Protecting Cayman Island Sharks: Monitoring, Movement and Motive

Protegiendo a los Tiburones de las Islas de Caimán: Monitoreo, Movimiento y Motivo

Protection des Requins aux Iles Cayman : Surveillance, Mouvement et Motivation

RUPERT ORMOND[1,2], MAUVIS GORE[1,2], ANNABELLE BLADON[3], OLIVER DUBOCK[1], JOHANNA KOHLER[1,2], and CATRIONA MILLAR[1,2]
[1]*Marine Conservation International, South Queensferry, Edinburgh, Scotland, United Kingdom.*
**rupert.ormond.mci@gmail.com*
[2]*Heriot-Watt University, Riccarton, Edinburgh, Scotland, United Kingdom.*
[3]*University of York, York, United Kingdom.*

ABSTRACT

In April 2015, the Cayman Islands gave full legal protection to all sharks and other elasmobranchs throughout its Exclusive Economic Zone. This was the culmination of a research programme initiated in 2008 to determine the status of sharks in Cayman waters and assess the need for their conservation. A Facebook linked citizen science scheme and interviews with fishers, as well as BRUVS and longline surveys, were used to monitor the principal species, among which Caribbean reef sharks (*Carcharhinus perezi*), blacktip sharks (*C. limbatus*) and nurse sharks (*Ginglymostoma cirratum*) are the most common, while tiger sharks (*Galeocerdo cuvier*), silky sharks (*C. falciformis*), oceanic whitetip sharks (*C. longimanus*) and great hammerhead sharks (*Sphyrna mokarran*) occur locally or seasonally in small numbers. The results of eight years of surveys indicate that shark abundance on Little Cayman is about three times that on the other two islands, and that while abundances in the Cayman Islands overall are higher than many Caribbean locations, they are markedly less than those within large protected or unexploited areas elsewhere or than in the historic past. To investigate the ranges of individual sharks in comparison to the Cayman Islands existing Marine Protected Areas (MPAs) medium-bodied species have been fitted with acoustic tags and larger-bodied ones with SPOT GPS tags. The results have revealed that while some individuals of smaller shark species may be semi-resident within a part of an island, they may also travel significant distances around or between islands. Two Caribbean reef sharks travelled from Grand Cayman to Little Cayman, a distance of about 150 km through water at least 1000 metres deep, one of them completing the return journey twice. Larger sharks were found to travel much greater distances: the majority of seven tagged tiger sharks travelled widely across the Caribbean basin, one returning seasonally to Grand Cayman for at least three further years, while among 18 tagged oceanic whitetip sharks many not only crossed the Caribbean but travelled in to the Gulf of Mexico. The scale of shark movements strongly supported the need for protection on a much larger scale than the existing MPA network could achieve. In further support of the case for shark conservation, an environmental economics study revealed that both residents and visitors value the marine life highly, more so than the islands' Caribbean culture or fishing. The Non-Consumptive Use Value of sharks to the Cayman Islands, through tourism and recreation, was estimated at US $46.8 to 62.6 million/yr, compared with an estimated Consumptive Use Value, if sharks were sustainably fished, of no more than US $1.3 million/yr.

KEYWORDS: Shark conservation, shark sanctuary, Cayman Islands, Caribbean reef shark, tiger shark, oceanic whitetip shark, shark migration, shark movement ecology, shark economic value

INTRODUCTION

In May 2016 we held a Cayman Shark Festival to celebrate the first anniversary of the Cayman Islands giving full legal protection to all shark and ray species, when the Cayman Islands National Conservation Law, 2013, section 17, came into effect. The event included a shark photography competition for divers, a poster competition for schools, short talks and demonstrations, as well as music by local traditional bands and dancing. It was attended by both visitors and local residents, fishers as well as divers, and children, as well as Cayman Island Government Department of Environment (DoE) staff. In affording legal protection to sharks throughout Cayman waters, the Cayman Islands joined the ten or so other countries, including notably the Bahamas, Maldives, and Palau, that have established shark sanctuaries covering part or all of their Exclusive Economic Zone (MPA Atlas 2016, The Pew Charitable Trusts 2017).

The need for such measures to help conserve shark species has become widely recognised since the extent of the decline in shark abundance, and the scale of their slaughter over the past 25 years, became appreciated. It is generally considered that by the beginning of the present century an estimated 26 - 73 million sharks were being caught each year (Clarke et al. 2006), mainly to meet the demand of the Asian shark-fin trade, with the result that across the world's oceans the populations of many species are now thought to have declined by over 90%, compared to pre-exploitation levels (Baum et al. 2003, Baum and Myers 2004, Robbins et al. 2006, Ferretti et al. 2008, Graham et al. 2010). This collapse in shark abundance has affected not only the major ocean basins, but also marginal seas including the Gulf of Mexico and the Caribbean (Baum and Myers 2004, Ferretti et al. 2008, Ward-Paige et al. 2010). Ward-Paige et al. (2010) notably concluded, based on data from over 75,000 dives, that human impacts, principally fishing, has led to the broad-scale absence of sharks on reefs in the greater Caribbean, sharks other than nurse sharks being largely absent around Cuba, Jamaica, Dominican Republic, and Puerto Rico, as well as through most of the Antilles and the Central and South America coasts. Following their latest assessment the IUCN shark specialist group now consider that among sharks six species are now Critically Endangered, four species Endangered, and 24 species Vulnerable (Dulvy et al. 2008, IUCN 2016). Thus developing measures to protect especially the larger-bodied sharks has become a matter of urgency.

Besides a straight-forward concern for the conservation of biodiversity, it has been widely proposed that large-bodied sharks play a key role in maintaining the health of marine environments including coral reefs (Dulvy et al. 2004, Myers et al. 2007, Ferretti et al. 2010). For reefs it is hypothesised that sharks as apex predators may regulate a trophic cascade that

influences the health and abundance of corals. If large sharks regulate the abundance of middle level predators, which in turn may regulate the abundance if herbivorous fishes such as parrotfishes (Scaridae) and surgeonfishes (Acanthuridae), which in turn help regulate the abundance of reef algae, that otherwise can outcompete corals, then a collapse in the numbers of large sharks could in principal result in a large reduction in the abundance of corals. However, a recent in-depth review (Roff et al. 2016) has concluded that while sharks perform important ecological roles, so far the evidence to support the hypothesised shark -driven trophic cascades is equivocal, especially since it appears that most reef-associated shark species do not act as apex predators but instead function as mesopredators, along with a variety of other larger reef fish species. Their conclusions have however been questioned (Ruppert et al. 2016), implying that more work is needed on this topic.

In addition to their ecological role, sharks and also rays are increasingly valued as a source of tourist income, with shark watching becoming almost as popular among SCUBA divers as is whale (and dolphin) watching more generally. While in 1998, whale & dolphin watching was estimated to be ongoing in 87 countries and territories, to involve more than 9 million participants per year, and be worth more than US$1 billion per year, by 2008 it was estimated to involve 13 million participants per year in 119 countries and territories, generating a total annual income of $2.1 billion (Hoyt 2008, O'Connor et al. 2009). Although it only developed some time later, by 2010 shark and ray tourism was estimated to involve at least 376 operators in at least 29 countries (Gallagher and Hammerschlag 2011), and to be generating US$314 million of economic expenditures per year (Cisneros-Montemayor et al. 2013). In fact the oldest example of elasmobranch tourism is believed to be one that has been operating in Grand Cayman since the early part of the last century. This is the tourist attraction most widely known as "Stingray City", where up to a hundred wild Southern stingrays (*Dasyatus americana*) come to be fed daily and can be experienced close-up while snorkelling or bathing. Up to a thousand or more visitors a day may be taken by boat to the site, which is regarded as the most popular tourist attraction in the Caribbean (Department of Environment, Unpublished a). The rays have been estimated to be worth approximately US$1.75 million each in terms of the revenue generated, yet until 2015 these rays were not subject to any legal protection.

Concerning sharks in the Cayman Island, while small numbers were not infrequently sighted by SCUBA divers, they have not in recent decades been regarded as abundant. The Cayman Islands were doubtless not unaffected by the region-wide decline in shark numbers brought about by intense commercial and recreational fishing (Bonfil 1997, Shepherd and Myers 2005, Ward-Paige et al. 2010) that apparently did not peak until the 1990s (Pauly 2010). In addition, however, during the middle part of the last century (1900s) the Cayman Islands were the base for a modest commercial shark fishery that had a small number of vessels covering wides areas of the western Caribbean, targeting in particular nurse and tiger sharks for their skin to be exported for the production of sharkskin leather. Otherwise, at the start in 2008 of the work described here there was little known about which were the main species present in the Cayman Islands, or their relative abundances. Given the islands' isolated position, separated by very deep water from continental coasts and shelf (see *Study Area*) it could not be assumed that species occurrence or abundance would reflect that of adjacent continental areas.

Thus a long-term project was initiated to address the following questions:

i) What shark species are present around the Cayman Islands,
ii) What are their relative abundances,
iii) Are measures desirable to give protection to some or all species or populations, or are the exiting Marine Protected Areas adequate, and
iv) Are other shark related management measures advisable in relation to the marine tourist industry?

This paper provides an overview of the information and results obtained to date and indicates how they influenced the DoE's decision to recommend the full protection pf sharks through Cayman waters. More detailed accounts of the scientific results are in hand.

STUDY AREA

The Cayman Islands are a cluster of three islands in the north-west Caribbean, approximately midway between Jamaica and Cuba (Figure 1). The largest island, Grand Cayman, which accounts for most of the population and commercial and tourist activity, is approximately 40 by 20 km in size. About 100 km away to the north-east are the two smaller "sister islands" of Little Cayman and Cayman Brac, each about 20 by 5 km (Figure 1 inset). The three islands lie adjacent to the Cayman Ridge which separates deep water (about 3000 m) immediately to the north from the Cayman Trench (about 5000 m) immediately to the south. All three islands are almost completed surrounded by a well-formed fringing reef characterised by a broad terrace at about 15 m, beyond which is a sharp deep reef face, the famous (to divers) "Cayman Wall". In some places however the fringing reef is separated from the shore by sandy lagoons, known locally as "sounds". In particular the north-west portion of Grand Cayman features a large bay enclosing an approximately 10 km wide (up to 5 m deep) lagoon known as North Sound. Parts of this sound and other smaller ones are lined with well-developed mangrove forest.

The reefs and associated biota have been the object of extensive research and monitoring by or under the auspices of the Cayman Islands Department of the Environment (DoE). Most appear to be still in relatively good condition compared to most other parts of the Caribbean (Department of Environment, a situation aided by the establishment over 25 years ago of a network of Marine Parks and Conservation / Replenishment Areas. These occupied about 25% of the coast of the three islands (Figure 2), with proposals to increase the extent of these Marine Protected Areas (MPAs) due for implementation.

METHODS AND RESULTS

Species Occurrence

Early in the project, to gain information on the species of shark present in the Caymans, besides undertaking our own surveys (*see next section*) we involved the public in two ways. First we undertook in depth interviews with a large proportion of the islands' fishers. There are few full-time fishers on the islands, but perhaps a hundred or so boat-owners (DoE Cayman Islands, unpublished report b) fish part-time to supplement other income. Second we established a Facebook based reporting scheme and promoted it among divers (especially local diving centre staff) and interested local people and visitors. This group, "Cayman Island Sharks and Cetaceans" (we were also seeking information on local cetaceans) now has over a thousand members, many of whom remain active.

The results of both surveys suggested that Caribbean reef (*Carcharhinus perezii*) and nurse (*Ginglymostoma cirratum*) sharks were relatively common, and that blacktip (*C. limbatus*), oceanic whitetip (*C. longimanus*), and lemon (*Negaprion brevirostris*) sharks were not uncommon, while

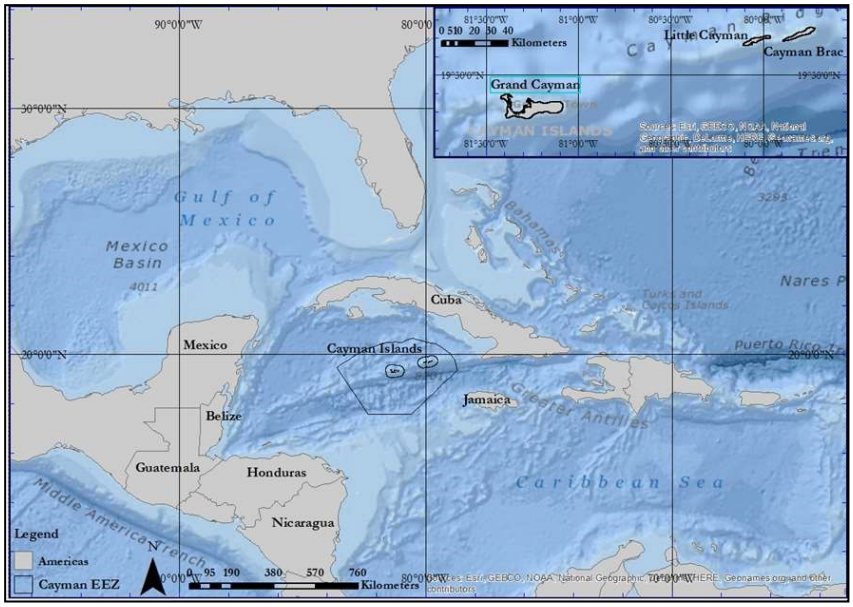

Figure 1. Map to show the location of the Cayman Islands in the north-west Caribbean, including the largest island Grand Cayman to the south-west, and the two "sister islands" of Little Cayman and Cayman Brac approximately 150 km to the north-east. Inset shows the three islands in more detail. The lines surrounding the islands indicate the extent of territorial waters (closer) and the exclusive economic zone (further). Map source: DoE GIS layers

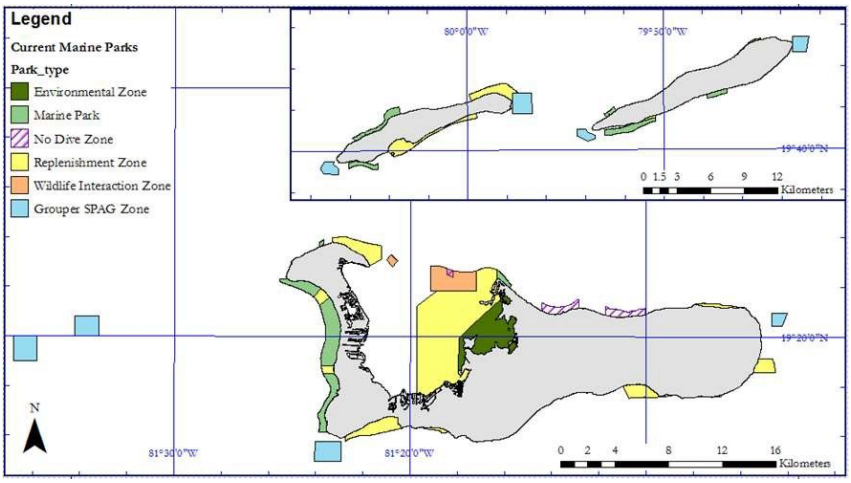

Figure 2. Map to show the extent of different types of Marine Protected Area (MPA) on each of the three Cayman Islands, Grand Cayman (main map), and Little Cayman and Cayman Brac (inset). Map source: DoE GIS layers.

tiger (*Galeocerdo cuvier*), great hammerhead (*Sphyrna mokarran*), scalloped hammerhead (*S. lewini*), whale (*Rhincodon typus*) and blue (*Prionace glauca*) sharks were also occasionally encountered. Subsequent reports and our own survey work have largely supported the information we were provided, save that contrary to reports we have no evidence for the occurrence of bull sharks on the islands, and suspect that prior reports were of large female Caribbean Reefs. Nor during the past nine years have we had any confirmed sightings of dusky sharks (*C. obscurus*) or shortfin makos (*Isurus oxyrinchus*). Scalloped hammerheads used to be observed regularly at the grouper and snapper spawning aggregation sights that are present in locations of the ends of the islands, but are now rarely seen. In contrast we discovered during the course of the project that silky sharks (*C. falciformis*), mostly sub-adult, may be caught mainly offshore, especially around the banks to the west and north-west of Grand Cayman.

Relative Abundance

Two methods were used to gain more quantitative information on the relative abundance of the more common species. First we used Baited Remote Underwater Video Stations (BRUVS), a now widely used technique (Meekan and Cappo 2004, Cappo et al. 2004, Meekan et al. 2006, Brooks et al. 2011, White et al. 2013, Espinoza et al. 2014), to record the sharks that were attracted by scent to reef locations around the three islands. Initially our BRUVS consisted of a traditional hand-held video camera recording images to tape contained in a simple underwater housing and mounted on a heavy iron frame from which a 1.5m long bait arm was extended. At the end of the arm was suspended a bait bag containing approximately 300 g of cut fish (usually imported-frozen Pacific Mackerel). However as soon as higher resolution waterproof "GoPro" cameras became available we switched to these and to a lighter, plastic frame weighed down and stabilised by dive weights placed around the base. On each occasion four BRUVS were deployed at stations typically 500 m to 1 km apart, at a series of standard locations around all three islands. They were left in situ for as long as the cameras could record, initially for 90 minutes using tapes, and subsequently for up to two hours as higher capacity memory cards and batteries became available. Following retrieval recordings were downloaded to a hard drive and the resulting videos viewed and visits to the BRUVS by different shark species noted.

Secondly, we also employed "Scientific Longlining" which likewise has been widely used to estimate shark comparative abundance (Simpendorfer 2004, Pikitch et al. 2005, Brooks et al. 2011). While similar in essence to commercial longline fishing, with a series of baited hooks being hung from a 2 m line supported from the surface by a series of buoys, scientific long-lining as used by us differed in that a) we used only 30 hooks attached to a line no more than 500 m in length, and b) we patrolled the line at intervals of 30 minutes to retrieve any sharks that were caught, thus minimising the risk of mortality. The sharks were identified, measured and tagged, both with a conventional numbered tag (attached to the dorsal fin) and in many cases with an acoustic and / or satellite tag (see below). Catch data enabled catch rates to be generated for comparison between species or with data from studies elsewhere. Catch rates were calculated as catch per unit effort (CPUE) in units of number caught per hook per hour.

To date we have data from 1048 BRUVS deployed over an eight year period. An example of the data obtained is shown in Figure 3 which compares the overall frequency with which Caribbean reef sharks were recorded on each of the three islands. As the figure indicates this species appears to be about three times more abundant on Little Cayman (mean 0.27 sharks/hour) than on either of the other two islands (Grand Cayman 0.8 sharks/hour; Cayman Brac 0.09 sharks/hour). Figure 4 compares the mean detection rates for the same species pooled across islands for the years 2008 to 2016. The abundance of Caribbean Reef Sharks appears to have declined slowly to 2010, to have increased sharply to the highest level recorded in 2012, but then declined again by 2016 to close to the original levels. Figure 5 shows the mean detection rates for all shark species combined for each of the three Cayman Islands and compares the rates with similar data from the Bahamas (Brooks et al. 2011) and from reef areas in the Indian Ocean and Australia (Meekan et al. 2006, Clarke et al 2012, Gore et al. unpublished data) where sharks are either protected or little exploited. It should be noted however that the species involved at the Indo-West-Pacific Ocean locations are different, albeit of the same genera and playing a similar ecological role.

An example of the catch data from the scientific longlining (Figure 6) compares the overall mean catch rates of a second species, the blacktip shark (*C limbatus*), between the three Cayman islands. Again the CPUE for Little Cayman appears to be much higher (0.026/hook/hour) than for either Grand Cayman (0.005 hook/hour) or Cayman Brac (0.001 hook/hour). The longline catch rates for blacktip shark also show significant differences between years (Figure 7), with abundance apparently increasing until 2012 before falling sharply again through 2013 to 2016.

Shark-logger Programme

More recently we have introduced a third method for monitoring reef shark abundance which, as a citizen science / volunteer programme, also has the advantage of promoting public awareness. Our "Shark-logger" project takes the Facebook reporting scheme one stage further by recruiting regular divers (mostly dive centre staff) and asking them to record not only when they do see a shark while diving, but also those dives when they do not. This enables us to allow for variable effort and by calculate values of mean sightings per dive, comparable to the data reported by Ward-Paige et al. (2010). In addition we ask the observers to note whether the shark appears tagged i.e. with a numbered dorsal tag. To data we have 878 logged dives (738 on Grand Cayman and 140 on Little Cayman) during which 328 sharks were sighted. Four of these sharks carried our conventional tags.

As an example of the data generated Figure 8 shows the monthly variation in the mean sighting rates for the two commonest reef species as recorded over the first year of the project's operation. The data suggest that on the Cayman Islands Caribbean reef sharks are about twice as abun-

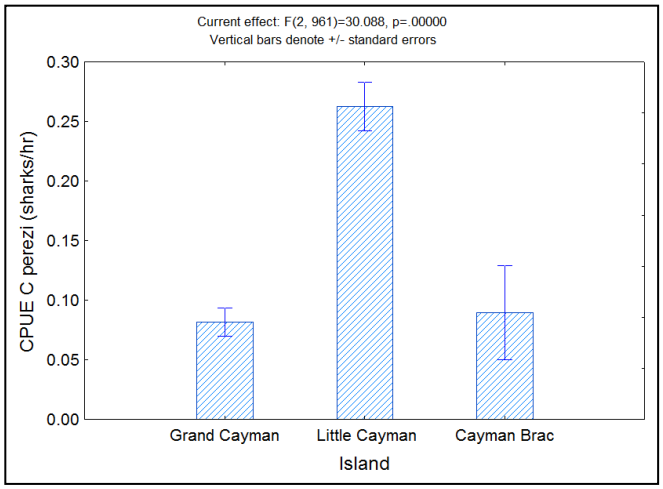

Figure 3. Mean abundance of Caribbean Reef Sharks (*Carcharhinus perezi*) on each of the three Cayman Islands as observed on Baited Remote Underwater Video Stations (BRUVS) between 2009 and 2016. Total n = 1048.

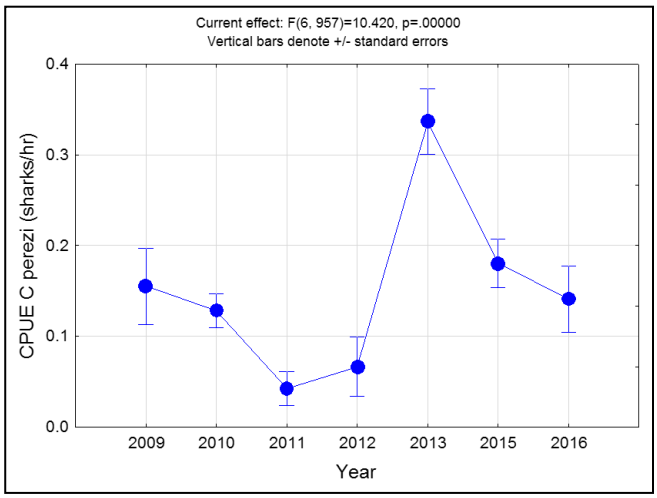

Figure 4. Variation in mean abundance from year to year of Caribbean Reef Sharks (*Carcharhinus perezi*) as observed on Baited Remote Underwater Video Stations (BRUVS) pooled across all three Cayman Islands between 2009 and 2016. Total n = 1048.

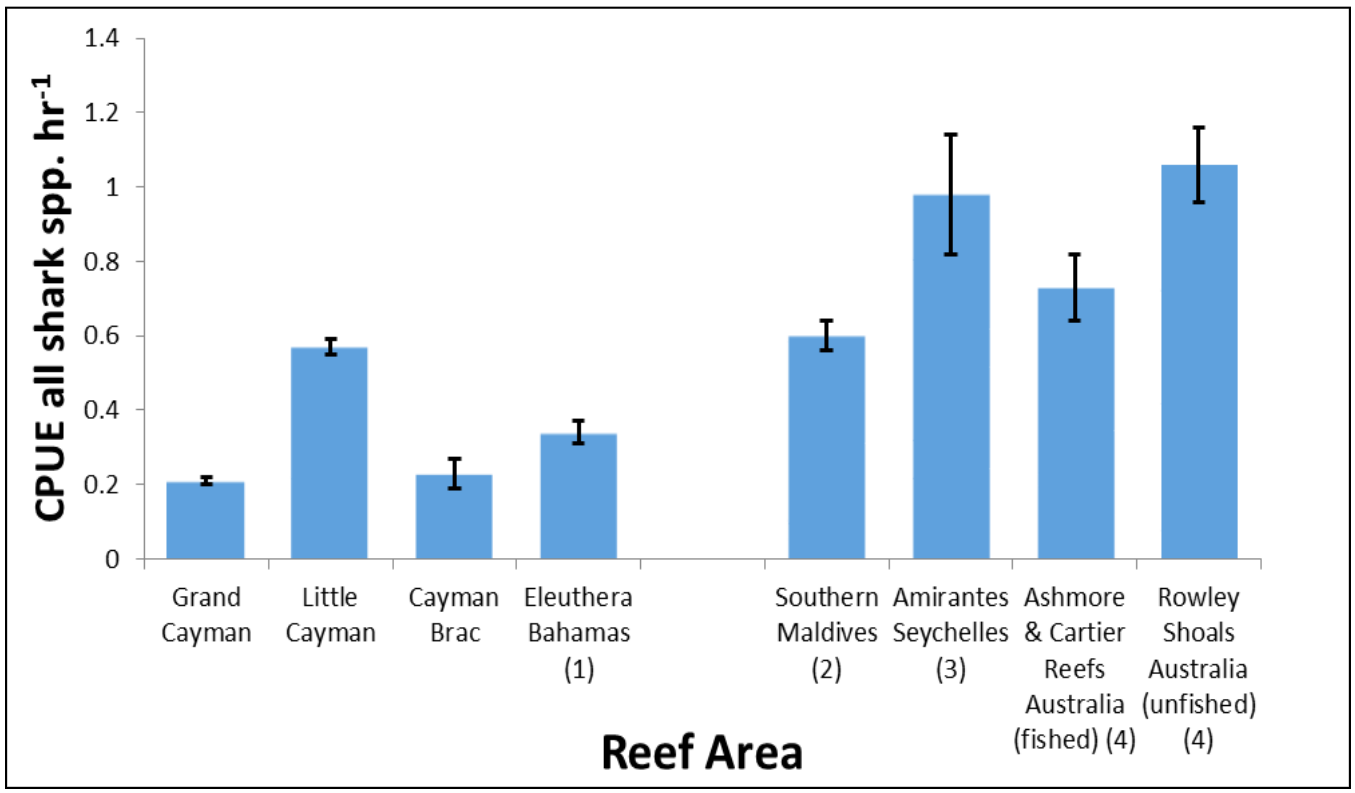

Figure 5. Mean CPUE on BRUVS of all shark species combined in each of eight reef area, four (to left) in the Caribbean, four in the Indian Ocean (to right) (error bars = standard errors). Note the species recorded are different in the two regions. Source of data other than present study (1) Brookes et al. (2011), (2) Clarke et al. (2016) (3) R.F.G. Ormond & M.A. Gore unpublished data, (4) Meekan et al. (2006).

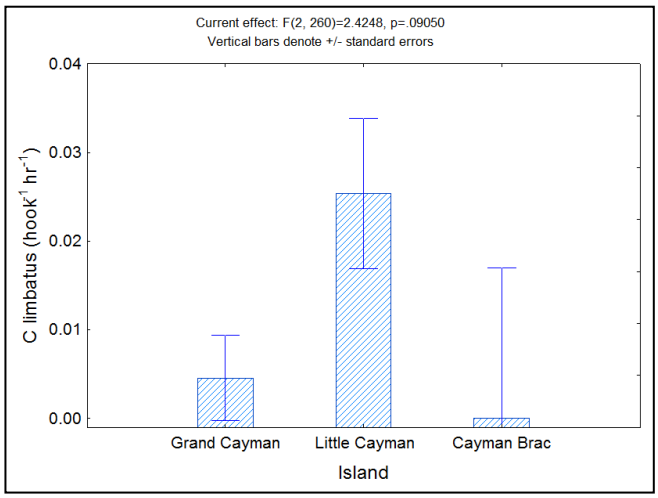

Figure 6. Mean catch rates of Blacktip Sharks (*Carcharhinus limbatus*) on each of the three Cayman Islands as obtained during scientific longlining (see text for explanation) between 2009 and 2016.

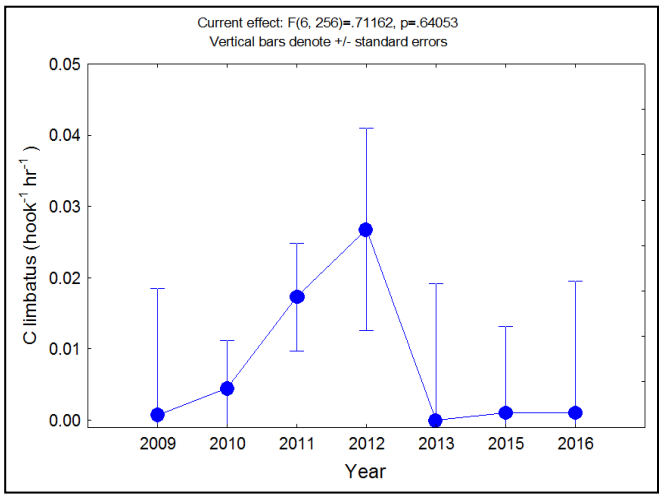

Figure 7. Variation in mean catch rate by year between 2009 and 2016 of Blacktip Sharks (*Carcharhinus limbatus*) pooled across all three Cayman Islands as obtained during scientific longlining (see text for explanation).

dant as nurse sharks. At the same time the data indicate possibly marked variation in observation rates during the course of the year, nurse sharks being most frequently observed in May and June, and Caribbean reef sharks in September.

Shark Movement Patterns

A key question in relation to the issue of whether or not the existing MPAs on the Cayman Islands are large enough to afford effective protection to the main shark species was whether the home or foraging ranges of individuals could frequently be contained within individual MPAs, or were much larger. To investigate this we followed other researchers in tagging smaller-bodied species with acoustic tags (Heupel et al, 2004, Chapman et al. 2005, Heupel et al. 2010, Clarke et al. 2011), and larger-bodied species with satellite tags (Bonfil et al. 2005, Rowat and Gore 2007, Gore et al. 2008).

All adult and sub-adult Caribbean reef and blacktip sharks that appeared to be in good condition, as well as a few individuals of some other species, were tagged by inserting surgically under the skin of the abdomen an acoustic pinger (Vemco V9 and V16) generating a regular pulse (at 69 kHz) detectable by listening gear over a distance of 100 – 300 m. Detections were obtained via a network of about 40 acoustic receivers (Vemco VR2W) that were located at sites around the three islands, many of which had been installed for use during an earlier study of Nassau Grouper (Semmens et al. 2006), and others of which were obtained for the present project. Receivers were collected and data downloaded typically at intervals of 6 – 12 months. However due to faults on some receivers, it has not been possible to analyse the patterns of detections at all stations. Instead data from the same side of an island (North, East, South or West) have been pooled, with the exception that stations on the northern side of Grand Cayman have been processed as two groups a) those to the west outside or inside of North Sound and b) the remaining stations further east along the northern side.

Tiger and oceanic whitetip sharks were if practicable tagged with SPOT5 satellite tags (Wildlife Computers) that were fixed to the upper part of the dorsal fin. The tags are designed to fix a position using GPS within about a minute and then transmit that information via an Argos satellite to a receiving ground station. This work was undertaken in collaboration with our colleagues Guy Harvey (Guy Harvey Ocean Foundation, Grand Cayman), Mahmood Shivji (Nova SE University, Florida, USA) and Brad Wetherbee (University of Rhode Island, Rhode Island, USA) and will be reported on in more detail shortly.

To date a total of 70 sharks have been tagged with acoustic tags: 54 Caribbean reef sharks, nine blacktip sharks, three lemon sharks, two tiger sharks and two silky sharks. In each case about half the sharks tagged were male and half female. Of these sharks only 30 (42.9%) were detected again, even though in all cases the sharks were tagged in the vicinity of the receiver network. Of the sharks detected 25 were Caribbean reef sharks (detection rate 36.4%), 2 blacktip sharks (detection rate 22.2%), and one each a lemon shark, a tiger shark and a silky shark. Notably four of the Caribbean reef sharks (two male and two female) were recorded to move between islands, and of these two moved between Grand Cayman and Cayman Brac, covering a distance between stations of approximately 150 km.

Examples of the movement behaviours of individual sharks are shown in Figure 9 and Figure 10. The former shows for different months from 2013 to 2016 the parts of the island of Grand Cayman on which one shark was detected. The shark is mainly detected within the North Sound (NS) sector of Grand Cayman and appears as if it is semi-resident in that area. However, it was not detected every month, and notably each year, in the period July to September, was also regularly detected in the more eastern portion of the north side of the island (N). Figure 10 shows the detection pattern for another (female) Caribbean Reef

Shark, one of the individuals that was detected both on Grand Cayman and on Little Cayman. This individual also appeared to be resident in the North Sound (NS) sector of Grand Cayman and for most of the time was only detected in that area. However in a period between June to October each year the shark appeared to move about, visiting the North and East parts of Grand Cayman, and in 2013 and 2015 travelling as far as Little Cayman, before in the former case at least returning to Grand Cayman.

Plots of the SPOT tag data revealed movements of both tiger and oceanic whitetip sharks on an even larger scale. Example plots for each species are shown in Figures 11 and 12. Together with our collaborators we have tagged 18 oceanic whitetip sharks and 7 tiger sharks. Figure 11 shows the reliable locations recorded for the first tiger shark we tagged, in North Sound, in December 2010. From there within the next 273 days the shark moved first north-west to the entrance to the Gulf of Mexico, then east to the south coast of Cuba, then south across the Caribbean to the eastern coast of Honduras, and finally north-west again to the east coast of the Yucatan Peninsula, in Mexico. Further, because it also carried a longer-lived acoustic tag, we detected this same individual in the North Sound area of Grand Cayman for three further years, in each case during the December – January period.

Figure 12 shows a comparable plot for an oceanic whitetip shark, tagged off Grand Cayman in April 2014 and detected for a further almost two years. During this time the individual not only spent significant periods of time in an ocean area due west of Jamaica, but also visited Honduras, Belize, the Yucatan Peninsula (twice) and travelled someway north in to the Gulf of Mexico, almost to the latitude of Tampa, Florida. Comparing the plots of the two species (tigers versus oceanic whitetips) it is of note that while all the individuals of both species moved extensively across the Caribbean, none of the tiger sharks appear to have left it, whereas many of the oceanic whitetips have did so, travelling at least some way in to the Gulf of Mexico.

Economic Value

Besides conservation and ecological considerations, the Cayman Island DoE was also interested to assess the economic value of sharks to the Cayman Islands. To investigate this issue we undertook work to estimate in relation to sharks some of the elements of both the "Use" and "Non-Use" Values that environmental economics has come to recognise (Moran and Pearce 1994, Perlman and Adelson 1997)

These elements potentially included:

i) Consumptive Direct Use (e.g. of shark products such as meat, fins, oil and hides,
ii) Non-Consumptive Direct Use, such as occurs as a result of shark-related tourism or recreation,
iii) Indirect-Use value, such as the benefits to fisheries or tourism that may be the result of healthy or more stable marine habitats,
iv) So-called Option or Bequest Value, the potential value that might arise as a result of the discovery of some new use of sharks (e.g. perhaps in medicine), and
v) The animals' Existence Value, meaning the amount people are prepared to pay simply to know that a species continues to survive or to thrive.

In order to investigate the Non-Consumptive Direct se and the Existence values of sharks in the Cayman Islands, we designed an environmental economics questionnaire

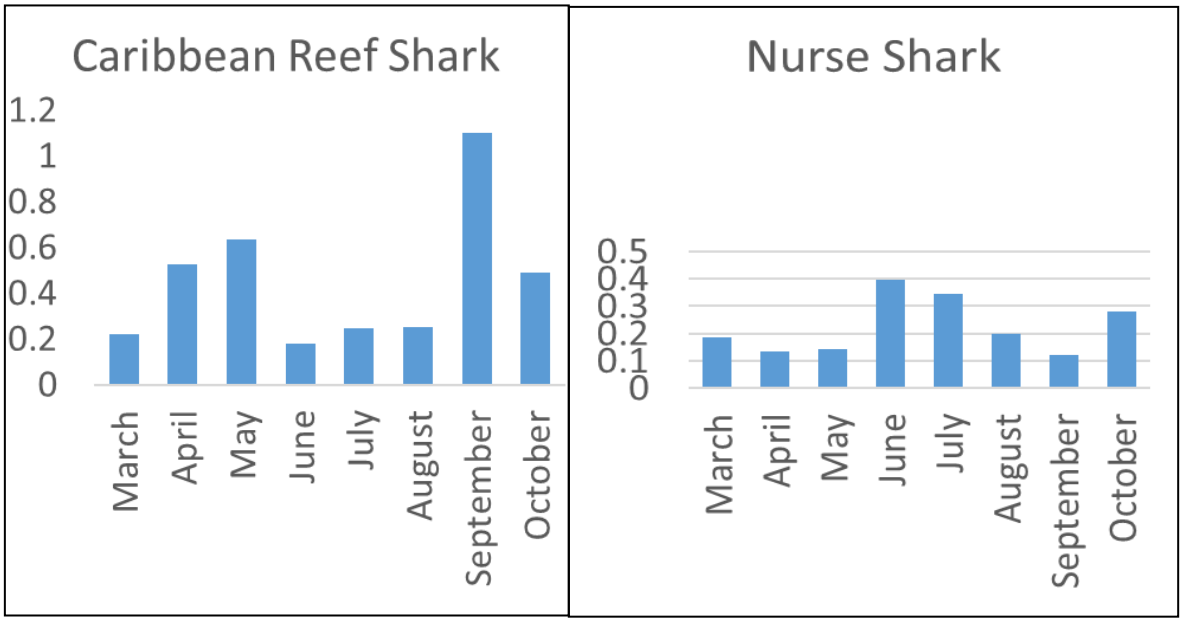

Figure 8. Mean number of sharks per dive recorded by SCUBA divers participating in the "shark-logger" project during different months of the year (2016) – left: Caribbean Reef Shark (*Carcharhinus perezi*); right: Nurse Shark (*Ginglymostoma cirratum*). Total number of dives during the period n = 878.

and interviewed a total of 458 Caymanians, Cayman residents (non-Cayman nationals with permission to reside or work in the Cayman Islands) and visiting tourists.

As one method of estimating the current non-Consumptive Direct Use of sharks in Cayman, we first asked respondents about the aspects of the Cayman Islands that influenced their decision to live in or to visit the Cayman Islands: its beaches (sun & sea), its Caribbean culture, the opportunities for fishing (of different types), marine life related activities, or the islands' terrestrial wildlife. Focussing on the islands' marine environment, we then asked what features of the marine life most attracted them to the Cayman Islands: their impressive dive sites, the corals, the marine mammals, sharks, or other marine megafauna such as turtles. We then both a) partitioned the known income from tourism and recreation between these different elements and sub-elements, assuming that each could be val-

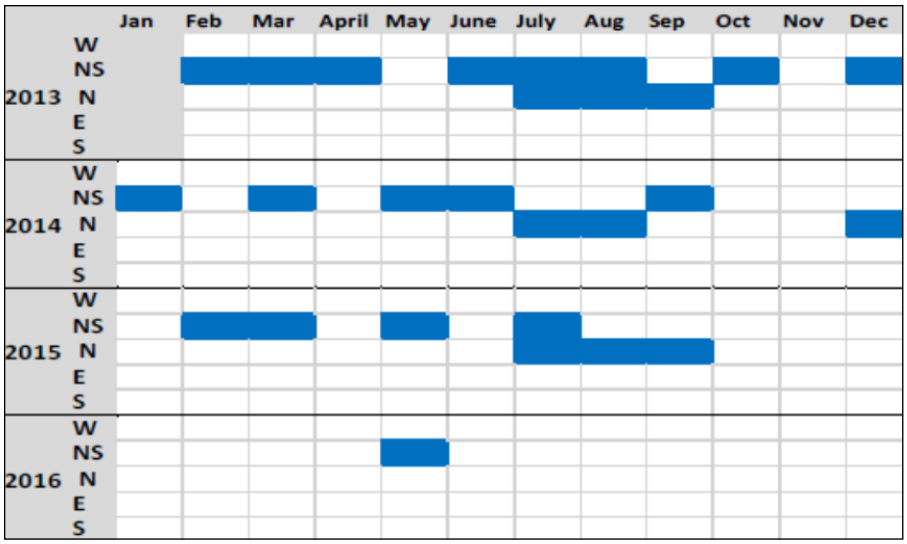

Figure 9. Figure illustrating the parts of Grand Cayman Island on which a single acoustically tagged Caribbean Reef Shark (*C. perezi*) (# xxx) was detected as present month by month since being tagged in February 2013. Different lines indicate different parts of the island: W – west, NS – North Sound and adjacent reef, N – north (more eastern portion), E – east, and S – south; blue infill indicates months in which the tag was detected by one or more acoustic receivers within that sector.

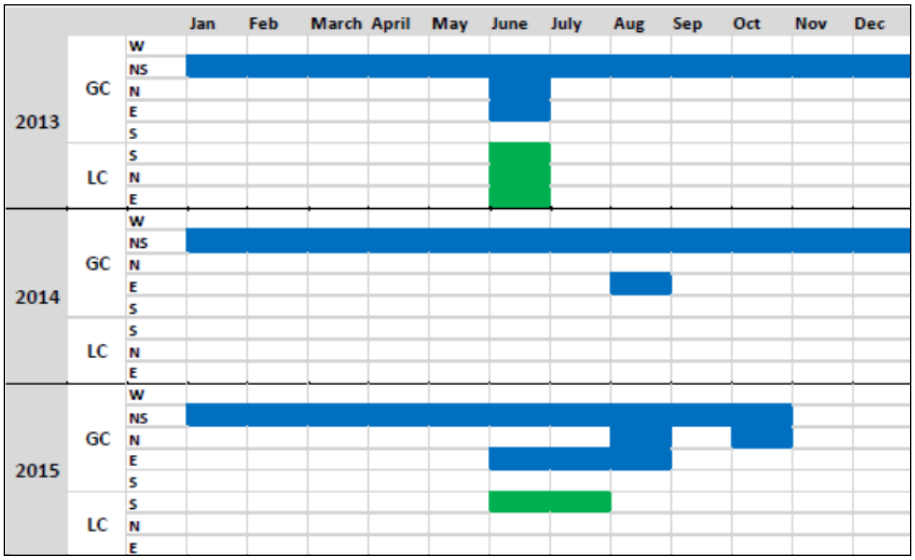

Figure 10. Figure illustrating the parts of Grand Cayman and Little Cayman Islands on which a second acoustically tagged Caribbean Reef Shark (*C. perezi*) (# 130, female) was detected as present month by month since between January 2013 and December 2015. Abbreviations as per Fig. 7; blue infill indicates months in which the tag was detected on Grand Cayman, green infill months in which it was detected on Little Cayman.

ued in proportion to its relative importance as judged by respondent, and b) enquired of visitors how much they were spending to visit.

The responses received to the stage one question are summarised in Figure 13. They illustrate that for visitors, on average, the marine life of the islands was clearly the most important factor driving their visit, ahead of beach life and Caribbean culture. For residents "sun and sea" counted equally with the marine life as their most important reasons for living in the Caymans. For both groups fishing opportunities were on average the least important reason for being in the Cayman Islands. Turning to the different elements of marine life, impressive dive sites and sharks were on average rated as less important than the other characteristics listed above, but sharks were nevertheless rated as a significant feature, scoring a mean of 6.0 (on a scale of 0 -10) among visitor respondees, and 7.2 (out of 10) among residents. In support of this assessment some visitors stated they were willing to pay up to US $1,000 or more for a reasonable opportunity of seeing sharks in the wild. Depending on the measures used to estimate relevant visitor income we estimated the Non-Consumptive Use Value of sharks in the Cayman Islands to be between US $46.8 and 62.6 million per year. This compares we estimate with a direct use of the shark population, if fish sustainably for meat, fins, oil and leather, of no more than US $1.3 million, even after the stocks was permitted to recover to four times the current population levels.

DISCUSSION

As will be evident from the above, our work on the project over the past eight years has largely answered our initial questions. The combined information from BRUVS and longline surveys on the one hand, and our own and independent diver observation on the other, have firmly identified the principal shark species present around the Cayman Islands. Caribbean reef sharks are the commonest species over the outer / fringing reefs, but blacktip sharks may also be encountered there, as are nurse sharks. Nurse and to a lesser extent lemon sharks are the main species observed in the sounds. Occasionally solitary tiger and great hammerhead sharks have been seen in North Sound, where both have been observed to target the southern stingrays, but both species are also very occasionally seen on the outer reef, and the tiger sharks seem to be present mainly if not only during mid-winter. Offshore, within sight of the islands, both oceanic whitetip and silky sharks seem to occur regularly in small numbers. In contrast, we have been unable to confirm the presence in the Cayman Islands of either dusky shark, which appear possibly absent from the north-west Caribbean (Campagno et al. 2005), or bull sharks, which may be absent given their requirement for freshwater influenced habitat for breeding (Campagno et al. 2005), although female bull sharks have now been found capable of migrating considerable distances from remote islands to find suitable pupping grounds (Lea et al. 2015). Nor have been able to confirm the reported occurrence of shortfin mako sharks, though this seems more plausible, given their published range (Campagno et al. 2005). Also, while well before the start of our study small schools of scalloped hammerhead sharks used to be seen by divers at the grouper spawning aggregation sites, main-

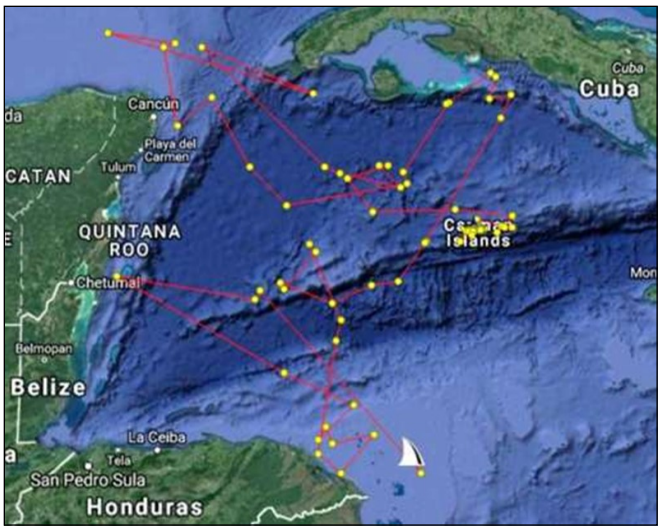

Figure 11. Chart showing sample successive locations of a 2.47 metre long female Tiger Shark (*Galeocerdo cuvier)* tagged with a SPOT5 satellite tag between it being caught in North Sound, Grand Cayman on 15th December 2010, and its final detection 273 days later. The same shark is known to have returned to the Cayman Islands subsequently because its acoustic tag was detected by the Cayman array seasonally for three further years.

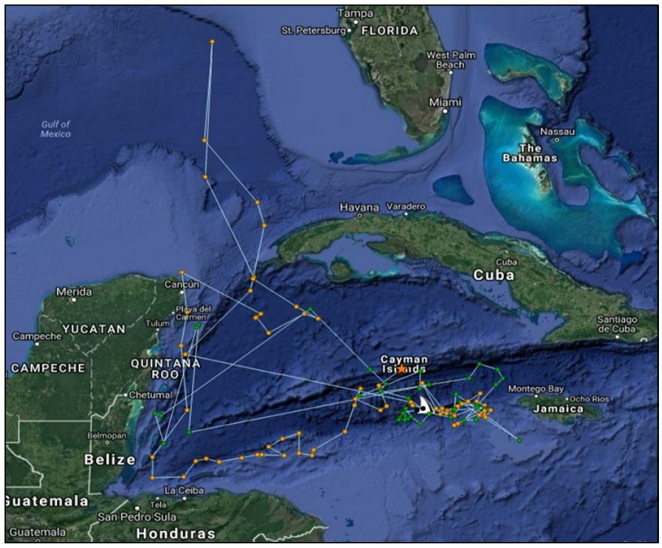

Figure 12. Chart showing sample successive locations of a 2.19 metre long male Oceanic Whitetip Shark (*Carcharhinus longimanus*) tagged with a SPOT5 satellite tag between it caught off the north coast of Grand Cayman on 26th April 2014, and its final detection 644 days later.

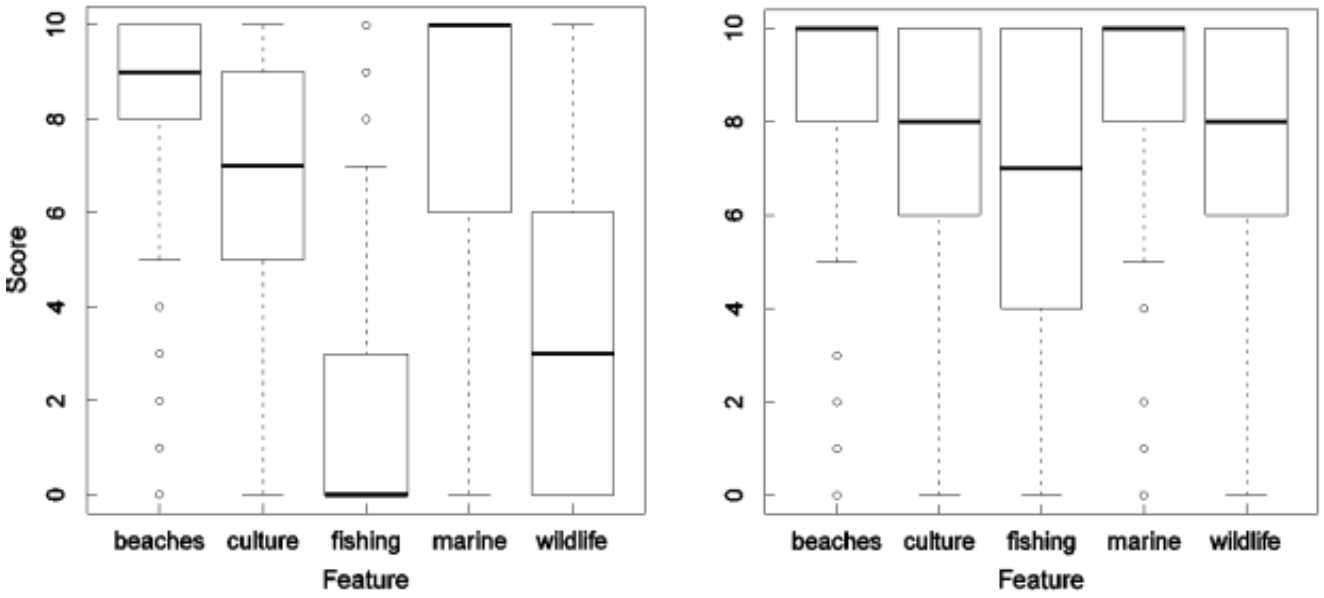

Figure 13. Box and whisker plots to illustrate the relative importance of different features of the Cayman Islands to the decisions of visitors (left, n = 180) and residents (right, n = 195) to visit or live in the Cayman Islands. The features respondents were asked to discriminate between were (from left to right): sun & sand (beaches), Caribbean culture, fishing opportunities; marine wildlife; other wildlife. In the plots the heavy horizontal lines indicate the median values, the upper and lower margins of the boxes indicate the second and third quartiles, the whiskers indicate the standard errors and the open symbols the extreme values.

ly off Little Cayman, they have not been recorded there in recent years, although we have recently received a single report of three sharks. Many species that are well known from the continental coasts of the Caribbean and Gulf of Mexico appear absent from the islands, presumably as a result of lack of habitat and the islands' separation from those areas by very deep water. However there will undoubtedly be additional species present in the deep water near the islands, though we have yet to investigate this possibility systematically.

Our relative abundance data, both from BRUVS and from scientific longlining (Figures 3 and 6) indicate that most of the species present are two or three times more likely to be encountered on Little Cayman than on either of the other two islands. Little Cayman is widely considered to have the best reefs and densest reef fish populations (Department of the Environment, Unpublished b). It has a larger proportion of its coast protected as MPAs (Figure 2), and the smallest number of regular fishermen (Department of the Environment, Unpublished c). However our data analysis has not as yet indicated whether healthier coral and fish populations are the cause or the result of the greater numbers of sharks, or whether both are independent consequence of better protection or less human impact. Thus we are not able as yet to comment on current debate regarding the potential role of sharks on stabilising reef ecology (Myers et al. 2007, Ferretti et al. 2010, Roff et al. 2016, Ruppert et al. 2016). When we observed increased CPUEs in some of our BRUVS and longline data through 2012 and 2013 (figs 4 & 7) we were encouraged to consider that shark populations might be recovering as a result of the public awareness campaign promoting shark conservation that we had been developing since the start of the project. In consequence the return to low numbers through 2015 and 2016 was disappointing. However, despite the low standard errors in these Figures (4 & 7) we are not yet fully confident that this variation in mean CPUE accurately reflects inter-annual changes in shark abundance. It is possible that they reflect instead slight differences in the times of sampling between years or in the amounts of sampling on different islands. Further analysis of the full dataset is currently underway to explore these possibilities.

Both our BRUVS and longline data also suggest, on comparison with similar data from elsewhere, that the overall abundance of sharks in the Cayman Islands is currently higher than that in most Caribbean areas, but not as high as in a few areas in places such as the Bahamas and Belize, where sharks have been protected (Pikitch et al. 2005, Chapman et al. 2007, Brooks et al, 2011). A similar conclusion is reached if the diver sightings rates from our sharklogger project, or those shown for the Cayman Islands in the Caribbean-wide study of Ward-Paige et al. (2010) are compared with their data from other regions. Similarly, overall shark abundance in the Cayman Islands is also well below that recorded in some relatively unexploited or well protected areas in the Indian Ocean or Australia (Meekan et

al. 2006, Clarke et al. 2012, Gore et al. unpublished data). This comparison lends support to the interpretation that while sharks in general may be two or three times as abundant in the Cayman Islands as in most other parts of the Caribbean, their current population levels are nevertheless very low compared to those that once existed in the region (Bonfil 1997, Heithaus et al. 2007a, Stallings 2009, Ward-Paige et al. 2010), or elsewhere (Nadon et al. 2012).

It should be stressed that while discussing shark abundance we are considering, so far, only *relative* abundance. Both BRUVS and longline data only provide indirect indicators of abundance allowing comparisons between sites or times. Even the abundances of different species can not be reliably compared since different species likely have different tendencies to be attracted to BRUVS or caught on longlines. In any case relative abundance data does not allow us to estimate population density or size, unless we also have information on the local home range sizes of species or separate information such as mark-recapture data from which effective population size can be estimated as has been attempted for some other shark species (Castro & Rosa 2005, Chapple et al. 2011, Gore et al. 2016).

Our acoustic tag data have confirmed the conclusion of Chapman et al (2007) that many Caribbean reef sharks appear to be essentially semi-resident within a particular reef area. However the data also revealed two other important aspects of the behaviour of this species. Firstly, over the half the individuals released were not detected by the receiver network. Since receivers are located at regular intervals around all three islands and we do not have evidence that catching and surgery caused significant mortality, this suggests that a high proportion of individuals were simply passing through the locations where they were captured rather than resident in the immediate vicinity. This may be because they were truly vagrant individuals, wandering over very large areas. Or it may be, since Chapman et al. (2007) also report an archival satellite (PAT) tagged Caribbean reef shark descending to a depth of 356 m, that some of these undetected individuals were semi-resident, but only within very much larger areas of seabed, extending into much deeper water (perhaps 500 metres or more), than previously realised. As described in the *Study Area* section, the reefs on the Cayman Islands drop away in to very deep water within only a short distance of the upper reef face.

Secondly, we recorded four individuals that moved between islands and two that travelled as far as from Grand Cayman to Little Cayman, and back, covering in each direction a distance of about 150 km, and travelling through water that over most of that distance was at least 1000 metres deep. It was reported by Chapman et al. (2005) that some individuals of this species may travel distances greater than might have been assumed for a supposed resident species, but the distance between Grand Cayman and Little Cayman significantly exceeds the maximum of 30 km (across open water >400m deep) described to date (Chapman et al. 2005). The distance is more comparable with the observation by Heupel et al. (2010) of an acoustically tagged grey reef shark (*C. amblyrynchos*), the ecologically comparable carcharhinid in the Indo-Pacific, travelling 134 km between reef areas. Our data suggest that a) some Caribbean reef sharks may routinely travel long distances over or between reef areas, and that b) this may be on a seasonal basis, perhaps to mate or pup. This latter interpretation is supported by the fact that the female illustrated in Fig. 9 travelled from Grand Cayman to Little Cayman on two occasions, exactly two years apart, and by knowledge that the species is recorded to produce a litter of 3 – 6 pups every second year (Castro et al. 2009).

We had anticipated at the start of the project that we would be able to get a separate indication of the size of the populations of the main shark species from the rates of recapture (by longlining) or re-sighting (by divers) of the sharks tagged with conventional external tags. We have had a small number of recaptures of tagged sharks and some re-sightings by divers participating in our shark-logger programme. But in each case there have been less than 10, amounting to both a small proportion of the sharks newly caught or sighted, and a small proportion of the sharks originally tagged. Unless tags are being lost from the sharks at a much greater rate than normal, these observations suggest that the sharks caught or observed represent only a small proportion of a much larger population pool. Since both the overall catch and sightings rates of sharks are relatively low and the extent of the reefs around the islands not that great, this again suggests that many of the individuals seen on the reef may be mixing over a much larger area of seabed, perhaps as large as 10,000 km^2, than previously supposed.

As previously indicated, information on the movement patterns of individuals is also important both for assessing whether or not MPAs of a particular size-range are likely to be of value in affording significant protecting to at least a proportion of the population. The distances covered by many of our acoustically tagged Caribbean reef sharks supports the observation of Chapman et al (2005) that some individuals of this species may travel distances of 10 km or more, taking them well beyond the bounds of MPAs established on a such a scale, such as those in the Cayman Islands. Bond et al (2012) nevertheless found that there was a significantly higher abundance of Caribbean reef sharks within compared to without the approximately 30 x 10 km. diameter Glover's Reef Marine Reserve, Belize. But taken with our data the evidence suggests that to be provided with adequate protection, this and comparable shark species require MPAs on the scale of at least the individual Cayman Islands, if not throughout the combined territorial waters.

The data resulting from the satellite tagging of the tiger and whitetipped oceanic sharks provides a further tranche of evidence relevant to this issue. It is clear that both these species travel widely across the Caribbean, supporting evidence of trans-oceanic migration by tiger sharks from other studies (Kohler et al. 1998, Heithaus et al. 2007b, Meyer et al. 2009, Meyer et al. 2010, Ferreira et al. 2015), including notably of one individual travelling at least 8,000km between Western Australia and southeast Africa (Heithaus et al. 2007b). Similarly satellite tagged oceanic whitetip sharks have been recorded as travelling up to 4000 km from tagging sites in the central Pacific (Musyl et al. 2011) and 1940 km from a tagging site in the central Bahamas (Howey-Jordan et al. 2013). Clearly the existing Cayman Islands MPAs will be of only limited benefit to these two

species. Individual tiger sharks may spend part of their time within one or two of the current MPAs during the month or two they are in the Cayman Islands, while the oceanic whitetips caught of the Cayman Islands probably rarely enter the MPAs, since the existing conservation areas cover a relatively narrow coastal strip. The scale of movement of these two species supports the case for their protection not only throughout Cayman waters, which do cover a significant portion of the north-west Caribbean (Figure 1), but through a reasonably high proportion of the whole Caribbean basin. There is thus a case also for cooperation on a regional level with adjacent countries, notably Honduras, which was among the first countries to give full protection to sharks (Pew Charitable Trusts 2016, MPA Atlas 2017).

The iconic conservation status of some of the larger shark species apart, protective measures are more likely to be implemented and enforced if both government and people support the measures and can see value in them. Our estimate of the Non-Consumptive Use value of sharks to the Cayman Islands is important in this context. Our figure of US $46.8 to 62.6 million per year does not include all aspects of total economic value (i.e. optional or bequest values), but is surprisingly similar to comparable estimates made in other studies for other countries, the best known examples being of US $78 million per year for the Bahamas (Cline 2008), and US $18 million per year for the Micronesian territory of Palau (Vianna et al. 2012). It is notable however that whereas both of these estimates are largely based on the value of shark-diving, when SCUBA divers pay to visit sites where wild sharks are provisioned, feeding of sharks is prohibited in the Cayman Islands. Nevertheless it appears that SCUBA divers visiting the Cayman Islands are willing to pay a premium, in part because during normal dives they more likely to see a wild shark than in many other locations. In this connection it is interesting that whereas a recent environmental economics assessment of the touristic value of the northern Great Barrier Reef (Australia) (Farr et al. 2014) concluded that visitors valued the opportunity to see whales and dolphins more highly than the opportunity to see sharks, in the Cayman Islands we found the reverse to be the case, likely because the Cayman Islands are considered a premier SCUBA diving destination, but not somewhere that visitors come expecting to encounter cetaceans.

Even though legal protection for a species is very important and knowledge of its economic value, especially if not used non-exploitatively invaluable, vital also to secure the conservation of species is the support of the public in general and of the relevant stakeholders in particular. It is for this reason that our public awareness programme (involving press, radio and TV items, talks and promotional events, such as the shark festival) is critical, and that our relationship with the Cayman Island brewery "Caybrew" especially significant. Not long after the beginning of the project Caybrew agreed to the development, production and sale of a new brand "Whitetip", each can and bottle of which carries a strapline highlighting the case for shark conservation, and from which, for the sale of each drink, 5 cents is donated to local shark conservation work. Not only was this we believe the first "Conservation Beer" to be produced and marketed anywhere, but Caybrew's generosity was compounded by the fact that the beer proved to have an excellent taste, won a Caribbean-wide award and sold extremely well. The subliminal message that sharks are to be appreciated rather than feared undoubtedly contributed to the wide public support for shark conservation in the Cayman Islands that we found during an on-line survey prior to the passing of the shark protection legislation

ACKNOWLEDGEMENTS

The work summarised in this paper was supported by two grants from the UK Government under the Overseas Territories Environment Programme and the Darwin Initiative, and by smaller grants from the Save Our Seas Foundation, Caybrew Ltd, and Fosters Food Fair. The authors also wish to acknowledge the considerable assistance and support received from the Cayman Islands Department of the Environment (DoE) and to thank in particular Gina Ebanks-Petrie, Tim Austin and their many staff who gave of their time. Thanks are also due to the Guy Harvey Ocean Foundation for support in kind, and to Edd Brooks, Mahmood Shivji and Brad Wetherbee for scientific advice and support. The authors also thank Louisa Neves, Kirsty Richards, Beth Taylor, Richard Easton and Peter Davies for fieldwork assistance throughout individual campaigns.

LITERATURE CITED

Baum J.K., R.A. Myers, D.G. Kehler, B. Worm, S.J. Harley et al. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**:389–392.

Baum J.K. and R.A. Myers. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters* **7**:135–145.

Bond, M.E., E. Babcock, E.K. Pikitch, D.L. Abercrombie, N.F. Lamb et al. 2012. Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. *PLoS One 7: e32983.* doi:10.1371/journal.pone.0032983.

Bonfil, R. 1997. Status of shark resources in the southern Gulf of Mexico and Caribbean: implications for management. *Fisheries Research* **29**:101–117.

Bonfil, R., M. Meyer, M.C. Scholl, R. Johnson, S. O'Brien, H. Oosthuizen, S. Swanson, D. Kotze, and M Paterson, 2005 Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* **310**:100–103.

Brooks E.J., K.A. Sloman, D.W. Sims D.W., and A.J. Danylchuk (2011) Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. *Endangered Species Research* **13**:231-243.

Cappo, M., P. Speare, and G. Death. 2004. Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology* **302**:123–152.

Castro J.I., C.M. Woodley, and R.L. Brudek. 2009 Observations on the reproductive cycles of some viviparous North American sharks. *International Journal of Ichthyology* **15**:205-222.

Castro, A.L.F. and R.S. Rosa. 2005. Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol das Rocas Biological Reserve. *Brazil Environmental Biology of Fishes* **72**:213–221.

Chapman, D.D., E.K. Pikitch, E.A. Babcock, and M.S. Shivji. 2005. Marine reserve design and evaluation using automated acoustic telemetry: a case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. *Marine Technology Society Journal* **39**:42–53.

Chapman, D.D., E.K. Pikitch, E.A. Babcock, and M.S. Shivji. 2007. Deep -diving and diel changes in vertical habitat use by Caribbean reef sharks, *Carcharhinus perezi*. *Marine Ecology Progress Series* **344**:271–275.

Chapple, T.K., S.J. Jorgensen, S.D. Anderson, P.E. Kanive, A.P. Klimley, L.W. Botsford et al. **2011**. A first estimate of white shark, *Carcharodon carcharias*, abundance off Central California. *Biology Letters* **7**: 581 –583.

Cisneros-Montemayor, A.M., M. Barnes-Mauthe, D. Al-Abdulrazzak, E. Navarro-Holm, and U.R. Sumaila. 2013. Global economic value of shark ecotourism: implications for conservation. *Oryx* **47**:381-388.

Clarke, S.C., M.K. McAllister, E.J. Milner-Gulland, G.P. Kirkwood, C.G.J. Michielsens, D.J. Agnew, E.K. Pikitch et al. 2006. Global estimates of shark catches using trade records from commercial markets. *Ecology Letters* **9**:1115–1126.

Clarke, C., J.S.E. Lea and R.F.G. Ormond. 2011. Reef-use and residency patterns of a baited population of silky sharks, *Carcharhinus falciformis*, in the Red Sea. *Marine and Freshwater Research* **62**:668–675.

Clarke C, J. Lea and R. Ormond. 2012. Comparative abundance of reef sharks in the Western Indian Ocean. Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia.

Cline, W. 2008. *Shark Diving Overview for the Islands of the Bahamas. Report of the Bahamas Ministry of Tourism.* Cline Marketing Group, Nassau, Bahamas. 11 pp.

Compagno, L., M. Dando, and S. Fowler. 2005. *Sharks of the World*. HarperCollins Publishers Ltd., London, England. 368 pp.

Department of Environment, Cayman Islands. Unpublished report (a). Report on Value of Southern Stingray Tourism.

Department of Environment Cayman Islands, Unpublished report (b). Health of Cayman Islands Coral Reefs.

Department of Environment Cayman Islands. Unpublished report (c). Fishing Pressure on Cayman Islands Coral Reefs.

Dulvy, N.K., R.P. Freckleton, and N.V.C. Polunin. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* **7**:410–416.

Dulvy, N.K., J.K. Baum, S. Clarke, L.I.V. Compagno, E. Cortes, et al. 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* **18**:459-402.

Espinoza M., M. Cappo, M.R. Heupel, A.J. Tobin, and C.A. Simpfendorfer. 2014. Quantifying Shark Distribution Patterns and Species-Habitat Associations: Implications of Marine Park Zoning. PLoS *ONE* ***9****(9): e106885*. https://doi.org/10.1371/journal.pone.0106885.

Farr, M., N. Stoeckl, and Rabiul Alam Beg. 2014 The non-consumptive (tourism) 'value' of marine species in the Northern section of the Great Barrier Reef. *Marine Policy* **43**:89–103.

Ferreira L.C., M. Thums, J.J. Meeuwig, G.M.S. Vianna, J. Stevens, R. McAuley, et al. 2015. Crossing latitudes - long-distance tracking of an apex predator. *PLoS ONE* ***10****(2): e0116916.* https://doi:10.1371/journal.pone.0116916.

Ferretti F., R.A. Myers, F. Serena, and H.K. Lotze. 2008. Loss of large predatory sharks from the Mediterranean Sea. *Conservation Biology* **22**:952–964.

Ferretti, F., B. Worm, G.L. Britten, M.R. Heithaus, and H.K. Lotze. 2010. Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* **13**:1055–1071.

Gallagher, A.J. and N. Hammerschlag. 2011. Global shark currency: the distribution, frequency, and economic value of shark ecotourism. *Current Issues in Tourism* **14**:797 –812.

Graham, N.A.J., M.D. Spalding, and C.R.C Sheppard. 2010. Reef shark declines in remote atolls highlight the need for multi-faceted conservation action. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**:543–548.

Gore M.A., D. Rowat, J. Hall, F.R. Gell, and R.F. Ormond. 2008. Transatlantic migration and deep mid-ocean diving by basking shark. *Biology Letters* **4**:395–398.

Gore M.A., P.H. Frey, R.F. Ormond, H. Allan, and G. Gilkes. 2016. Use of photo-identification and mark-recapture methodology to assess basking shark (*Cetorhinus maximus*) populations. *PLoS ONE 11(3): e0150160.* https://doi:10.1371/journal.pone.0150160.

Heithaus, M.R., D. Burkholder, R.E. Hueter, L.I. Heithaus, H.L. Pratt, et al. 2007(a) Spatial and temporal variation in shark communities of the lower Florida Keys and evidence for historical population declines. *Canadian Journal of Fisheries and Aquatic Sciences* **64**:1302–1313.

Heithaus, M.R., A.J. Wirsing, L.M. Dill, and L.I. Heithaus 2007(b). Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia. *Marine Biology* **151**:1455–1461.

Heupel, M.R., C.A. Simpfendorfer, and R.E. Hueter. 2004. Estimation of shark home ranges using passive monitoring techniques. *Environmental Biology of Fishes* **71**:135–142.

Heupel, M.R., C.A. Simpfendorfer, and R. Fitzpatrick. 2010. Large–scale movement and reef fidelity of Grey Reef Sharks. *PLoS ONE* ***5****(3): e9650.* https://doi:10.1371/journal.pone.0009650.

Howey-Jordan, L.A., E.J. Brooks, D.L. Abercrombie, L.K.B. Jordan, A. Brooks, et al. 2013. Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the Oceanic Whitetip (*Carcharhinus longimanus*) in the Western North Atlantic. *PLoS ONE* ***8****(2): e56588.* https://doi:10.1371/journal.pone.0056588.

Hoyt, E. 2008, Whale watching. Pages 1219-1223 in: W.F. Perrin, B. Würsig and J.G.M. Thewissen (eds.) *Encyclopedia of Marine Mammals, 2nd Edition.* Academic Press, San Diego, California USA.

IUCN. 2016. *IUCN Red List of Threatened Species. Version 4*, update 2016-3. http://www.iucnredlist.org. Accessed 1 December 2016.

Kohler, N.E., J.G. Casey, and P.A. Turner. 1998. NMFS cooperative shark tagging program, 1962–93: an atlas of shark tag and recapture data. *Marine Fisheries Review* **60**:1 –87.

Lea, J.S.E., N.E. Humphries, C.R. Clarke, and D.W. Sims. 2015. To Madagascar and back: long-distance, return migration across open ocean by a pregnant female bull shark *Carcharhinus leucas*. *Journal of Fish Biology* **87**:1313-1321.

Meekan, M. and M. Cappo. 2004. Non-destructive techniques for the rapid assessment of shark abundance in Northern Australia. Report prepared for the Department of Agriculture Fisheries and Forestry. *Australian Institute of Marine Science*, Townsville, Queensland, Australia.

Meekan, M., M. Cappo, J. Carleton, and R. Marriott. 2006. Surveys of sharks and fin-fish abundance on reefs within the MOU74 Box and Rowley Shoals using baited remote underwater video systems. Report prepared for the Department of the Environment and Heritage. *Australian Institute of Marine Science*, Townsville, Queensland, Australia.

Meyer, C.G., T.B. Clark, Y.P. Papastamatiou, N.M. Whitney, and K.N. Holland. 2009. Long-term movements of tiger sharks (*Galeocerdo cuvier*) in Hawaii. *Marine Ecology Progress Series* **381**:223–235.

Meyer, C.G., Y.P. Papastamatiou, and K.N. Holland 2010. A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. *Marine Biology* **157**:1857–1868.

Moran, D. and D. Pearce. 1994. *The Value of Biodiversity*. World Conservation Union, Biodiversity Programme, Earthscan Publications, London, United Kingdom.

MPAtlas. 2016. *Shark Santuary*. http://www.mpatlas.org/category/shark-sanctuary/ viewed 1.12.2016.

Musyl, M.K., R.W. Brill, D.S. Curran, N.M. Fragoso, L.M. McNaughton, et al. 2011. Post-release survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. *Fishery Bulletin* **109**:341–368.

Myers, R.A., J.K. Baum, T.D. Shepherd, S.P. Powers, and C.H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**:1846–1850.

Nadon, M. O., J.K. Baum, I.D. Williams, J.M. McPherson, B.J. Zgliczynski, et al. 2012. Re-creating missing population baselines for Pacific reef sharks. *Conservation Biology* **26**:493–503.

Perlman, D.L. and G. Adelson. 1997. *Biodiversity: Exploring Values and Priorities in Conservation*. Blackwell Science, Malden, Massachusetts, USA.

O'Connor, S., R. Campbell, H. Cortez, and T. Knowles. 2009. Whale Watching Worldwide: tourism numbers, expenditures and expanding economic benefits. Report for the International Fund for Animal Welfare, Yarmouth, Massachusetts USA, prepared by Economists at Large.

Pauly, D. 2010. *Sea Around Us: A Ten-Year Retrospective, 1999 to 2009*. Sea Around Us Project, Fisheries Centre, University of British Columbia, Vancouver, Canada.

Pikitch E.K., D.D. Chapman, E.A. Babcock, and M.S. Shivji. 2005. Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). *Marine Ecology Progress Series* **302**:187–197.

Robbins W.D., M. Hisano, S.R. Connolly, and J.H. Choat. 2006. Ongoing collapse of coral-reef shark populations. *Current Biology* **16**:2314-2319.

Roff, G., C. Doropoulos, A. Rogers, Y-M Bozec, N.C. Krueck, E. Aurellado, M. Priest, C. Birrell, and P.J. Mumby. 2016. The ecological role of sharks on coral reefs. *Trends in Ecology & Evolution* **31**:395-407.

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

Ruppert, J.L.W., M-J Fortin, and M.G Meekan. 2016. The ecological role of sharks on coral reefs: Response to Roff et al. *Trends in Ecology & Evolution* **31**:586-587.

Semmens B.X., P.G. Bush, S.A. Heppell, B.C. Johnson, C.M. McCoy, et al. 2006. Defining the biogeography of a spawning aggregation to inform marine reserve planning and evaluation in the Cayman Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute* **59**:638.

Shepherd T.D. and R.A. Myers. 2005. Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecology Letters* **8**:1095–1104.

Simpfendorfer, C., R. Hueter, U. Bergman, and S. Connett. 2002. Results of a fishery-independent survey for pelagic sharks in the western North Atlantic, 1977–1994. *Fisheries Research* **55**:175–192.

Stallings, C.D. 2009. *Fishery-Independent Data Reveal Negative Effect of Human Population Density on Caribbean Predatory Fish Communities*. *PLoS ONE 4(5): e5333.* https://doi.org/10.1371/journal.pone.0005333.

The Pew Charitable Trusts. 2017. *Fact Sheet: Shark Sanctuaries around the World*. http://www.pewtrusts.org/en/research-and-analysis/fact-sheets/2016/03/shark-sanctuaries-around-the-world.

Vianna, G.M.S., M.G. Meekan, D.J. Pannell, S.P. Marsh, and I.J. Meeuwig. 2012. Socio-economic value and community bene fits from shark-diving tourism in Palau: a sustainable use of reef shark populations. *Biological Conservation* **145**:267–277.

Ward-Paige, C.A., C. Mora, H.K. Lotze, C. Pattengill-Semmens, L. McClenachan, et al. 2010. *Large-Scale Absence of Sharks on Reefs in the Greater-Caribbean: A Footprint of Human Pressures*. *PLoS ONE 5(8): e11968*. https://doi:10.1371/journal.pone.0011968.

White, J., C.A. Simpfendorfer, A.J. Tobin, and M.R. Heupel. 2013. Application of baited remote underwater video surveys to quantifying spatial distribution of elasmobranchs at an ecosystem scale. *Journal of Experimental Marine Biology and Ecology* **448**:281–288.