Reef sharks: recent advances in ecological understanding to inform conservation

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Sharks are increasingly being recognized as important members of coral-reef communities, but their overall conservation status remains uncertain. Nine of the 29 reef-shark species are designated as data deficient in the IUCN Red List, and three-fourths of reef sharks had unknown population trends at the time of their assessment. Fortunately, reef-shark research is on the rise. This new body of research demonstrates reef sharks' high site restriction, fidelity and residency on coral reefs, their broad trophic roles connecting reef communities and their high population genetic structure, all information that should be useful for their management and conservation. Importantly, recent studies on the abundance and population trends of the three classic carcharhinid reef sharks (grey reef shark *Carcharhinus amblyrhynchos*, blacktip reef shark *Carcharhinus melanopterus* and whitetip reef shark *Triaenodon obesus*) may contribute to reassessments identifying them as more vulnerable than currently realized. Because over half of the research effort has focused on only these three reef sharks and the nurse shark *Ginglymostoma cirratum* in only a few locales, there remain large taxonomic and geographic gaps in reef-shark knowledge. As such, a large portion of reef-shark biodiversity remains uncharacterized despite needs for targeted research identified in their red list assessments. A research agenda for the future should integrate abundance, life history, trophic ecology, genetics, habitat use and movement studies, and expand the breadth of such research to understudied species and localities, in order to better understand the conservation requirements of these species and to motivate effective conservation solutions.

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INTRODUCTION

Sharks are large predators on coral reefs, and yet these species, and their ecological role in these ecosystems, were often overlooked until recently. For example, neither Sale's (1991) classic book nor the follow-up edition (Sale, 2006) make any mention of sharks. This might be attributed to the long exploitation history on coral reefs, which resulted in the virtual elimination of these predators on many coral reefs around the world long before modern scientific studies were conducted in these ecosystems (Jackson *et al.*, 2001; Pandolfi *et al.*, 2003). Coral reefs are, however, used by a variety of shark species (White & Sommerville, 2010) and they form critical habitat for those sharks that remain resident on reefs throughout their life cycle, here termed reef

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sharks. Fishing surveys on the Great Barrier Reef, Australia, for example, have found that most surveyed shark species occurred at or near reefs, particularly at sites with hard-coral cover, emphasizing the importance of coral-reef habitat to these species (Chin *et al.*, 2012; Espinoza *et al.*, 2014). Scientific research focused on reef sharks has increased substantially in the past few decades, and along with growing recognition of the importance of these species there is also recognition that they face many threats. Most notably, as coral reefs have been degraded over the past century, reef sharks have continued to face exploitation pressure and habitat loss (Jackson *et al.*, 2001; Pandolfi *et al.*, 2003; Bellwood *et al.*, 2004; Hoegh-Guldberg *et al.*, 2007; Sandin *et al.*, 2008). Recently, climate change has also been postulated to pose an additional threat to these species through effects on physiology and the suitability of coral-reef habitat (Chin *et al.*, 2010).

Directed research effort is required to ensure the design and implementation of effective conservation measures that encompass the suite of reef-shark diversity. The IUCN Red List is the primary tool used to define global shark extinction risk and conservation statuses, and has been important for shark conservation, as evidenced by the recent CITES listings of five shark species listed as vulnerable and endangered by the Red List (Vincent *et al.*, 2014; CITES, 2015). Up to date knowledge of reef-shark diversity, ecology and population statuses is critical for conservation prioritization, and as such, the current ability of reef-shark research to serve as aids for conservation needs to be assessed. This review (1) presents the first synthesis of the scientific literature on reef sharks focusing specifically on ecological research, (2) assesses the extent to which current knowledge may contribute to IUCN Red List evaluations and (3) identifies gaps in reef-shark research and suggests priority research directions to foster reef-shark conservation.

METHODS

Reef sharks were defined as those species that use shallow tropical coral reefs as their primary habitat. The final species list was determined primarily using the habitat descriptions by Compagno *et al.* (2005), following initial consideration of each species whose habitat description included 'reef' or 'coral', those species with multiple habitat types indicated, and for which tropical coral reefs were not their primary habitat, were removed. As such, those large pelagic sharks that frequent coral reefs but are not reef-restricted and those sharks that inhabit only rocky reefs were excluded. Additionally, the following species were removed because coral reefs are not their primary habitat: bluegrey carpetshark *Heteroscyllium colcloughi* Ogilby 1908, blind shark *Brachaelurus waddi* (Bloch & Schneider 1801), brownbanded bambooshark *Chiloscyllium punctatum* Müller & Henle 1838, nervous shark *Carcharhinus cautus* (Whitley 1945), spot-tail shark *Carcharhinus sorrah* (Müller & Henle 1839) (A. Chin, pers. comm.), spotted *Orectolobus maculatus* (Bonnaterre 1788), ornate *Orectolobus ornatus* (de Vis 1883) and cobbler *Sutorectus tentaculatus* (Peters 1864) (C. Huveneers, pers. comm.). For some species, there was insufficient information to confidently assess them as reef sharks, but if the little information available suggested that they live on coral reefs, they were retained.

For each reef-shark species, a Web of Science (WoS) search was conducted on 19 April 2015 using the species' scientific and common names as search terms, including

synonyms. Abstracts from conference proceedings and papers that only briefly referenced the species were removed. Reef-shark papers that were not located in the original WoS search but were referenced elsewhere in the literature were also included. Three additional studies were located in September 2015 in a follow-up search.

Each paper was classified based on the subject matter of the study; papers on multiple subjects were classified into multiple categories. 'Physiology' was used for any study on the physiology or biochemistry of reef sharks and their proteins and cells. 'Behaviour' includes studies of the use of senses, mating, aggression, reaction to humans and locomotory behaviour. 'Habitat use' includes use of nursery or mating grounds, habitat preferences and characteristics, aspects of their distribution and studies of movement and spatial use. 'Basic biology' is a broad category that includes general descriptions of the species' biology and natural history; studies of form, function and general external morphology (including teeth and feeding mechanics); reproductive biology studies (such as egg case descriptions) not included in the physiology, behaviour or habitat use categories; interactions with other species that do not include predation or parasitism; growth studies and studies of condition. 'Diet' includes studies of feeding, including stomach content and stable-isotope analysis. 'Genetics' include studies of population genetics and structure as well as multiple paternity, genetic aspects of parthenogenesis, characterization of genomes and genes, microsatellite identification and sequencing and investigations of polyploidy. 'Parasites' include all references pertaining to parasites found in the target species, including bacterial disease. 'Abundance' was used for studies providing estimates or indications of a species' abundance or density in an area or through time, including fishing surveys. The 'socio-economic and conservation' (SEC) category includes studies discussing a human dimension or aspect of conservation, including fisheries and shark eco-tourism. The category 'captive' was used for studies on husbandry and keeping of sharks in captivity. 'Taxonomy' was used for studies discussing reef-shark taxonomic units or redefining reef-shark taxonomy, and for accounts of fossils. 'Other' was used for anything else, including reviews, studies of methodology and records of first occurrence.

REEF-SHARK DIVERSITY AND OVERVIEW OF RECENT ADVANCES

In total, 29 reef-shark species are considered here (Table I). These species are taxonomically and functionally diverse spanning three orders [Heterodontiformes (bullhead sharks), Orectolobiformes (carpet sharks) and Carcharhiniformes (ground sharks)] and seven families (Table I and Fig. 1). From a life-history perspective, reef sharks are also a diverse group of fishes, with estimated maximum total lengths (L_T) ranging from 60 to 370 cm and estimated trophic levels ranging from 3·1 to 4·2 (Table I).

The total number of studies on reef sharks has risen rapidly, particularly over the past 30 years, with a total of 1101 studies identified in the literature review [Fig. 2(a)]. Physiological studies of the nurse shark *Ginglymostoma cirratum* (Bonnaterre 1788) ($n = 366$), a model organism, are most common in this body of literature [Fig. 3(a)]. Without considering any physiology studies, there are a total of 604 reef-shark studies [Fig. 2(a)]. The taxonomic focus of these reef-shark studies is highly uneven, with over half focused on just four species: *G. cirratum* ($n = 167$) and the three classic carcharhinid reef sharks [blacktip reef shark *Carcharhinus melanopterus* (Quoy &

TABLE I. Reef-shark species of the world including their estimated size (maximum total length, L_T, from Compagno et al., 2005 except where otherwise indicated) and trophic level (T_L, from Froese & Pauly, 2015), as well as information derived from the IUCN Red List: the current status (Vu, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient) and year of most recent assessment (additional regions and years on the same line refer to separate regional assessments of the species in addition to the global status assessment), population trend (as indicated in most recent IUCN Red List report: ↓, a decreasing trend; −, a stable trend; ?, an unknown trend), distribution [Au, Australia; EA, eastern Atlantic; EP, eastern Pacific; IP, Indo-Pacific (excluding Australia); Med, Mediterranean; WA, western Atlantic; WI, west Indian Ocean; WP, western Pacific (northern Asia)] and fisheries use (targeted, by-catch: Y, yes; N, no)

Order/Family[a]	Species	Common name	L_T (cm)	T_L	IUCN Red List Status	Trend	Distribution	Targeted	By-catch
Het/He	Heterodontus mexicanus	Mexican hornshark	70	4·2	DD-2006	?	EP	N	Y
	Heterodontus quoyi	Galapagos bullhead shark	61	3·5	DD-2004	?	EP	N	Y
Ore/Or	Eucrossorhinus dasypogon	Tasselled wobbegong	>125		NT-2003	→	IP/Au	Y	Y
	Orectolobus japonicus	Japanese wobbegong	>107	3·8	DD-2007	?	WP	Y	Y
	Orectolobus wardi	Northern wobbegong	63	4·0	LC-2003	−	Au	N	N
	Orectolobus hutchinsi	Western wobbegong	200	4·0	DD-2008	?	Au	N	Y
	Orectolobus floridus*	Floral banded wobbegong	75	3·8	DD-2008	?	Au	N	Y
	Orectolobus reticulatus*	Network wobbegong	Unk	3·7	DD-2011	?	Au	N	N
Ore/Hs	Chiloscyllium arabicum*	Arabian carpetshark	54	4·1	NT-2008	?	WI	N	Y
	Hemiscyllium freycineti	Indonesian speckled carpetshark	72	3·4	NT-2011	?	IP (New Guinea)	Y	Y

TABLE I. Continued

Order/Family[a]	Species	Common name	L_T (cm)	T_L	IUCN Red List Status	Trend	Distribution	Targeted	By-catch
	Hemiscyllium michaeli	Michael's epaulette shark	69[a]	3·5	NT-2012	?	IP (New Guinea)	N	N
	Hemiscyllium ocellatum	Epaulette shark	107	3·4	LC-2003 IP: NT-2003	–	IP/Au	Y	Y
	Hemiscyllium henryi	Henry's epaulette shark	81·5[b]	3·5	DD-2012	?	IP-NG	N	N
	Hemiscyllium strahani	Hooded carpetshark	80	3·4	Vu-2003	?	IP-NG	N	N
	Hemiscyllium trispeculare	Speckled carpetshark	79	3·5	LC-2003	?	Au	N	N
	Hemiscyllium hallstromi[*]	Papuan epaulette shark	77	3·5	Vu-2003	?	IP-NG	N	N
	Hemiscyllium galei[*]	Cenderwasih epaulette shark	>57[b]	3·4	DD-2012	?	IP-Indonesia	N	N
Ore/Gi	*Ginglymostoma cirratum*	Nurse shark	300	4·2	DD-2006 WA: NT-2006	?	WA/EA/EP	Y	Y
	Nebrius ferrugineus	Tawny nurse shark	320	4·1	Vu-2003 Au: LC-2003	→	IP/Au	Y	Y
	Pseudoginglymostoma brevicaudatum	Shorttail nurse shark	75	3·8	Vu-2004	?	WI	N	Y
St	*Stegostoma fasciatum*	Zebra shark	354	3·1	Vu-2003 Au: LC-2003	→	IP/Au	Y	Y
Car/Sc	*Atelomycterus marmoratus*	Coral catshark	70	4·1	NT-2003	?	IP	Y	Y
	Autohalaelurus labiosus[*]	Blackspotted catshark	67	4·1	LC-2003	?	Au	N	N

TABLE I. Continued

Order/Family[a]	Species	Common name	L_T (cm)	T_L	IUCN Red List Status	Trend	Distribution	Targeted	By-catch
Car/Ca	Carcharhinus albimarginatus	Silvertip shark	300	4·2	NT-2007	?	WI/IP/EP	Y	Y
	Carcharhinus amblyrhynchos	Grey reef shark	255	4·1	NT-2005	?	IP/WI/Au/EP/WP	Y	Y
	Carcharhinus melanopterus	Blacktip reef shark	<200	3·9	NT-2005	→	WI/IP/Med/EP/WP/Au	N	Y
	Carcharhinus perezi	Caribbean reef shark	295	4·5	NT-2006	→	WA	N	Y
	Carcharhinus galapagensis	Galapagos shark	370	4·2	NT-2003 Au: DD-2003	?	EA/WA/WI/EP/IP/Au	Y	Y
	Triaenodon obesus	Whitetip reef shark	200	4·2	NT-2005	?	WI/IP/Au/WP/EP	Y	Y

Orders:: Het, Heterodontiformes; Ore, Orectolobiformes; Car, Carcharhiniformes. Families: He, Heterodontidae; Or, Orectolobidae; Hs, Hemiscylliidae; Gi, Gingly-mostomatidae; St, Stegostomatidae; Sc, Scyliorhinidae; Ca, Carcharhinidae.
*Indicates a little known species that is most likely a reef shark.
[a] Allen & Dudgeon, 2010.
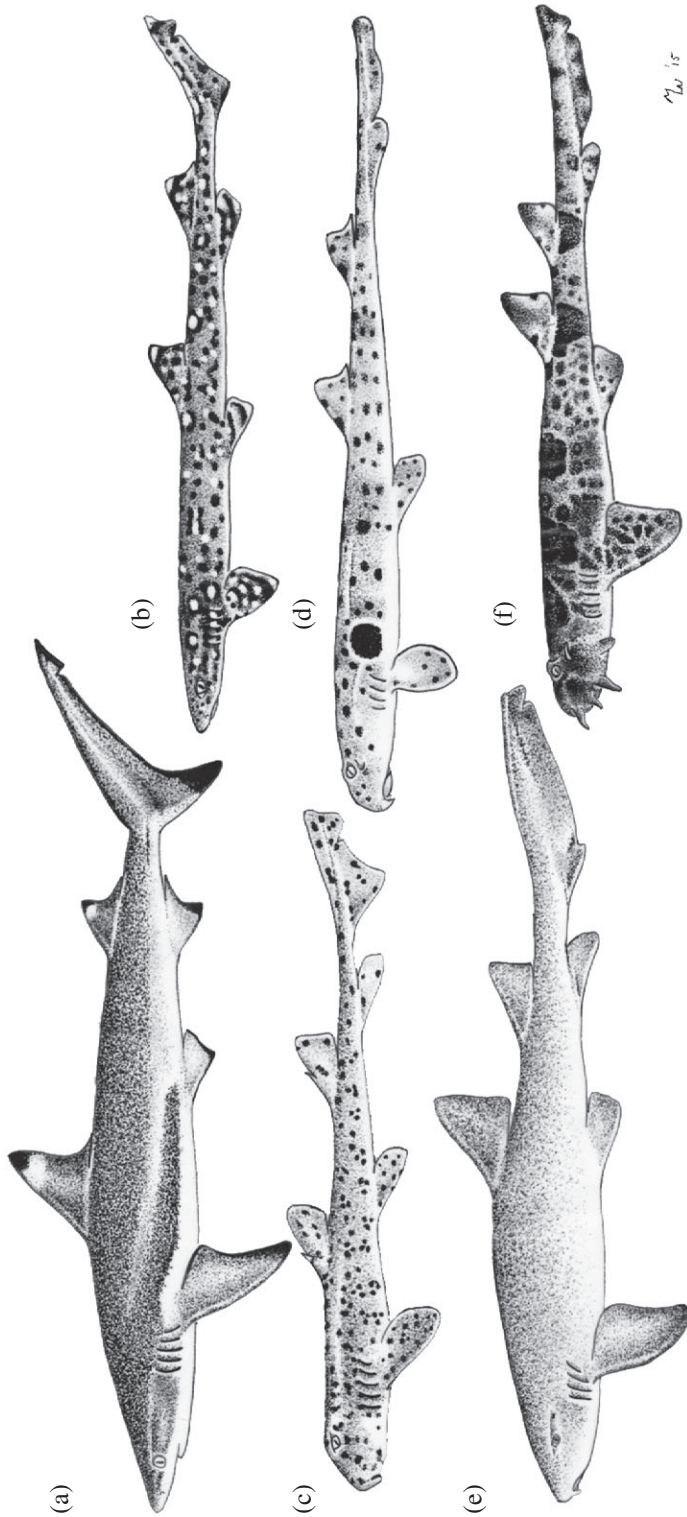[b] Allen & Erdmann, 2008.

FIG. 1. Representative sharks from each reef-shark family considered, except for Stegostomatidae, which is similar in form to Orectolobidae. (a) Carcharhinidae: *Carcharhinus melanopterus*, (b) Scyliorhinidae: *Atelomycterus marmoratus*, (c) Heterodontidae: *Heterodontus quoyi*, (d) Hemiscylliidae: *Hemiscyllium ocellatum*, (e) Ginglymostomatidae: *Ginglymostoma cirratum* and (f) Orectolobidae: *Orectolobus wardi*.

Gaimard 1824) ($n = 119$), grey reef shark *Carcharhinus amblyrhynchos* (Bleeker 1856) $n = 110$ and whitetip reef shark *Triaenodon obesus* (Rüppell 1837) ($n = 101$)] [Figs 2(b) and 3(b)]. Fewer studies have been devoted to the Caribbean reef shark *Carcharhinus perezi* (Poey 1876) ($n = 53$), the Galapagos shark *Carcharhinus galapagensis* (Snodgrass & Heller 1905) ($n = 51$), the zebra shark *Stegostoma fasciatum* (Hermann 1783) ($n = 47$), the epaulette sharks [family Hemiscylliidae, $n = 44$, although most of these studies (72%) focused on a single species, the epaulette shark *Hemiscyllium ocellatum* (Bonnaterre 1788)] the silvertip shark *Carcharhinus albimarginatus* (Rüppell 1837) ($n = 39$) and other ginglymostomids besides *G. cirratum* ($n = 38$) [Figs 2(b) and 3(b)]. The heterodontids, orectolobids and scyliorhinids remain understudied: <10% of reef-shark studies examined any of these groups even though they comprise over one third of the species; most of their studies (56%) were published recently [Fig. 2(b)].

Besides physiology studies, most reef-shark research has focused on habitat use (21%) or basic organismal biology (20%) [Fig. 2(c)], with data typically obtained from fisheries catches or underwater observations. Studies pertaining to reef-shark abundance have risen rapidly in the past decade and now comprise the third highest research focus [15%; Fig. 2(c)]. There has been a steady focus on reef-shark behaviour (12%) over time, with most of these studies describing agonistic displays and behaviour towards humans, foraging behaviour, locomotory performance, the use of the senses or mating behaviour; almost all behaviour studies (93%) were of *G. cirratum* or the carcharhinid species. In addition, numerous studies have characterized the diversity and biology of reef-shark parasites [11%; Fig. 2(c)], covering all reef-shark groups besides Scyliorhinidae. Characterization of reef-shark parasites could open a new avenue of research in which parasites are used to assess contemporary and historical movement patterns of their hosts (Caira & Euzet, 2001). There has also been a steady rise in the studies dealing with reef-shark taxonomy [8%; Fig. 2(c)], reflective of taxonomic uncertainties and recent discoveries of new species in Orectolobidae and Hemiscylliidae (Last *et al.*, 2006; Allen & Erdmann, 2008; Goto, 2008; Corrigan & Beheregaray, 2009). Fewer studies to date have examined reef-shark genetics (6%) or diets (5%) [Fig. 2(c)].

Here, a review of the reef-shark literature deemed most relevant to conserving these species is undertaken, namely studies focused on reef-shark ecology (habitat and diet), genetics, abundance, socio-economics and conservation. Although there is still much to learn, research in these areas has increased substantially in the past decade [Fig. 2(c)], making a synthesis of this new knowledge now possible.

HABITATS, MOVEMENT AND HOME RANGES

Reef sharks are coastal species with preference for the structurally complex habitats of reefs with high coral cover (Chin *et al.*, 2012; Espinoza *et al.*, 2014; Rizzari *et al.*, 2014*a*; Table SI, Supporting Information). Beyond this general characterization, interspecific habitat preferences vary widely. The tawny nurse shark *Nebrius ferrugineus* (Lesson 1831), *H. ocellatum*, *S. fasciatum* and *C. melanopterus* prefer shallow habitat in lagoons and on sand and reef flats and ledges (Heupel & Bennett, 2007; Papastamatiou *et al.*, 2009*a*, *b*, 2010; Speed *et al.*, 2011, 2015; Chin *et al.*, 2013*b*; Rizzari *et al.*, 2014*a*). In contrast, *C. galapagensis* (Holzwarth *et al.*, 2006; Lowe *et al.*, 2006; Papastamatiou *et al.*, 2015; Table SI, Supporting Information), *C. perezi* (Garla *et al.*,
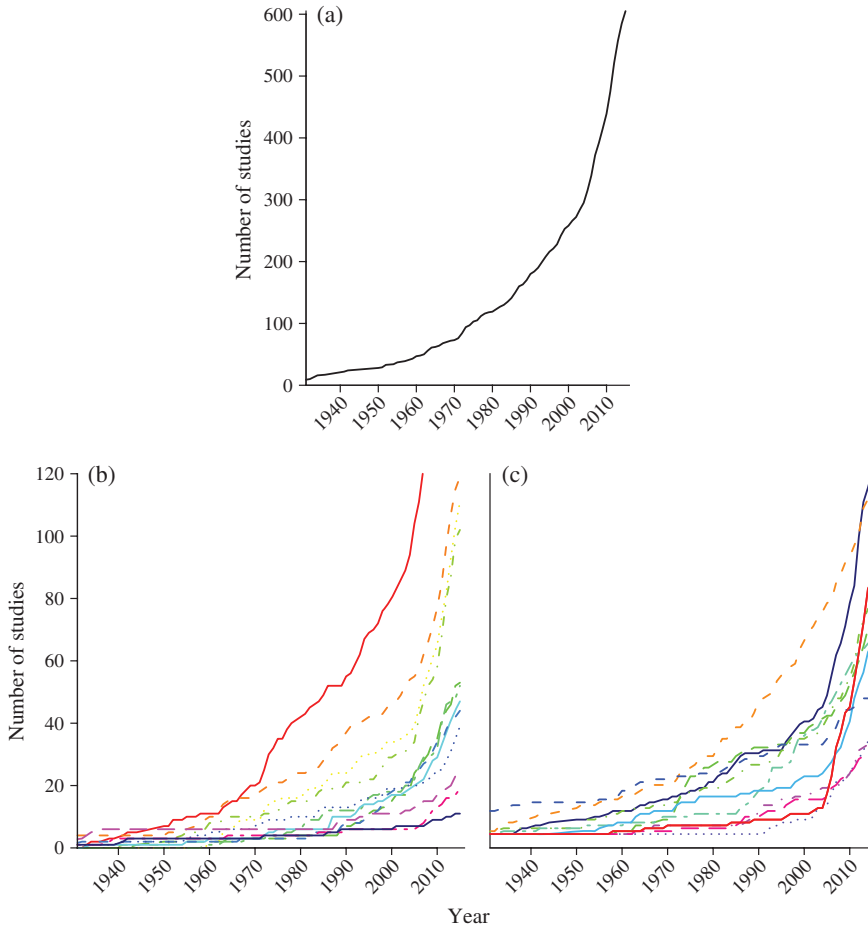
FIG. 2. The cumulative number of studies on reef sharks (excluding physiology studies) published in peer-reviewed journals by year (a) for all species and topics combined, (b) by species (or family) and (c) by topic. Other Ginglymostomatidae includes *Nebrius ferrugineus* and *Pseudoginglymostoma brevicauda-tum*. Each *x*-axis starts at 1931, although nine taxonomic studies occurred earlier, from 1867. The *y*-axis on (b) and (c) only extends to 120, but on (b) *Ginglymostoma cirratum* increases to 167 and on (c) habitat use extends to 126. For (b) and (c), legends are ordered from the category with the greatest to the least number of studies. *Ginglymostoma cirratum* (——), *Carcharhinus melanopterus* (– –), *Carcharhinus amblyrhyn-chos* (……), *Triaenodon obesus* (·– –·), *Carcharhinus perezi* (·– –·), *Carcharhinus galapagensis* (— —), *Stegostoma fasciatum* (——), Hemiscylliidae (– –), *Carcharhinus albimarginatus* (……), other Gingly-mostomatidae (— —), Scyliorhinidae (— —), Orectolobidae (·– –·) and Heterodontidae (——). Habitat use (——), basic biology (– –), abundance (——), other (— —), behaviour (·– –·), parasites (·– –·), socio-economics conservation (——), taxonomy (– –), genetics (……), captive (·– –·) and diet (— —).

2006; Chapman *et al.*, 2007) and *C. amblyrhynchos* (McKibben & Nelson, 1986; Dale *et al.*, 2011; Rizzari *et al.*, 2014*a*; Table SI, Supporting Information) prefer deeper sites with strong currents on exposed forereef slopes, crests and channels. Similarly, *C. amblyrhynchos* is fairly restricted to reef habitat (Chin *et al.*, 2012; Espinoza *et al.*, 2014) while *C. albimarginatus* has preferences for deeper sites further offshore (Stevens, 1984; Espinoza *et al.*, 2014). As a benthic species, *T. obesus* can
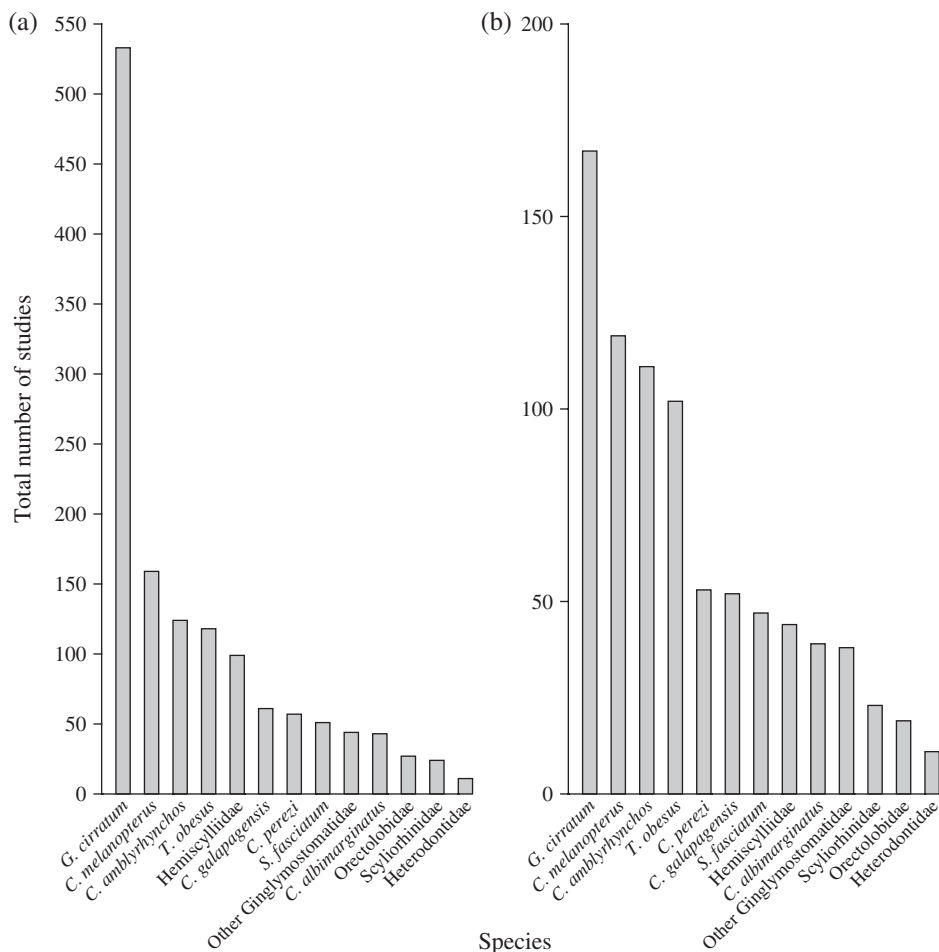
(a)

(b)

Fig. 3. Frequency distribution of peer-reviewed reef-shark studies (a) including and (b) excluding physiology studies by species (or group). Other Ginglymostomatidae includes *Nebrius ferrugineus* and *Pseudogingly-mostoma brevicaudatum*.

be widespread across habitat with high coral cover that provides rock ledges and coral heads for refuges and foraging (Randall, 1977; Whitney *et al.*, 2012*a*; Espinoza *et al.*, 2014). Although reef sharks may select habitat partially based on environmental variables such as coral cover, depth, complexity and temperature (Papastamatiou *et al.*, 2009*a*; Vianna *et al.*, 2013, 2014; Espinoza *et al.*, 2014), recent evidence suggests these effects are relatively weak and that biological factors such as competition may be more important (Heupel & Simpfendorfer, 2014; Espinoza *et al.*, 2015*a*).

Tagging and telemetry methods have been increasingly used over the past decade to track reef-shark movements and to delineate their habitat use, home ranges and long-distance movements. Thus far, these studies have focused on 10 reef-shark species: *C. amblyrhynchos* ($n = 14$ studies), *C. melanopterus* ($n = 13$), *C. galapa-gensis* ($n = 8$), *C. perezi* ($n = 6$), *G. cirratum* ($n = 6$), *T. obesus* ($n = 5$), *S. fasciatum* ($n = 2$), *C. albimarginatus* ($n = 3$), *N. ferrugineus* ($n = 1$) and *H. ocellatum* ($n = 1$).

Most of these studies have employed acoustic telemetry (Maljković & Côté, 2011; Espinoza *et al.*, 2015*b*; Heupel & Simpfendorfer, 2015), including the placement of acoustic receivers and transmitters on the sharks themselves (Holland *et al.*, 2009). Other methods include tagging for mark–recapture or resighting (Stevens, 1984; Garla *et al.*, 2006; Chin *et al.*, 2013*b*), pop-off satellite archival transmitting (PSAT) tags for studying depth use (Chapman *et al.*, 2007) and Argos satellite tracking (Meyer *et al.*, 2010; Papastamatiou *et al.*, 2010; Friedlander *et al.*, 2012). Additionally, movement has been studied directly using photo-identification surveys (Dudgeon *et al.*, 2008; Mourier *et al.*, 2012; Whitney *et al.*, 2012*a*).

Recent movement studies are providing compelling evidence of reef sharks' high site fidelity, residency and restricted home ranges over multiple years, even after seasonal and diel migrations (Speed *et al.*, 2010; Field *et al.*, 2011; Bond *et al.*, 2012; Chapman *et al.*, 2015; Espinoza *et al.*, 2015*a, b*; Table SI, Supporting Information). Home ranges vary from <1 to 10 km^2 in the smaller more sedentary, site-restricted species such as *C. melanopterus*, *T. obesus* and *G. cirratum* (Papastamatiou *et al.*, 2010; Whitney *et al.*, 2012*a*; Ferreira *et al.*, 2013; Table SI, Supporting Information) up to tens of km^2 in size in the larger, more mobile species such as *C. amblyrhynchos* and *C. perezi* (McKibben & Nelson, 1986; Garla *et al.*, 2006; Heupel & Simpfendorfer, 2015; Table SI, Supporting Information). Despite high residency, some individuals of *C. amblyrhynchos*, *C. galapagensis*, *C. perezi*, *T. obesus*, *S. fasciatum* and *G. cirratum* have been shown to make longer movements or migrations over tens of km throughout and between wider reef systems (McKibben & Nelson, 1986; Chapman *et al.*, 2005; Lowe *et al.*, 2006; Heupel *et al.*, 2010; Whitney *et al.*, 2012*a*; Dudgeon *et al.*, 2013; Table SI, Supporting Information).

In addition, movement studies are revealing interspecific and intraspecific variation in reef-shark habitat use, degree of movement and home range size. *Carcharhinus amblyrhynchos* movement is generally less restricted on continuous to semi-isolated reef habitat (Heupel *et al.*, 2010; Espinoza *et al.*, 2015*a*) [Speed *et al.* (2011) and Heupel & Simpfendorfer (2014) provide examples of site restriction in these systems] than it is on isolated oceanic islands and atolls separated by deep water (Field *et al.*, 2011; Barnett *et al.*, 2012; Speed *et al.*, 2012). *Carcharhinus perezi* does not show the same year-long residency on reefs in the Bahamas, which presumably have less seasonal temperature fluctuations, as it does on reefs further south (Garla *et al.*, 2006; Bond *et al.*, 2012; Brooks *et al.*, 2013). Body size, which can influence energy requirements, also affects interspecific and intraspecific habitat variation. For *C. amblyrhynchos*, *C. melanopterus* and *C. perezi*, activity space appears to increase with size and juveniles typically use shallower habitat closer to shore such as lagoons (Garla *et al.*, 2006; Chin *et al.*, 2013*a*; Rezzolla *et al.*, 2014; Table SI, Supporting Information). On the Great Barrier Reef, the larger *C. albimarginatus* displays wider movements, is less site attached and more likely to move between management zones than either *C. amblyrhynchos* or *T. obesus* (Barnett *et al.*, 2012; Espinoza *et al.*, 2015*b*). Similarly, in Fiji, one *C. albimarginatus* displayed pelagic behaviours in addition to its reef-associated habits (Bond *et al.*, 2015). Finally, there is also variation by sex, with females tending to be more resident and philopatric, and sometimes showing different spatial and temporal habitat use patterns from males (Speed *et al.*, 2011, 2012; Whitney *et al.*, 2012*a*; Brooks *et al.*, 2013; Table SI, Supporting Information). For example, female *C. melanopterus* off Moorea, French Polynesia use lagoons while males preferentially use the forereef (Mourier *et al.*, 2012). Males may show greater

movement than females due to dispersal or searching out females during mating season (Field *et al.*, 2011; Whitney *et al.*, 2012*a*; Espinoza *et al.*, 2015*a*, *b*; Table SI, Supporting Information).

The wealth of new information about reef-shark habitat and movement could help to inform effective management strategies for these species. Marine protected area (MPA) design, for example, will benefit from information about home-range size, habitat selection and exposure to anthropogenic stressors in different zoning regions (Chapman *et al.*, 2007; Wiley & Simpfendorfer, 2007; Espinoza *et al.*, 2015*b*). Movement studies can serve to evaluate MPA placement and design by evaluating the fidelity and residency of reef-shark species to particular protected zones (Heupel *et al.*, 2010; Bond *et al.*, 2012; Speed *et al.*, 2015). Moreover, tagging studies that include vertical movement reveal that certain reef-shark species prefer deeper waters and may exhibit seasonal or diel shifts in depth that could bring them out of MPAs around shallower reef habitat (Chapman *et al.*, 2007; Vianna *et al.*, 2013; Papastamatiou *et al.*, 2015). The occasional long-range movements identified in reef sharks also informs about wider population connectivity, with implications for reducing extinction vulnerability (Heupel *et al.*, 2010; Whitney *et al.*, 2012*a*; Mourier & Planes, 2013). The variation in habitat use between species, sizes and sexes should be further characterized using a combination of tagging, telemetry and population genetic techniques, and then incorporated into management plans as this variation may determine the effectiveness of MPAs.

DIETS AND TROPHIC ECOLOGY

Diet studies also provide an important window into the ecological role of reef sharks. About 30 studies have examined reef-shark diets and trophic ecology to date, most of which focused on carcharhinid reef sharks and utilized stomach content analysis of specimens captured during fisheries surveys. Carcharhinid reef sharks are generalists consuming a wide variety of reef-associated teleosts, cephalopods, crustaceans as well as the occasional elasmobranch (Stevens, 1984; Stevens & McLoughlin, 1991; Salini *et al.*, 1992; Wetherbee *et al.*, 1997; Papastamatiou *et al.*, 2006; Zhang *et al.*, 2006; Tavares, 2009). Apart from the Carcharhinidae, stomach content analysis of *H. ocellatum* found worms and crabs to be most important, followed by other crustaceans and small fishes (Heupel & Bennett, 1998). Also, one tasselled wobbegong *Eucrossorhinus dasypogon* (Bleeker 1867) was observed consuming another elasmobranch on the Great Barrier Reef (Ceccarelli & Williamson, 2012). Two stomach-content analyses revealed that *N. ferrugineus* consumes cephalopods and sea snakes (Smale, 1996; Masunaga *et al.*, 2008).

To date, only eight studies have employed stable-isotope analyses, but these studies have already shed light on reef-shark trophic ecology. Stable isotopes have, for example, been used to detect ontogenetic diet shifts, along with individual variation in these shifts, both directly by repeated measures of the same individuals through time and indirectly by relating stable isotopes to body size (Papastamatiou *et al.*, 2010; Speed *et al.*, 2012; Matich *et al.*, 2015). This approach also has provided evidence of competition in reef-shark communities: stable-isotope data for *C. perezi* at a provisioning site in the Bahamas showed that a few individuals with enriched δ^{15}N values were monopolizing the feeding (Maljković & Côté, 2011). Stable-isotope data have revealed interspecific differences in niche width between *C. perezi* and *G. cirratum* in Belize, including differences in δ^{13}C values that suggest resource partitioning

despite similar trophic levels (Tilley *et al.*, 2013). At Ningaloo Reef, Australia, *C. melanopterus*, *C. amblyrhynchos* and *T. obesus* have largely overlapping trophic levels, but *T. obesus* still feeds at a slightly lower trophic level, and it is believed to rely more on benthic herbivores and invertivores than piscivory (Speed *et al.*, 2012).

In addition, stable-isotope studies can help elucidate reef-shark habitats and prey bases (Borrell *et al.*, 2011; Speed *et al.*, 2012), thus providing complementary information to movement studies and new insights into these species' ecological roles on reef ecosystems. Diet information has already been used to parameterize models that suggest sharks play an important role in coral-reef food webs (Bascompte *et al.*, 2005). Recent studies have revealed that reef sharks can connect distinct reef habitats through their foraging, which, in addition to their omnivory, is hypothesized to help to confer stability to these ecosystems (Bascompte *et al.*, 2005; Rooney *et al.*, 2006). In the north-west Hawai'ian Islands, for example, an analysis of $\delta^{13}C$ coupled with telemetry work revealed that although *C. galapagensis* primarily inhabits and forages on shallow reefs, about one third of its resources are derived from deeper mesophotic reefs (Papastamatiou *et al.*, 2015). On Palmyra atoll, in the northern Line Islands, *C. amblyrhynchos* is the dominant shark on the forereef, but derives most of its resources from offshore pelagic sources, whereas adult *C. melanopterus*, which are smaller and less abundant, do forage mainly on the forereef (McCauley *et al.*, 2012*a*). A related study, combining telemetry with stable isotopes, revealed both low levels of mixing and distinct trophic ecologies ($\delta^{15}N$ and $\delta^{13}C$) and foraging success, as evidenced by body condition, between *C. melanopterus* living in Palmyra's eastern and western lagoons (Papastamatiou *et al.*, 2010).

GENETICS

Reef-shark genetics represent an emerging research area [Fig. 2(c)], although only nine studies have focused on the most relevant information for assessing reef-shark conservation status, namely reef-shark genetic population structure and gene flow and assessing cryptic biodiversity. With respect to the latter, Karl *et al.*'s (2012) *G. cirratum* study revealed that its Pacific populations may in fact be a different species from its heavily studied Atlantic populations. Other reef-shark studies have examined multiple paternity in *C. galapagensis* (Daly-Engel *et al.*, 2006) and *G. cirratum* (Saville *et al.*, 2002; Heist *et al.*, 2011), or sequenced genes and microsatellite loci for the Japanese wobbegong *Orectolobus japonicus* Regan 1906 (Chen *et al.*, 2013), *G. cirratum* (Heist *et al.*, 2003), *S. fasciatum* (Dudgeon *et al.*, 2006) or *C. amblyrhynchos* (Momigliano *et al.*, 2014), as well as other sharks related to the carcharhinid reef sharks (Keeney & Heist, 2003; Fitzpatrick *et al.*, 2011*a*), which should enable population genetic work in the future.

Population genetic studies thus far have provided evidence of high genetic structure and low genetic diversity for populations of four reef-shark species, *G. cirratum* (Karl *et al.*, 2012), *S. fasciatum* (Dudgeon *et al.*, 2009), *C. melanopterus* (Mourier & Planes, 2013; Vignaud *et al.*, 2013, 2014) and *T. obesus* (Whitney *et al.*, 2012*b*). One study of *C. amblyrhynchos* on the Great Barrier Reef found, however, very low genetic structure that is indicative of substantial dispersal for these populations (Momigliano *et al.*, 2015). Although these results are expected based on the residency patterns of these species, they should still help in assessments of their conservation status. First,

the information could help to justify effort for reef-shark conservation assessments at finer spatial scales (Dudgeon *et al.*, 2009). Second, these studies suggest there is limited potential for depleted populations of these reef sharks to be rescued from other regions with more abundant populations (Dudgeon *et al.*, 2009) while demonstrating a high potential for inbreeding. For instance, genetic diversity of *C. melanopterus* is greater on the large well-connected reefs of the Red Sea and the Great Barrier Reef, which promote dispersal, than on the fragmented reefs of French Polynesia, where it exhibits high genetic structure and low effective population size, probably due to inbreeding resulting from high natal philopatry of females to nursing grounds (Mourier & Planes, 2013; Vignaud *et al.*, 2013, 2014). These findings underscore the need for interconnected systems of MPAs for conservation of reef-shark genetic diversity (Vignaud *et al.*, 2014; Momigliano *et al.*, 2015). Further genetic work, however, is still required to quantity the benefits of dispersal as well as the severity and consequences of inbreeding depression for reef sharks. Finally, genetic studies can provide information on effective population size to aid in monitoring genetic diversity and abundance for shark populations (Dudgeon & Ovenden, 2015). Genetic studies can also complement the results of tagging and telemetry by demonstrating gene flow, dispersal and philopatry over longer time frames (Whitney *et al.*, 2012*b*; Mourier & Planes, 2013; Momigliano *et al.*, 2015).

ABUNDANCE

Studies aimed at quantifying reef-shark baselines, abundances and densities, and how these have changed over time, have increased greatly in the past decade [$n = 89$; Fig. 2(c)], but because of the dearth of available data there are still serious geographic and taxonomic gaps in understanding. Carcharhinid reef sharks were the focus of most (81%) abundance studies, with the three classic Indo-Pacific reef sharks (*C. amblyrhynchos*, *C. melanopterus* and *T. obesus*) accounting for 59% of these studies, and for two-thirds of those that inferred temporal or spatial (space-for-time) trends in abundance. Even for these well-studied species, however, abundance is well characterized only for Australia and some selected islands in the western and central Pacific, including Hawai'i and the Line Islands; little information exists about their Indian and western Pacific Ocean populations [Fig. 4(a)–(c)]. *Ginglymostoma cirratum* was investigated in 23% of all abundance studies, of which only one third inferred any temporal or spatial trends. Its abundance has only been studied in any detail in the western Atlantic Ocean, particularly in the Caribbean, despite a distribution that spans the eastern Pacific and eastern Atlantic Oceans [Fig. 4(d)]. The remaining reef-shark species were included in only 16% of abundance studies, and although 61% of those inferred trends in abundance, most were based on aggregate counts over multiple species (Heupel *et al.*, 2009; Nadon *et al.*, 2012; Rizzari *et al.*, 2015) or on small sample sizes (Joshi *et al.*, 2008; Chin *et al.*, 2012; Goetze & Fullwood, 2013).

A diversity of survey and analytical methods has been used to study reef sharks. Reef shark abundances have been quantified using fisheries-dependent data (48% of studies), underwater visual censuses (UVC) by divers (40%; of which 22% collected data through tourist operations) and video, including baited remote underwater videos (BRUV; 9%). Five studies (6%) used mark–recapture to estimate population size in their study area (Stevens, 1984; Heupel & Bennett, 2007; Dudgeon *et al.*, 2008; McCauley *et al.*, 2012*a*; Zanella *et al.*, 2012). Despite the variety of survey methods,
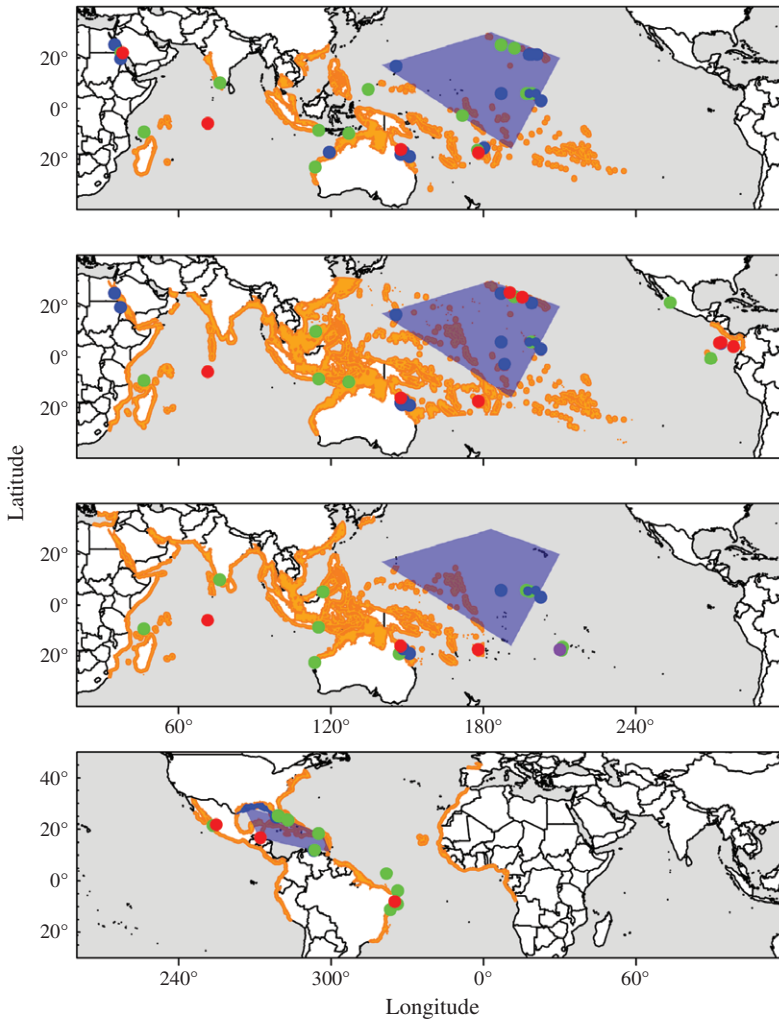
FIG. 4. Geographic location of abundance studies for the four best studied reef-shark species: (a) *Carcharhinus amblyrhynchos*, (b) *Triaenodon obesus*, (c) *Carcharhinus melanopterus* and (d) *Ginglymostoma cirratum* overlaid on maps of their global ranges (represented in orange), based on spatial data from the IUCN Red List (IUCN, 2015). ● denotes studies of abundance, ● denotes spatial studies, ● indicates a demographic analysis from genetic data and ● denotes studies including only estimates of density or abundance from a single location and time. ◀ were used for studies that examined a wider region rather than only a single, smaller locality. Maps made with Natural Earth and the R package PBSmapping (www.r-project.org; cran.r-project.org/web/packages/PBSmapping/index.html).

the analysis of abundance data has been largely limited to basic statistical methods, with most studies ($n = 51$) using linear regression or simpler methods to examine abundance, including 46% of the studies that inferred temporal or space-for-time trends, despite the largely non-normal nature of count data. The recognized importance of environmental covariates in affecting reef-shark abundance will mean that appropriate statistical techniques will be crucial for inferring trends in abundance (Nadon *et al.*,

2012; Richards *et al.*, 2012; Brooks *et al.*, 2013; Afonso *et al.*, 2014; Espinoza *et al.*, 2014; White *et al.*, 2015). The importance for robust modelling approaches driven by data from long-term programmes has already been recognized in temperate contexts (Rutterford *et al.*, 2015). Robust statistical analysis and long-term monitoring programmes should be made common practice for tropical reef systems as well.

Despite a paucity of time-series data to examine reef-shark trends in abundance, 17 such studies have been published, all but one in the past decade. Only seven of these studies, however, used time series longer than 10 years, and three of them analysed aggregate counts of multiple species some of which included just occurrence data (Heupel *et al.*, 2009; Ruppert *et al.*, 2013; Torres-Herrera & Tovar-Avila, 2014), reflecting the difficulty of obtaining good quality long-term data. Temporal studies have found a mixture of trends for all studied reef-shark species, with eight reporting declines, 10 finding evidence for positive population trends and five identifying population stability in at least some of their studied species. Two studies have demonstrated positive trends for the carcharhinid reef sharks (except for *C. albimarginatus*) and *N. ferrugineus* in the Great Barrier Reef Marine Reserve (Heupel *et al.*, 2009; Espinoza *et al.*, 2014). In contrast, there have been general declines for these same species (again except for *C. albimarginatus* which increased) at the Chagos Archipelago, Indian Ocean, over 30 years (Graham *et al.*, 2010). Declines were seen for both *T. obesus* and *C. albimarginatus* at Cocos Island in the eastern Pacific Ocean, although *C. galapagensis* occurrence appears to be increasing; also their populations appear stable at the nearby Malpelo Island (Soler *et al.*, 2013; White *et al.*, 2015). Elsewhere in the Pacific Ocean, temporal studies are known only from provisioned tourism enterprises at Fiji and Hawai'i, which found proportions of some species visiting the sites, such as *C. galapagensis*, *C. melanopterus* and *T. obesus* increasing with time at the expense of other species such as *C. albimarginatus* (Meyer *et al.*, 2009; Brunnschweiler *et al.*, 2014).

Most studies have either examined abundance across spatial scales spanning multiple islands or reef systems ($n = 34$) or only indicate abundance for a particular region or reef system ($n = 34$) without inferring temporal or spatial trends for some of the studied species. About 22 studies have used space-for-time analyses to infer historical population trends in areas lacking temporal data by comparing sites with fewer anthropogenic pressures to more heavily affected ones. Every space-for-time study found lower abundance (or occurrence) in areas with higher anthropogenic effect or fishing pressure. For instance, UVCs provide evidence that populations of *C. amblyrhynchos*, *C. galapagensis*, *C. melanopterus*, *T. obesus* and *N. ferrugineus* in the central-western Pacific Ocean (DeMartini *et al.*, 2008; Nadon *et al.*, 2012) and *C. perezi* and *G. cirratum* in the Caribbean (Ward-Paige *et al.*, 2010) are depressed on reefs around areas of high human density. Reef-shark populations have potentially declined to <10% of baseline levels on Pacific reefs (Nadon *et al.*, 2012). UVCs suggest that top predators, including sharks, make up a large portion of fish biomass at the reefs of the more remote north-west Hawai'ian Islands and Palmyra Atoll, while at the more populated main Hawai'ian Islands and Fanning Island, reef sharks are rarer and in some instances large species such as *C. amblyrhynchos* were either observed only rarely or not at all (Wetherbee *et al.*, 1997; Friedlander & DeMartini, 2002; Stevenson *et al.*, 2007). Similarly, these sorts of studies can also reflect the influence of fishing pressure on reef sharks, finding substantially higher abundances of populations inside reserves with stricter fishing regulations, including for those of *C. perezi* in Belize (Pikitch *et al.*,

2005) and *C. amblyrhynchos*, *C. melanopterus* and *T. obesus* on the Great Barrier Reef (Robbins *et al.*, 2006; Espinoza *et al.*, 2014; Rizzari *et al.*, 2015).

A global picture of reef-shark abundance remains difficult to formulate both because of the dearth of studies and because caution is needed when comparing conclusions amongst studies and sites. Survey methods can, for example, greatly influence density estimates (McCauley *et al.*, 2012*b*; Nadon *et al.*, 2012). For instance, UVCs conducted at smaller scales can overestimate true densities, which can lead to potentially erroneous conclusions about the role of sharks on reefs (McCauley *et al.*, 2012*b*; Trebilco *et al.*, 2013). Towed-diver surveys over a larger scale appear to provide more accurate estimates of reef-shark abundances (Richards *et al.*, 2011; McCauley *et al.*, 2012*b*): in the Line Islands, these surveys (Nadon *et al.*, 2012) estimated one tenth as many reef sharks as smaller transect surveys conducted in the same locations (Sandin *et al.*, 2008). Methods with higher detection abilities, but lower accuracy, such as baited video surveys, may also be desired when reef sharks are rarer, as found at heavily fished localities or if only presence–absence or relative abundance data are desired for studies of species richness or composition (Dennis *et al.*, 2005; Heagney *et al.*, 2007; Brooks *et al.*, 2011; Bond *et al.*, 2012; McCauley *et al.*, 2012*b*; Ruppert *et al.*, 2013; Espinoza *et al.*, 2014; Rizzari *et al.*, 2014*b*). Video surveys can also be used if estimates of total biomass are desired given the ease and accuracy of measuring size on video (Goetze & Fullwood, 2013; Rezzolla *et al.*, 2014). BRUVs are only slightly less accurate and efficient than typical fisheries-dependent methods of estimating abundance and are also non-invasive (Brooks *et al.*, 2011). Mark–recapture may be the best approach for estimating absolute abundances, but is of course a much more effort-intensive approach than BRUVs (McCauley *et al.*, 2012*b*). Estimating effective population size from a sample of microsatellite loci may provide an effective alternative when estimates of absolute abundance cannot be achieved (Dudgeon & Ovenden, 2015). If the few studies that estimated abundance in relatively isolated areas, such Aldabra Atoll, the north-west Hawai'ian Islands, the Line Islands and areas in the Red Sea (Stevens, 1984; Holzwarth *et al.*, 2006; Papastamatiou *et al.*, 2009*a*; Dale *et al.*, 2011; Hussey *et al.*, 2011; Obura *et al.*, 2011; McCauley *et al.*, 2012*b*), are to be useful in temporal or spatial comparisons or for setting baselines, both oceanographic variables and survey methodology will need to be carefully considered.

Habitat selection of the target species can also introduce bias into abundance estimates if not properly considered. For instance, the deepwater preferences of *C. albimarginatus* may require baited underwater remote cameras to overcome the depth limitations of divers in order to get systematic counts (Espinoza *et al.*, 2014). The shallower preferences of *C. melanopterus* (Hobson, 1963; Stevens, 1984; Papastamatiou *et al.*, 2009*a*, *b*; Rizzari *et al.*, 2014*a*) compared with other carcharhinid reef sharks mean that surveys in shallower reefs and lagoons will find them aplenty even when the forereef community is dominated by larger, more deepwater sharks (Papastamatiou *et al.*, 2009*a*; McCauley *et al.*, 2012*a*). Seasonal or diel changes in habitat use can also affect abundance estimates if these factors are not incorporated into survey design (Brooks *et al.*, 2013; Vanderklift *et al.*, 2014).

In lieu of time series or spatial data, other studies have used demographic models parameterized by estimates of mortality (Dudgeon *et al.*, 2008; Hisano *et al.*, 2011) and genetic models of effective population size based on microsatellite DNA diversity and mutation rates (Vignaud *et al.*, 2014) to infer population trends and the negative influences that fishing and human presence may have on reef sharks. Analysis

of historical records has also proved useful in demonstrating the potential extinction of *C. galapagensis* at Saint Paul's Rocks, an archipelago in the central Atlantic Ocean, where it was once quite abundant (Luiz & Edwards, 2011). Interviews with fishermen could also prove to be another useful tool for estimating historical abundance when no other options exist (Teh *et al.*, 2007).

Even with the rapid rise in reef-shark abundance knowledge, there is still a need for quality geographically and taxonomically diverse abundance data, particularly over long temporal scales, if the conservation status of reef sharks is to be reliably assessed. These monitoring programmes ideally should have standardized designs based upon the study species that account for the biases of the chosen survey methods. Lack of species specificity is also a widespread problem not only for fisheries-dependent data (Heupel *et al.*, 2009; Torres-Herrera & Tovar-Avila, 2014), but also has happened in UVC studies (Sandin *et al.*, 2008; Williams *et al.*, 2011; Ruppert *et al.*, 2013), particularly when a species is counted too rarely to support independent analysis (Ward-Paige *et al.*, 2010; Nadon *et al.*, 2012). Citizen science is a logistically feasible, effective and relatively inexpensive alternative to standardized surveys that can collect abundance data over large spatial and temporal scales as long as tourism operators have training and links to researchers with statistical expertise (Huveneers *et al.*, 2009; Ward-Paige *et al.*, 2010; Vianna *et al.*, 2014).

THREATS

Fishing currently poses the greatest threat to reef-shark species globally (Dulvy *et al.*, 2014), but most exploitation has occurred in the absence of fisheries data, and as such the effects of fishing on reef-shark populations remain poorly understood. Overall, there have been reports of fishing pressure, both targeted and as by-catch, for reef sharks in each family except Scyliorhinidae and Hemiscyllidae (Heupel *et al.*, 2009; Tavares, 2009; Meneses *et al.*, 2011; Aguilar *et al.*, 2014; Table SI, Supporting Information). Amongst species, the threat posed by fishing differs depending on life-history characteristics (Hutchings *et al.*, 2012) as well as by habitat preferences and associated exposure to fishing pressure. For instance, *T. obesus* is not as susceptible to fishing pressure as other reef sharks such as *C. amblyrhynchos*, partially because of its preference for shallow reef habitat which limits its capture in longline fisheries (Dennis *et al.*, 2005; Dale *et al.*, 2011; Chin *et al.*, 2012). Reef-shark fisheries records are sporadic: high catches of *C. amblyrhynchos* and *N. ferrugineus* have been reported from India (Joshi *et al.*, 2008; Kumar *et al.*, 2015), and for these species and *T. obesus* in Indonesia (White, 2007). Studies have also documented high landings in largely unreported artisanal fisheries, including in Madagascar, the Seychelles, Brazil and Mexico (Nageon de Lestang, 1999; Smith *et al*, 2009; Meneses *et al.*, 2011; Robinson & Sauer, 2013; Furlong-Estrada *et al.*, 2014). For instance, *G. cirratum* and *T. obesus* experience an intermediate ecological risk from artisanal gillnets and longlines in the Gulf of California (Furlong-Estrada *et al.*, 2014). Additionally, several recent studies have uncovered and assessed quantitative time series or spatial data on reef-shark populations, from which inferences about fisheries effects on reef-shark populations have been made. Other perceived threats to reef-shark species include pollution, biomagnification (the concentration of pollutants up the food chain) (Lyle, 1986; Al-Hassan *et al.*, 2000; Dulvy *et al.*, 2014) and disturbances to nursery grounds (Carrier & Pratt, 1998). These, in addition to habitat destruction, have been identified as important in the IUCN Red

List assessments, but remain unstudied and under discussed in the current literature (Dulvy *et al.*, 2014; IUCN 2015).

CONSERVATION STATUS

The IUCN Shark Specialist Group (SSG) has assessed all reef-shark species, and although the conservation status of most species was uncertain at the time of their assessment and many assessments are now a decade old, little new information is available to alleviate these uncertainties. Overall, five reef-shark species are assessed as vulnerable, 11 as near threatened, four as least concern and nine as data deficient (Table I). Given the difficulty of assessments, it is not surprising that the majority of reef-shark species (59%) were last assessed in or before 2005 (Table I); but this was also the year when studies of abundance began to rise rapidly [Fig. 2(b)]. As such, most abundance studies (*e.g. C. amblyrhynchos*: 89%, *C. melanopterus*: 92%, *T. obesus*: 88%, *C. galapagensis*: 80%, *C. albimarginatus*: 79%, *C. perezi*: 75% and *G. cirratum*: 72%) have been published since a species' last red list assessment. Yet despite the rise of abundance studies there remains little information on long-term reef-shark population trends, often because studies were based upon short time series or low sample sizes with insufficient power to detect trends in abundance; the only species assessed in the last 5 years were newly described wobbegong and epaulette shark species. Uncertainty in reef-shark conservation status is reflected in the fact that at the time of assessment, 22 of the 29 species had uncertain population trends; five species (two vulnerable and three near threatened) had declining population trends while only two (listed as least concern) had stable populations (Table I). It is also suspected that as a group reef sharks may be more threatened and require more conservation attention than the current red listings suggest. As examples, global conservation assessments may mask conservation concerns at the regional or sub-regional level, reef-shark data collected at coarse taxonomic scales could mask declines in individual species, and many reef-shark population declines probably occurred prior to modern data collection (Jackson *et al.*, 2001).

The five reef shark species (two ginglymostomatids [*N. ferrugineus* and the short-tail nurse shark *Pseudoginglymostoma brevicaudatum* (Günther 1867)], two hemiscylliids (hooded carpet shark *Hemiscyllium strahani* Whitley 1967 and Papuan epaulette shark *Hemiscyllium hallstromi* Whitley 1967 and *S. fasciatum*), red listed as vulnerable in 2003 and 2004 (Table I), were assessed as such on the basis of limited ranges, habitat destruction and exploitation (Heupel & Kyne, 2003*a*, *b*; Pillans, 2003*a*; Pillans & Simpfendorfer, 2003; Nel *et al.*, 2004). Of these, only *N. ferrugineus* and *S. fasciatum*'s population trends were known. Along with reports of local *N. ferrugineus* extinctions in Thailand and India (Pillans, 2003*a*), there is now also evidence of its populations declining at Chagos Archipelago (Graham *et al.*, 2010), Fiji (Brunnschweiler *et al.*, 2014) and outside of the Great Barrier Marine Reserve (Espinoza *et al.*, 2014). Six studies have quantified *S. fasciatum* abundance, but only one, which used demographic models parameterized by mark–recapture data (Dudgeon *et al.*, 2008), documented temporal trends. There are no abundance studies of *P. brevicaudatum*, and no research effort has been devoted to the two hemiscylliid species possibly due to their small size and cryptic nature.

Since 2005, when *C. amblyrhynchos*, *C. melanopterus* and *T. obesus* were assessed as near threatened (Table I) based primarily on their restricted habitat, life-history

characteristics and exploitation history (Smale, 2005, 2009; Heupel, 2009), evidence has accumulated suggesting that each of these species faces a heightened risk of extinction and might be found to be more vulnerable when a new assessment is completed. Although population trends were unknown at the time of their assessments, numerous studies have since quantified *C. amblyrhynchos* ($n = 38$) and *T. obesus* ($n = 35$) abundance, providing evidence of populations declines in both (Robbins *et al.*, 2006; Heupel *et al.*, 2009; Graham *et al.*, 2010; Nadon *et al.*, 2012; Clarke *et al.*, 2013; Espinoza *et al.*, 2014; Rizzari *et al.*, 2015; White *et al.*, 2015), except for a few protected populations in Australia (Heupel *et al.*, 2009; Espinoza *et al.*, 2014). For *C. amblyrhynchos*, in addition to two temporal studies suggesting declines exceeding 90% (Graham *et al.*, 2010; Clarke *et al.*, 2013), 16 studies have shown high abundance at remote reefs and low abundance in affected areas and are evidence of historical declines (Table SI, Supporting Information). Moreover, *C. amblyrhynchos* population simulations show declines even under scenarios of moderate fishing pressure (Hisano *et al.*, 2011). Nine studies examining *T. obesus* population trends show a mix of positive and negative trends, whereas the 12 space-for-time studies consistently indicate declines. *Triaenodon obesus* is estimated to have declined by over 90% in the past 30 years at Chagos (Graham *et al.*, 2010) and by 77% over 20 years at Cocos in the eastern Pacific Ocean (White *et al.*, 2015). In contrast, populations appear to be stable at Malpelo Island in the eastern Pacific Ocean (Soler *et al.*, 2013) and increasing on the Great Barrier Reef (Espinoza *et al.*, 2014). Of the five studies that have examined *C. melanopterus* population trends, declines were found only at Chagos (Graham *et al.*, 2010). A recent population bottleneck was inferred in Moorea, French Polynesia, based on genetic evidence (Vignaud *et al.*, 2014). Such genetic studies also provide information on the low gene flow, inbreeding and susceptibility to habitat fragmentation in *C. melanopterus* populations in the Indo-Pacific, which is useful for conservation planning (Mourier & Planes, 2013; Vignaud *et al.*, 2013, 2014). Moreover, five studies show that *C. melanopterus* remains abundant at some remote and protected areas (Stevenson *et al.*, 2007; Papastamatiou *et al.*, 2009a; Obura *et al.*, 2011; McCauley *et al.*, 2012a, b; Vanderklift *et al.*, 2014). Overall, given that large populations of these three species have been observed recently only within MPAs or on uninhabited or remote reefs, reassessments of these three species in particular would be useful.

Although many of the remaining eight near threatened species were assessed about a decade ago (Table I), there is little new information about them in the scientific literature that could inform new red-list assessments. In general, the near threatened designation emphasizes research need since it often has arisen either from a paucity of information rather than a lack of threat or from balancing suspected threats in data-poor areas with lower extinction risk in protected parts of a species' range. For example, *E. dasypogon*, the Arabian carpetshark *Chiloscyllium arabicum* Gubanov 1980 and *C. albimarginatus* were each assessed as near threatened due to suspected population declines or suggested threats (Pillans, 2003b; Moore, 2009; Pillans *et al.*, 2009). The other five species, the coral catshark *Atelomycterus marmoratus* [Anonymous (Bennett) 1830], the Indonesian speckled carpetshark *Hemiscyllium freycineti* (Quoy & Gaimard 1824), Michael's epaulette shark *Hemiscyllium michaeli* Allen & Dudgeon 2010, *C. perezi* and *C. galapagensis*, might have also been classified in a threatened category had more information been available (Bennett *et al.*, 2003; White, 2003; Rosa *et al.*, 2006a; Kyne & Heupel, 2011; Dudgeon *et al.*, 2012). Uncertainty surrounding

the conservation status of *C. albimarginatus*, *C. perezi* and *C. galapagensis*, in particular, contrasts with the three carcharhinid reef-shark species previously discussed. The few studies that have been carried out provide evidence of extirpation, or nearly so, over parts of these species' ranges (Dennis *et al.*, 2005; Stallings, 2009; Ward-Paige *et al.*, 2010; Luiz & Edwards, 2011; Ruppert *et al.*, 2013). *Carcharhinus albimarginatus* is especially understudied, probably because its preference for deeper waters on outer forereefs prevents easy monitoring (Stevens, 1984; Friedlander *et al.*, 2012; Espinoza *et al.*, 2014) and so far it has typically only been analysed in taxonomically aggregated shark counts (Heupel *et al.*, 2009; Goetze & Fullwood, 2013; Shawky & De Maddalena, 2013; Table SI, Supporting Information).

The conservation status of the 13 reef-shark species currently designated as least concern or data deficient remains uncertain despite goals for research on their population statuses identified in their red-list assessments. Notably, *G. cirratum*, the most studied reef shark, is still designated as data deficient because its population dynamics are seldom studied: only four of the 18 abundance studies provide information useful for assessment. The abundance of any species within Heterodontidae has been studied only twice (Galván-Magaña *et al.*, 1989; Smith *et al.*, 2009) and within Hemiscyliidae only once (Heupel & Bennett, 2007), but none allowed for inference about population trends. No abundance, movement or population genetic studies have been conducted for reef sharks of the families Scyliorhinidae and Orectolobidae. Some of this trouble is due to the fact that species such as the floral banded wobbegong *Orectolobus floridus* Last & Chidlow 2008 and the network wobbegong *Orectolobus reticulatus* Last, Pogonoski & White 2008 are known from only a few specimens (Last & Chidlow, 2008; Last *et al.*, 2008; Huveneers & McAuley, 2009*a*; Corrigan & Huveneers, 2011). *Orectolobus reticulatus* may have satisfied criterion B for a threatened category due to its limited distribution (Corrigan & Huveneers, 2011), but having been only recently described (Last *et al.*, 2008) data were still limited at the time of its assessment. Based on their life-history characteristics and geographic extent, *G. cirratum*, the western wobbegong *Orectolobus hutchinsi* Last, Chidlow & Compagno 2006, the Mexican hornshark *Heterodontus mexicanus* Taylor & Castro-Aguirre 1972 and the Galapagos bullhead shark *Heterodontus quoyi* (Fréminville 1840), all of which are currently Data Deficient (Kyne *et al.*, 2004; Garayzar, 2006; Rosa *et al.*, 2006*b*; Huveneers & McAuley, 2009*b*), are also predicted to be threatened (Dulvy *et al.*, 2014).

Conservation-relevant reef-shark research remains focused on a few species and regions (Table I), even though most related red-list assessments identified uncertainties years ago that could have helped guide research focus. Even for well-studied species, geographic gaps still exist, particularly for populations outside Australia, the central Pacific Ocean or Caribbean. For instance, *C. galapagensis* has been mainly studied in Hawai'i despite populations across the Pacific Ocean, including Australia, and possible extirpation at St Paul's Rocks in the Atlantic Ocean (Luiz & Edwards, 2011) and *C. perezi* has been mainly studied at Glover's Reef in Belize. The IUCN Red List uses broad regional categories and only five reef-shark species received additional designations beyond their global assessment. For example, *G. cirratum* was designated as near threatened in the western Atlantic Ocean (a combination of its vulnerable status off South America and its least concern status in the Caribbean) (Rosa *et al.*, 2006*b*), but most of the work on it has been in the Caribbean, leaving a relatively poor understanding of the eastern Atlantic, Pacific and South American populations that may be more under threat (Castro & Rosa, 2005; Afonso *et al.*, 2014). Similarly, the

near threatened populations of *H. ocellatum* in New Guinea have been left unstudied despite almost meeting IUCN Red List criterion A3cde for vulnerable in 2003 (Bennett & Kyne, 2003). The overall lack of understanding of fine-scale reef-shark conservation statuses is problematic because of the high site fidelity and residency of reef-shark populations, which can lead to high degrees of population segregation and structure (Dudgeon *et al.*, 2009; Karl *et al.*, 2012; Vignaud *et al.*, 2014), but research still needs to expand geographically before the IUCN SSG will be able to undertake more regional assessments.

PROTECTING REEF SHARKS

Give the high site fidelity and residency typical of reef sharks, MPAs and shark sanctuaries could be effective conservation measures for these species provided their capacity for movement outside of reserves during dispersal, and seasonal and diel migrations, is understood and accounted for (Chapman *et al.*, 2005, 2007; Wiley & Simpfendorfer, 2007; Heupel *et al.*, 2010; Espinoza *et al.*, 2015b; Speed *et al.*, 2015). Starting in 2009 with Palau's Shark Haven Act, which prohibited all fishing of sharks in this country's exclusive economic zone, there has been a recent surge in the establishment of shark sanctuaries (Hoyt, 2014). There has also been a recent trend to explicitly include provisions for shark conservation in the management and design of sanctuaries and MPAs, including the Great Barrier Reef Marine Park in Australia, Papahānaumokuākea Marine National Monument in the Pacific and the Galapagos Marine Reserve in Ecuador (Hoyt, 2014). Already, there is evidence from eastern Australia that MPAs can promote recovery of fished reef-shark populations (Heupel *et al.*, 2009; Espinoza *et al.*, 2014). In general, MPAs covering a single reef could suffice for the conservation of juveniles or populations of small site-restricted species such as *H. ocellatum*, *T. obesus* or *C. melanopterus*, particularly on isolated reef systems, whereas protection of larger, wider roaming species such as *C. albimarginatus* and *C. amblyrhynchos*, will probably require an interconnected system of protected reefs (Chapman *et al.*, 2005; Heupel & Bennett, 2007; Heupel *et al.*, 2010; Espinoza *et al.*, 2015b; Speed *et al.*, 2015). The latter also will be required where promoting gene flow and reducing inbreeding is of concern (Mourier *et al.*, 2013; Vignaud *et al.*, 2013).

In addition to biological considerations, the conservation success of MPAs will depend on their quality, as measured by degree of community and fisher support, enforcement, monitoring, research and fragmentation, rather than their quantity (Hoyt, 2014). Reef-shark declines have been observed at ill-enforced protected areas (White *et al.*, 2015), and carcharhinid reef sharks have significantly lower abundance at no-take compared with no-entry sites on the Great Barrier Reef, which indicates that even limited human activities can contribute to population depletion (Robbins *et al.*, 2006; Rizzari *et al.*, 2015). In addition to effective enforcement, consistent monitoring would not only provide long-term information on the trends of populations in reserves, but could also provide extra surveillance for illegal fishing. Variable MPA benefits amongst species also compel an expansion of the taxonomic breadth of research effort so that knowledge exists to craft MPAs that are effective for more than just the few well-known charismatic species. Integration of multi-species and ecosystem-based management approaches should be the primary approach to MPA design in the future (Hoyt, 2014). Finally, evidence to date suggests that MPAs have limited spillover

effects, indicating that other regulations will be necessary to effectively conserve reef sharks (Ward-Paige *et al.*, 2010; Espinoza *et al.*, 2014), although few details of fisheries regulations were found in the literature review [Nageon de Lestang (1999) provide an example]. As such, there is a need to expand research of other management options beyond MPAs as MPAs alone cannot effectively conserve shark species on a global scale without the regulation and reduction of fishing effort (Baum *et al.*, 2003; Kinney & Simpfendorfer, 2009; Vignaud *et al.*, 2013).

Shark diving tourism is lucrative and serves as one additional tool that could motivate reef-shark conservation (Vianna *et al.*, 2012; Dicken, 2014). Although some changes in behaviour can occur as sharks interact with diving operations (González-Pérez & Cubero-Pardo, 2010; Cubero-Pardo *et al.*, 2011; Fitzpatrick *et al.*, 2011*b*), this eco-tourism should have minimal effect on their populations (Maljković & Côté, 2011; Vianna *et al.*, 2014). Sharks have been found to avoid areas of high human use, but this pattern is probably more reflective of fishing pressure and may be abated by the establishment of shark sanctuaries that incorporate conservation-minded diving practices (Garla *et al.*, 2006; Stallings, 2009; Ward-Paige *et al.*, 2010; Shawky & De Maddalena, 2013).

FUTURE RESEARCH NEEDS

Understanding both the population status and ecological role of reef sharks are proposed as priority research foci given the potential for such research to inform conservation and to motivate management measures of reef-shark populations potentially suffering declines. Overall, the current conservation statuses of reef sharks worldwide are only poorly understood from both geographic and taxonomic standpoints. A comprehensive global assessment of reef-shark conservation statuses would be built most effectively through a combination of integrated new research targeted on populations' abundance, movement patterns, trophic ecology and genetics. Most importantly, high quality long-term species-specific monitoring data are urgently required for reef-shark populations around the world: the continuation of existing monitoring programmes is strongly encouraged, as is the development of new programmes for data-poor areas and species. Additionally, tagging and telemetry studies could help inform population abundance assessments by revealing mechanisms behind spatial abundance gradients (Garla *et al.*, 2006; Heupel *et al.*, 2010), validating the methods and findings of abundance studies and evaluating if higher abundances within reserves are transient in nature or related to biases in sampling (Wiley & Simpfendorfer, 2007; Bond *et al.*, 2012; Vianna *et al.*, 2014; Espinoza *et al.*, 2015*b*). Knowledge of reef-shark population segregation by size and sex from movement and abundance studies could also aid in the design of MPAs that have specific goals to protect particular shark life-history stages from fisheries exploitation. Reef-shark conservation would also benefit from new genetic research to elucidate cryptic reef-shark diversity, as well as genetic structure and gene flow between populations (Dudgeon *et al.*, 2012; Chapman *et al.*, 2015). Genetic studies could also help to demonstrate whether high residency on single reefs leads to inbreeding (Mourier & Planes, 2013) and could give indications of longer-term dispersal in reef sharks, information that is inaccessible from telemetry data alone (Whitney *et al.*, 2012*b*; Vignaud *et al.*, 2014). Conservation prioritization could also benefit from

knowledge of effective population sizes and the likelihood of reef shark population rescue from localized depletion even when trends in abundance are available.

Over the past decade, conservation groups have promoted the importance of sharks to healthy ecosystems as a motivator for shark conservation, but such claims are premature given the current lack of knowledge about the role sharks play on coral reefs. If conservation is to be motivated in this way, convincing demonstrations of the ecological role of reef sharks are needed. To date, the few studies examining community consequences of shark losses have found little evidence of top–down control of reef fish communities by reef sharks (Ruppert *et al.*, 2013; Rizzari *et al.*, 2015). More studies examining reef-shark trophic interactions are needed, as are new stable-isotope analyses as these could elucidate both the how and why of reef-shark movement and demonstrate the extent to which mobile reef-shark species connect different reef habitats (Papastamatiou *et al.*, 2015).

Within the framework of the priority research foci proposed here, reef-shark research needs to expand both in taxonomic and geographic scope. Studies of the lesser known reef-shark species on diverse Indo-Pacific coral reefs, as well as in the less diverse eastern Pacific and western Atlantic Oceans, are required as are genetic studies to help illuminate cryptic reef biodiversity. The restricted spatial nature and high genetic structure of reef-shark populations underscores the fact that regional assessments on the scale of ocean basins will probably not suffice to summarize the local conservation status for most reef-shark species, specifically those having large geographic distributions. Although recognizably difficult given geographic gaps in knowledge, a more nuanced approach where possible would make clearer geographic variation in reef-shark conservation statuses. Ultimately, there needs to be tighter feedback between the conservation needs of reef-shark populations and the research devoted to them. Research has responded rapidly in the last few years to deficiencies in reef-shark knowledge, but researchers are encouraged to pay greater attention to IUCN Red List assessments, particularly data deficiencies. Conversely, conservation assessors should be helped to update reef-shark assessments as soon as possible so that conservation efforts are based upon the best and most recent available scientific evidence.

CONCLUSIONS

Research effort relevant to reef-shark conservation is relatively recent but is increasing rapidly in concert with the growing recognition of the importance of sharks on coral reefs. Most research has focused on *G. cirratum* and the three classic carcharhinid species, and studies of these are still geographically restricted, with most in Australia, the Line Islands, Hawai'i and the Caribbean. Consequently, there remain significant taxonomic and geographic research gaps, which need to be filled if global reef-shark conservation goals are to be set and achieved, and only a few species can currently be considered for reassessment by the IUCN Red List. Although available evidence suggests that reef-shark abundances are now substantially lower than historical baselines and that declines are ongoing, much uncertainty remains about current population trends because of the paucity of abundance data and focused research effort in this area. Existing reef-shark monitoring programmes need to be supported and continued, and new programmes focusing on data-poor species and areas should be developed. The latter could be integrated with dive tourism and citizen science. MPAs should remain

an important tool for reef-shark conservation, although research should be expanded into other management options. Research programmes that achieve a critical synthesis of biodiversity, genetic, abundance, trophic ecology and movement knowledge will be best prepared to assess reef-shark susceptibility to extinction, the effectiveness of protected areas for these species and the consequences that depletions in reef-shark populations will have for their ecosystems.

Supporting Information

Supporting Information may be found in the online version of this paper:
Table S1. List of the literature returned by the Web of Science search for each reef shark species and used in the review. The species and topic of each piece of literature are given.

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