Assessing elasmobranch populations at Hurawalhi Island Resort (Maldives)

MAR533 Marine Conservation Project
MSc Marine Conservation

Author: Francesca Waters
Project supervisors: Dr Robert Puschendorf, Tamaryn Sawers and Frances Budd

18.09.2023

Acknowledgements

The Ministry of Fisheries, Marine Resources and Agriculture, the Ministry of Defence and the Maldives Civil Aviation Authority provided the research permit and approvals to conduct drone operations. The Ministry of Environment have granted Hurawalhi Island Resort candidacy for 'Other Effective Conservation Measures' status in September 2022.

Executive summary

Following elasmobranch (shark and ray) global declines, sanctuaries (no-take marine reserves) have been designated as a conservation measure. The Maldives shark and ray sanctuary was implemented in 2010 to stop the rapid decline of shark species, caused primarily from overfishing of the regions' multiple shark fisheries. The paucity of monitoring data since the implementation has impacted the ability to determine the efficacy of the sanctuary. Baseline data is crucial to begin long-term monitoring to assess changes in community dynamics, and therefore, to determine species recovery. Understanding the influence of environmental variables is also useful to improve localised conservation measures for these species.

This paper presents information on elasmobranch communities surrounding Hurawalhi Island Resort, Lhaviyani Atoll (Maldives). Hurawalhi Island Resort is surrounded by lagoon, reef and sandflat habitat types where elasmobranchs are frequently sighted. Over a 6-week period, four sites were surveyed using the roving diver technique that targeted lagoon and reef habitat types. From 170 sightings, ten species were identified including three sharks (*Carcharhinus melanopterus, Carcharhinus amblyrhynchos* and *Nebrius ferrugineus*), four sting rays (*Pastinachus sephen, Urogymnus asperrimus, Pateobatis jenkinsii* and *Taeniura meyeni)*, two mobula rays (*Mobula kuhlii and Mobula alfredi*) and one eagle ray (*Aetobatus ocellatus*). Shannon Weiner Diversity Index (0.44), mean species richness (1.67) and Pielou's evenness (0.67) were recorded. These values suggest a low elasmobranch diversity according to the index as well as in comparison to other elasmobranch community research. The lagoon habitat type was found to have higher elasmobranch diversity (0.54) compared to reef habitat type (0.35). However, with further investigation, differences in diversity values within the habitat types varied greatly. This indicates that habitat type was not an influential factor for species diversity, and instead it is suggested that prey abundance in each site holds higher importance. It should be noted that nine species of the species recorded are listed in the Threatened categories in the IUCN Red List, indicating Hurawalhi's Island Resorts current importance to these species. These diversity indices can be applied to calculate long term changes of species diversity in future monitoring of the study area.

Relative abundance calculations of 1.68 elasmobranchs/hour, 1.55 sharks/hour and 1.15 rays/hour were recorded. The influence of the following environmental variables on relative abundance was investigated; tidal phase, tide hight, tidal range, moon phase, time of day, temperature, wind direction and speed. The time of day emerged as the only significant environmental predictor impacting elasmobranch abundance. Higher activity rates at crepuscular periods were associated with (1) foraging behaviour due to their sensory advantage in low light conditions compared to prey species and (2) movement into shallow warmer water to aid with digestion. Disturbance during these periods may impact daily energetic budgets and therefore, reducing anthropogenic

activity should be considered in the construction of resort conservation strategies. Other environmental variables should be reassessed at species level when the sample size increases with future monitoring.

Unmanned remote vehicle surveys have proven effective to offer insights into elasmobranch diversity and density in shallow sandflat habitats. Only *C. melanopterus* were identified in this habitat, calculating a mean density of 0.656 individuals/km^2 (*SE* 0.13). The majority of *C. melanopterus* detected were juveniles (<100cm), ranging from 38.1 cm - 114.4 cm with a mean total length of 57 cm. The shallow sandflat habitat was identified as a key habitat for juvenile *C. melanopterus,* which was assumed to be utilised to minimise the risk of predation. The high temperatures experienced by habitats with shallow water depth may rise over juvenile *C. melanopterus* thermal tolerance as a result of climate change. Ultimately this may impact survival rates and therefore, the *C. melanopterus* population. Introduction of shading to the sandflat habitat around the island could be explored to reduce water temperature whilst maintaining the predation protection provided by the shallow water depth.

Overall, this work demonstrates a relatively simple methodology to assess elasmobranch communities and populations generating baseline data for long-term monitoring. Assessing spatial distribution and the drivers of movement on a local scale will be valuable in understanding species responses to future changes in environmental conditions in the context of stressors such as climate change.

Impact summary

Sharks and rays play an important ecological role in maintaining tropical coastal habitat health by controlling other species' abundance, distribution and diversity. These large marine megafauna are also an important aspect of the Maldives tourism industry and therefore, for both of these reasons, conserving shark and ray population is a high priority for resorts. The reduction in shark numbers caused primarily by the expansion of shark fisheries led to the declaration of the Maldives shark sanctuary in 2010. This legislation restricts all fishing of shark and ray species with-in the exclusive economic zone (EEZ). There is, however, little research on the success of this conservation strategy. To determine the efficacy of national and local conservation measures, it is crucial to gather baseline data of shark and ray species diversity and relative abundance to begin long-term monitoring.

This study generates baseline data of the shark and ray populations around a resort island in the Maldives. This includes the assessment of relative species abundance, spatial distribution and diversity, and explores which environmental factors influence the patterns found. Juvenile blacktip reef sharks are regularly sighted in shallow waters around the island. This study provides a methodology to calculated shark density and to measure size to confirm their life stage, using an unmanned aerial vehicle (drone).

This project was undertaken in collaboration with the Manta Trust's Maldives Manta Conservation Programme (MMCP) which is a Maldivian charity that co-ordinates and conducts research to conserve manta rays and their close relatives. This study operated from Hurawalhi Island Resort, Lhaviyani Atoll, a partner of the MMCP, and alongside Prodivers dive centre, who are also located on the resort island. Hurawalhi Island Resort was also named a candidate for the 'Other Effective area-based Conservation Measures' (OECM) by the Ministry of the Environment. An OECM is an area that is achieving the long-term and effective conservation of biodiversity outside of national marine protected areas. OECM's are managed at a local scale and therefore, to achieve the OECM status, the resort must provide ecological survey data and a management plan with objectives of long-term positive conservation outcomes. If successful, Hurawalhi Island Resort will be the first OECM designated in the Maldives and pave the way for a network of OECMs submitting specific elasmobranch surveys to aid in the national assessment for sharks and rays.

The data from this research found that although assessment of the shark and ray diversity was low, all sites were used by shark and ray species that are considered as Threatened according to the ICUN Red List. Therefore, conservation decisions and protection should be inclusive for all locations surveyed in the resorts' conservation management plan. High abundances were recorded in the morning and evening periods, which could feed into spatial planning and timing of water activities and boat traffic. By avoiding these times of high abundance, the resort could reduce disturbing foraging or resting activities of the local elasmobranch population. Finally, juvenile blacktip reef sharks were found in high numbers using shallow marine environment around the island, potentially identifying the area as an Important Shark and Rays Area (ISRA).

This work is important to the MMCP as the relatively simple methodology has generated the baseline data for long term monitoring of these populations. Furthermore, the data collected from this study was used in the OECM application to supplement the fish surveys and provide information to improve the conservation management plan.

Introduction

Elasmobranchs (sharks and rays) have a high economic and ecological global importance, playing a vital role in the trophic dynamics of marine ecosystems (Bornatowski *et al*., 2014; Frisch *et al*., 2016). Shark and ray diving tourism has been recognised as an economical avenue for many countries, attracting over 600,000 tourists globally (Cisneros-Montemayor *et al.*, 2013; Martin and Hakeem, 2006). These species, however, are highly vulnerable to overfishing, with over a third now included as Threatened according to the ICUN Red List (ICUN, 2022). Their K-selected life history traits contributing to their vulnerability include low fecundity, slow growth rates, long gestation period and late maturity (Cortés, 2000; Stevens *et al*., 2000). Following global declines over the last few decades, a variety of elasmobranch conservation measures have been introduced (Musick *et al*., 2000; MacKeracher *et al.*, 2019). Notably of which are elasmobranch sanctuaries (Ward-Paige and Worm, 2017).

The Maldives is an archipelago in the Indian ocean that experienced a rapid decline of elasmobranch populations in the region (Davidson, 2012). The archipelago spans 820km north to south, the 26 host various habitats such as coral reefs, seagrass meadows and lagoons, with a previously rich diversity of elasmobranchs (Andréfouët *et al*., 2006; Andréfouët *et al*., 2012; Gischler *et al.*, 2014; Saleem and Nileysha, 2011). The main cause of the decline was the over exploitation by the multiple shark fisheries which stimulated the designation a shark sanctuary in 2010 (Ali and Sinan, 2015; Anderson and Ahmed, 1993; The President's Office, 2010). This conservation measure therefore prohibits fishing, possession, trade and sale of all sharks, rays, skates and sawfish within the economic exclusive zone (916,189 km^2).

After recent assessments, the blacktip reef shark (*Carcharhinus melanopterus*) has been identified as one of the most abundant elasmobranch species in the Maldives archipelago (Dryden *et al*., 2020). Their small home range of 0.5km and unique natural markings on *C. melanopterus* fins can be used effectively to recognise individuals within a geographic population (Mukharror *et al*., 2019; Papastamatiou *et al*., 2009). This species has been listed as globally Vulnerable on the IUCN red list, with a globally decreasing species population trend (Simpfendorfer *et al*., 2020). This calls for a focus for a detailed assessment regarding their conservation level within the Maldives. It is worthwhile to mention that many shark and ray species, such as, the grey reef shark (*Carcharhinus amblyrhynchos*), reef manta ray (*Mobula alfredi*), whale shark (*Rhincodon typus*) and shorthorned pygmy devil ray (*Mobula kuhlii*), that are sighted in the Maldives are listed as globally Endangered on the IUCN red list.

The Sharkwatch Programme was created as a nationwide approach to assess changes to the shark population following the sanctuary implementation (Ushan and Wood, 2010). Data on shark sightings during diving activities were only recorded from 2009-2013, which indicates the termination of the programme. More recent elasmobranch population studies in the Maldives have only focused on manta rays and whale sharks (Anderson *et al.*, 2011; Stevens *et al.*, 2018; Riley *et al.*, 2010). To begin effectively monitor population recovery and assess the efficacy of this conservation strategy, baseline assessments of elasmobranch communities are crucial (Jachmann, 2001).

Underwater visual census (UVC) surveys, using the roving diver technique (RDT), have high success in detecting species with high mobility and a low sighting rate (Moreno *et al*., 2022). This technique enables surveys of large areas in short time periods and can be applied to coral reef, seagrass and lagoon habitats (Schmitt *et al*., 2002). This method can be a tool to assess population characteristics without impacting fine-scale spatial distributions, as is experienced with bait plumes produced using baited techniques (Taylor *et al.*, 2013). Due to recent advances in technology, unmanned aerial vehicles (UAV) are an increasingly popular technique for studying distributions of large marine fauna in shallow water habitats (Kiszka *et al*., 2016). This method allows survey coverage of inaccessible areas for UVC methods, such as shallow sand flats, combined with the ability to measure the length of individuals to estimate ontogenetic stage (Perry *et* al., 2018; Ramos *et al.*, 2022).

Various environmental factors affect elasmobranch spatial distribution and behaviour, including time of day, tidal phase, tide height, tidal range, water temperature, moon phase, wind direction and speed, (Anderson *et al*., 2011; Schlaff *et al*., 2014: Hammerschlag *et al*., 2017; Vianna *et al.*, 2013). Abiotic factors often interact and differ in their level of influence between species, ontogenetic stage, sex and location (Weideli *et al.*, 2019). Abiotic factors can often interact, such as the changes in water depth, as a result of the tides, can impact localised water temperature and therefore water chemistry (E.g. pH and dissolved oxygen levels) (Elston *et al.*, 2022). Elasmobranchs daily routines are heavily influenced by temperature due to their ectothermic nature (Papastamatiou *et al.*, 2015). It is important to consider the influence of biological factors, such as reduced predation risk, that may outweigh the high metabolic cost of selecting a shallow a high temperature habitat with reduces dissolved oxygen levels. Understanding habitat use and the interactions between abiotic and biological factors is important for applying appropriate localised conservation measures.

This study aimed to characterise the diversity, distribution and relative abundance of elasmobranch species around Hurawalhi Island Resort, Lhaviyani Atoll, using UAV and RDT surveys. Specifically, the objectives were to determine: (1) elasmobranch community diversity, species relative abundance and fine-scale spatial distribution, (2) the influence of environmental variables on habitat use and (3) to validate UAV usage for elasmobranch identification in shallow sandflat habitats and ontogenetic estimation. Hurawalhi Island Resort was identified as a candidate for the 'Other Effective area-based Conservation Measures' (OECM) programme, which are protected areas that are managed at a local scale. To achieve the OECM status, the resort must provide ecological survey data of the proposed area and a management plan to showcase the environmental conservation work being conducted by the resort. The data from this study will supplement the fish surveys in the OECM application and provide information to improve the conservation management plan.

Methods

Study area

This study was carried out in the Maldives, specifically in the coral reef, lagoon and shallow sandflat habitats surrounding Hurawalhi Island Resort (5° 31.28208' N, 73° 26.4927' E), north Lhaviyani Atoll. Sampling occurred from 29th May to 5th July at four sites and along one transect (Figure 1). The locations varied in depth, habitat coverage and spatial distribution and were chosen to target areas of high elasmobranch abundance. The first site, 'House Reef' is a shallow coral reef flat starting at a depth of 2m descending on a gentle slope to 15m, located near a channel habitat. The second site, 'East Lagoon' is a sandy lagoon with an average depth of 5m containing coral outcrops. The third, 'Aquarium', is a coral reef at a depth of 2m sloping to 25m, and the fourth, 'West Lagoon', has a consistent depth of 2m with predominantly seagrass meadow habitat. The transect surveyed sandflat habitat parallel to the shoreline of the east of the island, with a depth of <1m (Figure 1).

All sites are accessible to the resort guests to snorkel at any time and diving activities regularly take place at 'East Lagoon', 'House Reef' and 'Aquarium' between 9:00 – 12:00 and 14:00 – 18:00 (MVT +1). Lhaviyani Atoll experiences two seasons: Northeast Monsoon (Apr – Nov) and SW Monsoon (Dec – Mar). The study was conducted during the Northeast Monsoon which is characterised by northeast wind direction and higher levels of precipitation.

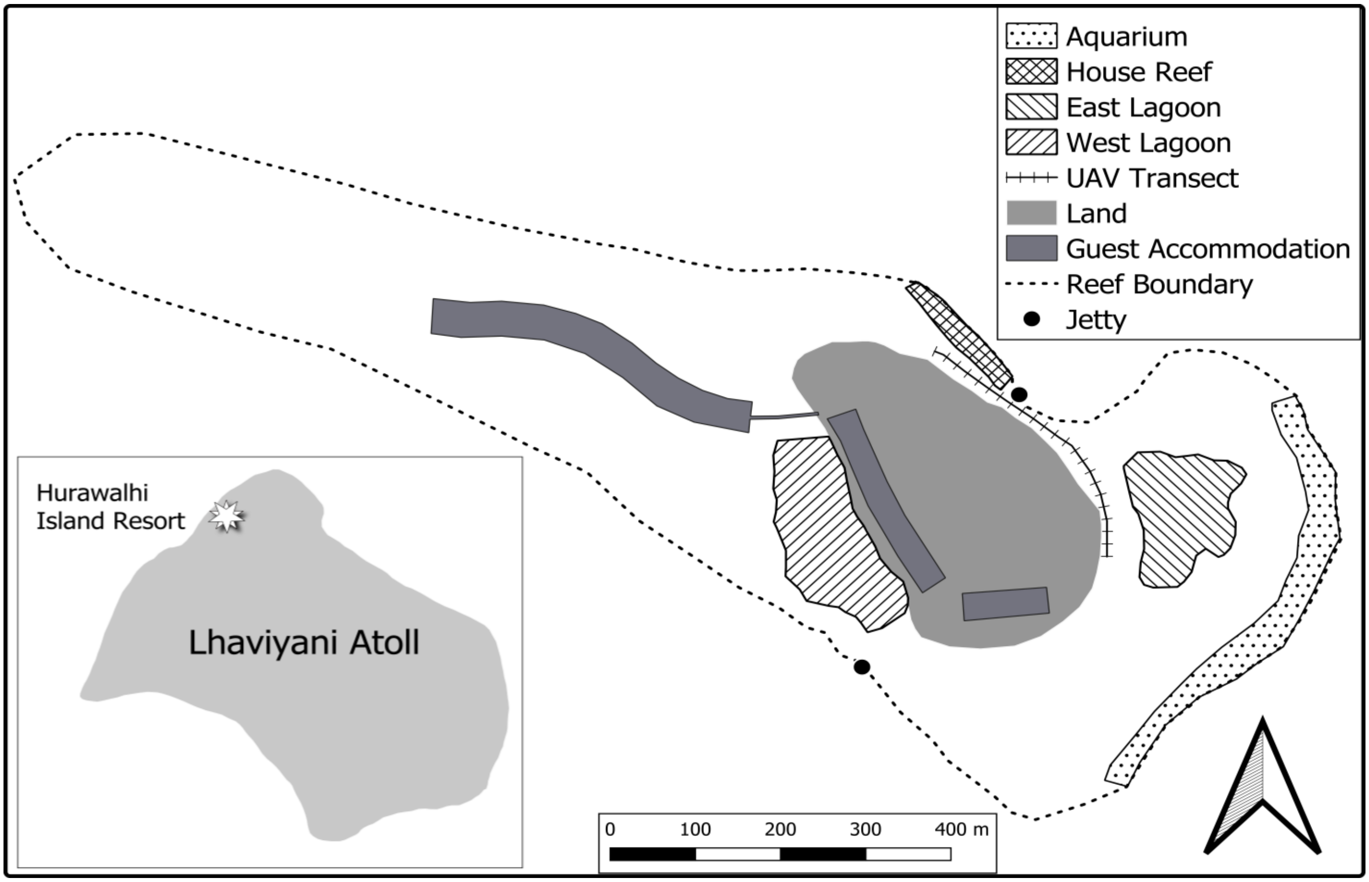


Figure 1. (a) Location of study area in reference to Lhaviyani Atoll (5° 31.28208' N, 73° 26.4927' E). (b) Location of the sites and transect route around Hurawalhi Island Resort. The jetty indicates areas of high boat traffic and guest accommodation limited length and location of the UAV transect.

Roving diver technique

The RDT surveys were conducted at all four sites; 'Aquarium', 'East Lagoon', 'House Reef' and 'West Lagoon'. The surveys consisted of snorkelling freely for one hour without assigned direction. Due to the low sighting rate of elasmobranchs, the method increases efficiency of surveying large areas in shorter time periods than conventional underwater transect methods (Ward-Paige and Lotze, 2011). Surveys were conducted at crepuscular periods (commencing 1 hour after sunrise and before sunset), when the target species exhibit increased activity, and at midday (commencing at either 11:00 or 14:00), to coincide with normal resort activities (Hammerschlag *et al*., 2017; Vianna *et al*., 2013). A total of 60 surveys were conducted, rotating between sites, resulting in each site being surveyed 15 times. Each elasmobranch individual sighted was identified to species. Double counted individuals, identified through morphometrics and markings, were removed from the dataset. This was only needed to differentiation *C. melanopterus* and was carried out by using their unique dorsal and caudal fin markings (Mukharror *et al*., 2019). Due to data collection logistical issues, data for midday surveys at 'Aquarium' site were obtained using dives and snorkels (40-60 minute duration) conducted by Prodivers. Elasmobranchs were identified by experienced dive instructors or dive guides.

Unmanned aerial vehicle

Using a DJI AIR 2s quadcopter integrated with a 13.05 x 8.82 mm camera sensor (www.dji.com), surveys were conducted between 7:00 and 8:00, as stated by the permit. The UAV followed a 0.35 km transect parallel to the shoreline, with an altitude of 11m and the camera at nadir (at 90 degrees facing downwards). This gave a width of 0.0245 km and a total of 8.575 km^2 area covered. The DJI Go app was used to pilot the UAV through an iPhone 11 connected to a remote control. Video footage (4K Ultra HD: 3840×2160) was captured for each survey at 29 frames/second. When an individual was sighted, video was stopped, and an image (20 MP: 5472×3648) was captured with the body of the shark as straight as possible before re-starting the video recording. Metadata of the acquired images were recorded in an EXIF (exchangeable image file format) file, which incorporates information such as altitude and GPS (global positioning system) coordinates. Video footage was reviewed using a PC (LG 24mb65py; www.lg.com) with a 24" (1920 x 1200) display to identify to species level if this was not possible to do during the flight. The total number of individuals for each species identified were counted to calculate the species abundance and density. Total length of each individual was measured in pixels using GIMP software (www.gimp.org) (Figure 2). To reduce the impact of sea-surface distortion on submerged individuals, frames with minimal distortion were selected from video footage (Colefax *et al*., 2020). Drone surveys were restricted to days with wind speed below 15 knots and when the sea state was 3 or below on the Beaufort scale to ensure detectability and altitude accuracy (Raoult *et al*., 2020).

Figure 2. Total length of sharks measured from snout to the end of caudal fin. Measurements followed curvature of the body to improve accuracy.

Environmental

This study focused on the following factors: time of day, tidal phase, tide height, tidal range, water temperature, wind direction, wind speed and moon phase. All of which have demonstrated influence on elasmobranch movement and are relevant to the study location (Anderson *et al*., 2011; Schlaff *et al*., 2014: Hammerschlag *et al*., 2017; Vianna *et al.,* 2013). The tidal phase, tide height (water level relative to mean lower low tide at the start of the survey) and tidal range were recorded using online tide charts (https://tides4fishing.com/mv/maldives/horsburgh-atoll). Water temperature was measured using a Suunto Zoop Nova dive computer (Finland, www.suunto.com). Wind direction and speed (knots) data were obtained via Windguru weather forecast (Kuredu, Lhaviyani) (https://www.windguru.cz/810). Moon phase was recorded via online moon phase calendars (https://www.timeanddate.com/moon/phases/maldives/male).

Analysis

All analysis was conducted in R Software version 4.2.3 (R Core Team, 2023) linked with R Studio version 6.1 (R Studio Team, 2012).

Diversity and relative abundance

Shannon-Wiener Diversity Index (herein; Shannon's), mean species richness and Pielou's evenness was calculated for the RDT dataset using the vegan R package (Heip, 1974; Shannon and Weaver, 1949). This diversity index has been chosen as it considers both richness and evenness. Measuring evenness was important due to multiple species surveyed having a relatively low abundance compared to the more dominant species, such as *C. melanopterus*. The species accumulation curve function in the vegan R package was used to report the accuracy of the study to estimate the total number of species in the area (Oksanen *et al.* 2018). Relative species abundance during RDT surveys was calculated in individuals / hour. Densities of species detected during UAV surveys were calculated using the strip transect methodology with the formula $D = [n/(w \times L)]$ (Buckland *et* al., 2005). Where n is the number of individuals detected, w is the strip width (measured using a measuring tape on land), and L is the length of the transect (km). This method assumes that all elasmobranch species were detected along the transect. Densities were expressed in number of animals per km^2.

Correlation with environmental variables

Generalised linear models were used to investigate relationships between the environmental predictor variables and three response variables including; 'elasmobranch', 'sharks' and 'rays'. Models fitted with different numbers of explanatory terms were compared on their model parsimony using the value produced by Akaike's

Information Criterion (AIC). The most parsimonious model was chosen, and significant relationships identified from the model were interrogated by conducting a one-way analysis of variance (ANOVA) using the accepted statistical test. For each ANOVA, the relevant assumptions were checked using Anderson-Darling test (for normality) and the dispersion of the response variable.

Length measurement

To calculate length of individuals from the UAV surveys, ground sampling distance (GSD) was derived using the barometer altitude sensors (Ramos *et al*., 2022). The GSD was calculated using the following formula:

$$\text{GSD (m/pix)} = \frac{[\text{sensor width(mm) x flight altitude(m)}]}{[\text{focal length(mm) x image width(pix)}]}$$

The GSD was used to scale size for each individual. An object of known length was used to test accuracy of GSD.

Results

Elasmobranchs were observed at all sites, with a total of 170 sightings of 10 species during the 60 surveys (Table 2). This included three sharks, four sting rays, two mobula rays and one eagle ray, with the species encountered in order of decreasing abundance: blacktip reef shark (*Carcharhinus melanopterus)*, spotted eagle ray (*Aetobatus ocellatus*), cowtail stingray (*Pastinachus sephen*), porcupine ray (*Urogymnus asperrimus)*, shorthorned pygmy devil ray (*Mobula kuhlii*), grey reef shark (*Carcharhinus amblyrhynchos*), tawny nurse shark (*Nebrius ferrugineus*), Jenkin's whipray (*Pateobatis jenkinsii*), round ribbontail ray (*Taeniura meyeni*) and reef manta ray (*Mobula alfredi).* These elasmobranchs are represented in three Orders, of which *Carcharhiniformes* contributed two species, followed by *Orectolobiformes* with one species, and *Myliobatiformes,* with seven species. No species were sighted on 18% of the surveys.

Diversity

A Shannon's value (H') of 0.44 with a mean species richness (S) of 1.67 was calculated including data from all sites (Table 1). As a higher Shannon's value equates to a more diverse community (0 - 4.5), lagoon habitat type (0.54) was more diverse compared to reef habitat type (0.35) (Shannon and Weaver, 1949). Shannon's values also varied between sites. The difference was greater, however, between sites within reef habitat type (0.1) compared to 'House Reef' and 'East Lagoon' in different habitat types (0.07). Community evenness can impact species diversity results and therefore, Pielou's evenness index (J') was calculated (0-1). 'House Reef' received a high evenness score (0.87), which was followed by 'East Lagoon' (0.72), 'West Lagoon' (0.65) and 'Aquarium', which has a low evenness score (0.43) (Table 1). Diversity indices reported larger differences between sites compared to habitat type grouping.

Table 1. Mean species richness (S), Shannon's index (H') and Pielou's evenness (J') for factors 'Habitat' and 'Site' surrounding Hurawalhi Island Resort.

Factors		S	H'	J'
Habitat	Reef	1.5	0.35	0.64
	Lagoon	1.83	0.54	0.68
Site	All sites	1.67	0.44	0.67
	Aquarium	1.22	0.3	0.43
	House Reef	1.73	0.4	0.87
	East Lagoon	1.73	0.47	0.72
	West Lagoon	1.93	0.61	0.65

Species accumulation curves

The gradient of the species accumulation curve including all sites is still increasing, indicating that more survey effort is required to reliably conclude that the entire community has been recorded (Figure 2). Species estimators provided the potential range of the number of species within the elasmobranch community from the lowest with Chao's estimator at 9.1 to first-order jackknife with the highest estimate of 13.3. The estimator's range is relatively small, suggesting that a small number of additional surveys should be added in future conduction of this methodology to increase confidence in the extensive sampling of the sites. Due to differences established between sites for elasmobranch diversity, species accumulation curves were calculated for each site

(Figure 2b, c, d, e). Increasing gradients of the curves were found for all sites, concluding that further sampling should be included for all sites for future monitoring.

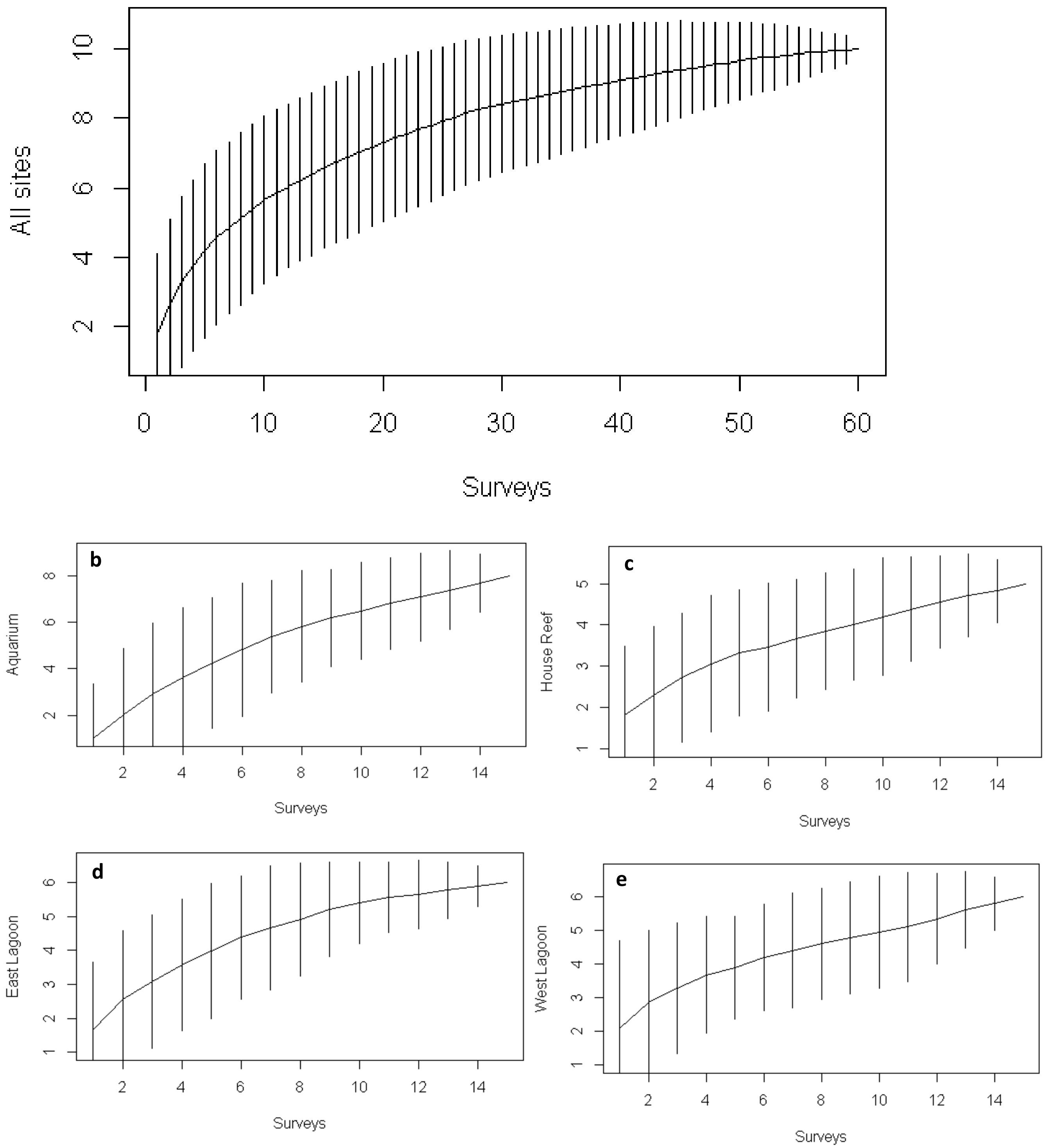


Figure 2. Species accumulation curves derived from the cumulative number of roving diver technique (RDT)

surveys for all sites (a), Aquarium (b), House Reef (c), East Lagoon (d) and West Lagoon (e). Bars represent 95% confidence intervals derived from standard deviation.

Density and relative abundance

During the eight UAV surveys following the transect, 44 individuals were observed and *C. melanopterus* was the only elasmobranchs species detected. There was high confidence for the identification of the species due to the characteristic curved pectoral fins, as well as the ability to see the individuals dorsal fin markings from shore (Rieucau *et al*., 2018). The relative abundance was 5.63 individuals / transect (*SE* 1.9) and the mean density of *C. melanopterus* was 0.656 km² (*SE* 0.13).

A relative abundance of 2.83 elasmobranch/hour was calculated for the RDT surveys (Table 2). There were 101 sharks sighted and 69 rays, making the relative abundance 1.68 sharks/hour and 1.15 rays/hour. All species had a low abundance per survey, with the highest number of individuals from one species was six *C. melanopterus.* Relative abundance of the two dominant species were 1.55 /hour and 0.57 /hour for *C. melanopterus and A. ocellatus,* respectively. The difference in relative abundance of sharks and rays calls for investigation into the influence of environmental factors for total elasmobranch abundance as well as for these two dominant species to determine differences for conservation measures.

Table 2. The total (Σ) and mean number of sharks per hour recorded for each site, with standard deviation (SD). Elasmobranch species abbreviated as follows: blacktip reef (BT), grey reef (GR), tawny nurse (TN), spotted eagle ray (SE), cowtail stingray (CT), porcupine ray (PC), round ribbon tail (RRT), Jenkin's whipray (JW), reef manta ray (RM), shorthorned pygmy devil ray (SPDR). IUCN Red List Status refers to the global assessment (CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern; DD: Data Deficient; NE: Not Evaluated).

	IUCN STATUS		AQUARIUM	HOUSE REEF	EAST LAGOON	WEST LAGOON	ALL SITES
BT	VU	Σ	11	29	28	24	93
		Mean	**0.73**	**2**	**1.87**	**1.6**	**1.55**
		SD	0.96	1.36	1.46	1.59	1.42
GR	EN	Σ	3	2	0	0	5
		Mean	**0.2**	**0.13**	**-**	**-**	**0.08**
		SD	0.41	0.35	-	-	0.28
TN	VU	Σ	0	0	2	1	3
		Mean	**-**	**-**	**0.13**	**0.07**	**0.05**
		SD	-	-	0.35	0.26	0.22
SE	VU	Σ	5	12	2	15	34
		Mean	**0.33**	**0.8**	**0.13**	**1**	**0.57**
		SD	0.72	1.32	0.35	1	0.96
CT	NT	Σ	1	0	7	8	16
		Mean	**0.07**	**-**	**0.47**	**0.53**	**0.27**
		SD	0.26	-	0.52	0.64	0.48
PC	VU	Σ	2	1	5	1	9
		Mean	**0.13**	**0.07**	**0.33**	**0.07**	**0.15**
		SD	0.35	0.26	0.9	0.26	0.52
RRT	VU	Σ	1	0	0	0	1
		Mean	**0.07**	**-**	**-**	**-**	**0.02**
		SD	0.26	-	-	-	0.13
JW	VU	Σ	0	0	1	1	2
		Mean	**-**	**-**	**0.07**	**0.07**	**0.03**
		SD	-	-	0.26	0.26	0.18
RM	VU	Σ	1	0	0	0	1
		Mean	**0.07**	**-**	**-**	**-**	**0.02**
		SD	0.26	-	-	-	0.13
SPDR	EN	Σ	1	5	0	0	6
		Mean	**0.07**	**0.33**	**-**	**-**	**0.1**
		SD	0.26	1.29	-	-	0.66
SHARKS		Σ	14	32	30	25	101
		Mean	**0.92**	**2.13**	**2**	**1.67**	**1.68**
		SD	0.67	1.22	1.21	1.18	1.09
RAYS		Σ	11	18	15	25	69
		Mean	**0.73**	**1.2**	**1**	**1.67**	**1.15**
		SD	0.36	0.74	0.45	0.58	0.55
TOTAL		Σ	25	50	45	50	170
		Mean	**1.67**	**3.33**	**3**	**3.33**	**2.82**
		SD	0.48	0.94	0.79	0.82	0.78

Model selection

To investigate the influence of environmental variables, an iterative approach was applied for each response variable; 'elasmobranchs', 'sharks' and 'rays', to select the most accurate model (Table 3). Most dominant species, *C. melanopterus* and *A. ocellatus* were also included as a response variable, however other species were not analysed individually due to inadequate number of sightings. Each variable contained over-dispersed non-normal data, therefore required analysis using a negative binomial generalised linear model. Models with varying number of parameters were compared using the "dredge" function in the MuMIn package, using the assumption of a lower AIC score and improved deviance to indicate the most accurate model. Models included 'Site', 'Time of day' and 'Tidal phase'. An ANOVA using the chi-squared test of independence was used to identify which environmental factors may have influenced elasmobranch abundance. Tukey's post hoc test was applied to identify significant differences between the means of the groups within the factors, while controlling for the family-wise error rate.

Site

In the final models, 'site' was significant for elasmobranch, shark and *C. melanopterus* abundance (df = 3, p = .011; df = 3, p = .001; df = 3, p = .01). Using the Tukey test, no significance differences in abundance for elasmobranchs were found between the sites; however, elasmobranch abundance was lower at 'Aquarium' compared to the 'House Reef' (p = .08) and with 'Aquarium' compared to 'West Lagoon' (p = .08) (Figure 3a). The Tukey test determined that shark abundance was significantly lower at 'Aquarium' compared to the 'House Reef' (p = .01) and lower at 'Aquarium' compared to 'East Lagoon' (p < .05) (Figure 3b). For *C. melanopterus,* abundance was only significantly different between 'House Reef' and 'Aquarium' (p = .04; Figure 3c).

Time of day

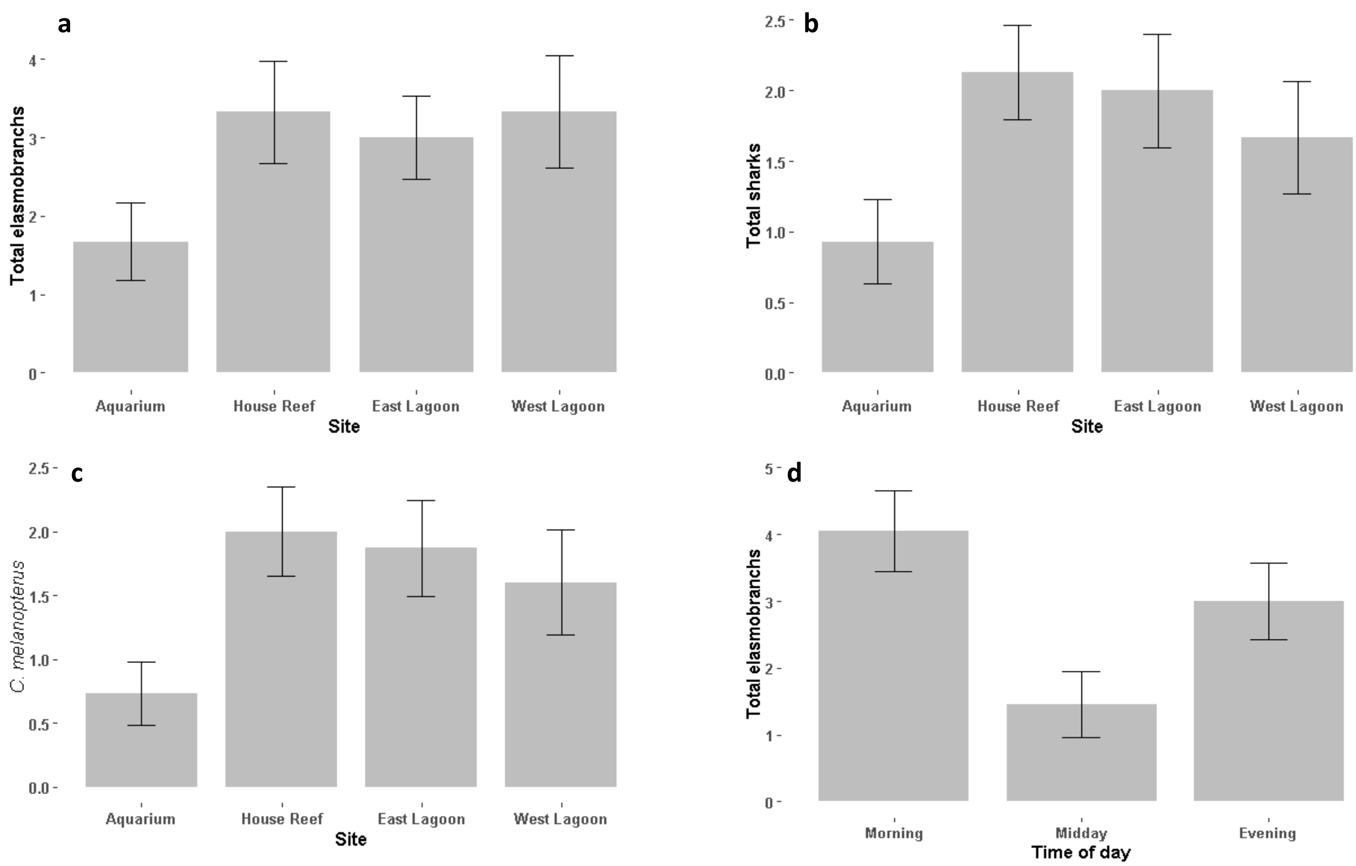
Time of day was found to influence elasmobranch relative abundance (df = 2, p < .001). The abundance pattern at various times of day can be observed in Figure 3d, where the highest mean abundance of elasmobranchs was recorded during the morning (4.05/hour), followed by evening (3/hour) and then midday (1.45/hour). The Tukey test revealed significant differences in abundance only occurred between the morning and midday periods (p < .001). This relationship was also found for sharks (p = .01; Figure 3e), rays (p < .01; Figure 3f), *C. melanopterus (p* = .01; Figure 3e) and *A. ocellatus (p* = .01; Figure 3h*)*.

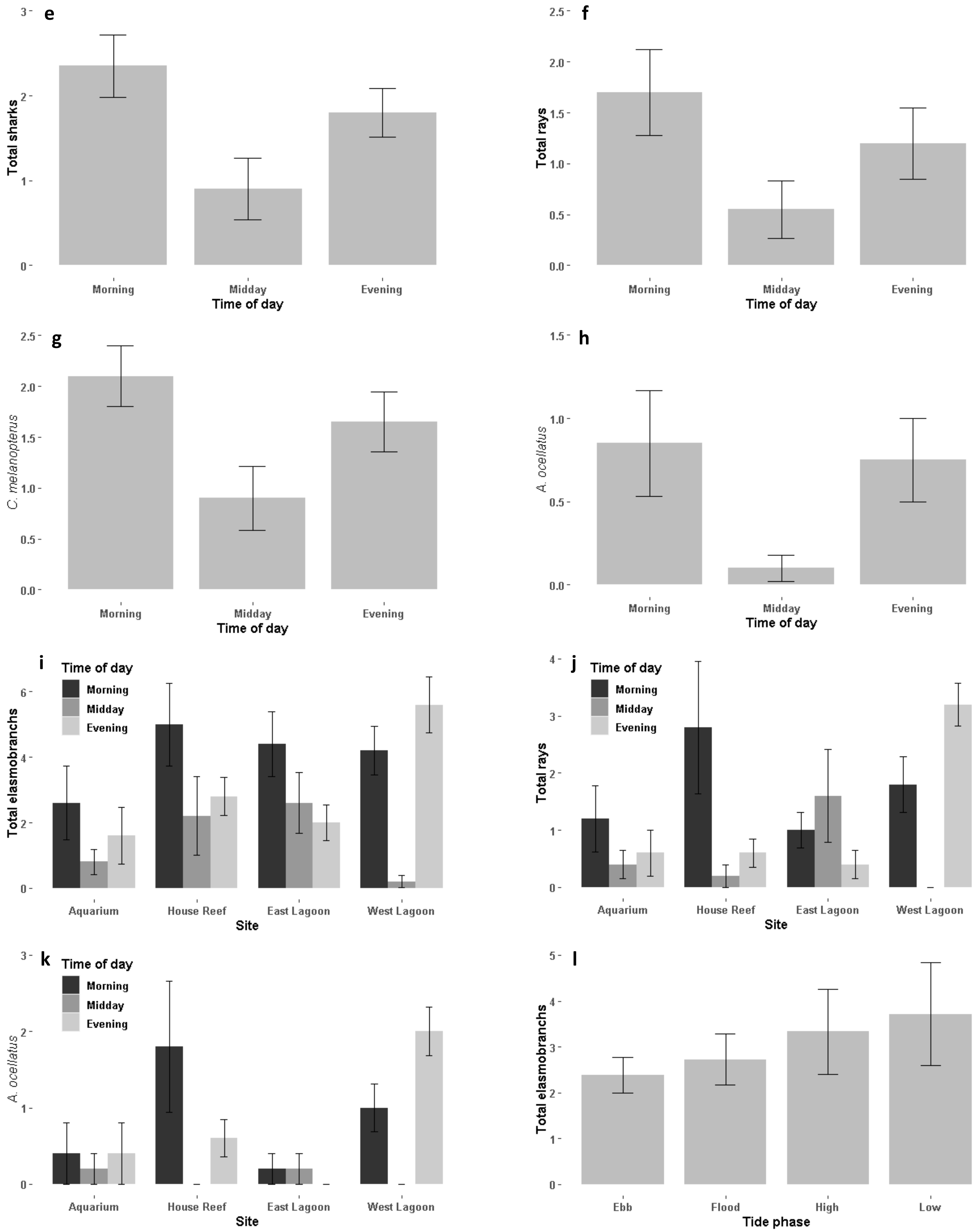
Time of day and site interacted to have a significant effect on elasmobranch abundance (df = 6, p < .001, Figure. 3i). The Tukey test determined significant differences in elasmobranch abundance at 'West Lagoon'. Highest mean abundance was found in the evening surveys (5.6/hour) that had a significant difference compared to midday surveys (0.2/hour) (p < .01). This was also seen for morning surveys (4.2/hour) compared to midday surveys (*p* = .02).

There was no site and time of day interaction for shark abundance, however, for ray abundance, 'House Reef' had a higher abundance in the morning (2.8/hour) compared to midday (0.2/hour) *(p* = .04) *(*Figure 3j). The mean abundance was higher in the evening (3.2/hour) compared to midday surveys when no rays were sighted *(p* < .01)*. Aetobatus ocellatus* had similar relative abundances at 'Aquarium' and 'East Lagoon' during the three-time period, following the same trend as established for ray abundance at 'House Reef' and 'West Lagoon' (Figure 3k). Although, no sightings were recording both midday survey periods and 'East Lagoon' evening surveys.

Tidal flows

Tidal phase was found to influence elasmobranch abundance, where ebb phase had the lowest mean abundance, followed by increasing abundance for flood then high tide, with low tide having the highest mean abundance (*df* = 3, *p* = .01; Figure 3l). Tidal phase had no relationship with shark or ray abundance.





e
Total sharks
3
2
1
0
Morning
Midday
Evening
Time of day
f
Total rays
2.5
2.0
1.5
1.0
0.5
0.0
Morning
Midday
Evening
Time of day
g
C. melanopterus
2.5
2.0
1.5
1.0
0.5
0.0
Morning
Midday
Evening
Time of day
h
A. ocellatus
1.5
1.0
0.5
0.0
Morning
Midday
Evening
Time of day
i
Time of day
Morning
Midday
Evening
Total elasmobranchs
6
4
2
0
Aquarium
House Reef
East Lagoon
West Lagoon
Site
j
Time of day
Morning
Midday
Evening
Total rays
4
3
2
1
0
Aquarium
House Reef
East Lagoon
West Lagoon
Site
k
Time of day
Morning
Midday
Evening
A. ocellatus
3
2
1
0
Aquarium
House Reef
East Lagoon
West Lagoon
Site
l
Total elasmobranchs
5
4
3
2
1
0
Ebb
Flood
High
Low
Tide phase

Figure 3. Mean relative abundances of total elasmobranch, sharks, rays, *C. melanopterus* and *A. ocellatus with* standard error.

Ground sampling distance

Measurements of all 44 *C. melanopterus* individuals recorded during the UAV surveys were calculated, ranging from 38.1 cm to 114.4 cm with a mean length of 57 cm.

Discussion

Knowledge on elasmobranch recovery remained low in the Republic of the Maldives despite nationwide implementation of elasmobranch conservation measures in 2010. The present study attempted to fill this knowledge gap by providing baseline data assessing elasmobranch communities around a resort island. This research that can be scaled up by independent application to other locations in the archipelago or incorporated into future annual OECM ecological surveys. Of the ten species recorded, nine are listed as globally Threatened according to the IUCN Red List. This includes the two most abundant species, *C. melanopterus* and *A. ocellatus*, which are both listed as Vulnerable, and therefore, show the importance of these sites. The Shannon's (0.44) and mean species richness (1.67) values recorded, however, indicates that Hurawalhi Island Resort has an overall low elasmobranch community diversity. This was not expected as Hurawalhi Island Resort has been identified as an ecologically significant area for shark and rays with the appointing of the OECM candidacy. Furthermore, Shannon's values at the higher end of the metric have been recorded in elasmobranch diversity research in similar tropical habitats (Hsu *et al*., 2022; Karuppasamy *et al*., 2020). The Shannon's index usually ranges from 1.5 –3.5 which may suggest a statistical error (Ortiz-Burgos, 2016). The highly mobile and elusive nature of elasmobranch species combined with the small spatial and temporal scale of this study has produced a small sample size. This may have unanticipatedly resulted in negatively biased Shannon's values that have underestimated the diversity (Konopiński, 2020). This would limit the comparison between other studies, however, the values recorded can still be useful for identifying differences between habitat type and sites in the current study.

Higher Shannon's value was recorded for lagoon habitat type compared to reef habitat. This was unexpected as the opposing trend has previously been recorded (Madduppa *et al*., 2012; Rizzari *et al*, 2014). Diversity studies that include both habitat type and prey abundance suggest that prey availability may be a more important predictor of predator habitat use than the habitats' suitability (Tickler *et al*, 2017). This may explain the higher diversity recorded in the lagoon habitat type as the stingray and eagle ray species contributed to half of the species diversity. These species prefer to predate on less mobile prey which are found extensively over sandy benthic environments, of which characterise the lagoon habitat at the study location (Bade et al., 2014; Collins et al., 2007; Schluessel et al., 2010; Serrano-Flores et al., 2019). This interpretation means that the lagoon habitats around Hurawalhi Island Resort are particularly important for the stingray and eagle ray species as a foraging ground.

It is important to add that the low Shannon's value received for site 'Aquarium' reduced the mean score for reef habitat type. With further investigation, the low mean species richness combined with low Pielou evenness index indicates an increase of rare species at 'Aquarium' site (Vinet and Zhedanov, 2010) (Table 1). Shannon index is based on evenness, and this is likely impacted by the larger number of rare species recorded. Therefore, although reef habitat type received the lower Shannon's value compared with lagoon habitat type, this does not reflect that the highest number of species were recorded at reef habitat type sites (n = 8). One of the rare species was *M. Alfredi,* which are commonly present in Lhaviyani atoll during the Southwest Monsoon (Nov – April) (Anderson *et al*., 2011). This highlights the potential effect that seasonality may have on the elasmobranch community in the study location. Elongating the study period over the span of a year may offer deeper insights with regards to this temporal factor.

Elasmobranchs have a low rebound capacity, indicating that species abundance recovery likely to take decades (Smith *et al*., 1998). The current study calculated a relative abundance of 1.68 sharks/hour (Table 2). Shark abundance has been previously recorded in the Maldives via the Maldives Sharkwatch Programme which focused on the ten most surveyed sites from 2009-2013 (Sattar *et al.*, 2014). The locations where data collection took place were not disclosed for site protection, making it difficult to discern meaningful comparison with the current study's fine-scale assessment. Broader analysis, however, estimated that Lhaviyani Atoll had an average encounter rate of 3 sharks/hour. Comparison of these calculations would suggest a decrease in shark abundance at Lhaviyani Atoll. The Sharkwatch Programme, however, uses encounter rate to measure abundance and this does not account for double counted individuals. Furthermore, the dataset includes a larger ranges of habitat types, including 'channels' where *C. amblyrhynchos* are observed in groups of 30 – 60 (Economakis and Lobel, 1998). This likely skewed the comparison as no groups were observed in the current study and where *C. melanopterus* accounted for 92% shark sightings. It is therefore unlikely that shark populations have decreased in abundance over the last decade from comparing results from the Sharkwatch Programme.
Relative abundance for the most dominant species, *C. melanopterus,* was 1.55/hour. In 2011, underwater visual census following chumming recorded *C. melanopterus* mean relative abundance of 0.03/hour in the three most southern atolls (Clarke *et al*., 2012). These data suggest that *C. melanopterus* abundance has greatly increased to 1.55/hour in the 12-year period. However, again it is difficult to establish dependable changes in relative abundance due to differences in location. No comparable studies have assessed elasmobranch diversity on a fine scale in the study area, and therefore, continuous monitoring is needed to reliably assess changes in elasmobranch abundance.

Conversely to previous research, habitat type did not have a significant influence on elasmobranch abundance (Dale *et* al, 2011; Robbins, 2006). Elasmobranch abundance recorded at reef site 'House Reef' was more closely matched with both lagoon sites compared to the other reef site; 'Aquarium' (Figure 3X). This could be attributed to the large variation in depth and benthos within the lagoon and reef habitat types. There were, however, several species that were only sighted in one habitat type. A difference between the spatial distribution and relative abundance of the three shark species was observed. *Carcharhius melanpoterus* was sighted at all sites, whereas C. amblyrhynchos was sighted only in reef habitat and *N. ferrugineus* in lagoon habitat. *Nebrius ferrugineus* were observed exhibiting resting behaviour on all occasions which suggests that the lagoon habitats were more likely to provide shelter from swell. The segregation of *C. amblyrhynchos* and *C. melanopterus* has been previously documented in Palmyra (Papastamatiou *et al*., 2018). These species share similar life-history strategies and therefore, the low relative abundance and the absence of *C. amblyrhynchos* at lagoon sites, may be the result of inter-specific competition (Svanbäck and Bolnick, 2007). It may be likely that as the larger of the two species, *C. amblyrhynchos* has a competitive advantage in the channel habitats (Sabando *et al*., 2020). *Carcharhinus amblyrhynchos* are known to commonly use channel habitats where strong currents increase fish biomass (Economakis and Lobel, 1998; Muller-Karanassos *et al*., 2021). Due to survey method limitations, channel habitats located on either side of the study island was not included in the present study. This means that the apparent low abundance of the globally Endangered *C. amblyrhynchos* should therefore be treated with caution when describing the elasmobranch community around Hurawalhi Island Resort.

Time of day emerged as the most influential variable impacting elasmobranch abundance patterns. Abundance was lowest during the midday surveys compared to the crepuscular periods (morning and evening) (Figure 3). The findings align with results by Hammerschlag *et al*. (2017), where higher abundances of sharks in these crepuscular periods were also found. This pattern is presumed due to sharks' sensory advantage compared to their mobile prey species in the low light condition (Gardiner *et al*., 2012). This could indicate that the habitats in the current study are used by sharks for foraging. Conversely, investigation into the impact of temperature on shark activity found that activity only peaked in the evening period when body temperature was cooling (Papastamatiou *et al*., 2015). In the current study, however, shark abundance was higher by 0.55/hr in the morning compared to the evening period. This may be explained by different habitat use, with sharks potentially moving into shallower warmer waters to aid in digestion, the avoidance of other shark species (Di Santo and Bennett, 2011; Papastamatiou *et al*., 2018).

No rays and only one shark was observed in the 'West Lagoon' during midday surveys (Figure 3j; 3i). Previous work found that stingrays move to actively exploit optimal thermal conditions (Elston *et al*., 2022). As 'West Lagoon' was characterised with a consistent shallow depth of ~2m, it is likely that the water temperature rose with sunlight exposure throughout the day. It could be assumed that elasmobranchs chose to avoid 'West Lagoon' at midday to ensure that their physiological processes are continually optimized. This means that this site is potentially inhabitable during the hottest periods of the day during the study months, highlighting the importance of habitat connectivity (Carr *et al*., 2017; McLeod *et al*., 2009).

The reduced abundance experienced at midday periods may also be a result of avoidance from anthropogenic disturbance. Human exclusion zones have been found to have a significantly higher mean density and biomass of sharks compared to no-take zones (Frisch and Rizzari, 2019). The midday surveys were conducted during the hours when guest activities took place and this included activities such as, snorkelling, diving, jet skis riding and transport between islands resulting in overall increased boat traffic. This area of research may be important for further research in the Maldives as fishing pressure is already removed. If future monitoring of elasmobranch population reveals that recovery is slower than expected, investigating the impact of anthropogenetic disturbance could be interesting to discover any corelations. If found to be an important influence, the application of designating and enforcing no-entry reserves within the Maldives could improve national and local elasmobranch conservation measures.

In this study, tidal phase was found to influence elasmobranch relative abundance. Previously identified elasmobranch tidal movement patterns have been attributed to conserving total energy expenditure. An estimation was calculated that tidally assisted swimming could potentially conserve up to 6 % for leopard sharks (Ackerman *et al*., 2000). The direction of movement in relevance to the tidal flow was not measured in this study, making it difficult to discern the interpretation of this significant relationship. The relationship was not identified within the shark or ray groupings, and this discrepancy potentially indicates that a statistical error has occurred. Therefore, tidal phase should not be considered as a driver of movement for this study area and that further investigation into the influence of this variable is required.

Other environmental variables did not have a significant effect on elasmobranch abundance. Although all of these factors were previously found to influence abundance, analysis in the current study used groupings with various species due to low abundances (Morgan, 2017). The variation of life histories within these groups suggest that environmental variables could impact some species differently (O'Shea et al., 2010). The influence of the other environmental variables could instead be re-evaluated at a species level following future monitoring to obtain a larger data set.

The use of an UAV to survey habitat restricted from underwater visual census techniques has proven effective to offer deeper insights to elasmobranch abundance and spatial distribution. *Carcharhinus melanopterus* was identified with high confidence, enabling a density calculation (0.656 individuals/km² *SE* 0.13). Due to the large transect width and most *C. melanopterus* individuals detected on the shoreline (<0.5m water depth), relative abundance calculated per survey may be more representative (5.63 individuals/transect *SE* 1.9).

Ground sampling distance values of individual total length collected a ranged from 38.1-114.4cm, with a mean of 57cm. As a consequence of discrepancies experienced at differing UAV altitudes, only the relative altitude that provided accurate results when testing against an object of known length was used (11m absolute altitude).

Carcharhinus melanopterus are considered juvenile when their total length is less than 100cm and they exhibit high residency to nursery habitats until permanent departure (Lyle, 1987). The detection of the smallest individuals along the shoreline (<0.5m water depth), with larger individuals in the deeper water (0.5-2m water depth) is consistent with these shifts in habitat usage related to ontogeny (Papastamatiou *et al*., 2009). Water depth has a strong association with juvenile *C. melanopterus* nurseries, speculating that use of shallow sandflats is a strategy of predation avoidance (Chin *et al*., 2013a). With predicted growth rate of juvenile *C. melanopterus* at 6.53cm/year, these habitats are important for *C. melanopterus* populations as individuals will use the nursery habitat for survival over several years (Chin *et al*., 2013b).

As previously mentioned, shallow habitats experiencing higher temperatures during midday periods (Di Girolamo *et al*., 2012). Juvenile *C. melanopterus* have been found to have a moderate thermal tolerance compared to adults, with the ability to acclimatise to water temperatures of 31°C (Bouyoucos *et al*., 2020). These temperatures, however, were avoided when possible and suggest the boundary of their upper thermal tolerance. Sea surface temperatures over the study period rose to 30°C and predicted rising water temperatures as a result of climate changes may force juveniles to move into deeper water for thermal refuge (DiGirolamo *et al*., 2012). Introduction of shading to the shoreline areas could be explored to reduce water temperature whilst maintaining the predation protection provided by the shallow water depth.

Conclusion

Overall, this research provides baseline data for the elasmobranch community surrounding Hurawalhi Island Resort. This has enabled the start of continued long-term monitoring that is required to assess the efficacy of national and local conservation measures on community diversity and relative abundance. Data collected from this study has been important due to the contribution to the first Maldivian OECM application. Understanding the influence of time of day has offered insights into improving Hurawalhi Island Resort's conservation management plan, with suggestion of reducing anthropogenic disturbance during crepuscular periods. The use of an UAV has detected important grounds for juvenile sharks and provides evidence to ensure these locations receive effective management with respect to rising sea temperatures.

Word count: 5802

References

Ackerman, J. T., Kondratieff, M. C., Matern, S. A., and Cech, J. J. (2000) ‘Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California’, *Environmental Biology of Fishes*, 58.

Ali, K., and Sinan, H. (2015) ‘National Plan of Action for the Conservation and Management of Sharks in the Maldives’, *Ministry of Fisheries and Agriculture*. Available at: 〈http://mrc.gov.mv/assets/Uploads/Sharks-Plan-Maldives.pdf). (Accessed 26 July 2023).

Anderson, R.C., Adam, M.S. and Goes, J.I. (2011), ‘From monsoons to mantas: seasonal distribution of *Manta alfredi* in the Maldives’, *Fisheries Oceanography*, 20(2), pp.104-113.

Anderson, R.C. and Ahmed, H. (1993) ‘The shark fisheries of the Maldives’, *FAO Technical Report*, *Ministry of Fisheries and Agriculture, Male, Republic of Maldives*, pp.77.

Andréfouët, S., Menou, J.L. and Naeem, S. (2012) ‘Macro-Invertebrate Communities of Baa Atoll, Republic of Maldives’, *Biodiversity, Resources, And Conservation of Baa Atoll (Republic of Maldives): A Unesco Man and Biosphere Reserve*.

Andréfouët, S., Muller-Karger, F.E., Robinson, J.A., Kranenburg, C.J., Torres-Pulliza, D., Spraggins, S.A. and Murch, B. (2006) ‘Global assessment of modern coral reef extent and diversity for regional science and management applications: a view from space’, *Okinawa: Japanese Coral Reef Society, In Proceedings of the 10th international coral reef symposium*, 2, pp. 1732-1745.

Bade, L. M., Balakrishnan, C. N., Pilgrim, E. M., McRae, S. B. and Luczkovich, J. J. (2014) ‘A genetic technique to identify the diet of cownose rays, *Rhinoptera bonasus*: Analysis of shellfish prey items from North Carolina and Virginia’, *Environmental Biology of Fishes*, 97, pp.999–1012.

Bornatowski, H., Navia, A.F., Braga, R.R., Abilhoa, V. and Corrêa, M.F.M. (2014) ‘Ecological importance of sharks and rays in a structural food web analysis in southern Brazil’, *ICES Journal of Marine Science,* 71, pp.1586–1592.

Bouyoucos, I. A., Morrison, P. R., Weideli, O. C., Jacquesson, E., Planes, S., Simpfendorfer, C. A., Brauner, C. J. and Rummer, J. L. (2020) ‘Thermal tolerance and hypoxia tolerance are associated in blacktip reef shark (*Carcharhinus melanopterus*) neonates’, *Journal of Experimental Biology*, 223(14).

Carr, M.H., Robinson, S.P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacker, E.J. and Williams, M. (2017) ‘The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment’, *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27, pp.6-29.

Chin, A., Heupel, M., Simpfendorfer, C. and Tobin, A. (2013a) ‘Ontogenetic movements of juvenile blacktip reef sharks: Evidence of dispersal and connectivity between coastal habitats and coral reefs’, *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23(3), pp.468–474.

Chin, A., Tobin, A.J., Heupel, M.R. and Simpfendorfer, C.A. (2013b) ‘Population structure and residency patterns of the blacktip reef shark *Carcharhinus melanopterus* in turbid coastal environments’, *Journal of Fish Biology*, 82(4), pp.1192-1210.

Clarke, C., Lea, J. and Ormond, R. (2012) ‘Comparative abundance of reef sharks in the Western Indian Ocean’, *In Proceedings of the 12th international coral reef symposium, Cairns, Australia*, pp.9-13.

Colefax, A.P., Kelaher, B.P., Pagendam, D.E. and Butcher, P.A. (2020) ‘Assessing white shark (*Carcharodon carcharias*) behavior along coastal beaches for conservation-focused shark mitigation’, *Frontiers in Marine Science*, 7.

Collins, A. B., Heupel, M. R., Hueter, R. E. and Motta, P. J. (2007) ‘Hard prey specialists or opportunistic generalists? An examination of the diet of the cownose ray, *Rhinoptera bonasus’*, *Marine and Freshwater Research*, 58, pp.135–144.

Dale, J.J., Stankus, A.M., Burns, M.S. and Meyer, C.G. (2011) ‘The Shark assemblage at French Frigate Shoals Atoll, Hawai ‘i: species composition, abundance and habitat use’, *PLoS One*, 6(2), pp.16962.

Di Santo, V. and Bennett, W.A. (2011) ‘Is post-feeding thermotaxis advantageous in elasmobranch fishes?’ *Journal of Fish Biology*, 78(1), pp.195-207.

Di Girolamo, A.L., Gruber, S.H., Pomory, C. and Bennett, W.A. (2012) ‘Diel temperature patterns of juvenile lemon sharks *Negaprion brevirostris*, in a shallow-water nursery’, *Journal of Fish Biology*, 80(5), pp.1436-1448.

Dryden, C., Basheer, A., Grimsditch, G., Musthaq, A., Newman, S. and Shan, A. (2020) ‘A rapid assessment of natural environments in the Maldives’, *Gland, Switzerland: IUCN and Government of Maldives.*

Economakis, A.E. and Lobel, P.S., (1998) ‘Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean’, *Environmental Biology of Fishes*, 51, pp.129-139.

Elston, C., Cowley, P. D., von Brandis, R. G. and Lea, J. (2022) ‘Stingray Habitat Use Is Dynamically Influenced by Temperature and Tides’, *Frontiers in Marine Science*, 8.

Frisch, A. J., and Rizzari, J. R. (2019) ‘Parks for sharks: human exclusion areas outperform no-take marine reserves’, *Frontiers in Ecology and the Environment*, 17(3), pp. 145–150.

Frisch, A.J., Ireland, M., Rizzari, J.R., Lönnstedt, O.M., Magnenat, K.A., Mirbach, C.E. and Hobbs, J.P.A. (2016) ‘Reassessing the trophic role of reef sharks as apex predators on coral reefs’, *Coral Reefs*, 35, pp.459-472.

Gardiner, J.M., Hueter, R.E., Maruska, K.P., Sisneros, J.A., Casper, B.M., Mann, D.A. and Demski, L.S. (2012) ‘Sensory physiology and behavior of elasmobranchs’, *Biology of sharks and their relatives,* 1, pp.349-401.

Gischler, E., Storz, D. and Schmitt, D. (2014) ‘Sizes, shapes, and patterns of coral reefs in the Maldives, Indian Ocean: the influence of wind, storms, and precipitation on a major tropical carbonate platform’, *Carbonates and Evaporites*, 29, pp.73-87.

Hammerschlag, N., Skubel, R.A., Calich, H., Nelson, E.R., Shiffman, D.S., Wester, J., Macdonald, C.C., Cain, S., Jennings, L., Enchelmaier, A. and Gallagher, A.J. (2017) ‘Nocturnal and crepuscular behavior in elasmobranchs: a review of movement, habitat use, foraging, and reproduction in the dark’, *Bulletin of Marine Science*, 93(2), pp.355-374.

Heip, C. (1974) ‘A new index measuring evenness’, *Journal of the Marine Biological Association of the United Kingdom*, 54(3), pp.555-557.

Hsu, H. H., Yacoubi, L., Lin, Y. J., le Loc’h, F., Katsanevakis, S., Giovos, I., Qurban, M. A., Nazeer, Z., Panickan, P., Maneja, R. H., Prihartato, P. K., Loughland, R. A. and Rabaoui, L. J. (2022) ‘Elasmobranchs of the western Arabian Gulf: Diversity, status, and implications for conservation’, *Regional Studies in Marine Science*, 56.

Karuppasamy, K., Jawahar, P., David Kingston, S., Venkataramani, V. K., and Vidhya, V. (2020) 'Elasmobranch diversity, conservation and management along Wadge Bank, South India', *Indian Journal of Animal Research*, 54(3), pp. 367–372.

Konopiński, M. K. (2020) 'Shannon diversity index: A call to replace the original Shannon's formula with unbiased estimator in the population genetics studies', *PeerJ,* (6).

Lyle, J.M. (1987) 'Observations on the biology of *Carcharhinus cautus* (Whitley), *C. melanopterus* (Quoy & Gaimard) and *C. fitzroyensis* (Whitley) from northern Australia', *Marine and Freshwater Research*, 38(6), pp.701-710.

Maciel, E.A. (2021) 'An index for assessing the rare species of a community', *Ecological Indicators*, 124, pp.107424.

MacKeracher, T., Diedrich, A. and Simpfendorfer, C.A. (2019) 'Sharks, rays and marine protected areas: A critical evaluation of current perspectives', *Fish and Fisheries*, 20(2), pp.255-267.

Madduppa, H.H., Farhan, A.R. and Suhendra, D. (2012) 'Fish biodiversity in coral reefs and lagoon at the Maratua Island, East Kalimantan', *Biodiversitas Journal of Biological Diversity*, 13(3).

Martin, R.A. and Hakeem, A.A.A. (2006) 'Development of a sustainable shark diving ecotourism industry in the Maldives: challenges and opportunities', *Maldives Marine Research Bulletin*, 8, pp. 56.

McLeod, E., Salm, R., Green, A. and Almany, J. (2009) 'Designing marine protected area networks to address the impacts of climate change', *Frontiers in Ecology and the Environment*, 7(7), pp.362-370.

Morgan, C.J. (2017) 'Use of proper statistical techniques for research studies with small samples', *American Journal of Physiology-Lung Cellular and Molecular Physiology*, 313(5), pp.873-877.

Mukharror, D.A., Susiloningtyas, D., Handayani, T. and Pridina, N. (2019) 'Blacktip reefshark (*Carcharhinus melanopterus*) individual's identification in Morotai waters using its fin's natural markings', *AIP Conference Proceedings*, 2202(1).

Muller-Karanassos, C., Filous, A., Friedlander, A.M., Cuetos-Bueno, J., Gouezo, M., Lindfield, S.J., Nestor, V., Marino, L.L., Mereb, G., Olsudong, D. and Golbuu, Y. (2021) 'Effects of habitat, fishing, and fisheries management on reef fish populations in Palau', *Fisheries research*, 241, pp.105996.

Musick, J.A., Burgess, G., Cailliet, G., Camhi, M. and Fordham, S. (2000) 'Management of sharks and their relatives (*Elasmobranchii)*', *Fisheries*, 25, pp. 9-13.

Ortiz-Burgos, S. (2016) 'Shannon-Weaver Diversity Index', Kennish, M.J. (eds) *Encyclopedia of Estuaries. Encyclopedia of Earth Sciences Series*. Springer, Dordrecht.

O'Shea, O.R., Kingsford, M.J. and Seymour, J. (2010) 'Tide-related periodicity of manta rays and sharks to cleaning stations on a coral reef', *Marine and Freshwater Research*, 61(1), pp.65-73.

Papastamatiou, Y. P., Watanabe, Y. Y., Bradley, D., Dee, L. E., Weng, K., Lowe, C. G. and Caselle, J. E. (2015) 'Drivers of daily routines in an ectothermic marine predator: Hunt warm, rest warmer?', *PLoS ONE*, 10(6).

Papastamatiou, Y.P., Bodey, T.W., Friedlander, A.M., Lowe, C.G., Bradley, D., Weng, K., Priestley, V. and Caselle, J.E. (2018) 'Spatial separation without territoriality in shark communities', *Oikos*, 127(6), pp.767-779.

Perry, C.T., Figueiredo, J., Vaudo, J.J., Hancock, J., Rees, R. and Shivji, M. (2018) ‘Comparing length-measurement methods and estimating growth parameters of free-swimming whale sharks (*Rhincodon typus*) near the South Ari Atoll, Maldives’, *Marine and Freshwater Research*, 69(10), pp.1487-1495.

Ramos, E., Yauri, S., Castelblanco-Martínez, N., Arreola, M., Quade, A., and Rieucau, G. (2022) ‘Drone-based photogrammetry assessments of body size and body condition of Antillean manatees’, *Mammalian Biology*.

Raoult, V., Colefax, A. P., Allan, B. M., Cagnazzi, D., Castelblanco-Martínez, N., Ierodiaconou, D., Johnston, D. W., Landeo-Yauri, S., Lyons, M., Pirotta, V., Schofield, G., & Butcher, P. A. (2020) ‘Operational protocols for the use of drones in marine animal research’, *Drones*, 4(4), pp. 1–35.

Rieucau, G., Kiszka, J.J., Castillo, J.C., Mourier, J., Boswell, K.M. and Heithaus, M.R. (2018) ‘Using unmanned aerial vehicle (UAV) surveys and image analysis in the study of large surface-associated marine species: a case study on reef sharks *Carcharhinus melanopterus* shoaling behaviour’, *Journal of fish biology,* 93(1), pp.119-127.

Riley, M.J., Hale, M.S., Harman, A. and Rees, R.G. (2010) ‘Analysis of whale shark *Rhincodon typus* aggregations near South Ari Atoll, Maldives archipelago’, *Aquatic Biology*, 8(2), pp.145-150.

Rizzari, J.R., Frisch, A.J. and Magnenat, K.A. (2014) ‘Diversity, abundance, and distribution of reef sharks on outer-shelf reefs of the Great Barrier Reef, Australia’, *Marine Biology*, 161, pp.2847-2855.

Robbins, W.D. (2006) ‘Abundance, demography and population structure of the grey reef shark (*Carcharhinus amblyrhynchos*) and the white tip reef shark (*Triaenodon obesus*)(Fam. *Charcharhinidae*)’, *Doctoral dissertation, James Cook University.*

Sabando, M.A., Rieucau, G., Bradley, D., Caselle, J.E. and Papastamatiou, Y.P. (2020) ‘Habitat-specific inter and intraspecific behavioral interactions among reef sharks’, *Oecologia*, 193, pp.371-376.

Saleem, A. and Nileysha, A. (2011) ‘Characteristics, status and need for conservation of mangrove ecosystems in the Republic of Maldives, Indian Ocean’, *Journal of the National Science Foundation of Sri Lanka*, 31(1-2).

Sattar, S. A., Wood, E., Ushan, M. and Ali, K. (2014) ‘Overview of the Sharkwatch Programme: 2009 – 2013’, *Marine Research Centre, Marine Conservation Society.*

Schluessel, V., Bennett, M. B. and Collin, S. P. (2010) ‘Diet and reproduction in the white-spotted eagle ray Aetobatus narinari from Queensland, Australia and the Penghu Islands, Taiwan’, *Marine and Freshwater Research*, 61, pp.1278–1289.

Schmitt, E., Sluka, R. and Sullivan-Sealey, K. (2002) ‘Evaluating the use of roving diver and transect surveys to assess the coral reef fish assemblage off southeastern Hispaniola’, *Coral Reefs*, 21, pp.216-223.

Serrano-Flores, F., Pérez-Jiménez, J. C., Méndez-Loeza, I., Bassos-Hull, K. and Ajemian, M. J. (2019) ‘Comparison between the feeding habits of spotted eagle ray (*Aetobatus narinari)* and their potential prey in the southern Gulf of Mexico’, *Journal of the Marine Biological Association of the United Kingdom*, 99, pp.661–672.

Simpfendorfer, C., Yuneni, R.R., Tanay, D., Seyha, L., Haque, A.B., Fahmi, Bin Ali, A., Bineesh, K.K., Gautama, D.A., Maung, A., Sianipar, A., Utzurrum, J.A.T. and Vo, V.Q. (2020) ‘*Carcharhinus melanopterus*. The IUCN Red List of Threatened Species 2020: e.T39375A58303674’. Available at: https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T39375A58303674.en. (Accessed 16 August 2023).

Smith, S.E., Au, D.W. and Show, C. (1998) ‘Intrinsic rebound potentials of 26 species of Pacific sharks’, *Marine and Freshwater Research*, 49(7), pp.663-678.

Stevens, G.M., Hawkins, J.P. and Roberts, C.M. (2018) ‘Courtship and mating behaviour of manta rays *Mobula alfredi* and *M. birostris* in the Maldives’, *Journal of Fish Biology*, 93(2), pp.344-359.

Stevens, J.D., Bonfil, R., Dulvy, N.K. and Walker, P.A. (2000) ‘The effects of fishing on sharks, rays, and chimaeras (*chondrichthyans*), and the implications for marine ecosystems’, *ICES Journal of Marine Science*, 57, pp.476–494.

Svanbäck, R. and Bolnick, D.I. (2007) ‘Intraspecific competition drives increased resource use diversity within a natural population’, *Proceedings of the Royal Society B: Biological Sciences*, 274(1611), pp.839-844.

Taylor, M.D., Baker, J. and Suthers, I.M. (2013) ‘Tidal currents, sampling effort and baited remote underwater video (BRUV) surveys: are we drawing the right conclusions?’, *Fisheries Research*, 140, pp.96-104.

The President’s Office, Government of the Maldives (2010) ‘Government to Impose Ban on Trade and Export of Sharks and Shark Products’, *Press Releases*, 9 March, Ref: 2010-183. Available at: https://www.presidency.mv/Press/Article/998. (Accessed 26 July 2023).

Tickler, D.M., Letessier, T.B., Koldewey, H.J. and Meeuwig, J.J. (2017) ‘Drivers of abundance and spatial distribution of reef-associated sharks in an isolated atoll reef system’, *PLoS One*, 12(5), pp. 0177374.

Ushan, M. and Wood, E. (2010) ‘Maldives Sharkwatch report for 2009-2010', *Marine Research Centre, Marine Conservation Society.*

Vianna, G. M. S., Meekan, M. G., Meeuwig, J. J. and Speed, C. W. (2013) ‘Environmental Influences on Patterns of Vertical Movement and Site Fidelity of Grey Reef Sharks (*Carcharhinus amblyrhynchos*) at Aggregation Sites’, *PLoS ONE*, 8(4).

Vinet, L. and Zhedanov, A. (2011) ‘A ‘missing’ family of classical orthogonal polynomials’, J*ournal of Physics A: Mathematical and Theoretical*, 44(8), pp.085201.

Ward-Paige, C.A. (2017) ‘A global overview of shark sanctuary regulations and their impact on shark fisheries’ *Marine Policy*, 82, pp.87-97.

Ward-Paige, C.A. and Lotze, H.K. (2011) ‘Assessing the value of recreational divers for censusing elasmobranchs’, *PLoS One*, 6(10), p.e25609.

Ward-Paige, C.A. and Worm, B. (2017) ‘Global evaluation of shark sanctuaries’, *Global Environmental Change*, 47, pp.174-189.

White, E.R., Myers, M.C, Flemming, J.M. and Baum, J.K. (2015) ‘Shifting elasmobranch community assemblage at Cocos Island—an isolated marine protected area’, *Conservation Biology*, 29(4), pp. 1186–1197.