Nuanced differences in shark assemblages in protected and fished locations and drivers of their habitat use: implications for conservation

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Abstract

Growing awareness that sharks may play a key ecological role in maintaining marine ecosystem health, together with observed population depletions on a global scale, has led to increased focus on their conservation. Declines in shark populations may be particularly important in coral reef ecosystems, where there is evidence that they influence the fish community structure that underpins the resilience of reefs, potentially impacting the livelihoods of millions of people worldwide. There is therefore a need to understand both how human activities, particularly fishing, impact reef shark assemblages and also the natural drivers of shark distribution within their habitat, so that conservation efforts can be prioritised and measures to foster recovery designed.

Few places in the oceans remain untouched by fishing, with even remote areas impacted by fishers motivated by high value catches and the depletion of local stocks. Locations that lie at opposite ends of the spectrum of fishing pressure can, however, help us to understand the degree and nature of fishing's impact on sharks and the ecosystems they inhabit and, where shark assemblages are relatively intact, provide insights into the ecology of sharks in the absence of anthropogenic disturbances. I analysed baited remote underwater video data from two large reef systems with an order of magnitude difference in known legal and illegal shark fishing. I chose the Chagos marine reserve, a remote and protected reef system in the central Indian Ocean, as my protected, 'unfished', location. For a 'fished' comparator, I used an area of reefs and shoals in northwest Australia (hence Australian Shoals) with a long history of shark fishing by domestic and foreign vessels.

Contrary to my expectations, indices of shark species richness and abundance revealed no significant differences between locations. However, size spectra and assemblage composition at each location revealed a greater abundance of bigger sharks, and of large mobile species in the less fished Chagos, and proportionally more individuals of smaller demersal species in the Australian Shoals. This suggests that the impact of differing levels of fishing on species richness and abundance can be partly masked by an increase in smaller sharks, potentially in response to the removal of their larger competitors. Comparison of the distribution of teleost biomass in the lower trophic groups suggests that higher shark biomass in Chagos is also leading to a higher biomass of herbivorous fishes that are important for reef resilience.

Taking Chagos as a reference site, I then modelled the shark assemblage indices and species composition against variables related to both habitat and the structure of the fish assemblage to determine the drivers of the spatial distribution of sharks within the reserve. Shark species richness, abundance and biomass, and assemblage composition were all primarily correlated with fish biomass rather than habitat, but depth and reef type were also important in explaining which sharks were found where.

My analyses suggest that protection from fishing leads to a more ecologically valuable shark assemblage, in terms of the proportional abundance of apex level species and individuals, but the effects of fishing may not be detected in richness and total abundance metrics due to shifts in the composition of the assemblage. Protection of sharks from fishing is clearly important, but modelling of abundance drivers within protected reefs also suggests that prey biomass should be given equal protection, and that a wide range of habitat niches are required to meet the needs of a mixed species assemblage. A wide range of measures has been implemented to tackle overfishing of sharks, including gear modifications, quotas in targeted fisheries, finning bans and spatial management including shark sanctuaries. Where possible, ‘no-take’ marine reserves that prevent depletion of both sharks and their prey, and that encompass a wide range of reef types and depths, would also appear instrumental for the recovery of reef shark populations.

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Statement of candidate contribution

Having completed my course of study and research towards the degree of Master by research (by thesis), I hereby submit my thesis for examination in accordance with the regulations and declare that the thesis is my own composition, all sources have been acknowledged and my contribution is clearly identified in the thesis. For any work in the thesis that has been co-published with other authors, I have the permission of all co-authors to include this work in my thesis, and there is a declaration to this effect in the front of the thesis, signed by me and also by my supervisor.

The thesis has been substantially completed during the course of enrolment in this degree at UWA and has not previously been accepted for a degree at this or another institution.

Publications arising from this thesis

I expect two publications to arise from this thesis following completion:

(1) "Nuanced differences between shark populations reveal impacts of fisheries pressure."
Authors: **David M Tickler**[1*], Tom B Letessier[1], Mark G Meekan[3], Heather J Koldewey[2], Jessica J Meeuwig[1].
Target journal: Conservation Biology

(2) "Prey abundance drives spatial distribution of sharks in an intact reef ecosystem."
Authors: **David M Tickler**[1*], Tom B Letessier[1], Heather J Koldewey[2], Jessica J Meeuwig[1].
Target journal: Functional Ecology

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Introduction

The decline of shark populations has been observed in all oceans and habitats, driven largely by decades of incidental bycatch and targeted fishing for their fins and meat [1]. Reductions of up to 90% in both commercial fisheries' catch per unit effort [2,3] and in diver observations [4] on reefs show sharp declines in shark abundances in both pelagic and coastal ecosystems. The loss of sharks in coral reef ecosystems is of particular concern, given the important ecosystem role they play in regulating reef communities, and the consequences for reef resilience. For instance, an increase in mid-level or 'meso' predator fish biomass due to reduced shark predation can lead in turn to increased predation on primary consumers and reduced grazing of turfing algae. This in turn impacts the ability of reefs to recover from damage, bleaching events and other disturbances [5]. Olds et al. [6] also found that reefs inside green zones in the Great Barrier Reef Marine Park, where sharks are protected, were more resilient to nutrient influxes and turbidity from coastal flooding.

Designing measures to protect and recover reef shark populations requires both an ability to assess the level of degradation in a given area, and an understanding of the ecological drivers that shape reef shark assemblages. Yet despite evidence of rapid declines understanding the manner and extent to which fishing has impacted sharks, and consequently what protection might hope to achieve, is made difficult by the absence of baseline data that describe pre-exploitation species richness, abundance, biomass and species composition of shark assemblages [7]. Truly pristine areas may no longer exist given the far reach of fishing and other human activities. However, it is possible to identify locations that lie at relative extremes of a given stress gradient, in this case the level of shark fishing, and compare them in order to determine the effects of that stressor on the shark assemblage. Such comparisons then allow the assessment of other locations against those criteria. It should then also be possible to identify places that lie at the 'least impacted' end of such gradients and use them as quasi-pristine reference sites in which to study the relatively natural ecology sharks in order to improve the implementation of conservation measures.

Given the sensitivity of large slow growing species such as sharks to fishing mortality[8,9], fishing pressure would be expected to manifest itself in reductions in abundance and species richness as populations decline or are locally extirpated.

Additionally, reductions in the mean size of populations have been observed as a response to fishing due to the removal of larger individuals by selective fishing practices and life history changes such as smaller size at maturity in response to reduced intra-species competition [10]. Therefore, measures of species richness, abundance, and size spectra/biomass should detect differences in fishing pressure between areas. Given the ecosystem role of sharks, reductions in abundance and biomass of sharks may also be reflected in changes to the fish community structure, a result of the release of meso-predator species from competition and predation risk [11].

To test this approach on a broad geographic scale, I compiled data from two large expanses of reef habitat with very different fishing histories. The Chagos marine reserve (Chagos) has been a no-take marine protected area since 2010, before which a relatively small commercial purse seine and long line fleet operated [12], with illegal fishing on the order of 50 vessels per year also impacting the area [13,14]. My comparison site, an area of reefs off north west Australia (the Australian Shoals), has experienced an order of magnitude more commercial fishing activity during the past decade [15,16]. Situated 200 km from Indonesia, one of the world's major shark fishing nations, the Australian Shoals has experienced a high level of illegal fishing, with estimates of 600 vessels visiting the region annually [17].

I here analyse data derived from baited remote underwater video surveys conducted in 2011 in the Australian Shoals and 2012 in Chagos. In Chapter One, I compare the reef-associated shark assemblages and associated fish communities of a protected area with a relatively light history of shark fishing (the Chagos marine reserve), with a collection of reefs with an order of magnitude higher fishing stress (the Australian Shoals) in order to determine which measures of shark assemblage condition best reflect differences in fishing pressure and to see if there are corresponding changes in fish community structure. Having determined how protection influences the assemblage as whole, in Chapter Two I use Chagos as a reference site to explore the natural drivers of spatial variation in the reef shark assemblage in an area with low fishing pressure to understand what features of a protected area of reefs are important to sharks. Combined, these two analyses help us to understand the relative level of impact that fishing has had on sharks at a particular location, and to design spatial management measures that will best promote recovery of impacted populations.

Chapter One

Indicators of impact: The effect of varying fishing pressure on the reef-associated shark assemblage of two Indian Ocean coral reef systems.

1.1 Summary

Due to their relative inaccessibility, protected coral reefs remote from human populations might be expected to provide the best examples of 'pristine' habitats and fish biomass for use as baselines in conservation and management planning. To examine the impact of a difference in fishing pressure on sharks I compared the isolated and largely uninhabited Chagos marine reserve (Chagos) with a group of reef systems off north west Australia (the Australian Shoals) that, although similar in terms of depth, topography and habitat, have experienced an order of magnitude higher shark fishing effort. Species richness, relative abundance and size structure of sharks, and the biomass of the associated fish assemblage were quantified using stereo baited remote underwater video systems (stereo-BRUVS) around reefs at the two locations. Despite their different proximity to population centres and exposure to fishing, species richness and overall abundance of reef sharks were similar in both locations (1.96 hr^{-1} and 2.06 hr^{-1}, $t = -0.46$, $p = 0.63$). Assemblage composition was significantly different ($F_{[1, 295]} = 11.755$, $p = <0.001$), with Chagos having a higher abundance of grey reef and silvertip sharks while the Australian Shoals showed a greater abundance of white tip reef sharks. Mean length of grey reef sharks was greater in Chagos (100.1cm vs. 92.9cm, $t = 2.36$, $p = 0.03$), with the length frequency distribution skewed towards larger size classes ($X^2 = 32.9$, $p < 0.01$). Biomass pyramids also differed, with greater biomass of both sharks and herbivorous fishes in Chagos, and greater meso-predator biomass in the Australian Shoals ($F_{[1, 385]} = 8.30$, $p = <0.01$). I conclude that measures of shark abundance or species richness may not always detect fishing pressure on sharks due to changes in assemblage composition, in this case increased abundance of smaller sharks in the Australian Shoals in response to reduced competition. However there are measurable differences in the species composition of the assemblage between a heavily and a lightly fished location. By comparing the trophic groups in the fish assemblages, I find evidence that the greater proportion of larger shark species in the better protected location may be indirectly be driving greater abundance of low trophic level species important to resilience in coral reef ecosystems.

1.2 Introduction

The past 50 years has seen a rise in the scale and intensity of human impacts on the marine environment [18]. Industrialised fishing has led to systematic over-exploitation of fish populations [19,20]; pollution from sources such as refuse disposal and agricultural runoff has led to problems such as algal blooms and entanglement and smothering of marine animals [21-23]; ballast water discharge and aquaculture have facilitated the introduction of non-native and sometimes invasive species [24-26]; and rises in the average ocean temperature and acidity due to increasing atmospheric CO_2 have stressed corals and other reef-building and shelled organisms [27]. Together these factors have placed a combination of acute and chronic stresses on marine ecosystems at local, regional and global scales [28,29].

Coral reefs are amongst the most biologically diverse areas of the oceans, providing a range of important ecosystem services including fisheries resources and coastal protection to an estimated 500 million people worldwide [30,31]. As with other marine environments, they have been subjected to a matrix of stressors including rising water temperatures, eutrophication, and the extraction of reef material for construction [32,33] and their conservation has become a priority for securing both the health of tropical marine ecosystems and the human populations that rely on them [34-36]. In parts of the Caribbean, East Africa and South East Asia, a long history of exploitation has also left reefs changed beyond recognition [37-40] but remote areas with little or no human settlement and associated extractive activities offer a chance to preserve and study coral reef systems in something approaching a ‘pristine’ state [41,42]. Importantly, these pristine areas are thought to be essential as baselines for conservation and management planning, since they give a picture of reef communities prior to the impact of anthropogenic activities. However, the extent that such areas truly represent pre-exploitation conditions is unclear, due both to the global reach of many of the human activities impacting reefs and reef communities, and the fact that such areas are often difficult for researchers to access, lack baselines and are thus data poor.

Such problems are particularly acute for any assessment of reef status that includes apex predators such as reef sharks. These predators are a key component of healthy coral reef ecosystems that play a pivotal role in structuring fish and invertebrate communities through their direct and indirect influences on lower trophic levels [5,11,43,44]. By influencing the abundance and behaviour of mid level (meso) predators, sharks can indirectly promote increased abundance of herbivores and detritivores, species that perform important ‘maintenance’ functions such as the suppression of smothering algae following eutrophication from flooding, or bleaching events, and may in turn make corals more resilient to stressors such as bleaching events and storms [5,6,45-47]. Sharks are, however, very easily impacted by human activities such as fishing and are targeted for their fins and meat, as well as being taken as bycatch in substantial numbers by pelagic fisheries targeting tunas and billfishes near reefs [13,48-53]. The k-selected life histories of many species (i.e. relatively slow growth, late maturity and low reproductive rate) mean that even relatively limited fishing pressure can cause rapid and substantial declines in numbers, and, where fishing methods selectively target larger, older individuals, result in a substantial reduction in biomass, mean individual size and the recovery capacity of the population [9]. Since sensitivity to fishing also varies across species, due to differing exposures to mortality risk and recovery potentials [54], impacted assemblages would also be expected to show reduced species richness, with larger, slower growing species either absent or at very low abundances.

Given their susceptibility, measures of the species richness, abundance, size, and species composition of the shark assemblage should provide an important indicator of fishing pressure at a site. Furthermore, because sharks are important structuring agents of fish communities, the composition of associated fish assemblages may also provide important metrics for comparing the relative health of shark populations and the extent to which they can be used as baselines for conservation and management strategies. I examined this hypothesis at the Chagos marine reserve (Chagos), in the Indian Ocean. This reserve was established in 2010 and, at 644,000 km^2 is the world’s largest no-take marine protected area (MPA). It is considered to be one of the least impacted reef ecosystems in the Indian Ocean. Long term (decadal) studies of coral cover, recruitment and resilience in Chagos have recorded high proportions of live coral cover, and rapid recovery from bleaching events [42]. Underwater visual census of reef fish indicates that fish biomass at Chagos is orders of magnitude higher, with greater biomass of high trophic level species, than that of both protected and unprotected locations in the populated western Indian Ocean [55], suggesting that its distance from population centres has conferred additional benefits to area. However, studies on sharks have been limited, with abundance estimates of reef sharks based on infrequent observations by divers between 1970 and 2006 [4] and incomplete data from fisheries observers on the composition of commercial by-catch and illegal fishing seizures

[13,56]. Though piece-meal, these data provide some evidence suggesting sharks have been impacted by commercial and illegal fishing activities in Chagos, with reductions in abundance of as much as 90% since the 1970s [4]. This has occurred despite other ecological indicators remaining apparently healthy [55]. In the absence of pre-exploitation baseline data, it is difficult to assess the magnitude of the impact of fishing on the shark assemblage at Chagos. However, it is still possible to estimate the health of shark and reef fish populations in Chagos by relative means, through comparison with other reefs in the Indo-Pacific that have a known history of fishing.

In February 2012, I used stereo baited remote underwater video systems (stereo-BRUVS) [e.g. 57] to make the first comprehensive survey of the reef shark assemblage following creation of the MPA. I compare our results with existing data stemming from a stereo-BRUVS survey conducted in 2011 of nine reefs and shoals in northwest Australia. The Australian Shoals has similar habitat characteristics to Chagos in terms of reef type, depth and area, but records indicate an order of magnitude more commercial and illegal, unreported and unregulated (IUU) fishing [17]. Similarities and differences between the two can therefore be used to assess the status of the shark assemblages at Chagos in light of lower fishing pressure. By comparing the attributes of the reef associated shark assemblages, the shark species composition and the relative abundance of fish biomass in different trophic groups, I test the following hypotheses:

1) Lower fishing pressure in Chagos will result in higher abundance, species richness, size and biomass of sharks in Chagos;
2) The species mix in Chagos will reflect more of the larger mobile species, consistent with the increased susceptibility of large slow growing shark species to fishing; and
3) The higher abundance of apex level sharks in Chagos will have had cascading effects on the fish assemblage, resulting in fewer mid level predatory fishes and more herbivores relative to the Australian Shoals.

With these data I also establish a reliable baseline description of the reef-associated shark assemblage in Chagos, following the creation of the marine reserve, against which future changes can be compared.

1.3 Materials and Methods

1.3.1 Survey locations

Video samples were obtained from two areas (Figure 1.1); the Chagos, and a group of submerged reefs and shoals near Ashmore and Cartier reefs in the Timor Sea off northwest Australia (referred to hereafter as the Australian Shoals). Chagos is an archipelago of over 60 individual islands, grouped into seven main atolls that lie approximately 600 km south of the Maldives between 04°50' to 07°40' S and 70°10' to 72°40' E. All reefs, except those in a 3 nautical mile (5.5 km) zone around Diego Garcia, are now part of the Chagos Marine Reserve, established in April 2010. Reef and lagoon habitats were sampled at seven sites around the two northernmost atolls, Salomon and Peros Banhos, at the submerged shoal at Victory Bank, at Brothers and Eagle Islands and Danger Bank along the western edge of the Grand Chagos Bank and at 60-80 m depth on a seamount to the south, all within the reserve. The Australian Shoals consist of a number of submerged reefs and banks between 12°31' to 13°54' S and 123°36' to 124°35' E, off the north west coast of Australia. Nine banks and shoals were surveyed across the area, with samples taken across features to encompass both reef flat and reef crest habitats.

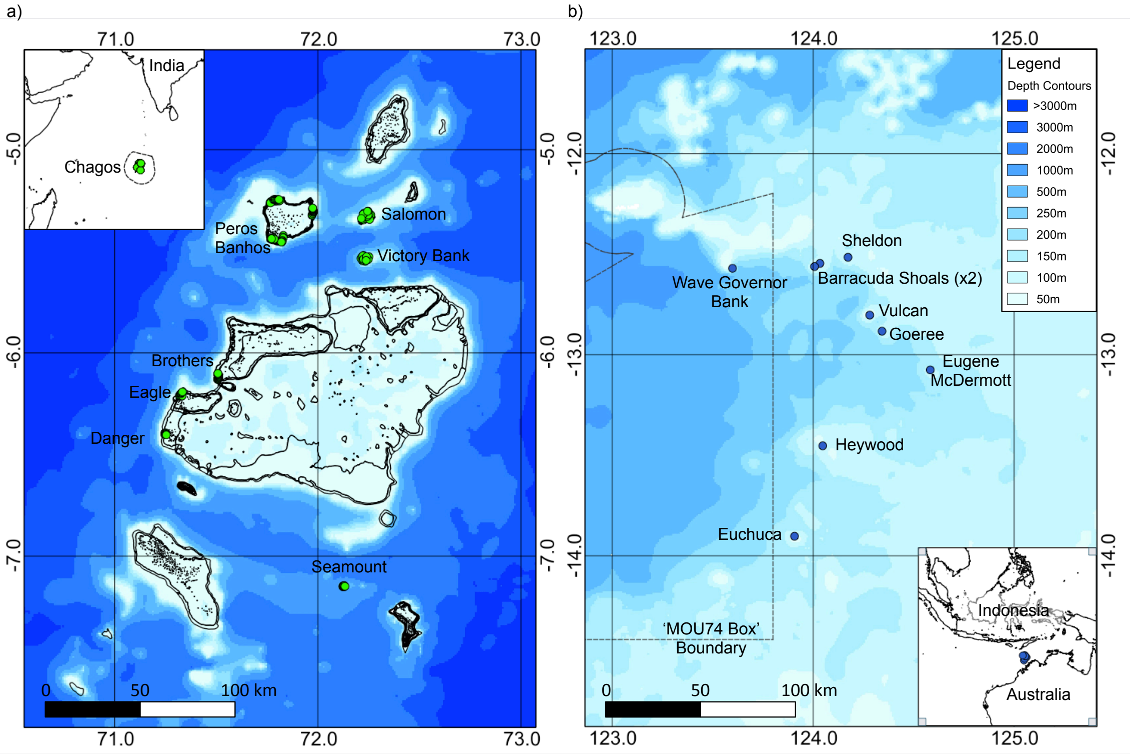

Figure 1.1: Location of sample sites in a) Chagos (n = 138) and b) the Australian Shoals (n = 248)

The Australian Shoals lie in a region that has been a traditional fishing ground for Indonesian boats for centuries, and fishing for shark, beche de mer (holothurians) and

Trochus continues legally in an area of Australian territorial waters just adjacent to the 2011 study site [58]. Depletion of the resources in this legal fishing area (known as the 'MOU 74 box' after the 1974 Memorandum of Understanding between Australia and Indonesia) is thought to have driven some Indonesian boats to fish illegally outside this are, including eastwards in the area surveyed in this study [17]. Additionally, commercial shark fisheries, and long line and purse-seine fisheries taking shark as bycatch, have operated in north west Australian waters as recently as 2009 landing up to 1,300 tonnes of sharks per year (average of 460 tonnes per year 2000-2009) [15,59], which included reef-associated species such as grey reef (*Carcharhinus amblyrhynchos*) and tiger sharks (*Galeocerdo cuvier*).

Chagos has also been impacted by legal and illegal fisheries, but to a lesser degree than Northwest Australia on the basis of available data. Commercial tuna fisheries operated until 2010, with shark bycatch estimated to be in the order of 35 tonnes per year in the period 2005-2010 [12]. Illegal fishing vessels, primarily from Sri Lanka, have operated throughout the pre- and post- protection periods and continue to be arrested within Chagos at the rate of around five per year [13]. Inspection of arrested vessels indicates that sharks comprise around 80% of seized catches [13] with grey reef and silvertip sharks (*Carcharhinus albimarginatus*) both represented. Price et al. [14] estimate the level of IUU fishing to be around 50 vessels per year, based on sightings by visiting yachts in Chagos and catch landings in Sri Lanka (a portion of which are assumed to come from Chagos). This contrasts with an estimated 600 vessels operating in north west Australian waters [17]. Data on fishing in the two locations from the literature are provided in Appendix 1.

1.3.2 Sampling activity

Video data for the Chagos were collected by a team from the University of Western Australia using stereo-BRUVS [57] during a three week expedition in February and March 2012 at 138 sampling stations within 13 sites; those for the Australian Shoals were collected in March and April 2011 at 248 stations across nine reefs and shoals by a team from the Australian Institute of Marine Science (AIMS) [60]. Stereo-BRUVS were chosen as a sampling method because they provide a reliable, repeatable and data-rich methodology for assessing the populations of sharks and fishes [61,62]. Moreover, the use of stereo-BRUVS avoids depth and time constraints imposed by SCUBA surveys and the destructive nature of scientific longlines, trawls or traps [63-65]. All sampling activity in Chagos was carried out under UWA ethical guidelines and was approved by the BIOT Administration and Scientific Advisory Group. Work carried out at the Australian Shoals was conducted in compliance with ethical guidelines at AIMS.

Stereo rigs consisted of two high definition digital video cameras (Sony Handycam™ models HX7 or HX12), housed in pressure resistant housings and fixed to a rigid bar held within a heavy frame that provides both stability and protection on the seabed [57,66]. A flexible bait arm, made from 15 mm plastic pipe and 1.5 m in length, was fixed between the cameras and baited with approximately 0.7 kg of pilchards (*Sardinops* spp.), roughly chopped to release blood and oil, and held in a mesh bait bag. Stereo-BRUVS were deployed for a minimum of one hour to allow for post-processing to be standardised to 60 minutes. In Chagos, the stereo-BRUVS were deployed at 138 sampling stations across the seven sites from the BIOT Patrol Vessel Pacific Marlin's fast rescue craft, and in the Australian Shoals at 248 sampling stations across the nine sites using the AIMS research vessel, the RV Solander.

1.3.3 Processing of stereo-BRUVS samples

All video imagery was converted to AVI format using Xilisoft™ video conversion software and analysed using the software package EventMeasure™ [67]. One hour of footage from one of the cameras in a stereo set (typically the left) was analysed from the time that the rig settled on the seabed. A trained analyst observed the resulting footage frame by frame and identified all fishes including sharks to family, genus and species level (where possible), with information for each identified species (sample code, frame number and time of occurrence, genus, species, etc.) recorded in a database by the software. Abundance was estimated as Max*N*, the maximum number of individuals of a given species in a single frame of video, as this is a consistent, conservative measure of relative abundance [57]. EventMeasure™ records Max*N* for each species based on the number of concurrent identification records created for each species by the analyst. To reduce operator bias, a second analyst checked species identifications and counts for each video. Stereo analysis using EventMeasure™ subsequently used the synchronised footage from both cameras to compute lengths for each animal by mathematically comparing the stereo images produced by the paired video frames with a calibration file based on a cube of known dimensions [67]. Length measurements with estimated error value greater than 10% of the measured length were rejected. Finally, habitat was classified by visual inspection of a still frame from each video sample. Habitat visible in the field of view of each BRUVS rig was classified as belonging to one of six dominant habitat groups (high-, medium- or low-relief hard corals, soft coral and macro-invertebrate dominated, rubble, or sand). Additional sample attributes (time of day, location and depth) were also obtained from the fieldwork logs (Table 1.1).

In addition to the sample attributes directly obtained from the image analysis, I estimated other sample attributes by calculation using external data sources. Mean weight for each species in a sample was calculated using species mean length and the length-weight relationship $W=aL^b$, where W is the estimated weight and L is one of fork, total or standard length [68]. Relative biomass for each species was calculated as the product of a species' Max*N* and its mean weight. Where species-specific coefficients for the length-weight equation were unavailable, the relationship for a similarly sized congener was used or, if again unavailable, for the genus or shape [69]. Where no individuals of a given species were measured on a sample, the mean length for the species from the same site or location was applied to the sample. The encounter rate (i.e. commonness) of sharks was calculated as the proportion of samples in which a shark was recorded. This was calculated for all shark species together, and for each individual species.

All species were classified as 'sharks' or 'fish' such that richness, abundance, mean length and biomass estimates could be derived for each group. Furthermore, as I was interested in the trophic structure of the shark and fish assemblage, I also extracted estimated trophic levels and diet classes for each species from Fishbase [68] and the literature using the methodology of Ruppert et al [5]. These were applied to each species so that abundance and biomass could be aggregated by trophic category.

1.3.4 Statistical Analyses

Except where mentioned below, all analyses were performed using R statistical software [70]; all summary metrics are reported as mean values and 95% confidence intervals (±1.96 standard errors).

Preliminary analyses tested for potentially confounding factors between the two areas and the adequacy of sampling effort. The areas were compared with respect to mean depth (t-test) and distribution of habitat classes (Chi square test). The effects of depth on shark diversity and abundance were tested using linear regression, and the mean depth of encounter for each species was calculated based on a weighted mean of sample depth by species abundance for each location to determine what affect differences in location depth were likely to have on the relative abundance of species. The effect of habitat class on shark diversity and abundance was tested using analysis of variance (ANOVA). Smoothed species accumulation curves, and extrapolated species diversity using the Chao2 richness estimator [71,72] were calculated at both locations using the software package EstimateS [73]. Data exploration was used to determine the shape and distribution of variables so that appropriate tests and their variants could be applied. Descriptive statistics for total abundance (MaxN), biomass and length were computed to determine mean and confidence interval for each variable at the two locations (Table 1.3). These results were used to determine the appropriate variation of the Student's T-test to apply (two tail, unequal sample size, unequal variance in all cases). Bar plots of the relative abundance of each shark species showed an order of magnitude difference between the most and least abundant, so a logarithmic transformation was applied to the data before testing for the similarities in assemblage structure, to increase the contribution of the lest abundant species to the analysis. Function *betadisper (*R package 'vegan') was used to determine beta-diversity to test the assumption of homogeneity of multivariate spread in the assemblage data before using permutational ANOVA (PERMANOVA).

1.3.5 Shark assemblage indices

Mean values per sample station (per hour) for shark species richness and abundance for all shark species at the two locations were compared using a t-test (2-tails, assuming unequal sample sizes and unequal variance, [74]). To assess the potential influence of habitat, shark species richness and total abundance were also calculated for a subset of sites in Chagos that were highly similar to the habitat (in terms of dominant habitat type) and topography (i.e. submerged banks) of the samples from the Australian Shoals. Encounter rates for sharks at both locations were compared using a Chi square test with Yates' correction for two categories [74].

1.3.6 Size comparisons for grey reef sharks

Sufficient observations were available for grey reef sharks at both locations to permit size comparisons between the locations based on this species. Fork lengths obtained from EventMeasure were converted to centimetres and mean observed length was compared between the two locations using a t-test as above. Length-frequency distributions were plotted using a kernel density function (*sm.density.compare* in the R package ‘sm’ [P1]) and the difference in distribution shape tested for using the Kolgomorov-Smirnof test [74] implemented in R through the function *ks.test*.

1.3.7 Differences in shark assemblage composition

Differences in shark assemblage composition between Chagos and the Australian Shoals were tested using permutational multivariate ANOVA (PERMANOVA), using the R function *adonis* (package ‘vegan’; [P2]) on a Bray-Curtis dissimilarity matrix of log-transformed species’ abundance data to reduce the influence of the most abundant species. Similarity percentage analysis (R function *simper;* package ‘vegan’) was used to determine the contribution of each species to the differences between locations.

1.3.8 Trophic pyramid analysis

Mean biomass pyramids for each location were constructed by summing mean biomass per hour (i.e. mean MaxN per hour multiplied by mean individual mass) for each species observed by half trophic levels (TL, from 2.0 to 4.5 in steps of 0.5). Differences between the biomass pyramids by location were tested using PERMANOVA with the R function *adonis*. The analysis was based on a Euclidian distance matrix, treating trophic categories as variables. A Euclidean distance for untransformed biomass was used since the range of values covered less than one order of magnitude and because I wanted to preserve the influence of zero values (relevant to trophic structure). The contribution of each trophic level to the difference between locations was determined using the R function *simper*. Additionally, all species were assigned a diet classification based on their trophic level and feeding habits following the methodology of Ruppert et al. [5] (Appendix 2) to create six diet classes: all sharks, teleost carnivores, herbivores, corallivores, planktivores and detritivores. Principal component analysis (function *rda,* package ‘vegan’, no constraining variables) was performed on a dissimilarity matrix calculated using log-transformed biomass at each site with diet classes as ‘species’. The result was visualised using a biplot.

1.4 Results

1.4.1 Sample location characteristics

Mean water depths of stereo-BRUVS deployments ranged from 5.4 to 82.2 m in Chagos (Table 1, mean 25.5 ± 2.6 m) and 18.0 to 81.3 m in the Australian Shoals (Table 2, mean 34.6 ± 1.4 m), with the deeper average deployments at the Shoals due largely to the lack of emergent reef at this locality. Although mean depth differed significantly (t

= -5.42, $p < 0.01$), shark abundance did not vary with depth ($R^2 < 0.001$; $F_{[1,384]} = 0.12$; $p = 0.72$). Habitat classes also varied significantly ($X^2_{adj} = 11.32$, $p < 0.001$) between locations, with 78.3% of sites classified as hard or soft coral dominated (59.4 and 18.8% respectively) and bare sand or rubble 21.7% in Chagos, whereas cover of hard and soft coral averaged 55.2% (29.8 and 25.4% respectively) and bare sand or rubble 44.8% on the Australian Shoals (Table 1.1). Both species richness and abundance of sharks were significantly higher where the dominant substrate category was hard or soft corals (ANOVA: $F_{[6,380]} = 4.39$, $p <0.001$). Historical data on the Oceanic Nino Index (ONI) indicates that although the samples were taken in subsequent years, broad scale environmental conditions, as represented by the ONI were the same [105].

Table 1.1: Summary of the number of samples (n), depth and habitat composition for survey sites in (a) Chagos and (b) the Australian Shoals

a) Chagos sites	Samples	Depth range [mean] (m)	Proportions of samples in habitat class (%)			
			Hard Coral	Soft Invert.	Rubble	Sand
Danger Bank	11	17.6 - 27.9 [24.3]	90.9	0.0	9.1	0.0
Eagle Island Lagoon	15	12.8 – 30.0 [23.6]	33.3	40.0	26.7	0.0
North Brother Bank	12	20.5 - 29.8 [24.7]	16.7	50.0	0.0	33.3
Diamante Island Lagoon	13	14.0 - 38.0 [23.8]	23.1	15.4	7.7	53.8
Diamante Island Reef	8	8.0 - 18.8 [12.6]	75.0	25.0	0.0	0.0
Grouper Ground	12	6.0 – 12.0 [8.8]	91.7	0.0	0.0	8.3
Ile de Coin Lagoon	10	5.4 - 37.9 [30.1]	100.0	0.0	0.0	0.0
Ile de Vache Marin	9	14.1 - 31.9 [21.5]	33.3	22.2	0.0	44.4
Salomon Atoll Lagoon	15	18.0 – 38.0 [26.8]	73.3	26.7	0.0	0.0
Salomon Atoll Reef	7	12.0 – 23.0 [19.3]	100.0	0.0	0.0	0.0
Sandes Seamount	10	68.3 - 82.2 [73.1]	0.0	30.0	0.0	70.0
Victory Bank Inner	8	9.0 – 20.0 [11.4]	75.0	12.5	12.5	0.0
Victory Bank Outer	8	19.1 – 40.0 [28.5]	100.0	0.0	0.0	0.0

b) Australian Shoals sites	Samples	Depth range [mean] (m)	Proportions of samples in habitat class (%)			
			Hard Coral	Soft Invert.	Rubble	Sand
Barracuda East	24	18.3 - 81.3 [34.6]	53.3	33.3	10.0	3.3
Barracuda West	24	18.6 - 81.3 [38.5]	22.7	36.4	22.7	18.2
Echuca	24	26.3 - 47 [33.6]	37.5	33.3	29.2	0.0
Eugene McDermott	24	19.2 - 40.4 [26.1]	37.5	33.3	29.2	0.0
Goeree	24	20.4 - 60.8 [37.5]	4.3	13.0	65.2	17.4
Heywood	64	25.0 - 46.4 [35.9]	38.7	9.7	32.3	19.4
Sheldon	24	18.3 - 49.8 [33.6]	0.0	43.5	56.5	0.0
Vulcan	24	31.4 - 44.3 [36]	29.2	20.8	41.7	8.3
Wave Governor Bank	16	20.4 - 46.2 [29.7]	18.8	31.3	50.0	0.0

1.4.2 Sharks assemblage characteristics

A total of 271 sharks were observed from 8 species representing 3 families in the Chagos (n = 138 samples), with 512 individuals, 9 species and 4 families recorded in the Australian Shoals (n = 248). Carcharhinids were the most represented family, with 7 species present across the two areas. Two Sphyrnidae and one species each from the Ginglymostomatidae and Triakidae families made a shared pool of 10 species (Table 1.2). Extrapolating observed species richness generated estimated maxima of 8.24 species of shark for Chagos (observed = 8) and 9 for the Australian Shoals (observed = 9), suggesting that the sampling effort had captured the main features of the shark assemblage in terms of species richness in both areas (Figure 1.2). The overlapping 95% confidence limits show that the locations did not differ in diversity. There was no significant difference between Chagos and the Australian shoals in terms of the mean sample values for shark species richness (SR = 1.09 vs. 1.23 hr^{-1}, t = 1.61, p = 0.12), total abundance (TA = 1.96 vs. 2.06 hr^{-1}, t = -0.46, p = 0.63) and encounter rate (ER = 74.6 vs. 75.4 %, $X^2_{adj} = 0.002$, p = 0.96) (Figure 1.3, Table 1.3). The lack of significant differences in species richness and abundance remained when the comparison was restricted to only those Chagos reefs with habitat characteristics similar to the Australian Shoals (SR = 1.19 vs. 1.23 hr^{-1}, TA = 1.98 vs2.68 hr^{-1}, Appendix 3).

Table 1.2: Abundance and encounter rates (ER) by species for Chagos and the Australian Shoals.

	Chagos (n=138)		Australian Shoals (n= 248)	
Species	Abundance (hr-1)	ER (% of samples)	Abundance (hr-1)	ER (% of samples)
Carcharhinidae				
Grey Reef *Carcharhinus amblyrhynchos*	1.33	58.0	1.10	59.3
Whitetip *Triaenodon obesus*	0.17	16.7	0.70	41.9
Silvertip *Carcharhinus albimarginatus*	0.17	10.1	0.08	7.3
Blacktip *Carcharhinus melanopterus*	0.09	8.7	-	-
Sicklefin Lemon *Negaprion acutidens*	-	-	0.04	4.0
Tiger *Galeocerdo cuvier*	0.01	1.4	0.00	0.4
Sliteye *Loxodon macrorhinus*	-	-	0.02	1.6
Sphyrnidae				
Great Hammerhead *Sphyrna mokarran*	0.01	1.4	0.06	5.6
Scalloped Hammerhead *Sphyrna lewini*	0.04	0.7	-	-
Ginglymostomatidae				
Tawny Nurse *Nebrius ferrugineus*	0.14	11.6	0.01	1.2
Triakidae				
Sicklefin Hound *Hemitriakis falcata*	-	-	0.05	2.0

Table 1.3: Summary statistics for the shark assemblages of Chagos and the Australian Shoals

All sharks	Chagos (mean ± CI)	Aus. Shoals (mean ± CI)	Statistical test (t-test or Chi-square)
Species Richness (hr^{-1})	1.09 ± 0.14	1.23 ± 0.19	$t_{[138,248]} = 1.61$, $p = 0.12$
Max*N* per (hr^{-1})	1.96 ± 0.35	2.06 ± 0.24	$t_{[138,248]} = -0.46$, $p = 0.63$
Encounter Rate (%)	74.6 ± 7.3	75.4 ± 5.4	$X^2_{adj} = 0.002$, $p = 0.96$

Grey reef sharks			
Mean total length (cm)	100.1 ± 4.6	92.9 ± 3.7	$t_{[97,211]} = 2.36$, $p = 0.03$

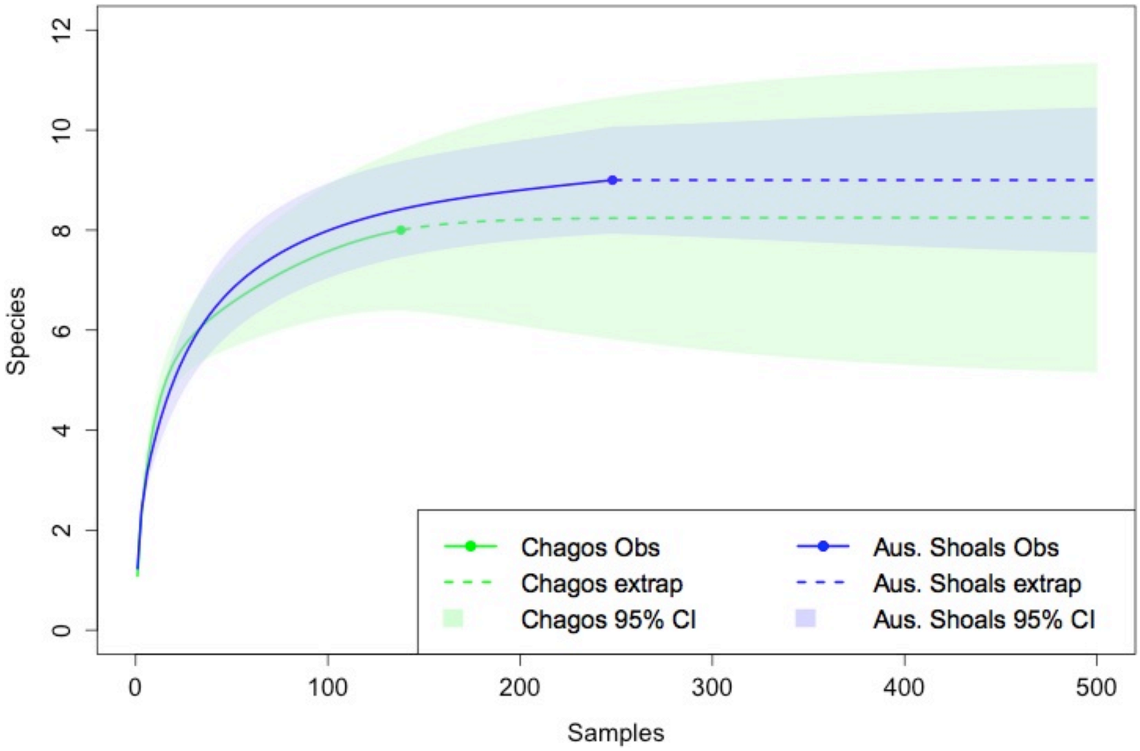

Figure 1.2: Species accumulation curves for Chagos (green) and the Australian Shoals (blue) showing extrapolated values (Chao2 formula) and 95% confidence intervals

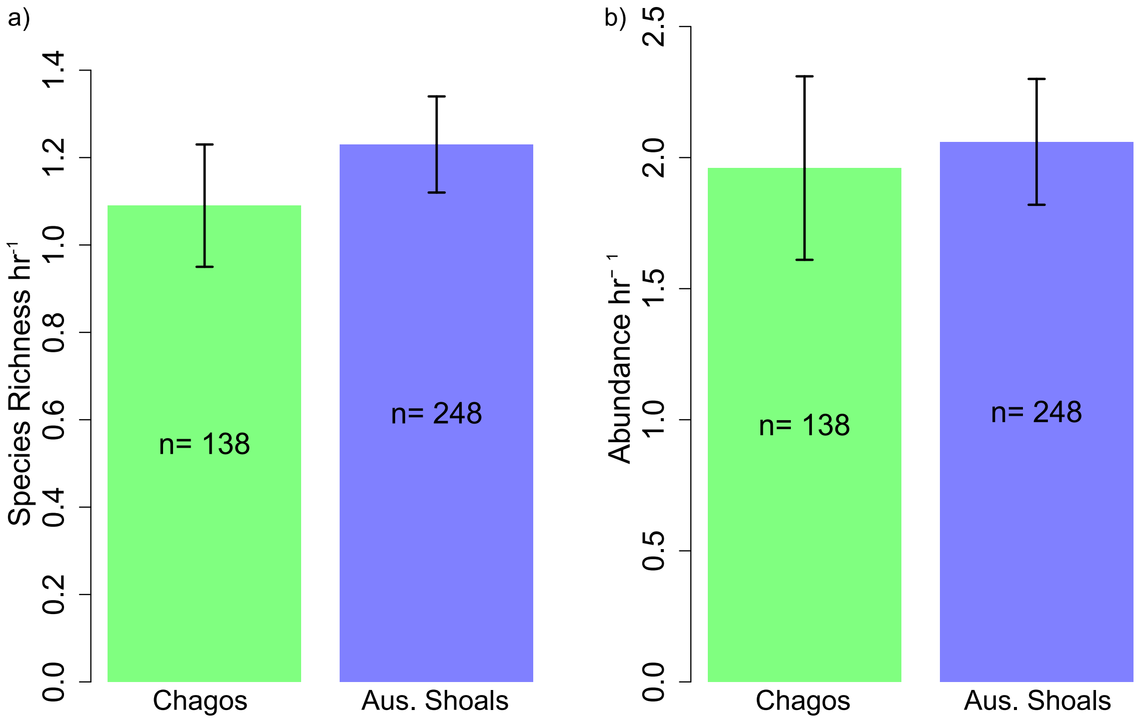

Figure 1.3: a) Mean shark species richness and b) mean abundance per hour for Chagos (green) and the Australian Shoals (blue).

1.4.3 Length-frequency distributions for grey reef sharks

Grey reef sharks were observed in relatively large numbers in both areas (67.5% and 53.5% of all shark sightings respectively), and size based comparisons between the two areas were performed using this species. After removing deployments where variations in range, orientation to the cameras or image quality made measurement unreliable, length data for the stereo-BRUVS samples were obtained for 97 animals in Chagos and 211 in the Australian Shoals. Mean total length was greater in Chagos than in the Australian Shoals (100.1 vs. 92.9 cm, $t = 2.36$, $p = 0.03$; Table 1.3, Figure 1.4a). Stereo-BRUVS derived length distribution in Chagos showed relatively more animals in larger size classes than the Australian shoals (Figure 1.4b; Two-sample Kolmogorov-Smirnov test, $D = 0.2646$, p-value = <0.001).

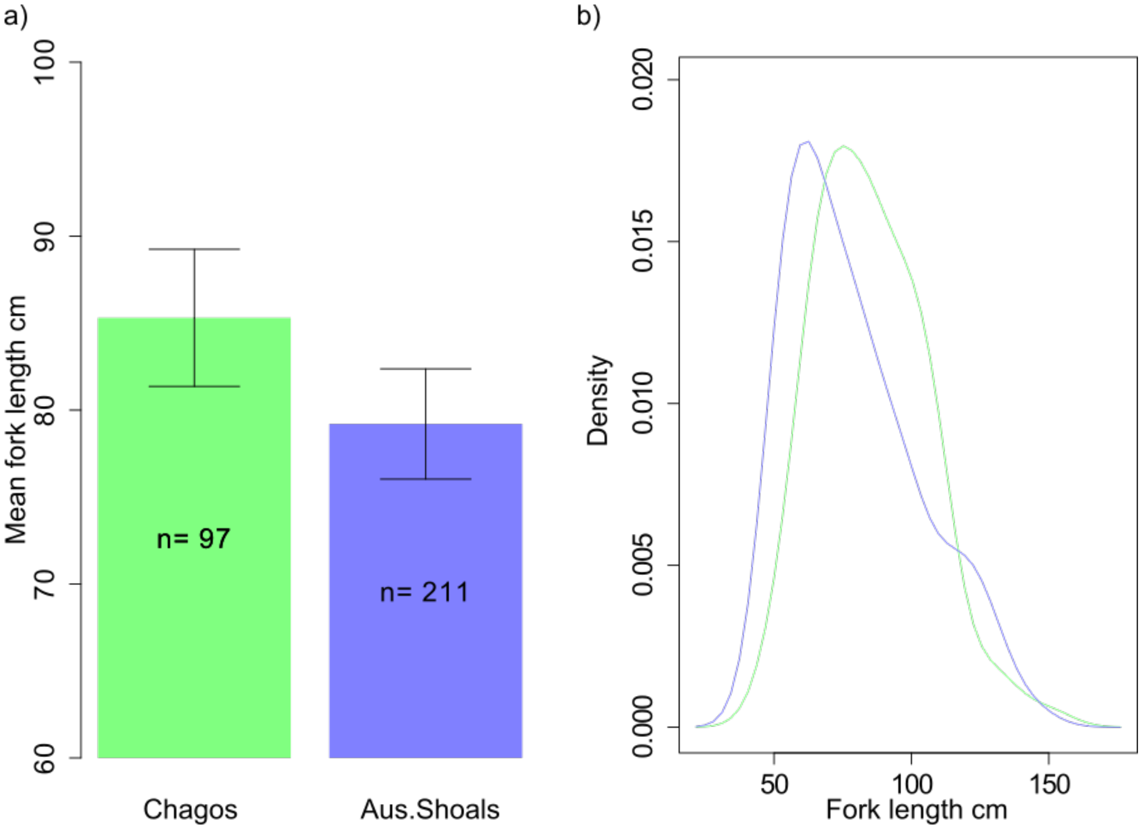

Figure 1.4: a) Mean total length and b) smoothed density functions for grey reef sharks in Chagos (green) and the Australian Shoals (blue). Two-sample Kolmogorov-Smirnov test on length distributions: $D = 0.2646$, p-value = <0.001

1.4.4 Spatial variability

Whilst overall shark abundance was similar (i.e. 1.96 hr^{-1} vs. 2.06 hr^{-1}), the composition of the shark assemblages in Chagos and the Australian Shoals differed significantly (Table 1.2 and Figure 1.5; F[1, 295] = 11.755, p = <0.001, 9999 perms). SIMPER analysis showed the relative abundance of grey reef, white tip and silvertip sharks to be the main contributors to the difference between areas (total contribution 77.3%).

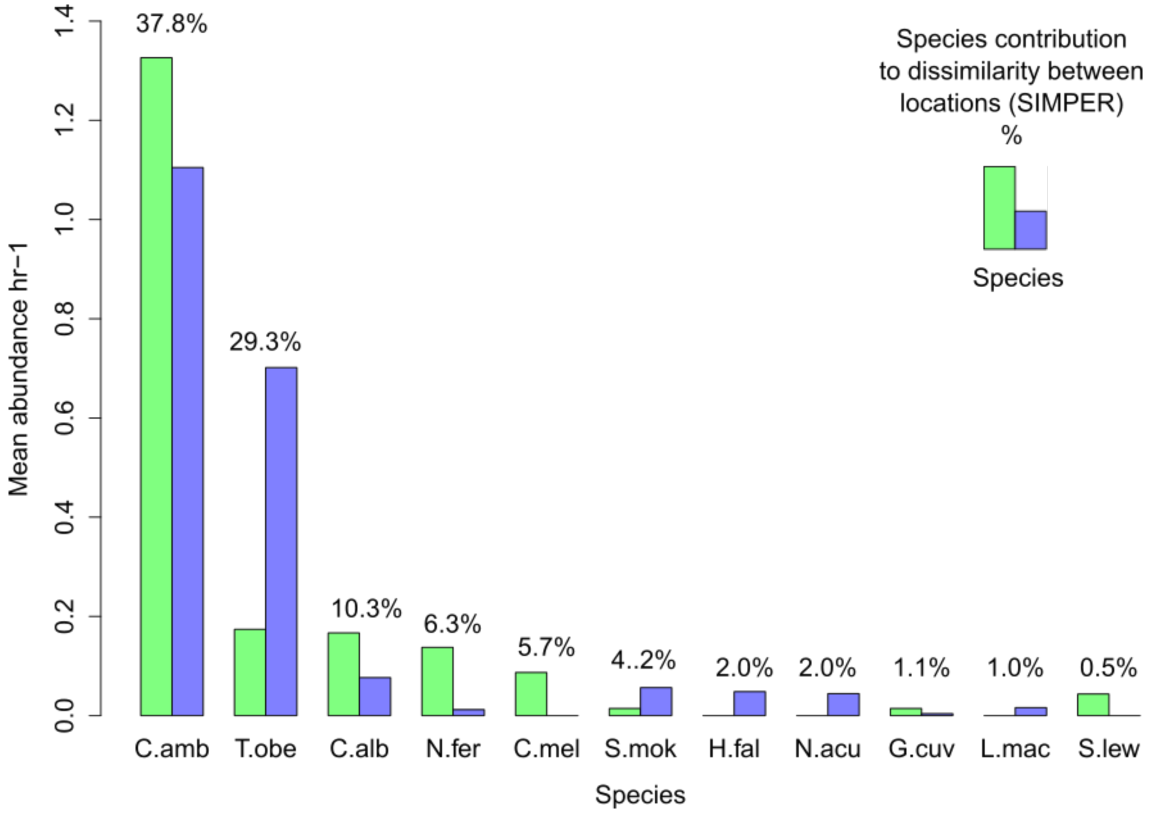

Figure 1.5: Mean abundance per hour by species for Chagos (green, n=138) and Australian Shoals (blue, n= 248). Ordered by percentage contribution of each species to difference in shark assemblage between the two areas (labelled above bars). Species abbreviations: C.amb = grey reef shark, T.obe = white tip reef shark, C.alb = silvertip shark, N.fer = tawny nurse, C.mel = black tip reef shark, S.mok = great hammerhead, H.fal = smooth houndshark, G.cuv tiger shark, L.mac = sliteye shark, S.lew = scalloped hammerhead.

1.4.5 Variations in biomass by trophic group

Total shark and fish biomass per sample was 68.8 kg hr^{-1} in Chagos and 64.5 kg hr^{-1} in the Australian Shoals and this overall difference was not significant ($t = 0.8$, $p = 0.41$). However, significantly greater biomass of apex predators (TL4.0+) was observed in Chagos (39.8 kg hr^{-1}) than the Australian Shoals (29.8 kg hr^{-1}, $t = 2.65$, $p < 0.01$). Lower trophic levels (TL<4.0) showed less biomass of mid-level predators (TL3.5 – TL4.0 and 3.0 to 3.5; 24.0 vs. 30.5 kg hr^{-1}) and greater biomass of herbivores (TL2.0) and detritivores (TL2.0 - TL2.5) (5.1 vs. 4.2 kg hr^{-1}) in Chagos compared with Australian Shoals (Figure 1.6a). PERMANOVA showed location had a significant effect on the distribution of biomass between classes ($F_{[1, 385]} = 8.30$, $p = <0.01$, 9999 perms) and SIMPER analysis showed that 70% of difference arising from relative biomass levels in the apex predator and meso-predator categories. The effect of shark and herbivore biomass on the separation of the two locations was confirmed by redundancy analysis using a distance matrix calculated on biomass in six diet categories. Shark and herbivore biomass were most strongly associated with the axis separating Chagos and the Australian Shoals in 2D ordination space (Figure 1.6b).

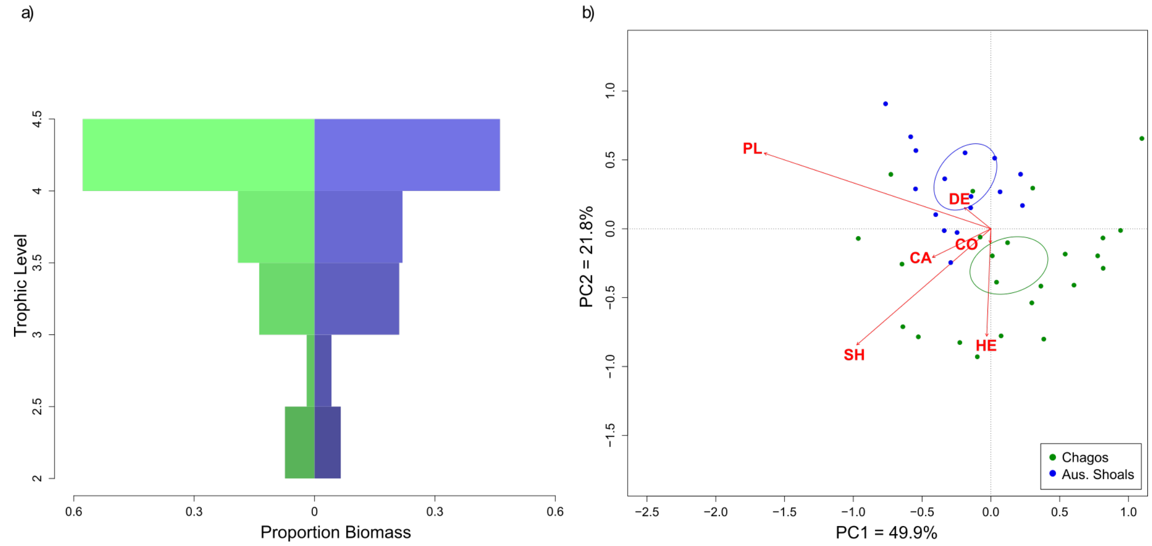

Figure 1.6: a) Distribution of total biomass per hour by trophic level (% of biomass in each band) in Chagos (green) and the Australian Shoals (blue); b) Ordination biplot of redundancy analysis results for sites in Chagos (green) and the Australian Shoals (blue) based on a distance matrix treating biomass in each diet category (SHarks, CArnivore, HErbivore, PLanktivore, COrallivore, DEtritivore) as species abundances.

1.5 Discussion

My study found the shark assemblages of Chagos and the Australian Shoals to be very similar in terms of the number of species observed (7 vs. 8), and the mean shark species richness (1.09 vs. 1.23 hr^{-1}) and abundance per sample (1.96 vs. 2.06 hr^{-1}). These similarities existed despite an order of magnitude difference in reported fishing catch and effort in the two locations. The Chagos Marine Reserve is remote (>600km) from any population centres and has been largely unpopulated for almost 50 years, whereas the Australian Shoals area is less than a day's travel – around 200km – from Indonesia, one of the world's most significant shark fishing nations [75] [17]. In concluding that the two locations are similar in terms of their sharks, I have taken into account the possibility that values for the assemblage indices might be impacted by differences in site depth or habitat, thus distorting the comparison. However, exploratory analysis of these factors indicated that environmental differences were either not correlated with abundance within the ranges sampled (in the case of depth) or would have been expected to produce larger estimates of abundance in Chagos than was observed (in the case of habitat). Similarly the Oceanic Nino Index (ONI), known to affect regional ocean temperature, productivity, and the movements of large predators, was equal (-0.6, or Weak La Nina) in both years, indicating that the two sets of data were collected under similar broad-scale environmental conditions. The similarity in overall abundance therefore suggests that the lower level of historical shark fishing at Chagos and its current no-take status have not impacted shark abundance as might be expected.

The first possible explanation for this contrary result is that reports of shark fishing in Chagos may have underestimated the number of sharks that have been removed. Graham et al. (2010) concluded from diver observations that there had been a reduction of around 90% in reef shark numbers between 1978 and 2006, implying high volumes of legal bycatch and IUU fishing. A second potential explanation is that a greater reduction in abundance of larger shark species in the Australian Shoals has allowed an increase in the abundance and range of smaller shark species less susceptible to fishing pressure, blurring the difference in total abundance at the two locations.

Two pieces of evidence support this latter hypothesis. Firstly, the greater mean length observed in Chagos for grey reef sharks, and the substantial skew in the length-frequency distribution towards larger animals there; and, secondly, the higher proportional abundance of larger species (grey reef and silvertip sharks) in Chagos, compared with the smaller species (white tip reef sharks, houndsharks and slit eye sharks) observed in the Australian Shoals. Fishing pressure is known to impact the length-frequency distribution of species, removing larger animals and truncating the distribution towards smaller size classes [76], and data from other locations in north west Australia show that larger more mobile species (such as grey reef and especially silvertip sharks) are disproportionately affected by shark fishing [77], possibly due to their greater movement range and consequent exposure to fishing activities off the reef. The observed similarity in shark assemblage metrics but difference in assemblage composition may therefore be analogous to the results of Bellwood et al. [78] who found that coral reef fish assemblages before and after a bleaching event showed similar levels of richness abundance and diversity, but had undergone a fundamental shift in composition to a new species mix.

It must, of course, be recognised that other factors, such as fundamental differences in biogeography, may also affect the observed structure of the shark assemblages in the two locations, and that long term structural differences cannot be reliably detected with the one-off surveys reported here. However other surveys of predator abundance elsewhere in NW Australia show a similar species pool in that region as is found in Chagos (ROWLEY SHOALS REF), and that species such as grey reef and silvertip sharks are found throughout the tropical indo-pacific, from the Seychelles to the Marshall Islands. It therefore seems plausible that the differences between Chagos and the Australian Shoals are not due to a fundamental difference in the natural sharks assemblages but rather external factors in the two locations, of which fishing pressure is one of the most markedly different.

My analysis of trophic structure suggests that the differences in shark assemblage composition between Chagos and the Australian Shoals may be having a cascading effect on lower trophic orders. The finding of higher levels of apex predator biomass in Chagos, lower biomass of mid-level species and higher biomass of herbivores was substantiated by principal components analysis (PCA) which found shark and herbivore biomass associated with the grouping of Chagos sites in an ordination biplot. The contrasting pattern observed in the Australian Shoals of higher biomass of mid-level species and lower biomass of low trophic species is consistent with changes in trophic structure predicted by models of ‘meso-predator release’ following a reduction in apex predator biomass [11,44] and predation effect. This contrast would likely be enhanced if smaller shark species were reclassified as 'meso-predators' in the analysis, as suggested by Heupel et al. [79]. Since herbivores and detritivores are believed to play a critical role in enhancing coral reefs resilience and recovery capacity (by, for example, suppressing the growth of algae during eutrophication or bleaching [5,6]), it follows that increased herbivore biomass may be associated with healthier reefs. Higher abundance of large apex-level shark species in Chagos may therefore not just be evidence of lower fishing pressure, but also partly explain the high levels of reef resilience documented in that area [42].

Though I do not challenge the conclusions of Graham et al. [4] that there has been a substantial reduction in total shark abundance in Chagos in past decades, the data suggest that the smaller magnitude of fishing effort has allowed the assemblage to retain a greater abundance of apex level species than in the Australian Shoals which I interpret as corresponding to differences in fishing pressure between the two locations.

Whilst all forms of shark fishing are now banned in Chagos, this is still a relatively young marine reserve. The long generation times of many of the shark species involved suggests that recovery of numbers from past fishing pressure, even with strong enforcement of the no-take MPA, will be necessarily slow [54]. While Edgar et al. [80] identify an age threshold of 10 years for an MPA to become effective, this is with respect to general fish biomass and richness levels, and may not pertain to the k-selected species investigated here. The other success factors identified in that study are 'large size', 'no-take' status, 'isolation by deep water' and 'effective enforcement'. Whilst Chagos clearly meets the first four criteria, enforcement of the no-take status remains a critical issue within the MPA. As such, monitoring the trajectory of reef shark abundance will provide critical feedback as to the effectiveness of MPA management. Smith [54] estimated the rebound potential of grey reef sharks in the Pacific, and calculated population growth rates of 5.4 - 7.8 $\%yr^{-1}$ based on life history parameters and assuming no fishing mortality. The lower estimate implies a 30% increase in abundance in 5 years, with the population doubling within 13 years, suggesting that stereo-BRUVS surveys at 5-year intervals should detect significant changes in reef shark abundance. Robbins [8] and Hisano [9] find that population growth rates for reef sharks are substantially reduced (and become negative) in the presence of fishing mortality, implying that any ongoing fishing pressure should be readily detected by such surveys.

In the absence of baseline data, snapshot surveys such as the Chagos survey can neither measure the absolute health of systems, nor gauge their trajectories. However, use of concurrent stereo-BRUVS samples for two large scale reef systems, in combination with supporting data on their histories and relative exposure to fishing, provide evidence about their *relative* condition and allow us to understand the effects of different levels of fishing pressure on shark assemblages at a broad geographical scale. By assessing the relative health of a little studied site with respect to an area with a better known history of fishing pressure, I have been able to position Chagos along on the spectrum of shark depletion, link this to relative fishing pressure, and establish a fresh baseline against which future change can be measured. With the increasing use of stereo-BRUVS as a standard monitoring technique and the growing number of large scale marine reserves, there is now the opportunity to extend this approach to a global network of sites giving valuable data on the relative conditions of reef shark populations and a measure of the level of human impact across their ranges.

Chapter Two

Drivers of abundance and spatial distribution in a relatively intact reef shark assemblage.

2.1 Summary

Sharks play major roles in structuring marine communities meaning that as shark populations decline globally there are clear implications for ecosystems and the services we derive from them. Understanding drivers of shark distribution and abundance is essential to understanding healthy ecosystems, as well as being needed to design management tools to protect and support the recovery of shark populations. An isolated and relatively pristine marine protected area such as the Chagos Marine Reserve (Chagos) represents a promising location in which to study natural drivers of shark demography.

I used baited underwater video data from 35 sites across Chagos with a range of habitat and depth characteristics. Shark assemblage data were analysed with respect to habitat (e.g. reef type, topography and depth) and biological characteristics (e.g. fish biomass, species diversity and evenness). Shark abundance was correlated to fish biomass, fish species evenness and site depth ($R^2 = 0.43$) while shark species richness ($R^2 = 0.44$) and biomass ($R^2 = 0.40$) were both correlated to fish biomass, fish species richness and reef type. Distance based redundancy analysis showed that assemblage composition was influenced by both habitat and biological factors, with fish biomass, depth and feature type both influencing the relative abundance of species. Orthogonal separation of grey reef sharks and silvertip sharks in the ordination plot indicated habitat partitioning between these closely related species, and observed depth ranges differed significantly. I also found evidence of ontogenetic habitat partitioning, with the mean length of grey reef sharks at the isolated Victory Bank (fork length = 71.1cm ± 3.6cm) significantly smaller than that at the main atolls surveyed (ANOVA $F_{[4,91]} = 6.49$, $p < 0.001$).

The correlation between prey biomass and shark abundance, species richness and biomass can be interpreted as implying that ecosystem-level protection will promote shark population recovery more effectively than species-specific measures that allow ongoing depletion of prey biomass. Since sharks of different species and ages use a wide range of niches defined by habitat and topography and depth, protection of a

comprehensive suite of habitats should also be a fundamental consideration in the design of protection regimes.

2.2 Introduction

As apex predators in marine ecosystems, sharks are believed to influence community structure through their direct impact on prey species abundance and behaviour and the cascading effects this has on lower trophic orders [5,11]. This influence has been compared to observations of predator-prey interactions in terrestrial ecosystems [81] where the removal and subsequent reintroduction of apex predators has resulted in large changes in community composition and habitat [82-84]. The terrestrial experience, together with emerging evidence from marine systems [44], imply that the removal of sharks may have serious effects on the structure and health of the ecosystem.

This structuring role may be of particular importance in coral reef ecosystems given evidence that reef community composition influences the resilience of reefs to stresses and pulse disturbances [6]. Degradation of coral reef ecosystems is of great concern as they support the highest diversity of fishes in the oceans [85] and over half a billion people depend directly on the services they provide [31]. Reefs are affected by a multitude of natural and anthropogenic stressors which often interact in a synergistic manner [32]: atmospheric and oceanic warming resulting from increased atmospheric CO_2 may amplify natural cycles of warming leading to more frequent and severe coral bleaching, and also lead to increased frequency of damaging storms, and the recovery of reefs affected by such pulse disturbances may be being hindered by accelerated algal growth caused by eutrophication from coastal activities. Such combinations of chronic and acute stressors have multiplicative affects on reef ecosystems, leading to dramatic and sometimes irreversible change [33].

With evidence of sharp declines in shark abundances observed around the world in both pelagic and coastal ecosystems, up to 90% reductions over only a few decades [2,3,86], coral reefs would appear to be caught between a matrix of bottom up stressors and the loss of the top down regulation provided by sharks [5]. Restoring the structural integrity and resilience of coral reef ecosystem therefore requires both the mitigation of stressors, to the extent possible, and measures to promote the recovery of shark populations.

To address this issue at the ecosystem level, marine protected areas (MPAs) have been proposed for coral reef systems to substantially limit all extractive activities and preserve or restore both reefs and the species they support [87]. Closing large areas to fishing is normally a decision involving substantial political and economic commitment, and the failure of so-called ‘paper parks’ to achieve their conservation objectives [e.g. 88] has led to some opposition to these comprehensive protection regimes in favour of species-specific or fisheries management interventions such as shark sanctuaries or gear restrictions [89]. Whilst quantifying the impact of MPAs requires data on the effectiveness of enforcement and the rate at which population recovery occurs, designing effective spatial management also needs us to understand the way in which species of conservation interest use MPAs. This requires an understanding of the natural drivers of spatial variation in shark abundance and demography at the assemblage and species level so that design of protection regimes will take account of movement ranges and variations in habitat preferences by species and ontogeny [90-92].

In Chapter One, I compared the overall abundance and composition of the shark and fish assemblage at Chagos to that in a location with a far higher level of fishing pressure. I found Chagos to be relatively pristine in terms of the composition of the shark assemblage despite some evidence of depletion. I now use the Chagos data to model relationships between assemblage indices and individual shark species’ abundances and environmental variables. Specifically, I identify the natural drivers of spatial variations in the abundance, richness and biomass of the Chagos shark assemblage and assess the drivers of species and ontogenetic variations in the shark assemblage composition.

2.3 Materials and Methods

2.3.1 Survey sites

Data analysed in this study were obtained from the Chagos marine reserve in the British Indian Ocean Territory (BIOT), central Indian Ocean (hereafter referred to as Chagos, Figure 1.1a). Chagos is an archipelago of over 60 individual islands, grouped into seven main atolls including the Great Chagos Bank, the largest atoll in the world. The reefs, islands and lagoons lie south of the Maldives between 04°54' to 07°39' S and 70°14' to 72°37' E. Reef and lagoon habitats were sampled across the two northern most atolls, Salomon and Peros Banhos, and along the western edge of the Grand Chagos Bank.

2.3.2 Data collection

Video data for Chagos were collected using stereo baited remote underwater video systems (stereo-BRUVS) [57] during a three week expedition to the region in February and March 2012. The method employed was similar to that used in other stereo-BRUVS studies [66]. Stereo-BRUVS were deployed at 138 sampling points at 13 sites around Chagos that reflected a range of depths (0-80m), habitats (reef/lagoon) and feature types (large atoll, small atoll, submerged atoll, and seamount), and were distributed across the Chagos reserve to allow for analysis of geographical differences. Rigs were baited with crushed pilchards (*Sardinops spp.*) to attract rarer predatory fish that might otherwise not enter the field of view of the cameras. Resident herbivorous fishes are captured in the FOV of the cameras as a result of normal movements about the reef. As a result, stereo-BRUVS bias the reef community sample towards predatory fishes, but in a consistent manner that makes comparison of samples obtained with this methodology valid. Sampling took place throughout the day and across the tide cycle to capture natural variations in the assemblages, and stereo-BRUVS were left to record for at least one hour to ensure that a standard 60 minute sample could be obtained from each site. Stereo-BRUVS were typically deployed in sets of four at each site, with morning, midday and afternoon deployments taking place.

2.3.3 Processing of the stereo-BRUVS samples

Video data was converted into relative abundance (as Max$N$) and length data using the methodology described in section 1.3. The 138 individual samples were allocated to 35 sites based on the location and time of day of the drops. This gave sufficient power for regression analyses whilst reducing the influence of outlying values of individual samples. Mean values per sample for abundance and length were calculated for each site. Species biomass was calculated using Length-Weight conversion parameters, as in Chapter 1. Diversity indices for the fish assemblages associated with each site were calculated as Shannon-Weiner diversity (H’) [93] and Pielou evenness (J) [94].

$$H' = -\sum_{i=1}^{S} p_i \ln{(p_i)}$$

$$J = \frac{H'}{\ln{(S)}}$$

Where p_i the proportion of individuals belonging to species i, and S = total species pool at a sample site.

Additional habitat and environmental variables were obtained from still images taken from the stereo-BRUVS, field logs and GIS data. The final set of variables in the data set comprised four dependent variables related to the shark assemblage (species richness, abundance, length and biomass) and 12 independent variables (including spatiotemporal, habitat and biological variables, Table 2.1).

All analyses were performed using the R statistical software and additional packages. Confidence intervals on means are reported as mean ± 1.96 standard errors.

2.3.4 Data exploration

Data exploration [95] was carried out in R to determine suitable modelling approaches and choice of variables. Scatter plots, box-plots, histograms, pair plots and co-plots were used to check for normality of the data, the presence of outliers, collinearity between explanatory variables and evidence of relationships between response and explanatory variables. The Shapiro-Wilks statistic was used to test the ability of log or square-root transformations to improve the normality of candidate variables in the data. Based on this, shark abundance was transformed using a log(x+1) transformation and fish biomass was square root transformed.

2.3.5 Univariate analyses

Relationships between shark species richness, abundance and biomass and candidate explanatory variables (Table 2.1) for the 35 sampling sites were analysed using multiple linear regression and regression trees [96]. To determine the best linear regression model, variable combinations were tested using the *leaps* function in the R package ‘leaps’ [P3]. The n/10 rule of thumb [97] was used to set the maximum number of independent variable to be included in the model, in this case three, and the adjusted R^2 was used as the measure of model fit. To visualise the goodness of fit, predicted values from the models were plotted against observed values. Regression trees drawn from the same pool of explanatory variables were calculated and plotted using the function *tree* in the R package ‘tree’ [P4].

Table 2.1: Variables used in univariate and multivariate modelling

Dependent variables	Abbreviation	Description
Shark abundance	TA	Max*N* from EventMeasure^{TM}
Shark species richness	SR	Calculated as number of species recorded per sample
Shark length	TL	From EventMeasure^{TM}
Shark Biomass	SB	Shark biomass calculated by species from average measured lengths per sample. Parameters for conversion from Fishbase [68]
Spatiotemporal variables		
Drop time	time	Time BRUV deployed
Drop location	lat, long	GPS position of deployment
Distance from Diego Garcia	distanceDG	Distance from Diego Garcia - used as a proxy for the level of protection afforded by the BIOT Patrol Vessel based there
Tide state	Tide	Tide tables used to calculate state of tide based on drop time: Slack (high/low tide ± 1 hour), Rising, or Falling
Depth of sample	Depth	Depth as measured by vessel sounder at time of stereo-BRUVS deployment
Environmental variables		
Live hard coral cover	LHCpc	Percentage live hard corals visible on still frame extracted from video data, estimated to the nearest 10%
Substrate type	Abiotic	Classification of substrate type into one of six types: High Relief Reef (HRC), Medium Relief Reef (MRC), Low Relief Reef (LRC), Sand Inundated Reef (SIR), Rubble Field (RUB), Sand (SAN)
Topography	GIS topo	Topographical classification from GIS shapefiles [98]. Factor with five levels: Bank, Lagoon, Rim, Shoal and Seamount
Biotic variables		
FishBiomass	FishBio	Aggregate fish biomass calculated by species from average measured lengths per sample. Parameters for conversion from Fishbase [68]
Average Fish Biomass	avgFishBio	Average individual fish biomass (i.e. average weight of fish seen in video sample)
Shannon-Weiner index (fish)	H'	Calculated for teleosts only based on abundance
Peilou species evenness (fish)	J'	Calculated for teleosts only based on abundance
Effective Species richness (fish)	ESRh	Effective species richness calculated from Shannon-Weiner index. Calculated as e^H

2.3.6 Multivariate analyses

Distance-based Redundancy Analysis (dbRDA, using the R function *capscale* in the package “vegan” [P2]) was used to test relationships between a shark assemblage dissimilarity matrix and habitat and biological variables at different sites. A Bray-Curtis dissimilarity measure on square-root transformed abundances was used to reduce the dominance of abundant over rarer species and an iterative process was used to test different combinations of variables with the *capscale* function. Subsets of possible constraining variables were passed to the *capscale* function and the proportion of explained variance was stored for each case. The function iterated through all possible combinations of independent variables and stored the best combination of each of 1 to n variables where n was the size of the variable pool (Appendix 4). Consistent with the linear regression approach, a maximum of three variables was chosen to avoid overfitting the solution. A biplot was used to visualise the results.

To compare the result of a constrained ordination and an unconstrained approach, k-means clustering (R function *kmeans*) was used on untransformed species abundance data to produce unconstrained groups of like sites for which mean species abundances were calculated. This result was superimposed on the ordination bi-plot by plotting star plots at the centroids of the unconstrained site groups.

As depth emerged as an important constraining variable in the ordination plot, the mean depth of observation of each species was calculated and the results plotted by species in descending order (shallowest to deepest) to visualise the separation. ANOVA was used to test whether species had a significant effect on mean encounter depth, and Tukey’s HSD was used to test which species differed significantly.

To test for a relationship between reef type and shark length, ANOVA was carried out on fork length data for grey reef sharks, grouped by reef type obtained from the GIS data set (five categories: atoll rim, atoll lagoon, bank lagoon, drowned atoll and seamount). Differences between treatments were tested using Tukey’s HSD.

2.4 Results

2.4.1 Linear regression analysis

All three univariate attributes of the shark assemblage (species richness, abundance and biomass) were strongly related to fish biomass, with R^2 values of 0.44, 0.44 and 0.40 respectively (Figure 2.1 a-c, Table 2.2 a-c). Examining the model fit by plotting predicted against observed values indicated that the models under-predicted the dependent variable at higher values. To corroborate the regression analysis, the importance of fish biomass as an explanatory variable for all three indices was substantiated by tree analysis, a non linear method, which placed mean fish biomass per sample at the first node in each case, with variables related to habitat and other dimensions of the reef fish assemblage at the lower nodes (Figure 2.1d-f).

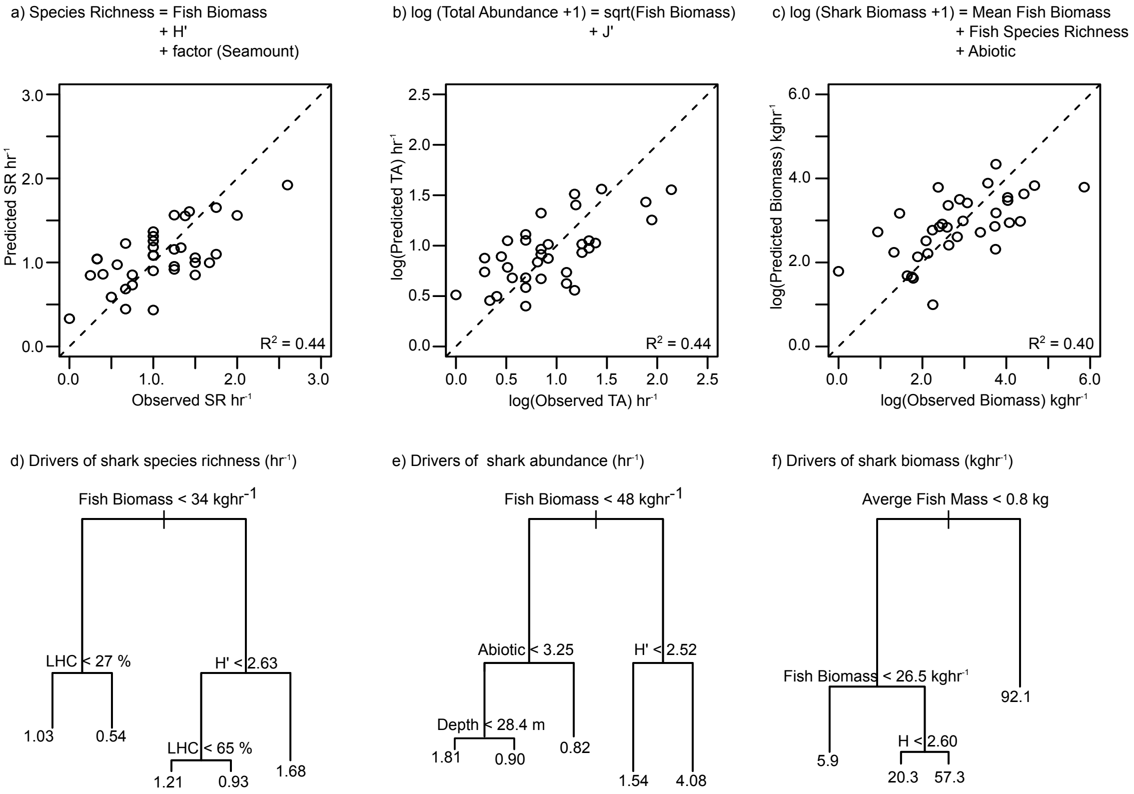

Figure 2.1 Predicted vs. observed values for linear models of a) Species Richness, b) Total Abundance and c) Shark Biomass per hour for Chagos. Tree diagrams below each model plot (d,e,f) show tree based regression results for the same assemblage indices.

Table 2.2: Linear regression model parameters for shark a) abundance, b) richness and c) biomass for the shark in Chagos

a) Shark species richness ~ Fish Biomass + ESRh + Seamount

	Value	t	p
Fish Biomass	0.011	4.017	<0.001
ESRh	0.036	2.481	0.02
seamount	0.647	2.438	0.02
	$R^2 = 0.44$	F = 8.002 on 3,31 df	$P < 0.001$

b) Ln(Shark abundance) ~ sqrt(Fish Biomass) + J

	Value	t	p
sqrt(Fish Biomass)	0.19473	4.759	4e-05
J	1.44036	2.094	0.044
	$R^2 = 0.44$	F = 12.34 on 2,32 df	$P < 0.001$

c) Shark biomass ~ Average Fish Biomass + Total Species Richness + Abiotic

	Value	t	p
Average Fish Biomass	1.61873	2.057	0.048
Abiotic	-0.33135	-2.043	0.050
	$R^2 = 0.40$	F = 6.933 on 3, 31 DF	$P = 0.001$

2.4.2 Multivariate analysis of shark assemblage composition

The results of the distance based redundancy analysis projected the shark assemblage data on two principal axes constrained by fish biomass, depth and a categorical variable for reef type (levels: bank, lagoon, atoll rim, submerged reef or seamount), with the majority of sites distributed along the fish biomass gradient (Figure 2.2). Grey reef sharks had the strongest association with the fish biomass gradient; silvertip sharks had the strongest association with the depth gradient and the topography factor ‘seamount’. Although rarer species observed had less clear associations, with the centroids plotted closer to the origin of the plot, there was alignment between black tip reef sharks and the lagoon habitat. Aggregating the sites into 4 groups using a k-means clustering method and overlaying star plots representing average species abundance in each group showed that the ordination found the natural gradients in assemblage composition associated with the different habitat zones in Chagos (Figure 2.2). Three reef shark species (black tip, white tip and tawny nurse) were a significant component (49%) of shark observations in shallower lagoon and bank habitats, and shallow reefs, but were scarce or absent on deeper sites. Grey reef sharks showed increasing importance along the gradient from lagoon to exposed reef (from 51% to 79% of the assemblage), but was supplanted by silvertip sharks (57%) in the seamount habitat, where hammerhead species (19%), were also a large component of the assemblage.

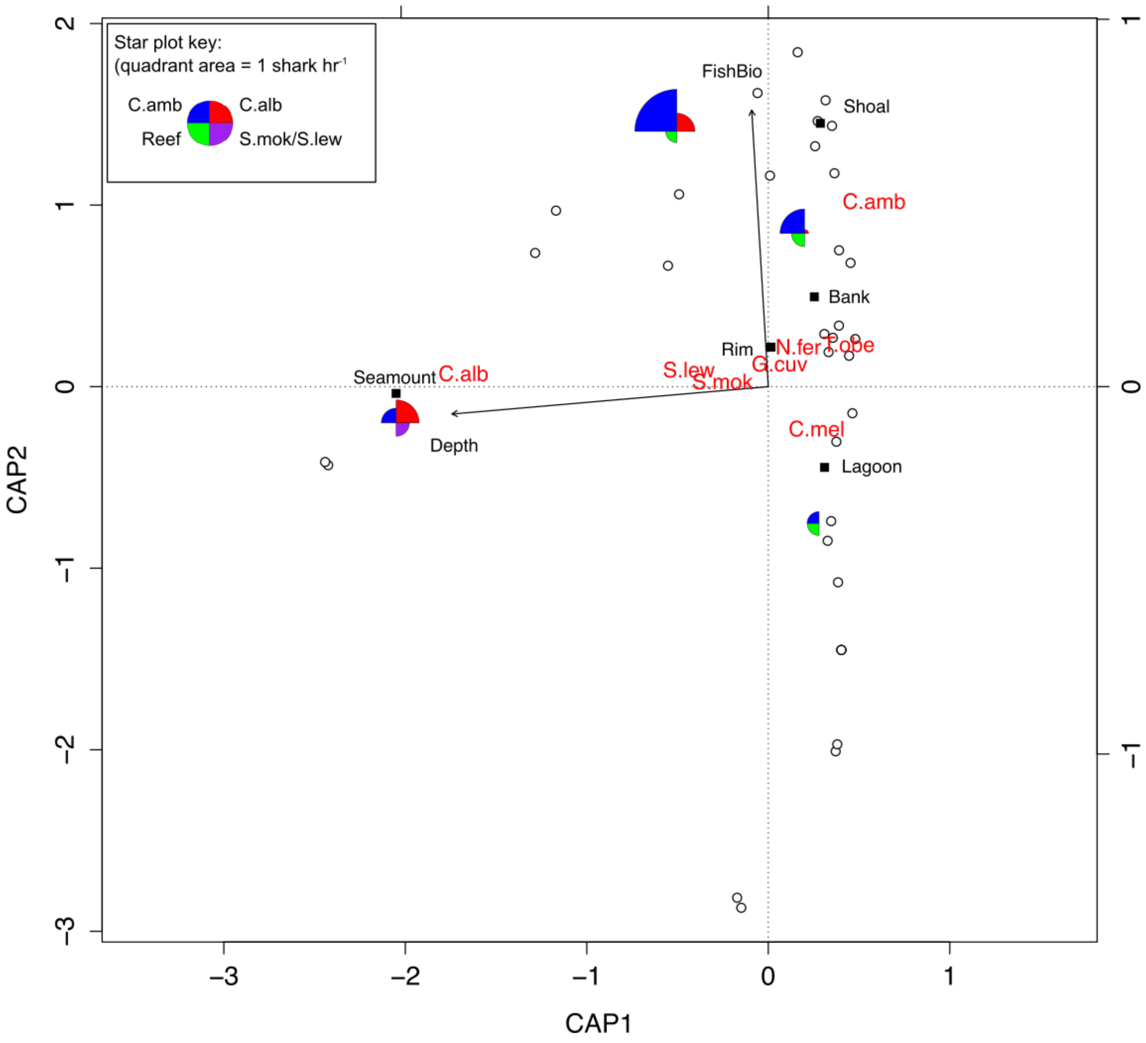

Figure 2.2: Ordination biplot of Bray-Curtis distances between sites using distance based redundancy analysis, with constraining variables (Fish Biomass, Depth and Habitat type) fitted. Star plots have been overlaid representing the mean abundance of species or species groups at the centroids of four unconstrained site clusters. Species abbreviations: C.amb = grey reef shark, T.obe = white tip reef shark, C.alb = silvertip shark, N.fer = tawny nurse, C.mel = black tip reef shark, S.mok = great hammerhead, H.fal = smooth houndshark, G.cuv tiger shark, L.mac = sliteye shark, S.lew = scalloped hammerhead.

2.4.3 Depth preferences amongst shark species

There was evidence of depth partitioning amongst the different shark species in the Chagos data (Figure 2.3). Two of the most abundant reef shark species showed overlapping but distinct depth ranges on the reefs where they were observed, with the mean depth for observation of grey reef sharks 23.6 ± 2.9 (range 6.0 – 73.0) metres, compared with 58.2 ± 13.1 (range 12.0 – 82.2) metres for silvertip sharks ($t = -4.97$, p-value < 0.001). Analysis of variance showed species to be significant in explaining the depth of shark observations (ANOVA $F_{[7,272]} = 33.4$, p-value < 0.001), and Tukey's Highly Significant Difference (HSD) test showed the shallower five species to be significantly different to the deepest three, showing habitat partitioning by depth.

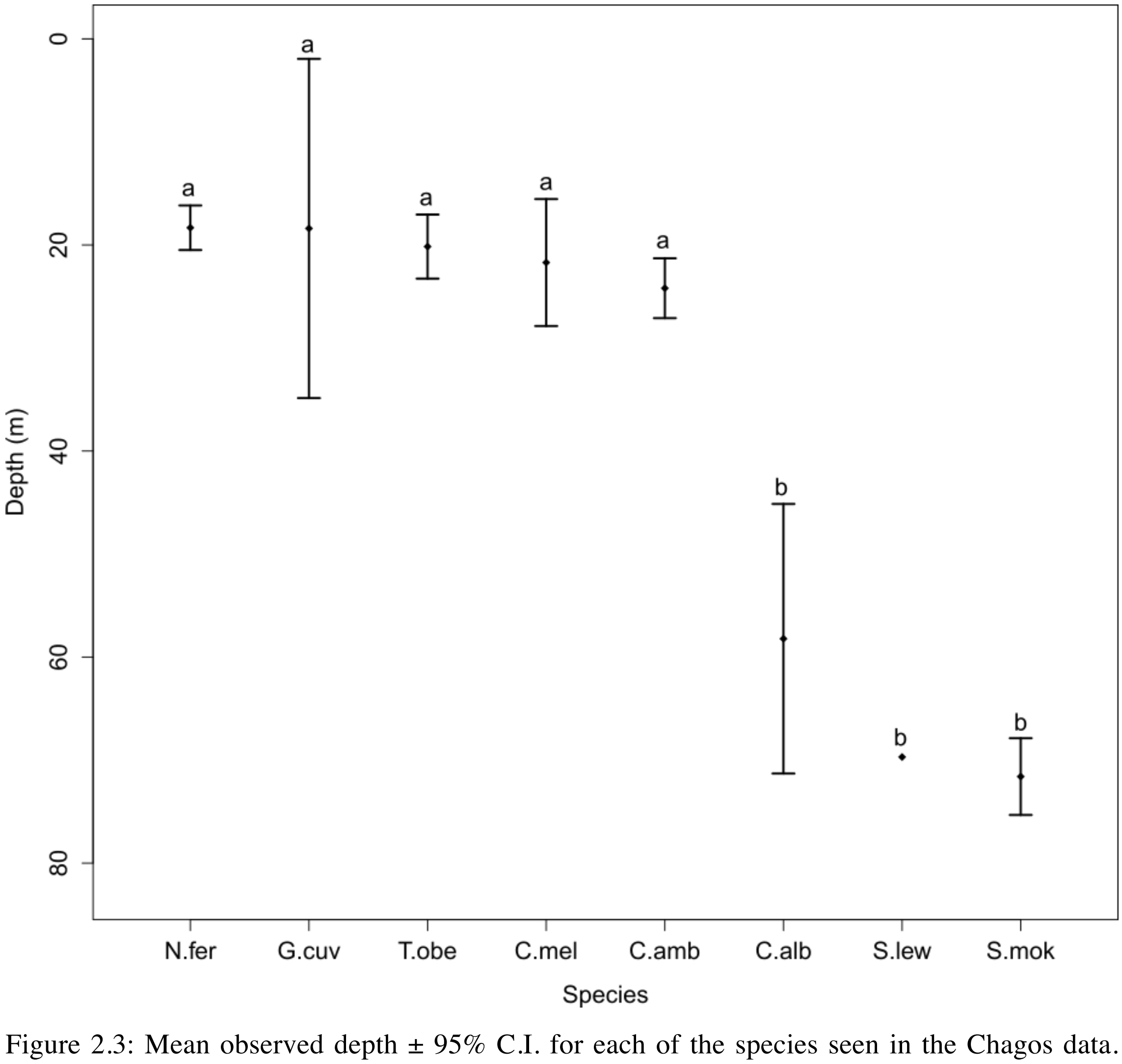

Figure 2.3: Mean observed depth ± 95% C.I. for each of the species seen in the Chagos data. Species abbreviations: N.fer = tawny nurse, G.cuv tiger shark, T.obe = white tip reef shark, C.mel = black tip reef shark, C.amb = grey reef shark, C.alb = silvertip shark, S.lew = scalloped hammerhead, S.mok = great hammerhead. Groups labelled with the same letter are not significantly different in Tukey's HSD test.

2.4.4 Size-specific habitat preferences

Fork length of grey reef sharks differed significantly with reef type (ANOVA $F_{[4,91]}$ = 6.49, $p < 0.001$, Figure 2.4). Tukey's HSD test found that mean length in the reef type 'drowned atoll' (mean 71.2 ± 3.6 cm) was significantly less than in either atoll rim (91.1 ± 6.8 cm) or atoll lagoon (92.0 ± 8.5 cm) habitat. The drowned atoll habitat was associated with the Victory Bank location, a submerged bank between the northern atolls and the Great Chagos Bank (Figure 1.1).

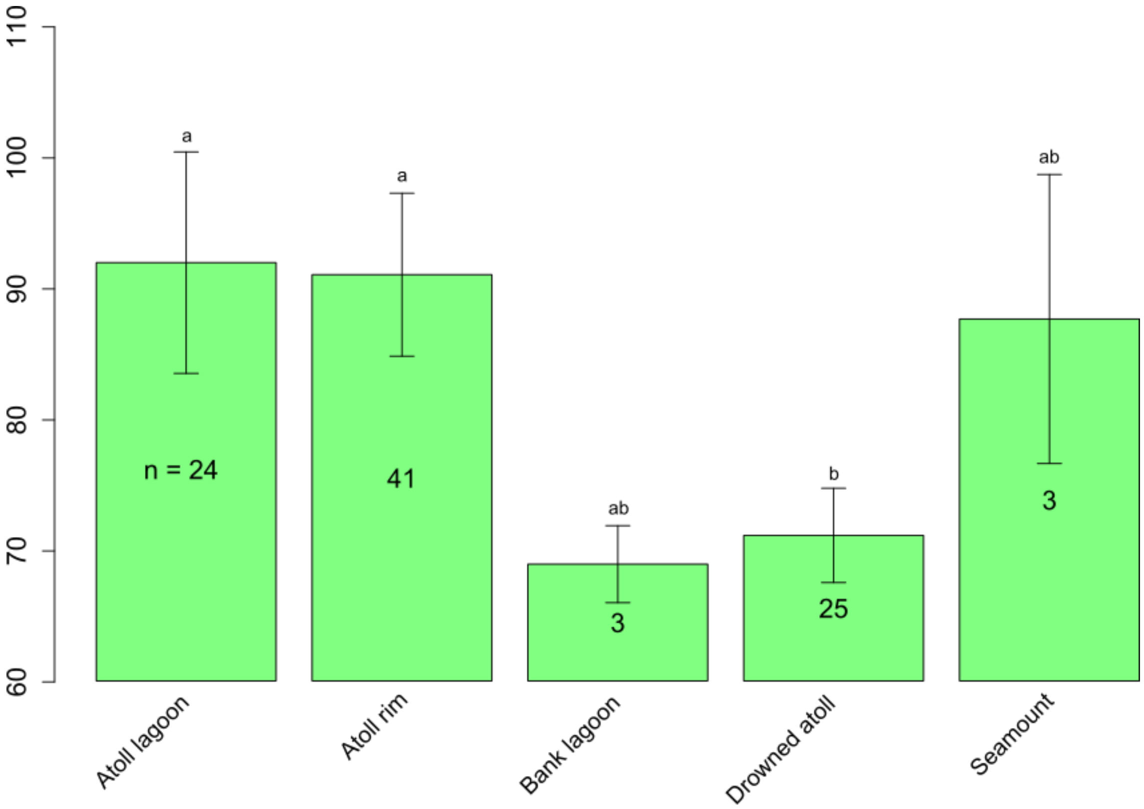

Figure 2.4: Mean length of grey reef sharks by habitat type (error bars ± 95% CI). Groups labelled with the same letter are not significantly different in Tukey's HSD test.

2.5 Discussion

Univariate and multivariate techniques both identified fish biomass as an important driver of both shark assemblage indices and species composition. However, whilst fish biomass was the primary factor driving shark species richness, abundance and biomass, habitat variables emerged as important drivers of the mix of shark species found at a site. Additionally, I found evidence of vertical partitioning by species, particularly between grey reef and silvertip sharks, and evidence suggestive of spatial partitioning by size, possibly reflecting ontogeny, within the grey reef shark population. In the latter case, the observed mean length of 71.2 cm at Victory Bank is comparable to this species size at birth (60-70cm [68]), suggestive of the presence of nursery areas on particular reef types assuming normal growth rates across sites. This hypothesis is supported by anecdotal evidence from subsequent visits to Chagos, where neonate grey reef sharks (umbilical scars still open) were encountered at Victory Bank during an acoustic tagging expedition in 2014. Overall, these results indicate that the shark assemblage varies widely in composition around the reefs of Chagos.

The relationship between overall shark abundance and fish biomass is consistent with other predator-prey studies, both marine and terrestrial, that indicate that models using prey availability are better predictors of large, mobile predators than those using habitat factors alone [99-101]. Heupel et al. [102] found that movement patterns of grey reef sharks in the southern Great Barrier Reef were best modelled using biological factors related to prey availability and reproduction, rather than environmental conditions. A direct implication of this result is that prey removal through fishing, even under conditions where sharks are protected, may have negative effects on reef shark populations. Furthermore, Wirsing et al. [81] suggest that such similarities in relationships between top marine and terrestrial predators and their respective prey implies similar ecological roles, and that lessons should be drawn for marine ecosystems from terrestrial examples such as the impact on ecosystem function of the removal of wolves from their habitats in the US.

The analysis of species-specific and ontogenetic variations across Chagos showed that habitat structure and depth were significant factors in shaping the shark assemblage at different sites around the marine reserve. This is consistent with observations of spatial and resource partitioning and species-specific habitat preferences in the literature, including tagging studies of white tip reef and grey reef sharks at Osprey Reef in the

Coral Sea [90], long line surveys in the French Frigate Shoals [103] and Hawaiian Islands [92], and stereo-BRUVS studies in north west Australia [77]. Sharks at Chagos used a broad spectrum of depth and habitat niches across the varied reef types within the marine reserve. This, together with the presence of habitat as an explanatory variable in the univariate model of species richness discussed above, suggests that the inclusion of a wide variety of habitat zones within the marine reserve is important in supporting the diversity of shark species observed there.

The ontogenetic segregation in the grey reef shark population, with the mean size of individuals found at submerged atoll (Victory Bank) 20 cm smaller than those found on the atolls immediately north of that site, is consistent with studies on this and other species that show changing habitat use with age. For example, Papastamatiou et al. [104] found ontogenetic shifts in habitat use by black tip reef sharks at Palmyra Atoll in the Pacific Ocean, from lagoon shallows to shelf environments, and Heupel et al. [91] found evidence of increased site fidelity amongst juvenile grey reef sharks in the Great Barrier Reef.

The results of this study support the findings of other studies, obtained using a variety of techniques, that mixed species assemblage of sharks require both healthy environments in terms of the prey availability and a wide range of habitat zones to accommodate differing species' habitat preferences and permit resource partitioning and ontogenetic changes in habitat and prey preference. The implication for conservation management aimed at preserving and promoting sharks is that species-specific protection regimes, such as shark sanctuaries, may be less effective if there is continued extraction of the fish biomass occurring, and that no-take areas and other ecosystem scale protection regimes that preserve the biomass and structure of prey communities may be more effective in supporting the recovery of shark populations. This is not to suggest that shark sanctuaries with continued teleost fishing may not be effective but simply that the persistence of unsustainable fishing practices may impair outcomes for shark conservation, even when sharks themselves are not directly targeted. Additionally, the importance of a wide range of habitat zones, and the fact that nominally resident reef species are capable of making long movements between reefs [91], implies that large marine reserves that encompass a wide variety of habitats within the boundaries of the protected area will be more effective in preserving species diversity in the shark assemblage and providing the habitat niches required at different life stages.

Edgar et al. [80] found that effective MPAs shared five key features: they were large, had no fishing, had good enforcement, and were isolated and old. Chagos is still a new reserve but it is a large, protected no take reserve, isolated from neighbouring countries by hundreds of kilometres of deep ocean. The abundant fish biomass its reefs, and the diverse range of habitats contained within its boundaries, from shallow reef flats in the atolls, to soft coral covered seamounts, may be yet another reason why it is expected to remain a hub and refuge of predator biodiversity in the Indian Ocean.

Conclusions

The resilience of marine ecosystems to natural and anthropogenic stresses depends in part on complex interactions between organisms and their habitat, and this is particularly true for the coral reefs that host a disproportionate share of the oceans' biodiversity. Fishing selectively removes elements of food webs, typically large predatory fishes and sharks, potentially destabilising delicately balanced systems and impairing their ability to recover from damage. In many parts of the world, this top-down and bottom-up assault on reefs has led coral to be replaced by algal barrens, and destroyed the fisheries, tourism and coastal protection services provided by healthy reefs. Protecting the health of marine ecosystems is of vital concern, not only to the millions who depend directly on them for livelihoods and the services they provide, but also for humanity as a whole.

There is growing evidence that sharks play a critical role in regulating reef ecosystems, and their systematic removal from oceans has contributed to weakening the resilience of reefs to a host of disturbances, from global warming to floods. Protecting reefs and conserving sharks are therefore fundamentally connected objectives.

I examined the impact of protection from fishing on shark assemblages by comparing a large protected area, Chagos, with a location where shark fishing has occurred on a large scale, and find that protection in Chagos impacts the structure of the shark assemblage, even where hypothesised effects on abundance and richness may not be readily apparent. The fact that no significant differences in shark abundance were detected despite an order of magnitude difference in recorded fishing effort appeared counter-intuitive. However, the differences in the species membership of the assemblage between the heavily and lightly fished locations offer a possible explanation, namely that reductions in the abundance of larger species has been compensated for by growth in the populations of smaller species. Heupel et al. [79] conclude that sharks occupy different trophic levels depending on both ontogeny and species, therefore removal of larger shark species may initiate a 'meso-predator release' within the shark assemblage as smaller individuals and species benefit from reduced competition and predation risk. A similar response to disturbance has been observed in reef fish assemblages where measures of abundance and species richness have remained unchanged despite a phase shift in assemblage composition [78]. My results suggest that these measures may also not detect disturbances in reef shark assemblages, where similar shifts in assemblage membership may occur, and that multivariate dimensions of species composition are also required to detect differences in fishing pressure. It should also be noted that an additional explanation of the lack of a significantly greater abundance of sharks in the Chagos marine reserve is the fact that these data were collected less than two years after formal protection began in October 2010. Grey reef sharks, for example, are mature at about 7 years with population doubling occurring after 13 years [54], meaning that sufficient time may not yet have passed to see measurable increase in shark numbers.

Based on the results from chapter one, I decided to use the Chagos Marine Reserve to model spatial drivers in a relatively intact shark assemblage. Modelling of assemblage indices and species composition identified fish biomass as the principal driver of assemblage metrics, with reef type and depth shaping the species mix. This accords with findings in the literature from studies of a variety of ecosystems and species: Prey biomass has been found to be an important predictor of predator distribution in both terrestrial and marine environments [99-101], and species specific and ontogenetic variations in habitat use have been described in studies of individual species and assemblages using a variety of survey methods [90-92,103,104]. These suggest that large fully protected areas promote sharks not only through the reduction of direct fishing mortality, but also through the protection they give to their prey and the broad spectrum of habitat niches they provide, as well as the direct protection from fishing mortality that they offer.

Understanding the function of marine ecosystems is complex. In this study, for example, the comparison of trophic pyramid structure in chapter one suggests that sharks influence meso-predator biomass, whilst prey (fish) biomass appears as an explanatory variable for shark abundance in chapter two. Sharks' diverse diets are certainly one explanation of how these two results can be reconciled, but it does go to show that relationships in marine food webs may be anything but simple, and the unpredictable feedback loops between trophic levels that follow from this mean that modelling the impact of population changes of a species or group of species will be fraught with challenges. Similarly, deciding on management actions based on the findings of studies is far from straightforward.

Management actions to support existing and recovering shark populations, and the ecosystems of which they form part, may take many forms depending on the specific economic, political and physical environment. Species specific fisheries management, for example through gear changes or quotas and trade restrictions, is a widely applied set of tools, as are more restrictive spatial management measures such as total or seasonal closures of areas or the creation of shark sanctuaries. Large no take reserves, involving the permanent closure of entire reef systems to fishing, may only be applicable under certain conditions, but my findings indicate that such large scale, no-take reserves may be the best means of restoring depleted reef shark populations and suggest that monitoring of these areas needs to take into account attributes of the reef shark assemblage as a whole in determining the effects of protection.

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Appendix 1: Shark fishing data from Chagos and the Australian Shoals

a) Chagos longline shark bycatch 2005-2010; source: Mees et al. [12]

Year	Sharks (t)
2005/2006	56.8
2006/07	14.4
2007/08	18.1
2008/09	16.4
2009/10	71.4
Mean	35.4

b) Chagos IUU fishing data

Species		Abundance in 11 catches*	Percent	Est. Catch tonnes yr^{-1} **
Blacktip shark	*Carcharhinus spp.*	244	30.2	21.4
Grey reef shark	*Carcharhinus amblyrhynchos*	208	25.7	18.2
Oceanic whitetip shark	*Carcharhinus longimanus*	94	11.6	8.2
White tip reef shark	*Carcharhinus spp.*	94	11.6	8.2
Blue shark	*Prionace glauca*	46	5.7	4.0
Hammerhead shark	*Sphyrna spp.*	37	4.6	3.2
Tiger shark	*Galeocerdo cuvier*	30	3.7	2.6
Silvertip shark	*Carcharhinus spp.*	28	3.5	2.5
Silky shark	*Carcharhinus spp.*	21	2.6	1.8
Bronze whaler shark	*Carcharhinus spp.*	4	0.5	0.4
Thresher shark	*Alopias spp.*	2	0.2	0.2
Bull shark	*Carcharhinus leucas*	1	0.1	0.1
Total				70.8

* Catch composition from Martin et al. [13]

** Total catch estimate based on catch per vessel from Martin et al. [13] and annual vessel totals from Price et al. [14].

c) North west Australia shark fishing data

Species		Catch (tonnes) 2001	2002	2003	2004	2005	2006	2007-9 (mean)	Mean 2000-9
Blacktip shark	*Carcharhinus spp.*	47	185	178	40	78	76	67	90
Sandbar (thickskin)	*Carcharhinus plumbeus*	79	72	88	209	762	0	63	155
Lemon shark	*Negaprion acutidens*	15	26	57	24	62	7	15	26
Hammerhead shark	*Sphyrna spp.*	23	43	45	33	114	27	28	41
Tiger shark	*Galeocerdo cuvier*	34	37	43	51	81	12	34	40
Pigeye shark	*Carcharhinus amboinensis*	29	25	32	43	83	43	46	44
Shovelnose/fiddler rays	*Rhinobatidae, Rhynchobatidae*	3	11	11	8	32	5	3	9
Grey reef shark	*Carcharhinus amblyrhynchos*	7	6	7	9	8	1	0	4
'Bronze whaler' shark	*Carcharhinus obscurus*	9	6	7	17	36	0	4	10
Spot-tail shark	*Carcharhinus sorrah*	0	0	3	0	0	0	12	4
Other sharks/rays		26	45	19	156	46	18	6	37
Total		272	456	490	590	302	189	278	459

Appendix 2: Diet classification of species

Species	Diet	Species	Diet
Abalistes stellatus	Carnivore	*Carangoides gymnostethus*	Carnivore
Acanthurus dussumieri	Detritivore	*Carangoides orthogrammus*	Carnivore
Acanthurus grammoptilus	Herbivore	*Carangoides plagiotaenia*	Carnivore
Acanthurus leucocheilus	Detritivore	*Caranx ignobilis*	Carnivore
Acanthurus leucosternon	Detritivore	*Caranx lugubris*	Carnivore
Acanthurus maculiceps	Detritivore	*Caranx melampygus*	Carnivore
Acanthurus mata	Planktivore	*Carcharhinus albimarginatus*	Carnivore
Acanthurus nigricans	Herbivore	*Carcharhinus amblyrhynchos*	Carnivore
Acanthurus olivaceus	Detritivore	*Carcharhinus melanopterus*	Carnivore
Acanthurus tennenti	Detritivore	*Centropyge bicolor*	Herbivore
Acanthurus thompsoni	Planktivore	*Centropyge multispinis*	Herbivore
Acanthurus tristis	Detritivore	*Centropyge tibicen*	Herbivore
Acanthurus xanthopterus	Detritivore	*Centropyge vroliki*	Herbivore
Aethaloperca rogaa	Carnivore	*Cephalopholis argus*	Carnivore
Aipysurus laevis	Carnivore	*Cephalopholis leopardus*	Carnivore
Alepes vari	Carnivore	*Cephalopholis nigripinnis*	Carnivore
Aluterus scriptus	Detritivore	*Cephalopholis spiloparaea*	Carnivore
Amblyglyphidodon leucogaster	Herbivore	*Cephalopholis urodeta*	Carnivore
Anampses lineatus	Planktivore	*Cetoscarus bicolor*	Herbivore
Anampses meleagrides	Planktivore	*Chaetodon auriga*	Corallivore
Anampses twistii	Planktivore	*Chaetodon falcula*	Carnivore
Aphareus furca	Carnivore	*Chaetodon guttatissimus*	Corallivore
Apolemichthys trimaculatus	Carnivore	*Chaetodon kleinii*	Corallivore
Aprion virescens	Carnivore	*Chaetodon lineolatus*	Corallivore
Atule mate	Carnivore	*Chaetodon lunula*	Corallivore
Balistapus undulatus	Carnivore	*Chaetodon madagaskariensis*	Corallivore
Balistoides conspicillum	Carnivore	*Chaetodon meyeri*	Corallivore
Balistoides viridescens	Carnivore	*Chaetodon trifascialis*	Corallivore
Bodianus axillaris	Carnivore	*Chaetodon trifasciatus*	Corallivore
Bodianus bilunulatus	Carnivore	*Chaetodon zanzibarrensis*	Corallivore
Bodianus diana	Carnivore	*Cheilinus chlorourus*	Carnivore
Caesio cuning	Planktivore	*Cheilinus fasciatus*	Carnivore
Caesio teres	Planktivore	*Cheilinus trilobatus*	Carnivore
Caesio xanthonota	Planktivore	*Chlorurus bleekeri*	Herbivore
Cantherhines dumerilii	Carnivore	*Chlorurus sordidus*	Herbivore
Canthigaster valentini	Herbivore	*Chlorurus strongylocephalus*	Herbivore
Carangoides coeruleopinnatus	Carnivore	*Chromis dimidiata*	Planktivore
Carangoides ferdau	Carnivore	*Chromis margaritifer*	Planktivore
Carangoides fulvoguttatus	Carnivore	*Chromis opercularis*	Planktivore

Chromis ternatensis	Planktivore	*Lethrinus enigmaticus*	Carnivore
Chromis viridis	Planktivore	*Lethrinus erythracanthus*	Carnivore
Chromis weberi	Planktivore	*Lethrinus microdon*	Carnivore
Cirrhilabrus exquisitus	Planktivore	*Lethrinus nebulosus*	Carnivore
Cirrhilabrus sp1	Planktivore	*Lethrinus olivaceus*	Carnivore
Cirrhilabrus sp2	Planktivore	*Lethrinus ornatus*	Carnivore
Coris batuensis	Carnivore	*Lethrinus ravus*	Carnivore
Coris gaimard	Carnivore	*Lethrinus rubrioperculatus*	Carnivore
Ctenochaetus striatus	Detritivore	*Lethrinus sp1*	Carnivore
Ctenochaetus truncatus	Detritivore	*Lutjanus bohar*	Carnivore
Dascyllus aruanus	Carnivore	*Lutjanus gibbus*	Carnivore
Dascyllus carneus	Planktivore	*Lutjanus rivulatus*	Carnivore
Dascyllus reticulatus	Planktivore	*Macolor macularis*	Carnivore
Dasyatis kuhlii	Carnivore	*Macolor niger*	Carnivore
Echeneis naucrates	Carnivore	*Macropharyngodon bipartitus*	Carnivore
Elagatis bipinnulata	Carnivore	*Malacanthus brevirostris*	Carnivore
Epibulus insidiator	Carnivore	*Malacanthus latovittatus*	Carnivore
Epinephelus fasciatus	Carnivore	*Melichthys indicus*	Carnivore
Epinephelus merra	Carnivore	*Melichthys niger*	Planktivore
Epinephelus multinotatus	Carnivore	*Monotaxis grandoculis*	Carnivore
Epinephelus polyphekadion	Carnivore	*Naso brachycentron*	Planktivore
Fistularia commersonii	Carnivore	*Naso brevirostris*	Planktivore
Forcipiger flavissimus	Carnivore	*Naso elegans*	Herbivore
Genicanthus lamarck	Planktivore	*Naso hexacanthus*	Planktivore
Gnathanodon speciosus	Carnivore	*Naso lituratus*	Herbivore
Gomphosus caeruleus	Carnivore	*Naso lopezi*	Planktivore
Gymnocranius grandoculis	Carnivore	*Naso unicornis*	Herbivore
Gymnosarda unicolor	Carnivore	*Naso vlamingii*	Planktivore
Gymnothorax javanicus	Carnivore	*Nebrius ferrugineus*	Carnivore
Halichoeres hortulanus	Carnivore	*Odonus niger*	Carnivore
Halichoeres zeylonicus	Planktivore	*Oxycheilinus digramma*	Carnivore
Hemitaurichthys zoster	Planktivore	*Oxycheilinus digrammus*	Carnivore
Heniochus acuminatus	Planktivore	*Oxycheilinus sp1*	Carnivore
Heniochus singularius	Corallivore	*Oxycheilinus unifasciatus*	Carnivore
Hipposcarus harid	Herbivore	*Paracirrhites arcatus*	Carnivore
Hologymnosus doliatus	Carnivore	*Paracirrhites forsteri*	Carnivore
Labrichthys unilineatus	Corallivore	*Parapercis millepunctata*	Carnivore
Labroides bicolor	Carnivore	*Parapercis signata*	Carnivore
Labroides dimidiatus	Carnivore	*Parapercis sp1*	Carnivore
Lethrinus amboinensis	Carnivore	*Parupeneus barberinus*	Carnivore
Lethrinus atkinsoni	Carnivore	*Parupeneus cyclostomus*	Carnivore
Lethrinus conchyliatus	Carnivore	*Parupeneus macronemus*	Carnivore

Parupeneus multifasciatus	Carnivore
Parupeneus pleurostigma	Carnivore
Parupeneus trifasciatus	Carnivore
Plagiotremus tapeinosoma	Carnivore
Platax teira	Carnivore
Plectroglyphidodon dickii	Herbivore
Plectroglyphidodon johnstonianus	Corallivore
Plectroglyphidodon lacrymatus	Herbivore
Plectropomus areolatus	Carnivore
Plectropomus laevis	Carnivore
Plectropomus leopardus	Carnivore
Plectropomus pessuliferus	Carnivore
Pomacanthus imperator	Carnivore
Pomacentrus caeruleus	Planktivore
Pomacentrus coelestis	Herbivore
Pomacentrus indicus	Planktivore
Pomacentrus nagasakiensis	Herbivore
Pseudanthias squamipinnis	Planktivore
Pseudobalistes flavimarginatus	Carnivore
Pseudobalistes fuscus	Carnivore
Pseudocheilinus evanidus	Carnivore
Pseudocoris heteroptera	Planktivore
Pseudodax moluccanus	Herbivore
Pseudojuloides kaleidos	Carnivore
Pseudojuloides severnsi	Detritivore
Pterocaesio digramma	Planktivore
Pterocaesio pisang	Planktivore
Pterocaesio tile	Planktivore
Pygoplites diacanthus	Carnivore
Scarus atrilunula	Herbivore
Scarus forsteni	Herbivore
Scarus ghobban	Herbivore
Scarus niger	Herbivore
Scarus oviceps	Herbivore
Scarus prasiognathos	Herbivore
Scarus rubroviolaceus	Herbivore
Scarus schlegeli	Herbivore
Scarus tricolor	Herbivore
Scolopsis bilineata	Carnivore
Scolopsis xenochrous	Carnivore
Scomberoides tol	Carnivore
Scomberomorus commerson	Carnivore
Siganus argenteus	Detritivore
Sphyrna mokarran	Carnivore
Sufflamen bursa	Carnivore
Sufflamen chrysopterum	Carnivore
Sufflamen fraenatum	Carnivore
Symphorus nematophorus	Carnivore
Taeniura lymma	Carnivore
Thalassoma amblycephalum	Planktivore
Thalassoma hebraicum	Carnivore
Thalassoma jansenii	Carnivore
Thalassoma lunare	Carnivore
Triaenodon obesus	Carnivore
Variola albimarginata	Carnivore
Variola louti	Carnivore
Zanclus cornutus	Carnivore
Zebrasoma desjardinii	Herbivore
Zebrasoma scopas	Herbivore

Appendix 3: Comparison of Chagos and Australian Shoals sites based on coral cover and habitat type

	n	Mean depth m	Abundance hr^{-1}				Species richness hr^{-1}	Encounter rate %
			All sharks	Grey Reef	Silvertip	White tip reef		
Chagos low coral average	40	24.0	1.98	1.40	0.00	0.30	1.23	85
Chagos submerged bank average	16	19.9	2.69	2.38	0.00	0.19	1.19	88
Aus. Shoals Mean	248	33.1	2.06	1.10	0.08	0.70	1.23	75

Appendix 4: R code for testing alternative constrained ordinations based on subsets of constraining variables

```
# Function to test adjR2 of various capscale models using all
possible variable combinations.
# Requires function combn() from package {combinat}
# Requires package {vegan}

#  install.packages("vegan")
#  install.packages("combinat")

capscalePermTest = function(x, y, measure = "bray") {

  # x is a matrix of species abundances by site
  # y is a set of constraining variables for the same set of
sites

  require(vegan)
  require(combinat)

  n = min(ncol(y),nrow(y)-2)
  n.names = ncol(y)
  varList = cbind(seq(1:ncol(y)),names(y))
  combArray = NULL
  bestInert = 0
  #   print(paste(n, "Variables to select"))
  #   print(paste("From ",n.names," possible"))


  # Loop through possible 1 to n variable combinations
  # and store the variable names with highest R2adj for each
level

  if (n > 1) {
    MaxR2adj = 0
    #     print(paste("iteration = ",1))
    for (j in 1:n.names) {
      BRUV.spe.cps = capscale(x ~ y[,j], distance = measure)
```

```
      R2adj = RsquareAdj(BRUV.spe.cps)$adj.r.squared
      #inert = BRUV.spe.cps$CCA$tot.chi/(BRUV.spe.cps$CCA$tot.chi
+ BRUV.spe.cps$CA$tot.chi)


      if (R2adj > MaxR2adj) {
        MaxR2adj = R2adj
        bestVar = j
        #bestInert = inert
      }
    }
    resultsArray = rbind(round(MaxR2adj,3))
    variablesArray = rbind(varList[bestVar,2])
    #inertArray = rbind(round(max(0,bestInert), 3))
    #     print(resultsArray)
    #     print(variablesArray)

    for (i in 2:n) {
      print(paste("iteration = ",i))
      MaxR2adj = 0
      combArray = as.data.frame(combn(n.names, i))
      #       print(combArray)
      for (j in 1:(ncol(combArray))) {
        varArray = combArray[,j]
        BRUV.spe.cps = capscale(x ~ ., y[,varArray], distance =
measure)
        R2adj = RsquareAdj(BRUV.spe.cps)$adj.r.squared
        #inert =
BRUV.spe.cps$CCA$tot.chi/(BRUV.spe.cps$CCA$tot.chi +
BRUV.spe.cps$CA$tot.chi)

        if (R2adj > MaxR2adj) {
          MaxR2adj = R2adj
          bestVar = varArray
          #bestInert = inert
        }
      }

      resultsArray = rbind(resultsArray,round(MaxR2adj,3))
      variablesArray = rbind(variablesArray,do.call(paste,
as.list(varList[bestVar,2])))
      #inertArray = rbind(round(max(0,bestInert), 3))
      #       print(resultsArray)
      #       print(variablesArray)
    }

  } else {

    MaxR2adj = 0
    for (j in 1:n.names) {
      BRUV.spe.cps = capscale(x ~ y[,j], distance = measure)
      R2adj = RsquareAdj(BRUV.spe.cps)$adj.r.squared
      #inert = BRUV.spe.cps$CCA$tot.chi/(BRUV.spe.cps$CCA$tot.chi
+ BRUV.spe.cps$CA$tot.chi)

      if (R2adj > MaxR2adj) {
        MaxR2adj = R2adj
        bestVar = j
        #bestInert = inert
      }
    }
    resultsArray = rbind(round(MaxR2adj,3))
```

```
    variablesArray = rbind(varList[bestVar,2])
    #inertArray = rbind(round(max(0,bestInert), 3))
  }

  results = data.frame(seq(1:n), variablesArray, resultsArray)
  colnames(results) = c("num","var","R2adj")
  rownames(results) = seq(1:length(resultsArray))
  results$var = as.character(results$var)

  cat(paste("***Best R2adj values of combinations of up to ",n,"
variables***"))
  cat("\n\n")
  print(results, right = FALSE)
  cat("\n")
  bestVars = unlist(strsplit(results[which(results$R2adj ==
max(results$R2adj)),2], split =" "))
  print(bestVars)
  bestModel = capscale(x ~ ., y[,bestVars], distance = measure)

  trialList = list("resTable" = results , "bestModel" =
bestModel, "bestVars" = bestVars)


}
```