

**Assessing sharks and rays in shallow coastal habitats using baited
underwater video and aerial surveys in the Red Sea**

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ABSTRACT

Years of unregulated fishing activity have resulted in low abundances of elasmobranch species in the Saudi Arabian Red Sea. Coastal populations of sharks and rays in the region remain largely understudied and may be at risk from large-scale coastal development projects. Here we aim to address this pressing need for information by using fish market, unmanned aerial vehicle and baited remote underwater video surveys to quantify the abundance and diversity of sharks and rays in coastal habitats in the Saudi Arabian central Red Sea. Our analysis showed that the majority of observed individuals were batoids, specifically blue-spotted ribbontail stingrays (*Taeniura lymma*) and reticulate whiprays (*Himantura* sp.). Aerial surveys observed a catch per unit effort two orders of magnitude greater than underwater video surveys, yet did not detect any shark species. In contrast, baited camera surveys observed both lemon sharks (*Negaprion acutidens*) and tawny nurse sharks (*Nebrius ferrugineus*), but in very low quantities (one individual of each species). The combination of survey techniques revealed a higher diversity of elasmobranch presence than using either method alone, however many species of elasmobranch known to exist in the Red Sea were not detected. Our results suggest that aerial surveys are a more accurate tool for elasmobranch abundance estimates in low densities over mangrove-associated habitats. The importance of inshore habitats, particularly for batoids, calls for a deeper understanding of habitat use in order to protect these environments in the face of unregulated fishing, mangrove removal, and anticipated developments along the coastline of the Saudi Arabian Red Sea.

TABLE OF CONTENTS

Examination Committee Page	2
Abstract	4
List of Abbreviations	6
List of Figures	7
List of Tables	8
1. Introduction	9
1.1 Sharks and rays in the Red Sea	9
1.2 Survey methods to assess elasmobranchs	12
1.3 Objectives	16
2. Methods	18
2.1 Study Site	18
2.2 BRUV surveys	21
2.2.1 BRUV design and sampling	21
2.2.2 Video annotation	23
2.2.3 Individual identification (MaxIND) of stingrays	24
2.3 UAV surveys	25
2.3.1 Pre-deployment and sampling parameters	25
2.3.2 Video annotation	27
2.3.3 Availability Correction Factor (ACF)	27
2.3.4 Perception Correction Factor (PCF)	28
2.3.5 Abundance	29
2.3.6 Density	30
2.4 Fish market surveys	30
2.5 Data analysis	31
3. Results	33
3.1 BRUV surveys	33
3.2 UAV surveys	34
3.3 Assemblage description	36
3.4 Paired BRUV and UAV samples	42
3.5 Fish market surveys	45
4. Discussion	46
5. Conclusion	57
Bibliography	59
Appendix	68

LIST OF ABBREVIATIONS

BRUV	Baited Remote Underwater Video
CPUE	Catch Per Unit Effort
FAO	Food and Agriculture Organization
FOV	Field of View
IUCN	International Union for Conservation of Nature
KAUST	King Abdullah University of Science and Technology
KSA	Kingdom of Saudi Arabia
MaxIND	Maximum number of Individuals
MPA	Marine Protected Area
UAV	Unmanned Aerial Vehicle
UVS	Underwater Visual Survey

LIST OF FIGURES

Figure 1.	Map of Thuwal lagoon system in the Saudi Arabian central Red Sea.	19
Figure 2.	Total BRUV and UAV survey effort.	21
Figure 3.	“Mini” BRUV unit system.	22
Figure 4.	Example of BRUV deployment.	24
Figure 5.	Example of MaxIND spot-pattern identification.	25
Figure 6.	Examples of identified species from UAV surveys.	27
Figure 7.	Proportions of the total elasmobranch assemblage between methods.	38
Figure 8.	Species accumulation curves.	40
Figure 9.	Relative abundance comparison from sandflat surveys.	42
Figure 10.	Relative abundance comparison from reef surveys.	44
Figure 11.	Relative abundance of elasmobranch species from UAV, BRUV and fish market surveys.	45

LIST OF TABLES

Table 1.	Summary of identifiable individuals from BRUV surveys using MaxIND.	34
Table 2.	Percentage of identified individuals that exhibited BRUV feeding attempts.	34
Table 3.	Perception Correction Factor interpretation.	35
Table 4.	Average densities of elasmobranchs in UAV surveys.	36
Table 5.	Catch per unit effort for UAV and BRUV surveys.	37
Table 6.	Mean number of individuals per species recorded from BRUV and UAV surveys.	38
Table 7.	Species richness and diversity indexes.	41

1. INTRODUCTION

1.1 Sharks and rays in the Red Sea

Sharks and rays (elasmobranchs) play complex and important ecological roles in the structure and function of marine ecosystems. Due to their highly varied diet, sharks control prey species in the pelagic and reef environment (Montgomery et al. 2019), whereas rays prey in shallow water ecosystems through predation and excavation of soft-bottom habitats. This top-down cascade acts as a vital check on a wide range of species in lower trophic levels and helps to maintain greater species richness and abundance by connecting trophic webs across habitats (Sergio et al. 2006). Despite the crucial roles they play in marine food webs and ecosystem dynamics, an alarming number of elasmobranchs have experienced precipitous population declines globally (Dulvy et al. 2008, 2014; Davidson et al. 2016). Many shark and ray species grow and mature slowly while producing relatively few offspring (Dulvy et al. 2014). These K-selected life-history traits make numerous species, especially large-bodied sharks, particularly vulnerable to overexploitation and susceptible to population decline (Dulvy et al. 2014). However, the removal of these larger predators can facilitate localized increases in mesopredator populations, increasing the top-down effect in nearshore environments (Myers et al. 2003). Declining populations and extirpations of sharks and rays will have substantial impacts on overall ecosystem health (Stevens et al. 2000). Many species of shark and ray utilize coastal waters as nursery habitats as they offer protection for juveniles and provide a wide range of prey items (Heupel et al. 2019). However, their proximity to land also exposes them to the adverse effects of human population growth. For instance, pollution, habitat loss and degradation,

and fishing exploitation jeopardize coastal populations of shark and ray. As such, it is vital to collect information regarding the abundance and species composition of elasmobranchs in coastal waters.

Of more than 1200 shark and ray species described to date (Dulvy et al. 2014; Steinke et al. 2017), only 64 are found in the Red Sea (Golani and Bogorodsky 2010; Golani and Fricke 2018), two of which are considered endemic (Bonfil and Abdallah 2004). The Red Sea is an extension of the Indian Ocean in which all 64 species are thought to have originated from (Compagno 1982). In comparison to other ocean basins, the elasmobranch fauna of the Red Sea has relatively low diversity. Currently, 53% of Red Sea shark and ray species are globally categorized as Endangered or Vulnerable, 23% are considered Near Threatened, and 19% are data deficient (IUCN, 2020; Appendix 1). The large proportion of threatened (Endangered and Vulnerable) species, in conjunction with the limited knowledge of coastal elasmobranchs in the Red Sea, is reason for concern and therefore an understanding of the abundance and assemblage of sharks and rays in the nearshore environment is of particular importance.

In Saudi Arabian Red Sea waters, sharks have been heavily exploited from as early as the 1970s (Bonfil 2003). Small-scale artisanal fishers use handlines, gillnets, and traps to target top predators on and around coral reefs (Sanders and GR 1989; Spaet and Berumen 2015; Jabado and Spaet 2017). These types of artisanal fisheries are a direct threat to smaller coastal species in addition to the larger shark species that use these areas as breeding and nursery areas (e.g., Jennings et al., 2008). Targeting sharks and rays in these critical habitats is detrimental to overall populations and is a chronic problem throughout the Red Sea (Hariri et al. 2006). With shark fisheries as profitable as industrial fisheries in the Red Sea (Tsfamichael and Pitcher 2006), overexploitation

along the entire Saudi Arabian Red Sea coast has led to potentially major population declines in many species (Berumen et al. 2019). Despite an explicit ban on landing and selling sharks and rays in Saudi Arabia in effect since 2008 (Kingdom of Saudi Arabia Royal Decree 57,543 of 23/08/1439), enforcement has been inconsistent and weak monitoring efforts offer limited data with which to evaluate management (Spaet 2019). In addition to unregulated fishing, current population threats may include inputs related to mangrove removal, pollution from coastal-based industries, and coastal development (Dulvy et al. 2014). Specifically, major coastal development projects fueled by the ambitious goals of the Kingdom's "Vision 2030" agenda present further threats to habitats of local populations of sharks and rays (Abdul Aziz et al. 2016). The plan includes "GigaProjects" that aim to promote economic diversification and the nascent tourism industry of Saudi Arabia. Unfortunately, these projects involve extensive development of the marine environment, particularly along vast stretches of hitherto relatively undeveloped coastline and islands. Fragmentation of critical habitats can impact the abundance and diversity of a wide array of marine life (Last et al. 2011). Under the imposing and synergistic pressures of overexploitation, habitat loss and degradation, and weak management, sharks and rays are increasingly threatened in the Saudi Arabian Red Sea.

In order to better inform management and protection for vulnerable species of sharks and rays, high-resolution data of species diversity and abundance is essential (Simpfendorfer et al. 2011). Survey methods to evaluate the status of elasmobranchs fall into one of two categories: fishery-dependent and fishery-independent. Each

technique comes with its own set of advantages, drawbacks, and opportunities for innovation.

1.2 Survey methods to assess elasmobranchs

Traditional, fishery-dependent survey techniques include data collection from fish markets, fisheries observer programs, or from fisheries logbooks (Carrier et al. 2018). This data includes both mandatory reporting from commercial fishermen (Walsh et al. 2002) as well as information from trained observers and estimates from recreational angling activity (Burgess et al. 2005; Harry et al. 2011). The fishing industry provides huge opportunities for cost-effective data collection as the process of industrial and recreational fishing is continuous and requires relatively little survey effort. Taken alone, however, these approaches have significant limitations. Fishing methods that target individual fish are biased towards capturing specific size classes of profitable species (Stevens et al. 2000). This kind of biased catch data may give an inadequate representation of diversity (e.g., discarded bycatch) and fail to account for threatened or rare species (Walker and Hislop 1998; Graham et al. 2001). In addition, participation, trust and, communication with local fishers is required.

Fisheries-independent methods are especially well-suited in regions like Saudi Arabia, where fisheries-dependent methods are challenging due to the lack of fisheries regulation and the resulting lack of data and documentation (Spaet and Berumen 2015). Additionally, fisheries-independent methods are particularly appropriate to study elasmobranchs due to the sensitive life-history traits and commonly cryptic behavior of sharks and rays (Cappo et al. 2004; Harvey et al. 2013; White et al. 2013; Espinoza et al. 2014). Fisheries-independent methodologies include techniques such

as scientific longline surveys, gillnets, and trawls, as well as underwater visual surveys (UVS) (Spaet et al. 2016). These techniques have built upon traditional, exploitative survey techniques to offer a more accurate understanding of species abundance and diversity and provide non-invasive means to sustainably observe sensitive populations (Simpfendorfer et al. 2011). Furthermore, these methods allow the user to survey areas of interest that may not be typically targeted by fisheries. Fisheries-independent gears are, however, limited by habitats in which the equipment can operate.

Despite advances in fisheries-independent techniques to sample elasmobranchs, there is a need to consider the appropriateness of the equipment and sampling method, as many are not suitable when working with endangered species or in marine protected areas, and as such non-extractive fisheries-independent surveys have become increasingly popular. The use and development of non-extractive methods to investigate the abundance and diversity of threatened and endangered species has been critical to alleviate issues regarding fishing in sensitive habitats, post-release mortality, and other sampling biases (White et al. 2013). Baited remote underwater video systems (BRUVs) present a minimally invasive approach to collecting ecological data that alleviates some issues associated with alternative methodologies. BRUV units are a robust frame consisting of a camera(s) system pointed towards a selection of cut or crushed bait fish within a mesh bag or box that can either be placed on the seafloor or suspended midwater in pelagic zones. Generally, BRUVs will stay in a single location for the duration of a survey, but the time, camera number and angle, bait, and general design vary between studies. The scent of the bait attracts animals into the field-of-view (FOV) of the camera and are subsequently recorded; those that are

indifferent to the bait may also enter the FOV coincidentally are also recorded (Cundy et al. 2017). BRUVs are used globally to study elasmobranch abundance, diversity, and behavior (Cappo et al. 2004, 2007).

BRUV surveys collect large quantities of information on the number of species and individuals as well as community structure (Cappo 2010). For example, BRUVs have been used to understand elasmobranch site fidelity, restriction, and residency (Broad et al. 2010), as well as predator-prey interactions and stimuli responses (Kempster et al. 2016; Ryan et al. 2018). Several methods to process and analyze BRUV data have been developed to describe the most common derivative; relative abundance. Typically, relative abundance is described as the maximum number of individuals per species in one video frame from BRUV data (MaxN) (Cappo 2010; Harvey et al. 2013; Whitmarsh et al. 2017). The usefulness of BRUV-derived data, however, largely depends on the population density of the study species at hand. Research involving low-density study species results in a lack of sampling power and replication, while high-density populations may overestimate actual abundance (Kilfoil et al. 2017; Kiszka and Heithaus 2018). To account for this bias and measure true abundance, Sherman et al., (2018) suggested the use of MaxIND, the maximum number of individuals detected over a deployment based on distinguishable markings on the body. Despite such attempts to reduce the bias in BRUV sampling, several other limitations remain. These challenges include potential damage to fragile habitats (e.g., coral reefs and seagrass beds), frequent obstruction of the FOV (orientation), and variability of behavior and camera attractiveness among different elasmobranch species (Edgar et al. 2004; Schobernd et al. 2014; Sherman et al. 2018). Additionally,

BRUV surveys are time-expensive, considering the length of time required to prepare the unit, the survey duration, and the post-processing required for each deployment (Ventura et al. 2016). These limiting dynamics, despite a considerable sampling effort, often lead to under-sampling. Alternative and more appropriate non-invasive tools should be considered in order to provide protection of fragile habitats and attempt to further reduce types of sampling bias, such as the use of Unmanned Aerial Vehicles (UAV).

In recent years, the use of UAVs (drones) has emerged as another non-invasive means to improve survey efforts, without even entering the water (Hodgson et al. 2017; Brack et al. 2018). Unmanned aerial vehicle surveys are able to sample areas that may be difficult to reach while allowing maximum spatial coverage in order to observe transient species. In coastal waters UAVs can provide a unique opportunity to sample absolute densities of elasmobranchs (e.g., Kiszka et al., 2016) and can be fully automated to increase reproducibility and reduce human bias, especially when working at small spatial scales ($<2 \text{ km}^2$) (Kiszka et al. 2016; Kiszka and Heithaus 2018). Post-flight analysis with UAVs are also advantageous as they provide a permanent video transect of sightings (Hodgson et al. 2013) and can be used for fine-scale mapping (Brack et al. 2018). The extent to which UAV surveys can be applied is limited by many factors, such as weather conditions (e.g., wind, glare, and turbidity), as well as observer bias (e.g., variations in user detection rate) and availability bias [e.g., animal present, but cannot be seen (Hodgson et al. 2013; Ferguson et al. 2018)] and may not provide true abundance and diversity estimates of conspecifics or co-occurring species. Nevertheless, UAV surveys are a powerful tool when used in

conjunction with other traditional survey techniques (e.g., mark-recapture) and have been shown to offer higher detection probabilities than traditional techniques depending on the aforementioned biases (Hodgson et al. 2017).

Understanding the biases of available survey techniques is fundamental to an informed selection of methodology. Method consistency is equally important to be able to study diversity across a range of habitats. A case in point from Kiszka et al. (2016) described the first direct estimates of shark and ray densities across barrier reef and sandflat habitats using UAV drone surveys in Moorea, French Polynesia. This study highlighted spatial heterogeneity in the distribution of elasmobranchs in shallow water, where sharks and rays preferred reef environments over sandflats and demonstrated the importance of understanding the relationship between distribution and density for management of threatened species. The combined use of both BRUV and UAV surveys will better describe potential data discrepancies between methods as well as identify specific limitations of each method. Furthermore, utilizing fish market surveys will characterize fisheries-targeted species to compare the suitability of fisheries-dependent assessments. This is particularly crucial when working in regions of low densities of elasmobranchs, such as the Saudi Arabian Red Sea (Spaet et al. 2016).

1.3 Objectives

The present study attempts to a) identify the associated biases of both BRUV and UAV surveys in both mangrove and reef-associated habitats, and b) quantify differences in abundance and diversity of elasmobranchs across these habitats in the central Saudi Arabian Red Sea. A combination of BRUV and UAV sampling techniques

was expected to provide a more detailed description of elasmobranch abundance and diversity compared to using either method alone.

2. METHODS

2.1 Study Site

Saudi Arabia has the most extensive coastline of the Red Sea, consisting of long reef systems that fringe the coastline and are typically backed by shallow water lagoons (Bird 2010). Thuwal lagoon, the survey site, is located between 22°18' and 22°20'N latitude and 39°04' and 39°05'E longitude along the western coast of central Saudi Arabia (Figure 1). This region of the Red Sea exhibits a seasonal sea-level change of 0.3-0.4m and a tidal range of less than 0.25m (Churchill et al. 2019). The western edge of the lagoon is composed of a long reef approximately 5 km long, where the northern end curves around a shallow sandflat region to a deep and narrow channel into the lagoon system (Figure 1). The inner lagoon ranges in depth between 3- 15m with shallow sandflats on either side. The eastern coastal edge of the lagoon shallows is fringed with 91.2 hectares of white mangrove (*Avicennia marina*), and the southern end of the lagoon has many smaller, shallower channels that exit the lagoon back into the Red Sea. There are two developments close to the site; Al Qadimah Military Port to the north, and King Abdullah University of Science and Technology (KAUST) to the east.



Figure 1. Map of Thuwal lagoon system in the Saudi Arabian central Red Sea. Black dots represent successful BRUV deployments used for analysis (sandflat= 49; reef= 11). Map depicts coral reef habitat on the west side of the lagoon, deep northern channel into the Red Sea, and mangrove habitat fringing the east side on the sandflat.

Surveys were conducted in a spatially stratified random design. The lagoon was split into two geographic features; coral reef (reef-associated) and sandflat (mangrove-associated).

Simultaneous BRUV and UAV surveys were conducted between August and November 2019 and conducted between 0730 and 1100 hours inside the Thuwal lagoon. Upon arrival, UAV surveys were conducted (section 2.3.1) before BRUV units were deployed (section 2.2.1). Each BRUV survey consisted of three replicates, where at least two units overlapped the UAV survey area (hereafter referred to as a “combined” survey). In the event of deployment failure during combined surveys, the alternative survey method was still attempted to collect temporal data. All BRUV data from deployments in the same survey day were pooled; however, due to single unit failure, there were not always three BRUV to one UAV survey deployments available (Figure 2).

Additional BRUV surveys (n=21) were conducted between April and August 2019 before permitting was issued for drone use in the Thuwal lagoon. The largest survey effort was in November (BRUV, UAV, & combined), and the lowest survey effort was in October (combined & UAV) and April (BRUV). No surveys were conducted in July.

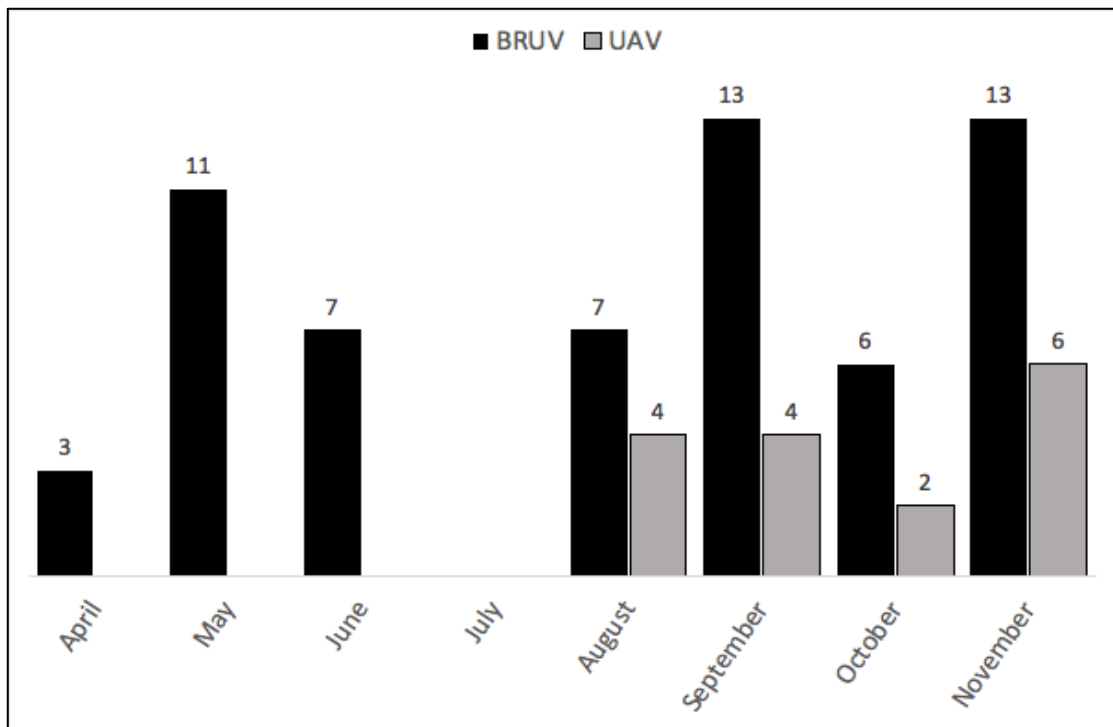


Figure 2. Total BRUV (black) and UAV (grey) survey effort from April 2019 to November 2019. No surveys were conducted in July.

2.2 BRUV surveys

A total of 87 BRUV deployments were conducted over 29 field-days between 29th April and 13th November 2019.

2.2.1 BRUV design and sampling

Miniature BRUV units were explicitly developed for shallow water habitats (Figure 3). GoPro HERO5 cameras (setting: Wide FOV) were mounted on the BRUVs 30cm above the seafloor. Approximately 1kg of chopped Indian mackerel (*Rastrelliger kanagurta*; Cuvier, 1816) was contained in a metal cage 60cm in front of the camera. In sandflat (shore) deployments, BRUV units were carried out to an appropriate depth (ca. 0.4-1m) and recovered on foot. For reef (boat) deployments (depth ca. 1-2m), BRUV units

were manually lowered from the boat and were recovered using a boat hook. BRUV units were made visible by an attached surface marker buoy.



Figure 3. Picture of BRUV unit, with GoPro, bait box, and marker buoy attached.

Three BRUV units were deployed at once and were left for a minimum deployment time of 90 minutes (“soak time”). The initial 10 minutes of footage were removed from analysis (reef-based), or the duration of time until any suspended sediment in the FOV settled out (sandflat-based) in order to remove any behavioral or visual bias from entering the environment. BRUV units were deployed at a minimum distance of 150m apart, to minimize the probability of double counting sharks and rays. Throughout the BRUV soak time, scientific personnel kept a minimum distance of 500m from the units during sandflat deployments, and 200m distance on reef deployments to minimize disturbances to animal behavior.

2.2.2 Video annotation

All BRUV deployment footage was reviewed by A. J. McIvor using the software VidSync (Neuswanger et al. 2016). Species validation was conducted by two independent reviewers (J. Cochran and C. Williams) who are experienced in Red Sea shark and ray identification (Figure 4). Video annotations included image view parameters, such as camera bias (proportion of seafloor visible in the video frame; defined in thirds) and visibility (water clarity as distance from the camera; to the bait box, $\leq 3\text{m}$, and $> 3\text{m}$) which were scored from 1-3, and FOV (the proportion of the video frame obscured by reef; defined in quarters) which was scored from 1-4 as described in Miller et al. (2017). In some cases, deterioration of visibility post deployment meant footage was cut short, or removed entirely from further analysis (e.g., sediment did not settle, or units were displaced after deployment). Time of arrival was recorded each time an individual entered or re-entered the FOV. Each arrival time was categorized as a new event before analysis.

Where previous studies have used time-to-first-arrival, the maximum number of individuals viewed at a single point in time (MaxN), or catch per unit effort (CPUE; the total number of individuals recorded in the footage), there is evidence to suggest that these may under-represent true abundance. In this study, the rarity of sharks and rays in the area render MaxN consistently small as the likelihood of two individuals in one frame was extremely low. MaxIND was used for batoids species, and MaxN was used for sharks to measure abundance.



Figure 4. Single frame from a video of a BRUV deployment showing typical placement in the habitat and typical visibility conditions. This example shows a positive identification of *Himantura* sp. attempting to access the bait.

2.2.3 Individual identification (MaxIND) of stingrays

When BRUV footage contained more than one ray individual, the event was re-analyzed in order to extract key frames from the video that showed variations in distinguishable features from rays in different events. Frames were compared among different ray events in a single BRUV locale, as well as between a whole deployment to identify unique individuals. No attempt was made to identify individuals over time (i.e., on different days). The most common species were the *Himantura* sp. (reticulate whipray) and *Taeniura lymma* (blue-spotted ribbontail ray), both of which have distinguishable spot patterns (Figure 5). In all batoid species that have been examined, spot patterns appear to be stable over the course of many years (e.g., *Aetobatus narinari* (spotted-eagle ray), González-Ramos et al. 2017; and *Megatrygon microps* (smalleye stingray), Boggio-Pasqua et al. 2019). Spot pattern was used when possible,

however, when a ray was perpendicular to the camera, only one side on the disk could be assessed (left/right). In this case, sex (presence of claspers), damage to disk/tail, and body to tail ratios were used (ImageJ, version 1.8.0; Schneider et al., 2012) to identify individuals. When two ray events were too similar to separate into two unique individuals, they were classed as a single ray to avoid overestimation of abundance estimates.

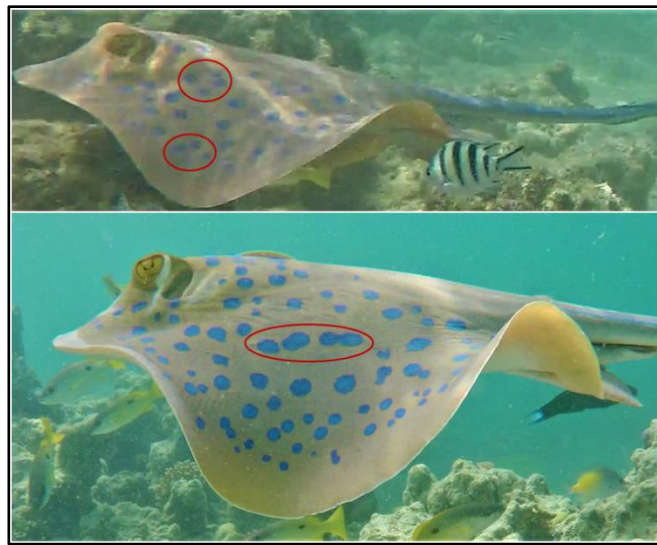


Figure 5. Example of two individuals of *T. lymma* with different spot patterns on the left pectoral wing. The differences enabling discrimination between the two individuals are highlighted with red circles.

2.3 UAV surveys

A total of 28 UAV surveys were conducted between 25th August and 13th November 2019.

2.3.1 Pre-deployment and sampling parameters

Aerial surveys were conducted using a commercially available DJI Phantom Pro 4 drone, at an altitude of 12m to ensure identification of target species while retaining

a broader spatial coverage. After take-off, pre-programmed missions were run using the program Altizure (www.altizure.com) in order to create repeatable transects. Each mission consisted of a 100m x 400m grid. The drone recorded a continuous video along a “lawn-mower” transect at a speed of $3\text{m}\cdot\text{s}^{-1}$ with a 50% overlap between transect strips. A polarized lens was used on the Phantom camera and was angled at 15 degrees from the sun to avoid glare. Videos were taken at 4k resolution to produce images stills of 8-megapixel quality. DJI Go 4 (<https://dji.com/goapp>) was used for take-off and landing, as well as manual flight paths when required (e.g., unexpected recovery of UAV due to low flying helicopters, $n=8$).

Field-of-view measurements were conducted during a pre-deployment analysis to determine the appropriate separation between line transects of the survey grid. Premeasured landmarks (e.g., cardinal marks) were used to determine the spatial coverage. A camera orientation (straight down/nadir vs. 9-degree angle) comparison was conducted during the pre-deployment analysis in order to decrease availability bias from sun glare. This study exercised minimum disturbance flight practices through optimal altitude testing and avoidance of sporadic flight movements as recommended by Hodgson and Koh (2016).

Species known to inhabit the study area from the pre-deployment trial were determined to have distinct disk and tail features (Figure 6) and were considered unique enough to not conduct a species identity trial using the multiple observer protocol. A total of 4.4% of all sightings could not be identified due to large plumes of suspended sediment from feeding/foraging rays that could not be seen or distinguished confidently ($n = 9$).



Figure 6. Examples of identified species from UAV surveys. Clockwise from top left: *Pastinachus sephen*, *Himantura sp.*, *Taeniura lymma*, *Aetobatus narinari*.

2.3.2 Video annotation

Flights were analyzed using VidSync at 0.25x speed. The observer was able to scroll frame by frame to identify individuals and record the time frame, species, habitat, and activity (moving, foraging, or stationary). Foraging was determined by excavation plumes of suspended sediment made by rays, or “shuffling” rays that exhibited “dig and search” behaviors.

2.3.3 Availability Correction Factor (ACF)

Availability bias, or the availability correction factor (ACF), is the number of elasmobranchs present in the survey area, which were not visible to the observer and were not counted as a result. Factors that influence availability are water

turbidity/clarity, depth of the target/water column, and diving behavior of the targeted species. The maximum depth was less than 5m at the study site (mangrove and reef), so benthic behavior and water column depth were discounted as factors affecting the visual detection of the target species. Water is typically clear in this shallow study site, and as such, it was assumed that availability bias due to water clarity was close to zero as every target object should be detected (Kiszka et al. 2016b). Sampling was restricted to wind conditions of Beaufort <2 (i.e., light breezes <11 km/h) to mitigate turbidity. Where conditions were of Beaufort 2, a Secchi disk was deployed to assess water clarity in order to confirm that the effects of turbidity were negligible. This study accounts for the most likely variables affecting availability bias in the local habitat and, as such, all sharks and rays inhabiting the study area at the time of the survey were available to be counted. Thus, the ACF used for this study is 1.

2.3.4 Perception Correction Factor (PCF)

Perception bias, or the perception correction factor (PCF), addresses the number of elasmobranchs available for counting but that are not detected by the observer. This may be due to observer fatigue and/or inattention, or from sun glare or low contrast between the target individual and the background. In UAV surveys, drone altitude and human error are the largest potential source of perception error. As ground sampling distance increases, the ability of the observer to identify targets decreases, as such, small individuals may be missed. For this reason, we adopted the guidelines set by Marsh and Sinclair (1989) that define the ability to detect an animal from a set distance (altitude: minimum animal size). Marsh and Sinclair (1989) recommend a maximum ratio of 274:1 for reliable detectability. In the current study, the UAV was

flown at a constant height of 12m, and the minimum animal size was estimated to be (disk-width) 0.15m (smallest encountered disk width, *T. lymma*; A. J. McIvor, personal observation). This offered a ratio of ~72:1 and is inside the guidelines of reliable detection based on the chosen altitude and smallest anticipated ray size. It was not expected that individuals smaller than 0.15m disk-width would be encountered during the study, and thus PCF correction was not required for altitude. However, target animals may not be counted and missed by the observer due to a variety of reasons. A double-observer technique was used to derive a PCF to assess the likelihood of detection bias from a single trained observer in order to correct for perception bias. A second observer (C. Williams) recorded the abundance and species in each UAV survey. Any discrepancies from the primary observer were noted and revisited by both observers to resolve differences in species or count. Two independent observers recorded detections, where " S_1 " represents the number of individuals reported by only observer one, " S_2 " is the number of individuals reported by observer two, and " b " is the number of individuals seen by both observers (Kessel et al. 2013).

$$PCF = \frac{(S_1 + b)(S_2 + b)}{b(S_1 + S_2 + b)}$$

If there were any uncertain matches, whether unidentifiable or unknown species, the count data was removed to avoid misidentification.

2.3.5 Abundance

The abundance estimation (N) for each UAV deployment was calculated using the equation of Rowat et al. (2009):

$$N = C \times ACF \times PCF$$

where C is the total count of individuals, ACF is the availability correction factor (1), and PCF is the perception correction factor (see also Kessel et al. 2013).

2.3.6 Density

To estimate the density of elasmobranchs, total count data from UAV transect surveys were collected. Each UAV transect was 100m wide × 400m long, and provided an area of 40,000m². Density (D) was calculated using the following formula:

$$D = \frac{N}{A}$$

where N is the number of individuals detected (abundance) and A is the area in meters. Species-specific density was calculated for both reef and sandflat habitats by expressing abundance per unit area (ha⁻¹).

2.4 Fish market surveys

Fish market surveys were conducted to identify if fisheries-dependent methods were a potential substitute or complement to the aforementioned independent survey methods and to determine if fisheries-targeted species were present in the general Thuwal region. Surveys were conducted opportunistically from 13th November, 2018, to 24th February, 2020, at the Thuwal central fish market. As many tables were surveyed as possible each time (typically 14-16 tables), where the total number of individuals of each species were reported per trip. In order to account for potential variation in the number of tables surveyed, number of tables in operation, and total volume of fish for sale on any given visit, relative abundance was used. Relative abundance was calculated by dividing the total abundance of each species in turn by the total abundance recorded.

2.5 Data analysis

All statistical analyses were conducted using R version 3.5.2 (R Core Team 2018). All statistical tests were given a significance cut-off value of ≥ 0.05 . A Shapiro-Wilk test and Filgner-Killeen test were used to assess the assumptions required for parametric tests through significance testing. Combined survey abundance observations highly deviated from normality ($W = 0.62278$, $p\text{-value} = 3.679\text{e-}09$), hence non-parametric methods were used for further analysis. Wilcoxon rank-sum tests were used to assess statistical differences in the data between habitat and method, as well as differences in combined samples.

As UAV surveys record all individual elasmobranch species along a transect (area-based sampling), whereas BRUV surveys record the MaxIND in a fixed location (time-based sampling), it was not appropriate to compare the raw observer abundance between the methods (Andradi-Brown et al. 2016). As the focus of this study was between methods across different habitats, abundance was standardized between methods by calculating the relative abundance of each species on each UAV transect or BRUV deployment. This was achieved by dividing the total abundance of each of the respective species by the total abundance of all study species recorded on the transect or deployment.

The comparison of species composition between methods relied on the relative abundance of different species. As such, the species richness and evenness were taken into consideration through the diversity indexes. Diversity indexes were standardized to a total abundance (sub-sample = n) that was less than the total community size of the smallest sample post-analysis. The discrepancy in sample size and the effect it has

on species richness can typically be corrected through rarefaction, as this assumes that the total abundance imbalance is due to differences in sampling technique and not the difference in actual abundance. Rarefaction, Shannon-Wiener, Simpson, true diversity, Hill's ration, and Piloni indices were derived using the *vegan* package in R (Oksanen et al. 2019). It is important to note that Shannon-Wiener considers species richness more than species evenness, whereas Simpson index has more weighting towards species evenness.

Species accumulation curves were used to estimate the number of species in the reef and sandflat environment detected by each method. Collector's curves were used to show the cumulative number of species observed in the sequence they were observed. Rarefaction curves were obtained using the *vegan* package (Oksanen et al. 2019), where observations were modeled over 100 iterations in a randomized order.

3. RESULTS

3.1 BRUV surveys

A total of 87 BRUV deployments were conducted over 29 field-days between 29th April and 13th November 2019. Seventeen videos were lost due to equipment failure (SD card corruption, battery defects, etc.), and ten videos were removed from analysis due to poor visibility (< 1m). From the resulting 60 deployments, 16 videos recorded a total of 61 elasmobranch capture events from five identified species. The vast majority (92%) of elasmobranch captures were from three species of ray: *T. lymma* (Dasyatidae), *Himantura* sp. (Dasyatidae) (Figure 4), and *Urogymnus granulatus* (mangrove whipray; Dasyatidae). The remaining eight percent of captures came from two species of shark: *Negaprion acutidens* (sicklefin lemon shark; Carcharhinidae), and *Nebrius ferrugineus* (tawny nurse shark; Ginglymostomatidae).

Stingrays accounted for 57 of the total 61 capture events, 43 of which could be distinguished from other conspecifics in the same deployment. A total of 6 *T. lymma* individuals were not able to be distinguished from other individuals of the species and were thus not added to the total. *Himantura* sp. were more likely to be seen more than once in the same video if present than *T. lymma*. Only one video showed two (*Himantura* sp. MaxN = 2) individuals in the same frame at the same time. Using MaxIND resulted in an additional 4 *T. lymma* and 2 *Himantura* sp. being identified during this study compared with MaxN (Table 1).

Table 1. Summary of identifiable individuals from BRUV surveys using MaxIND, where SF is sandflat, and R is reef.

	<i>T. lymma</i>		<i>Himantura</i> sp.	
	SF	R	SF	R
Videos present	7	2	6	1
Total observations	12	15	27	2
Identifiable individuals	9	4	8	1

Of all capture events in BRUV surveys, 37.5% of individuals attempted to feed from the BRUV bait box at least once (Table 2). Other than *T. lymma* and *Himantura* sp., only *N. acutidens* (n = 1) attempted to feed from the bait box, whereas both *N. ferrugineus* and *U. granulatus* did not make a feeding attempt.

Table 2. Percentage of identified individuals of *T. lymma* and *Himantura* sp. that exhibited feeding attempts on the bait box, where SF is sandflat, and R is reef. “-” indicates that the species were not observed in the reef habitat.

	Total		<i>T. lymma</i>		<i>Himantura</i> sp.	
	SF	R	SF	R	SF	R
Feeding attempt	37.5 %	-	7.14 %	-	77.78 %	-
No attempt	62.5 %	-	92.86 %	-	22.22 %	-

3.2 UAV surveys

A total of 28 UAV surveys were conducted between 25th August and 13th November, 2019. Due to equipment failure (n=3), interrupted surveys (e.g., military helicopters, territorial coastal birds), and visibility issues (waves present, but not wind), only 16 deployments were available for analysis; nine sandflat sites, and seven reef sites. UAV

surveys detected 206 individuals on 16 deployments, with at least one elasmobranch detection per deployment.

All capture events from UAV surveys were batoids; no sharks were detected. The majority of stingrays were from the family Dasyatidae: *T. lymma*, *Himantura* sp., and *Pastinachus sephen* (cowtail ray), and *Aetobatus narinari* (spotted eagle ray; Myliobatidae).

The double-observer derived perception correction factors (Table 3) reported very few observation deviations between observers ($n = 6$). Variations arose from species abundance of *T. lymma* and *Himantura* sp. (mean PCF: *T. lymma* 1.0 ± 0.06 cf. *Himantura* sp. 1.0 ± 0.04).

Table 3. Perception Correction Factor (PCF, see 2.3.4, following Kessel et al. 2013), where b = number of elasmobranchs seen by both observers, S_1 = number of elasmobranchs seen only by observer one, and S_2 = the number of elasmobranchs seen only by observer two.

Survey date	Total individuals observed	b	S_1	S_2	PCF
<i>T. lymma</i>					
25.08.2019	4	2	2	0	1.0
09.09.2019	18	16	1	1	1.0
29.09.2019	3	3	0	0	1.0
01.10.2019	4	2	1	1	1.1
04.11.2019	14	13	1	0	1.0
<i>Himantura</i> sp.					
09.09.2019	5	3	1	1	1.1
04.11.2019	6	6	0	0	1.0
13.11.2019	22	20	0	2	1.0

Higher densities of stingrays were found over sandflats (22 individuals $\text{ha}^{-1} \pm 11$ SE) than the reef (4 individuals $\text{ha}^{-1} \pm 2$ SE) (Table 4). UAV surveys observed a higher total density from the sandflat environment than both habitats combined due to the lack of *Himantura* sp. found over reef habitats and relatively high total abundance found in the sandflat environment (Table 4). High variances reduce the confidence of any statistical comparisons between *T. lymma* and *Himantura* sp. across the sandflat environment.

Table 4. Average density \pm standard error per hectare of elasmobranchs over sandflat and reef habitats for total abundance, *Taeniura lymma* density, and *Himantura* sp. density.

Average density (ha^{-1})	All	<i>T. lymma</i>	<i>Himantura</i> sp.
Sandflat	22 \pm 10.57	11 \pm 8.25	11 \pm 9.50
Reef	4 \pm 1.99	2 \pm 1.21	-

3.3 Assemblage description

A total of 206 and 26 elasmobranchs were recorded by UAV and BRUV surveys, respectively (Table 5). CPUE was derived from 60 BRUV deployments and 16 UAV deployments. There was a greater CPUE derived from UAV surveys generally (UAV: 22.07 cf. BRUV: 0.28), which was higher in sandflat surveys than reef surveys (SF: 30.08 cf. R: 4.46). However, the CPUE using BRUV surveys was higher in reef surveys compared to sandflat surveys (R: 0.39 cf. SF: 0.26).

Table 5. Catch per unit effort for UAV and BRUV surveys over reef (R) and sandflat (SF) habitats.

	UAV		BRUV		Total	
	R	SF	R	SF	UAV	BRUV
Effort (hours)	2.92	6.42	18.09	69.46	9.33	87.55
Total elasmobranch detection (<i>n</i>)	13	193	7	19	206	26
Catch per unit effort (CPUE)	4.46	30.08	0.39	0.26	22.07	0.28

There was a greater diversity observed over reef habitats when using BRUV surveys (λ reef = BRUV 0.612 cf. UAV 0.368), whereas a greater diversity was observed over the sandflat environment when using UAV surveys (λ sandflat = BRUV 0.549 cf. UAV 0.522) (Table 7). The combined species composition from BRUV and UAV surveys included seven species from five families (Table 6). The only two common taxa between survey types were *T. lymma* (total relative abundance: 48% BRUV cf. 49.5% UAV) and *Himantura* sp. (40% BRUV cf. 44.1%) (Figure 7). *Taeniura lymma* and *Himantura* sp. were observed using the sandflats and reef by both survey types, and *A. narinari* was detected in both habitats using only UAV surveys.

There was not a significant difference in the observed number of individuals in BRUV surveys between reef and sandflat surveys (Kruskal-Wallis chi-squared = 0.933, df = 1, p-value = 0.334). However, there were fewer species detected on sandflat surveys than reef (SF: 3 cf. R: 4) despite a larger sampling effort (Table 6).

UAV surveys observed a significantly higher abundance estimate of elasmobranchs on the sandflats than the reef (Kruskal-Wallis chi-squared = 5.785, df = 1, p-value = 0.016), as well as a higher number of species (SF: 4 cf. R: 3).

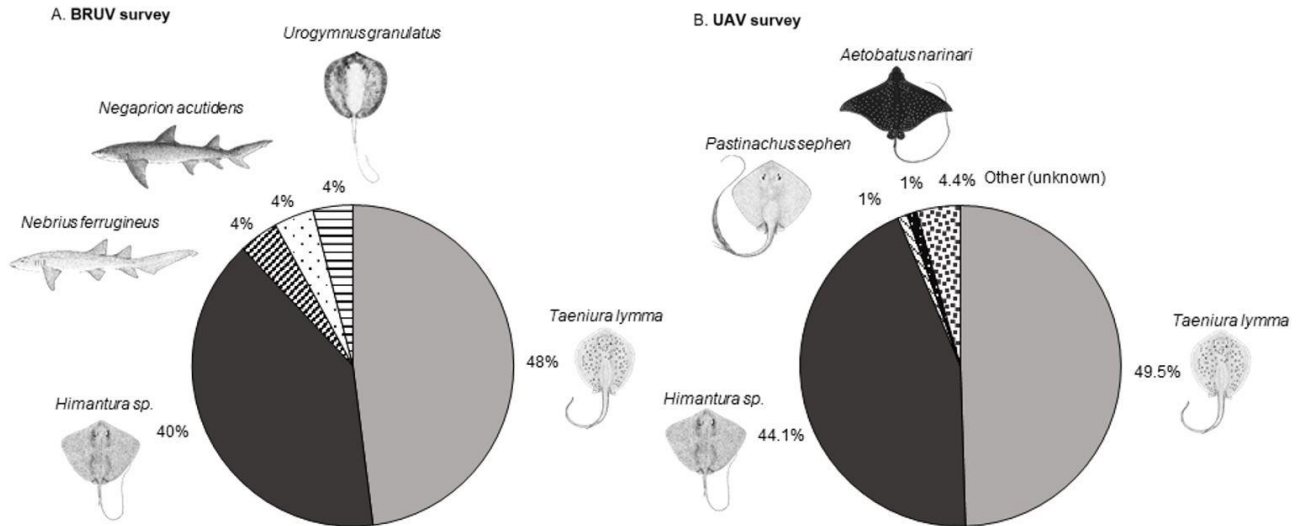


Figure 7. Proportions of the total elasmobranch assemblage that different species compose using two sampling techniques: (A) observed using BRUV surveys and (B) observed using UAV surveys. Images ©FAO.

Table 6. Mean \pm standard error of the number of individuals per species per site recorded from BRUV and UAV surveys over sandflat and reef habitats. BRUV data is shaded. “-” denotes that species was not recorded by survey type or at specific habitat.

Family	Genus Species	Sandflat		Reef	
		BRUV	UAV	BRUV	UAV
Dasyatidae	<i>Taeniura lymma</i>	0.31 \pm 0.15	9.44 \pm 2.83	0.67 \pm 0.42	2.43 \pm 0.43
	<i>Himantura sp.</i>	0.56 \pm 0.18	9.44 \pm 3.15	0.17 \pm 0.17	0.57 \pm 0.57
	<i>Urogymnus granulatus</i>	-	-	0.17 \pm 0.17	-
	<i>Pastinachus sephen</i>	-	0.22 \pm 0.15	-	-
Myliobatidae	<i>Aetobatus narinari</i>	-	0.22 \pm 0.22	-	0.14 \pm 0.14
Carcharhinidae	<i>Negaprion acutidens</i>	0.06 \pm 0.06	-	-	-
Ginglymostomatidae	<i>Nebrius ferrugineus</i>	-	-	0.17 \pm 0.17	-

Species accumulation curves typically highlight the influence of sampling effort on the total number of species detected, yet this does not hold for both survey methods in this study (Figure 8). Despite a greater sampling effort in BRUV deployments, this survey method failed to detect the same species as UAV surveys (Table 6). The species accumulation curve using BRUV surveys, ordered by collection, plateaus after three deployments on the reef, and six deployments on the sandflat, whereas the same plateau from UAV surveys is observed after five on the reef and two on the sandflat (Figure 8). The difference in deployment effort to observe the same plateau suggests that a greater effort (i.e., a larger number of deployments) is required to detect more species using BRUV surveys than UAV surveys.

Rarefaction curves from the sandflat surveys appear to level out towards an asymptote and suggest that it is unlikely that more species will be detected with a higher sampling effort. Reef-based curves do not show the same indications of leveling out, and it can be expected that reef-based surveys are likely to observe more species with more sampling. However, the rarefaction curve produced from UAV surveys over the reef environment is not as steep as the BRUV-reef surveys and so UAV surveys may not observe as many species as BRUV surveys with a greater number of deployments.

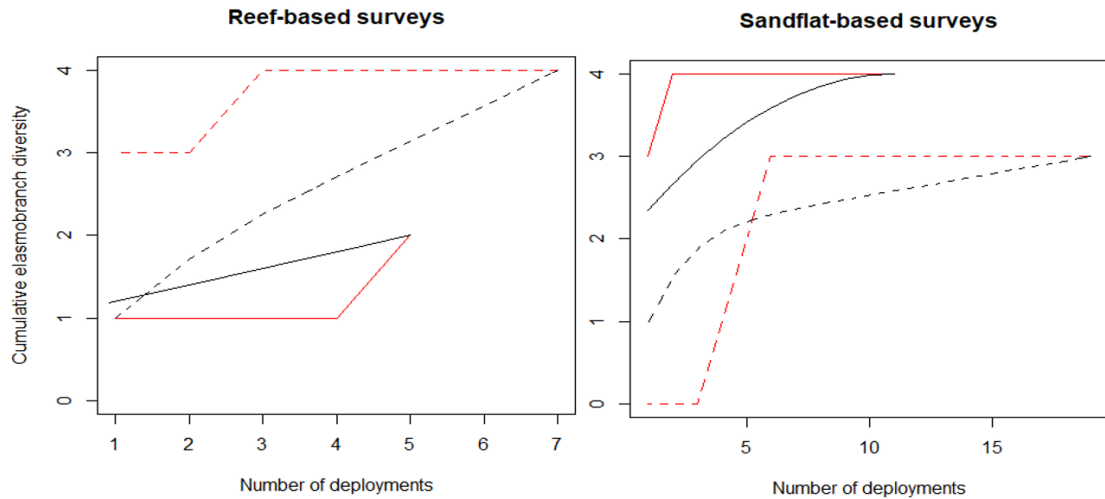


Figure 8. Species accumulation curve for BRUV (dashed lines) and UAV (solid lines) surveys in reef-based (left) and sandflat-based (right) collections. Collector's curve depicted in red, and rarefaction in black. Note difference in total number of deployments.

The comparison of species composition between methods relies on the relative abundance of different species. As such, the species richness and evenness were taken into consideration through the diversity indexes displayed in Table 7.

The diversity and richness were relatively similar between methods over sandflat surveys. Nonetheless, there was a relatively larger difference in evenness, indicating there is an uneven representation of the population size of the species present over the sandflat habitat. UAV surveys observed a higher relative abundance of specific species, whereas BRUV surveys observed a more similar relative abundance between the species observed over sandflat habitats. The difference in relative abundance was driven by the number of individuals of each species observed in the respective methods.

The rarefaction analyses show that there is a higher expected number of species using BRUV surveys over reef habitats (BRUV: 3.213 cf. UAV: 2.540) and sandflat habitats (BRUV: 2.811 cf. UAV: 2.685) than in UAV surveys. However, the sub-sample size used for standardization purposes was relatively small due to the limited number of individuals observed in BRUV-reef surveys (Table 7), and as such, the sensitivity of the test to sample size decreases the confidence in using rarefaction.

There was a more substantial discrepancy between the diversity and richness between methods over the reef environment, where BRUV surveys generally observed higher levels of diversity than UAV surveys. Pilou evenness suggests that there was more similarity between methods than habitat type in terms of diversity.

Table 7. Species richness and diversity indexes derived from BRUV and UAV surveys over the two sampled habitat types. BRUV data is shaded. Largest number per method is in bold. Rarefaction indices are standardized to six (where n is less than the total community size of the smallest sample; section 2.5).

Method; Habitat	Abundance	Rarefaction	Diversity		Evenness		
	Catch per unit effort (CPUE)	($n = 6$)	Simpson's Index (λ)	Shannon- Wiener Index (H')	True Diversity (eH')	Pilou evenness (J)	Hill's ratios ($E_{a:b}$)
BRUV; Sand	0.285	2.811	0.549	0.868	2.381	0.500	1.201
BRUV; Reef	0.387	3.213	0.612	1.154	3.170	0.442	1.165
UAV; Sand	30.078	2.685	0.522	0.802	2.230	0.377	1.139
UAV; Reef	4.457	2.540	0.368	0.650	1.915	0.335	1.130

3.4 Combined surveys

observed species from one survey type. Plot shows mean relative abundance of each species and method with standard error of the mean.

There was a significant difference in the relative abundance of *T. lymma* between method types in the sandflat surveys (Kruskal-Wallis chi-squared = 4.32, df = 1, p-value = 0.03). However, paired-sample Wilcoxon tests revealed that the mean relative abundance of *T. lymma* from BRUV surveys was not significantly different from that of UAV surveys (p-value = 0.08) and that BRUV surveys had a statistically lower mean relative abundance of *T. lymma* than UAV surveys (Wilcoxon-Mann-Whitney: V = 6.5, p-value = 0.003) (Figure 9). Wilcoxon-Mann-Whitney cannot compute exact p-value with ties (observations with the same value) or zeroes. Thus Kruskal-Wallis testing was deemed more reliable and is considered more appropriate for smaller sample sizes such as in this study (due to large quantities of zeros from BRUV data). Applying the Kruskal-Wallis test revealed a statistical difference in the relative abundance of *T. lymma* between methods in sandflat surveys. The difference in the relative abundance of *T. lymma* between BRUV and UAV sandflat surveys indicates that there may be biases associated with species-specific targeting between the methods; specifically, BRUV surveys did not detect as many individuals of *T. lymma*.

There was no significant difference in the relative abundance of *Himantura* sp. between methods of sandflat surveys using Kruskal-Wallis (chi-squared = 0.34, df = 1, p-value = 0.56) or paired-sample Wilcoxon testing (p-value = 0.62). The similarity in the relative abundance suggests that there is likely no bias towards targeting *Himantura* sp. in the sandflat environment using either method.

There were no instances where combined surveys observed *Himantura* sp. in both reef-based BRUV and UAV surveys, and thus relative abundance comparisons were only conducted using reef-based *T. lymma* samples.

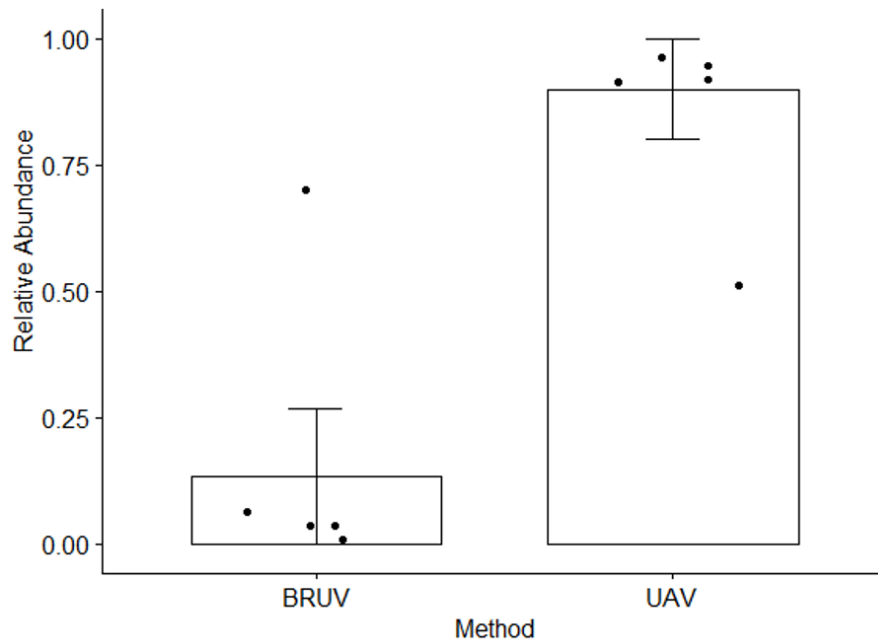


Figure 10. Bar plot of individual paired points of the relative abundance of *T. lymma* using only reef-based surveys. Each point represents the relative abundance observed from one survey type. Plot shows mean relative abundance between methods and standard error of the mean.

There was also a significant difference in the proportion of identified individuals of *T. lymma* between reef-based BRUV and UAV surveys (Kruskal-Wallis chi-squared = 6.56, $df = 1$, $p\text{-value} = 0.01$) (Figure 10), as the mean relative abundance was statistically different between methods when using paired-sample testing ($V = 0$, $p\text{-value} = 0.05$). The difference in test results is likely an artefact of data from reef-based BRUV surveys resulting in numerous zeros, and data from reef-UAV surveys often only detecting *T. lymma*, where values were ~ 0 and ~ 1 respectively.

3.5 Fish market surveys

A total of 53 individuals were reported from opportunistic fish market sampling. The most common taxa found were species in the family Carcharhinidae: *Carcharhinus sorrah* (spot-tail shark), *Carcharhinus melanopterus* (blacktip reef shark), *Triaenodon obesus* (whitetip reef shark), *Carcharhinus brevipinna* (spinner shark), *Negaprion acutidens* (sicklefin lemon shark), and *Carcharhinus falciformis* (silky shark) (Figure 11). Only a single member of family Ginglymostomatidae was found, *Nebrius ferrugineus*.

Only two shark species were found in both BRUV surveys and fish market surveys: *N. ferrugineus* and *N. acutidens*. There were no batoid species found throughout the sampling period at Thuwal central fish market, and so there was no overlap in species between UAV surveys and fish market surveys.

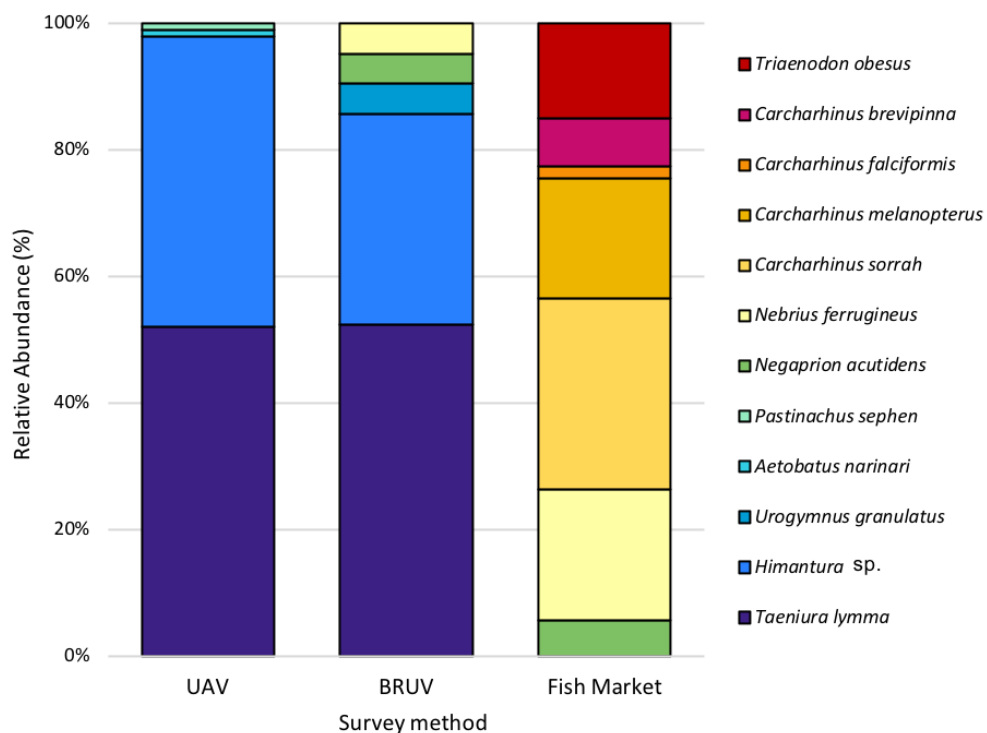


Figure 11. Percentage composition of elasmobranch species of UAV, BRUV, and fish market surveys. Fish market surveys were conducted opportunistically from 13th November, 2018, to 24th February, 2020.

4. DISCUSSION

This study investigated elasmobranch abundance and diversity using UAV and BRUV surveys in the nearshore habitats of the central Red Sea. Shark and ray species recorded in the reef and mangrove-associated environment represent 11% of the 64 elasmobranch species previously recorded for the Red Sea (Bonfil and Abdallah 2004; Golani and Bogorodsky 2010; Spaet and Berumen 2015; Golani and Fricke 2018). UAV surveys were more effective regarding abundance estimates, and UAV CPUE was two orders of magnitude greater than BRUV CPUE. Additionally, there was a higher abundance and density of batoids found over the sandflat environment using UAV surveys; UAVs in sandflats yielded a CPUE seven times greater than that in the reef environment. This was to be expected as shallow-water sandflats can serve as a nursery area for juveniles, as well as foraging and pupping grounds. Due to the potential overlap in methods, it is recommended that studies of abundance should use only one of the methods. Biodiversity studies, however, would benefit from the complementary nature of using both UAVs and BRUVs.

The diversity ($n = 7$) of species characterized by using both UAV and BRUV surveys was greater than either survey method alone. BRUV deployments are likely to observe more species in the reef environment with a greater survey effort, however, it is unlikely that either method would discover more species in the sandflat environment. Unsurprisingly, there were no batoids found in the fish market surveys. This is most likely due to their low economic value, and those that are caught as bycatch are likely released (Spaet and Berumen 2015; Jabado and Spaet 2017). However, UAV surveys did not observe any of the shark species reported in the fish market, and BRUV surveys

observed two shark species (one individual of each species). This suggests fisheries targeted species may not be present in the study site, or, due to the slow-moving and benthic nature of batoids, they are also unlikely to be captured by line and hook, gillnets, or long-lining by artisanal fishers (White and Potter., 2004; Vaudo and Heithaus 2009). Alternatively, fishing effort may not be occurring in the very shallow nearshore habitats studied.

The variation in composition between the present study and previous elasmobranch focused studies in the Red Sea was to be expected due to the difference in targeted habitat and methodologies used. Previous work using a combination of pelagic and benthic BRUVs (more than 275 BRUV hours) and scientific long-lining in the Saudi central Red Sea recorded a total species diversity of five elasmobranchs but did not record any batoid species (Spaet et al. 2016). It could be argued that the lack of rays in the environments of Spaet et al.'s study is merely a product of the trade-off between food and safety as a behavioral response to a perceived threat. Underwater visual surveys (UVS) may be a more appropriate method when assessing batoids in deeper water, despite the typical limitations associated with UVS. There is not enough published information on coastal elasmobranch stingray densities derived from UAV surveys to be able to compare the current results to other global regions. The difference in species composition between methods and habitats highlights the need for more rigorous investigations to quantify variations and the importance of method selection regarding species-specific research questions and habitat types.

Two distinct species dominated the species composition, *T. lymma* and *Himantura* sp. The variation in species detection in the sandflat environment is potentially driven by

either seasonal residency or spatial and temporal partitioning of the habitats. For example, *Himantura* sp. in the shallow sandflats of Shark Bay, Western Australia, were shown to have limited movement throughout the year and discrete changes in seasonal habitat use that drove the observed changes in abundance (Vaudo and Heithaus 2012). Similarly, *U. granulatus* typically do not exhibit seasonal changes and are thought to have a high degree of site fidelity (Davy et al. 2015; Kanno et al. 2019). However, *U. granulatus* display an ontogenetic shift in habitat preference from the use of mangrove-associated environments to reef once they hit maturity (disk width: 55-65cm; Last et al. 2016). In the present study, the only *U. granulatus* was observed in the reef-based BRUV surveys, and no smaller individuals were identified in UAV surveys in the sandflat environment. There is little information available in the residency and space use of *T. lymma*, yet preliminary data suggest that they are also highly resident to the lagoon system (A. J. McIvor, unpublished data). However, *Pastinachus* sp. are more transient (Vaudo and Heithaus 2012), and thus the lower detection rate could be from the lower residency of the species as they were less likely to stay in the survey area over time. Equally, *A. narinari* are also transient; they are known to frequent soft-bottomed sandflat regions midday when the water is typically warmer (i.e., energetically favorable; Matern et al. 2000), and often move between coastal (estuaries and lagoons) and coral reef/offshore habitats (Ajemian and Powers 2014). The variations in residency between species could lead to biases in species composition based upon the time of day and seasonality in which the surveys were conducted (i.e., August-November). Continued survey effort across seasons would be needed to identify species space use and densities to confirm this hypothesis.

Alternatively, I hypothesize that the comparatively high abundance of *T. lymma* and *Himantura* sp. to other ray species may be the result of competitive exclusion. There is a high dietary overlap between *Pastinachus* sp. and *T. lymma* in Ningaloo Bay, Australia (O'Shea et al. 2013). Therefore, the relatively low abundance of *P. sephen* in the sandflat habitat of the current study site in the Red Sea could be a result of a limit in food resources from either low infaunal abundances or prey item depletion from a high ray abundance of a similar dietary preference (e.g., *T. lymma*). As *Pastinachus* sp. grow to much larger adult sizes (disk width: 96-110cm) than *T. lymma* (disk width: 35cm) (Last et al. 2016), the increased size presumably decreases the perceived threat when feeding further from the sheltered environment and it is, therefore, more likely that there are fewer *P. sephen* individuals in the study area, and those that are present may not be resident. There is dietary partitioning between *T. lymma* and *Himantura* sp.; *Himantura* sp. has a diet primarily composed of crustaceans whereas *T. lymma* targets polychaetes, so overlap in space use does not create competition for prey (O'Shea et al. 2013). Whether the observed distribution of species in my study is dictated by habitat partitioning or species-specific low abundances, I would recommend UAV surveys as the ideal technique to acquire more distribution and abundance data to address this issue (due to the greater efficiency of UAV surveys compared to BRUVs).

Explaining the source of differences between the two survey methods is an essential step in accounting for the associated biases for future surveys. Deviations may be due to any and all of the following factors:

1. Area. There was a larger abundance recorded using UAV surveys compared to BRUV surveys. This was to be expected as each UAV flight path covered 4 ha^{-1} , whereas the total area of the bait plume from a BRUV was unknown and could be inconsistent between surveys dependent on the hydrodynamics of the site and tidal state. It was therefore not possible to compare densities between survey methods without calculating the area of BRUV samples. In any case, the CPUE of UAVs was consistently higher than the CPUE of BRUVs.
2. Composition. A large proportion of the total abundance was composed of *T. lymma* and *Himantura* sp. As shown by the percentage of the identified individuals of *T. lymma* attempting to feed on the bait (7% attempting to feed cf. 93% not attempting), not all species may be attracted to typical BRUV bait, or have an aversion to the unit that cannot be explained through this study. Some species were recorded in the BRUVs video but did not approach the BRUV units, which suggests that BRUV surveys may not be an appropriate way to account for all species. Likewise, the study design did not account for batoid distribution in response to depth. The discrepancy in abundance and composition between BRUV and UAV surveys could be in part due to stingrays preferring shallower depths where BRUV units were not able to be successfully submerged in. The dorsoventral compression of batoids allows them to exploit very shallow areas (Matern et al. 2000); however, this study intended to investigate both shark and rays. Thus, BRUVs were designed to be deployed in water deep enough to avoid a bias against larger elasmobranchs that also utilized the survey area.

3. Availability bias. UAV surveys could detect all individuals within the survey area, whereas BRUV surveys could only sample in a single direction parallel to the seafloor. BRUV surveys had a much lower CPUE than UAV surveys, which could be explained by the partial field of view the camera has of the study area. There could be elasmobranchs nearby but out of the video frame. This leaves the possibility that there could be a variance in detected abundance dependent upon the direction in which the BRUV was placed. In this study, the direction that the camera was facing relative to the shoreline was random. The possibility of using full-spherical (FS) camera technology (decreasing availability bias) could increase the detection probability, and thus the abundance estimate, of batoid species that may not directly approach the BRUV unit as many counts of MaxIND came from a ray making only a single pass across the FOV within a deployment (see Kilfoil et al. 2017 for exceptions). Further testing is required to quantify the behavioral-based biases of BRUV deployments. This could be investigated by deploying a UAV directly above a BRUV deployment to quantify the number of elasmobranchs using the area adjacent to the BRUV but outside the field of view.

4. Environmental conditions. Sea state is known to impact detection probabilities in aerial surveys negatively (e.g., Koski et al. 2009; Hammond et al. 2013), so surveys were only conducted in calm conditions (≤ 2 Beaufort; similar to Rowat et al. 2009; Westgate et al. 2014; Kiszka et al. 2016). Increased turbidity caused by wind and waves would likely have increased the availability bias (Colefax et al. 2019). Despite efforts to control this bias, the scope for investigating the

extent to which it impacted abundance estimates in this study was limited, especially with target species that did not have high contrast to the background (e.g., *T. lymma* over sand). However, it can be assumed that this was more challenging over the reef environment than the sandflat due to a higher level of habitat complexity. This challenge could describe the discrepancy in CPUE between BRUV and UAV surveys, where CPUE was higher over the reef than sandflat for BRUV surveys, opposite to that of UAVs.

Data quality is the primary issue regarding UAV surveys. UAV surveys could only identify ~95% of individuals to the species level. The batoid species encountered were distinguishable through disk shape alone; however, where foraging rays were excavating, the resultant plume would mask the individual entirely. It should be noted that prior knowledge of the species inhabiting the study site is imperative as some groups of species (e.g., species of eagle and reticulate rays) are morphologically similar, and UAV surveys may not be able to distinguish between them without ground-truthing. Throughout this study, consistent sampling was hindered by complications and inconsistencies regarding Coast Guard approval and permitting for boat and UAV use. As a result, sampling deployments for both BRUV and UAV surveys were not even across habitat types. However, based upon the CPUE of this study and previous studies, we do not believe that the differences in abundance were a result of differences in sampling effort.

BRUV surveys were able to collect more precise data on individuals. Distinguishable characters such as the presence of claspers and differences in spot patterns allowed for the confident identification of nearly all capture events. The main limitation in

BRUV surveys was caused by extreme bias from turbidity, where a large portion of the study site was inaccessible due to sediment being suspended during deployment and not settling out throughout the deployment. Turbid areas are important locations for future assessment, as typically, high turbidity in many shallow habitats can actually offer protection from visual predators and could potentially allow for an increased relative abundance (e.g., Roberts et al. 1992; Francis 2013; Cerutti-Pereyra et al. 2014). Besides, BRUV surveys do not provide precise data on spatial density as the extent of the bait plume, and thus the radius of attraction to the bait is usually unknown (Willis et al. 2000; Heagney et al. 2007). This study did not have access to real-time current data, and thus a dilution factor could not be determined to model the distance from which sharks and rays would have been attracted.

There was a greater abundance of stingrays found over the sandflats opposed to the reef habitat. This study focused on shallow-water investigation, and as such, reef-based surveys were prominently reef crest, where it is less likely that stingrays will settle or rest and, as such, all observed reef-survey rays were transient. Shallow reef crests have, however, been observed to function as a secondary refuge for juvenile rays in Orpheus Island, Australia (Martins et al. 2020). All sandflat regions were dominated by soft sediments, with infrequent patches of coral rubble or seagrass tufts. Habitat was not sampled for differences in microhabitat and abundance in this study and was assumed to be uniform within the two habitat types (i.e., reef and sandflat). Moreover, this study did not address the possibility that there may have been differences among sites within a habitat type in prey availability, or differences in potential predation (where human disturbance may also be considered a factor, see

Gill et al. 1996; Frid and Dill 2002; Beale and Monaghan 2004). However, previous studies have shown that microhabitat selection of giant shovelnose rays (*Glaucostegus typus*) did not adhere to predictions based on prey distribution, and that habitat preference was more heavily influenced by perceived predation risk instead (Vaudo and Heithaus 2013).

Stingrays are known to use shallow water habitats to avoid predation (Vaudo and Heithaus 2013). There is a positive correlation between reef shark abundance and the use of shallow-water habitats by stingrays (Bond et al. 2019). Saudi Arabia generally has very low abundances of sharks (Spaet et al. 2016), and as such, one can assume that the use of the shallow water environment is not heavily influenced by predictable spatial variation of sharks (e.g., Vaudo and Heithaus 2009). Both global lagoon and reef habitats are typically utilized by reef sharks, however, encounter rates in shallow reef flat habitats, such as surveyed in the current study, are far less frequent (Pikitch et al. 2005; Bond et al. 2012). Marine protected areas could have a net positive effect on shark populations that are currently targeted by artisanal fisheries in Saudi Arabia. An increase in reef sharks may have a potentially negative effect on the presence of stingrays in forereef environments as the probability of shark encounter increases. Thus, the threat of predation also increases, resulting in a potentially positive effect on stingray density in sandflat environments (such as Bond et al. 2019). The potential behavioral response would not directly affect the overall population abundance but could increase the vulnerability of those in the nearshore environment.

It is clear that the nearshore environment within the study site is used for feeding as there are many excavation pits, and many rays were identified as “feeding”. The study

site is relatively protected and has many mangrove-fringing (white mangrove; *Avicennia marina*) shallow embayments and is also seen as a suitable nursery habitat. Juvenile (disk width: 14-16cm) *T. lymma* were observed at the study site in January, March, and August (A. J. McIvor, personal observation), and this area is likely favorable as a potential nursery habitat for elasmobranchs. The complex structure of mangroves and high productivity could serve as a potential refuge for juvenile species. This study did not utilize size estimates of individuals and strongly suggests that future assessments should determine if the study meets the defined criteria as a nursery area (see Heupel et al. 2007 for free-swimming elasmobranch nursery criteria, and Hoff 2016 for oviparous species). Throughout April 2019/20, many observations were also made of 'close-following' and 'pre-copulatory biting' behaviors (see Chapman et al. 2003) from adult *T. lymma* in the shallow sandflat areas of the survey area (water depth > 50cm), as well as a few individuals being reported with fresh posterior disk excisions (A. J. McIvor, personal observation). These are clear signs of courtship and mating behaviors (Kajiura et al. 2000), indicating that the nearshore environment is also seasonally important for adult rays. It is unclear whether the mangrove-associated habitat in this study site is used as a nursery habitat or if there is an overlap in the spatial distribution of adults and juveniles year-round (i.e., use alone does not meet nursery criteria). Regardless, it is clear that the nearshore environment is of great importance for batoid species, and so more detailed biological data regarding the age and size classes of the species that utilize this habitat over time are required to aid in conservation efforts.

The Red Sea is the only region in the world that has a net increase in mangrove habitat (Almahasheer et al. 2016). The relative losses to Red Sea mangroves are driven by

coastal development (1972 to 2013) and have mostly been compensated for by afforestation projects (Almahasheer et al. 2016). However, coastal development in Saudi Arabia as part of Vision 2030 (<https://vision2030.gov.sa/>) could be a direct threat to these habitats. Major infrastructure projects for tourism (The Red Sea Project, NEOM, etc.) are underway in the northern Red Sea (PIF 2020), which could remove potential foraging and nursery habitats for shallow-water benthic elasmobranchs. The additional tourism is expected to drive a corresponding increase in boat traffic, necessitating more coastal development for docks and other infrastructure. Increases in boat traffic and the expansion of residential development could increase the aquatic pollution in the adjacent nearshore habitats. Although individuals can move from degraded habitats, species that exhibit philopatric behavior or residency will be at higher risk of depletion. Several species of shark have already seen a reduction or loss in nursery habitat from coastal development in other parts of the world, including *Negaprion brevirostris* (lemon sharks) in the Bahamas (Jennings et al. 2008) and *Carcharhinus plumbeus* (sandbar sharks) on the east coast of the United States (McCandless et al. 2002).

Understanding elasmobranch assemblages and abundances is an essential first step toward describing their ecological roles and developing effective strategies for their management. Future steps could include investigating seasonal patterns of the species described in this study, potential site preference, and infaunal community structure to assess the effects of mesopredator (stingray) removal or increase in these habitats. Saudi Arabia's coastline is evolving at an ever-increasing rate that could ultimately alter the nearshore habitats that are directly and indirectly vital to a large number of organisms. Understanding the community structure of elasmobranchs in

near- and inshore habitats will assist management in protecting critical areas of importance for specific species. Previous work has focused on offshore reefs ranging from 1-86km from land and emphasized the need for greater enforcement strategies to protect sharks (Clarke et al. 2012; Hussey et al. 2013; Spaet et al. 2016). Here, we have expanded upon this need by detailing the elasmobranch community of shallow-water habitats in the central Red Sea that are at risk from coastal development. In addition to emphasizing the importance of the nearshore environment to batoid species, we have shown the utility and benefits of using a commercially available drone to assess stingray abundances for the first time in the Red Sea.

5. CONCLUSION

This study provided an integrated approach to understanding the community composition of a nearshore habitat in the Saudi Arabian central Red Sea. The methods trialed in this study for assessing nearshore elasmobranchs provide a point of reference against which future surveys can be improved upon. A more comprehensive description was given using both BRUV and UAV surveys, as together they illuminated a higher diversity of elasmobranch presence than using either method alone, and despite their limitations are complementary to one another.

There was a distinct lack of sharks within this study (total: 2 individuals), further supporting the conclusions made by Spaet et al. (2016) that these low numbers are reason for concern. The lack of stingray species in other reef-based studies in the central Red Sea indicates that the sandflat regions of KSA are critical for batoid species, specifically *T. lymma* and *Himantura* sp. It is vital to understand the importance of an area in terms of spatial and temporal patterns of occupation in order to appropriately

assess the future effects of coastal development in the region. We suggest further investigation should be conducted in the habitat and space use of stingrays in the coastal regions of the Red Sea due to the likely exacerbation of anthropogenic impacts caused by the Kingdom's "GigaProjects" and potential decreases in habitat availability.

Our study demonstrated the advantages and disadvantages of both methods, along with their distinct biases. Future studies focusing on elasmobranch abundance should consider UAV surveys as a primary method across sandflat areas and may help identify species that require further sample techniques to investigate detailed biological questions, involving individual identification, sex, and other biometrics. Reef based surveys should continue to employ BRUV-based surveys to allow more cryptic species to be detected. However, the biases associated with each survey type in various habitats show that neither survey method is better than the other, but rather are indicative that a combination should be used to determine elasmobranch assemblage when possible.

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APPENDIX

Appendix 1. List of Red Sea elasmobranch species as detailed by Golani and Fricke (2018). Families are ordered according to Golani and Bogorodsky (2010), and species alphabetically. IUCN Red List status is according to the 2020 IUCN Red List of threatened species categories; Not Evaluated (NE), Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR). *Species endemic to the Red Sea region.

Family	Species	Common Name	Reference	IUCN Red List Status
Sharks				
Odontaspidae	<i>Carcharias taurus</i>	Sand tiger shark	Rafinesque 1810	VU
Odontaspidae	<i>Carcharias tricuspidatus</i>	Indian sandbar shark	Day 1878	NE
Lamnidae	<i>Isurus oxyrinchus</i>	shortfin mako shark	Rafinesque 1810	EN
Alopiidae	<i>Alopias pelagicus</i>	Pelagic thresher shark	Nakamura 1935	EN
Ginglymostomatidae	<i>Nebrius ferrugineus</i>	Tawny nurse shark	(Lesson 1831)	VU
Stegostomatidae	<i>Stegostoma fasciatum</i>	Zebra shark	(Hermann 1783)	EN
Rhincodontidae	<i>Rhincodon typus</i>	Whale shark	Smith 1828	EN
Carcharhinidae	<i>Carcharhinus albimarginatus</i>	Silvertip shark	(Rüppell 1837)	VU
Carcharhinidae	<i>Carcharhinus altimus</i>	Bignose shark	(Springer 1950)	DD
Carcharhinidae	<i>Carcharhinus amblyrhynchos</i>	Grey reef shark	(Bleeker, 1856)	NT
Carcharhinidae	<i>Carcharhinus amboinensis</i>	Pigeye shark	(Müller & Henle 1839)	DD
Carcharhinidae	<i>Carcharhinus brevipinna</i>	Spinner shark	(Müller & Henle 1839)	NT
Carcharhinidae	<i>Carcharhinus falciformis</i>	Silky shark	(Müller & Henle 1839)	VU
Carcharhinidae	<i>Carcharhinus limbatus</i>	Blacktip shark	(Müller & Henle 1839)	NT
Carcharhinidae	<i>Carcharhinus longimanus</i>	Oceanic whitetip reef shark	(Poey 1861)	CR

Family	Species	Common Name	Reference	IUCN Red List Status
Carcharhinidae	<i>Carcharhinus melanopterus</i>	Blacktip reef shark	(Quoy & Gaimard 1824)	NT
Carcharhinidae	<i>Carcharhinus obscurus</i>	Dusky shark	(LeSueur 1818)	EN
Carcharhinidae	<i>Carcharhinus plumbeus</i>	Sandbar shark	(Nardo 1827)	VU
Carcharhinidae	<i>Carcharhinus sorrah</i>	Spottail shark	(Müller & Henle 1839)	NT
Carcharhinidae	<i>Galeocerdo cuvier</i>	Tiger shark	(Péron & Lesueur 1822)	NT
Carcharhinidae	<i>Loxodon macrorhinus</i>	Sliteye shark	Müller & Henle 1839	LC
Carcharhinidae	<i>Negaprion acutidens</i>	Sicklefin lemon shark	(Rüppell 1837)	VU
Carcharhinidae	<i>Rhizoprionodon acutus</i>	Milk shark	(Rüppell 1837)	LC
Carcharhinidae	<i>Scoliodon laticaudus</i>	Spadenose shark	Müller & Henle 1839	NT
Carcharhinidae	<i>Triaenodon obesus</i>	Whitetip reef shark	(Rüppell 1837)	NT
Triakidae	<i>Iago omanensis</i>	Bigeye Houndshark	(Norman 1939)	LC
Triakidae	<i>Mustelus mosis</i>	Arabian smooth hound	Hemprich & Ehrenberg 1899	NT
Hemigaleidae	<i>Hemigaleus microstoma</i>	Sicklefin weasel shark	Bleeker 1852	VU
Hemigaleidae	<i>Hemipristis elongata</i>	Snaggletooth shark	(Klunzinger 1871)	VU
Sphyrnidae	<i>Sphyrna lewini</i>	Scalloped hammerhead	(Griffith & Smith 1834)	CR
Sphyrnidae	<i>Sphyrna mokarran</i>	Great hammerhead	(Rüppell 1837)	CR
Somniosidae	<i>Zameus squamulosus</i>	Velvet dogfish	(Günther 1877)	DD
Batoids (rays, wedgefishes, sawfishes)				
Pristidae	<i>Anoxypristis cuspidata</i>	Narrow sawfish	(Latham 1794)	EN
Pristidae	<i>Pristis zijsron</i>	Green sawfish	Bleeker 1851	CR
Narcinidae	<i>*Heteronarce bentuviai</i>	Elat electric ray	(Baranes & Randall 1989)	DD
Torpedinidae	<i>Torpedo panthera</i>	Panther electric ray	Olfers 1831	DD
Torpedinidae	<i>Torpedo sinuspersici</i>	Marbled electric ray	Olfers 1831	DD
Torpedinidae	<i>*Torpedo suessii</i>	Red Sea torpedo	Steindachner 1898	CR

Family	Species	Common Name	Reference	IUCN Red List Status
Rhinobatidae	<i>Glaucostegus halavi</i>	Halavi guitarfish	(Forsskål in Niebuhr 1775)	CR
Rhinobatidae	<i>Glaucostegus thouin</i>	Clubnose guitarfish	(Anonymous 1798)	CR
Rhinobatidae	<i>Rhina ancylostoma</i>	Bowmouth guitarfish	Bloch & Schneider 1801	CR
Rhinobatidae	<i>Rhinobatos punctifer</i>	Spotted guitarfish	Compagno & Randall 1987	NT
Rhinobatidae	<i>Rhynchobatus djiddensis</i>	Giant guitarfish	(Forsskål in Niebuhr 1775)	CR
Dasyatidae	<i>Brevitrygon imbricata</i>	Scaly whipray	(Müller & Henle 1841)	DD
Dasyatidae	<i>Himantura uarnak</i>	Reticulate whipray	(Forsskål in Niebuhr 1775)	VU
Dasyatidae	<i>Himantura gerrardi</i>	Sharpnose ray	(Gray, 1951)	NT
Dasyatidae	<i>Neotrygon kuhlii</i>	Masked ray	(Müller & Henle, 1841)	NE
Dasyatidae	<i>Pastinachus sephen</i>	Cowtail ray	(Forsskål in Niebuhr 1775)	NT
Dasyatidae	<i>Himantura fai</i>	Pink whipray	Bonfil & Abdallah, 2004	VU
Dasyatidae	<i>Taeniura lymma</i>	Blue-spotted ribbontail ray	(Forsskål in Niebuhr 1775)	NT
Dasyatidae	<i>Taeniurops meyeri</i>	Round ribbontail ray	(Müller & Henle 1841)	VU
Dasyatidae	<i>Urogymnus asperrimus</i>	Porcupine ray	(Bloch & Schneider 1801)	VU
Dasyatidae	<i>Urogymnus granulatus</i>	Mangrove whipray	(Macleay 1883)	VU
Rhinopteridae	<i>Rhinoptera jayakari</i>	Oman cownose ray	Boulenger 1895	NE
Rhinopteridae	<i>Rhinoptera javanica</i>	Flapnose ray	Müller & Henle 1841	VU
Gymnuridae	<i>Gymnura poecilura</i>	Longtail butterfly ray	(Shaw 1804)	NT
Gymnuridae	<i>Gymnura tentaculata</i>	Tentacled butterfly ray	(Valenciennes in Müller & Henle 1841)	DD
Myliobatidae	<i>Aetobatus narinari</i>	Spotted eagle ray	Euphrasen, 1790	NT
Myliobatidae	<i>Aetomylaeus milvus</i>	Ocellate eagle ray	(Müller & Henle, 1841)	EN
Mobulidae	<i>Mobula alfredi</i>	Reef manta ray	(Krefft 1868)	VU
Mobulidae	<i>Mobula birostris</i>	Oceanic manta ray	(Walbaum 1792)	VU
Mobulidae	<i>Mobula kuhlii</i>	Shortfin devil ray	(Müller & Henle 1841)	DD
Mobulidae	<i>Mobula tarapacana</i>	Chilean devil ray	(Philippi 1892)	EN

Family	Species	Common Name	Reference	IUCN Red List Status
Mobulidae	<i>Mobula thurstoni</i>	Bentfin devil ray	(Lloyd 1908)	EN