O'Sullivan & T. Mitchell, unpubl. data). None of the bite scars found on whale sharks in this study could be unambiguously attributed to killer whales, as virtually all were healed wounds that lacked the distinctive teeth rake marks that are definitive of attacks by these predators (Naessig & Lanyon, 2004).

Many whale sharks bore the evidence of collisions with boats and this phenomenon was probably responsible for the majority of lacerations, amputations and blunt trauma injuries. The parallel rows of deep lacerations found on the backs of many whale sharks provided clear evidence of strikes by ship propellers (Rommel *et al.*, 2007), while the large blunt trauma injuries on the head and flanks of whale sharks were probably mostly due to ramming by ship bows (Laist *et al.*, 2001). In the case of amputations, some of these injuries may have also have been due to predatory attacks, albeit most could be distinguished from ship strike by the circular edge of the wound [see Fig. 2(a)].

TABLE III. Apparent survival estimates for whale sharks with and without scarring at Ningaloo Reef and Seychelles based on Cormack–Jolly–Seber mark–recapture models

Model		Φ	S.E.	Lower 95% CI	Upper 95% CI
Ningaloo Reef					
Φ (s) p (t)	*Not Scarred*	0·858	0·033	0·781	0·911
	Scarred	0·929	0·033	0·830	0·972
Seychelles					
Φ (s) p (t)	*Not Scarred*	0·502	0·060	0·386	0·618
	Scarred	0·538	0·070	0·402	0·669

Φ, apparent survival; p, sighting probability; s, scarred or not; t, time.

Ramming of whale sharks by ocean-going vessels was well-recognized as a threat to this species in the early years of the 20th century (Gudger, 1940), but such deaths of whale sharks are rarely recorded today. Due to relatively thin sub-dermal fat layers, whale shark carcasses may sink quickly in comparison to whales (Ward-Geiger *et al.*, 2005) so that most deaths due to collisions probably go unnoticed (Stevens, 2007). Boat collisions, however, are still likely to reduce the survival probability of whale sharks, particularly since shipping traffic along coasts and in the open oceans has more than tripled since the 1940s (Lloyd's Register of Shipping, 1939–2005), and today's cargo vessels are larger and travel at much greater speeds. Mortalities due to shipping have been recorded in recent times; for example, a whale shark was struck and killed by a large vessel off the Seychelles in 2000 (unpubl. data). Other possible evidence of ship strikes comes from pop-up archival tag (PAT; Wilson *et al.*, 2006) deployments on whale sharks at Ningaloo Reef. These tags are designed to release and float to the surface once an animal remains at a constant depth and temperature for >2 days. During one deployment, a 4 m whale shark travelling at the surface along the Northwest Shelf, one of Australia's busiest shipping routes, suddenly descended to 900 m and remained there for 12 h (Wilson *et al.*, 2006). Given diving records of other animals and the water temperature at that depth (2° C) this behaviour may represent mortality due to a ship strike, although other causes (*e.g.* predatory attacks) cannot be excluded.

The proportion of whale sharks bearing predator bite scars and those with laceration and amputation and blunt trauma scars were similar (27 *v.* 26% of individuals, respectively). This does not necessarily mean, however, that they translated into a similar number of deaths. Lacerations and blunt trauma scars generally appeared more severe than bite scars because the former covered larger areas of the body and in the case of lacerations, propellers often left multiple scars on the same animal. Furthermore, bite scars tended to be most common on the fins, and evidence from Ningaloo suggests that animals can recover from even total fin amputation by bites (Fitzpatrick *et al.*, 2006). Thus, ship collisions may be responsible for greater mortalities of whale sharks, even if rates of scarring from this source are similar to bites.

Although minor scars (nicks and abrasions) are unlikely to alter individual survival probability, they may act as warning signs of other threats. Three of the Mozambique whale sharks possessed abrasions similar to those described from net-entangled cetaceans (Angliss & DeMaster, 1997). Tuna purse-seine fisheries in the western Indian Ocean catch small numbers of whale sharks (Romanov, 1998), while gillnet fisheries also occasionally catch whale sharks (Stevens, 2007). Five Mozambique whale sharks had minor abrasions or lacerations characteristic of small-boat propeller strikes (Rommel *et al.*, 2007). Similar scars have been noted at other aggregation sites (Graham & Roberts, 2007; Rowat *et al.*, 2007) and in some cases, were possibly caused by vessels used to view whale sharks (Rowat *et al.*, 2007). 'Go-slow' areas within aggregation sites, already used for some other slow-moving marine species (Laist and Shaw, 2006) and regulated through the whale shark code of conduct in Western Australia, may reduce the probability and severity of ship strikes.

The caudal fin was the area most commonly scarred. This is not surprising, given that these animals spend most of their lives in <100 m of water and much time swimming at the surface (Wilson *et al.*, 2006). For this reason, the caudal fin will be the body part most likely to be struck by a boat. The caudal fin may also be an attractive target for predators because it may be easier to grip with teeth and sever in contrast to the body trunk (Long and Jones, 1998).

Whale sharks at Ningaloo Reef had more bites (44% of individuals) and fewer lacerations and blunt trauma scars than those at either the Seychelles or Mozambique. Although this suggests that there may be higher rates of predation at Ningaloo and lower numbers of boat strikes, it needs to be recognized that these animals are highly migratory (Eckert & Stewart, 2001; Eckert *et al.*, 2002; Rowat & Gore, 2006; Wilson *et al.*, 2006; Bradshaw, 2007; Castro *et al.*, 2007) and that the healed scars observed at the study sites may have been accrued in distant parts of their range. Despite the incongruence of shipping activity and relative scarring rates among sites (*e.g.* there were more commercial vessels near Ningaloo despite a lower incidence of ship-related injuries), there is some evidence that small boat traffic at Ningaloo may be lower than at either the Seychelles or Mozambique. Ningaloo Reef is largely protected by an expansive marine park in a remote area of Western Australia, whereas the coastal areas around Mozambique and Seychelles are heavily populated and have a strong fishing presence. Furthermore, tiger sharks *Galeocerdo cuvier* (Peron & Lesueur) and other large species of requiem (Carcharhinidae) sharks (Fitzpatrick *et al.*, 2006) are regularly sighted by spotter planes during the peak whale shark season at Ningaloo Reef, and are also temporarily abundant in other areas immediately to the south, such as Shark Bay (Heithaus, 2001*b*). In contrast, large, predatory sharks are rarely spotted during aerial surveys during whale shark season in the Seychelles (unpubl. data).

The hypothesis that observed rates of scarring were indicative of relative mortality rates at two widely separated aggregations on opposite sides of the Indian Ocean experiencing different intensities of shipping traffic was not supported. The lack of a scarring effect on apparent survival may indicate that individuals surviving ship strike and predator attack are no more susceptible to premature mortality than their unscathed counterparts, but the relative contribution of different shipping rates to explain regional variance in survival patterns still cannot be ruled out. Despite the observation that there seem to be fewer commercial vessels around whale shark aggregation sites in the western Indian Ocean (Seychelles and Mozambique), large fishing vessels may still pose threats to whale sharks in this region. Whale shark deaths related to ship strikes from commercial and fishing vessels may contribute to the lower apparent survival rates observed in the Seychelles; however, better and longer-term mark–recapture data are required to confirm this. Indeed, even individuals with major scarring returned repeatedly to their aggregation sites, indicating that scarring itself is unlikely to alter survival or migration patterns. Whether scars are naturally or anthropogenically derived, whale sharks appear to be resistant to the hypothetical negative effects of injuries on survival, but may still demonstrate reductions in maturation time or reproductive output (Hiruki *et al.*, 1993).

It must also be assumed that estimates of apparent survival between the Ningaloo and Seychelles aggregations are comparable based on equal probabilities of permanent emigration. Capture histories analysed in the Cormack–Jolly–Seber framework provide estimates of apparent survival that are confounded with permanent emigration (White & Burnham, 1999), so a higher proportion of transients in one population will bias apparent survival estimates downward. Nonetheless, the large difference in apparent survival between Ningaloo and Seychelles suggests true differences in survival rates and requires longer-term data to verify adequately.

This analysis of three Indian Ocean whale shark populations based on photo-identification provided little evidence that major or minor scarring affects survival rates, despite the prevalence of injuries and scarring among the individuals examined. The magnitude of shipping-related deaths, however, remains unquantified and may only be revealed with dedicated large-ship surveys near known aggregation sites. Due to their apparent resilience to scarring, it is true that whale sharks may not fear shark, man or ship; however, current trends in population status suggest they are not as impervious to these threats as previously thought.

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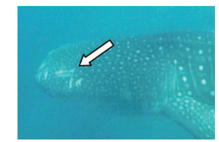
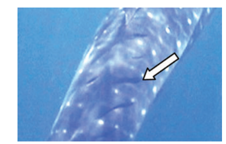
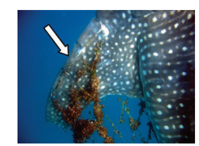
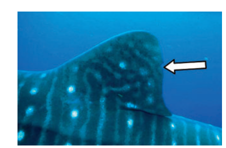
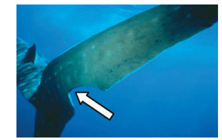
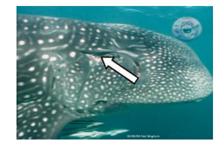
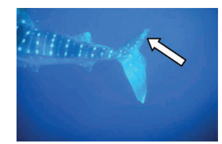
APPENDIX. Wound type, description and potential cause of scarring of *Rhincodon typus*. Shown are examples of 'abrasions' which are visible on the front and left side of the head, 'lacerations' showing parallel slashes along the caudal peduncle and cuts along the left pectoral fin with fishing net still attached, 'nicks' denoting a small piece of flesh removed from the trailing edge of the 1st dorsal fin, 'bites' showing a semi-circular piece of flesh removed from the trailing edge of the caudal fin, 'blunt trauma' indicating deep indentation and lacerations around the head, 'amputations' showing a caudal fin which has the top section removed, and 'other' indicating a large lump on the right side of the head.

Wound type	Description	Possible cause	Image
Abrasions	Superficial skin-deep wound. These may either be distinctive scratches or broad scrapes.	Collision with ship, benthos or floating debris	
Lacerations	A linear cut that penetrates the flesh. These are deep wounds that are generally clean (*i.e.* no ragged edges).	Vessel propeller or hull, fishing gear, or gaff	 
Nicks	Removal of a small piece of flesh from a fin's trailing edge. These usually have a geometric shape.	Vessel propeller or natural	

APPENDIX. Continued

Wound type	Description	Possible cause	Image
Bites	Semi-circular wound or removal of flesh from body or fin. These range from puncture marks, to complete removal of flesh or fins.	Attack by sharks or odontocete whales	
Blunt trauma	Unnatural indentation on the body. These often include scar tissue around the indentation.	Collision with a vessel	
Amputations	Partial or complete removal of fin. Unlike bites, fins that have been amputated have linear edges.	Vessel propeller or fishing gear	
Other	Uncommon wounds or irregularities such as abscesses, lumps or unusual markings.	Infection, parasite infestation