Unmanned Aerial Vehicle (UAV) surveys to compare foraging sea turtle density and distribution in two contrasting habitats in the Chagos Archipelago

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Abstract

Unmanned Aerial Vehicles (UAVs) facilitate observation of elusive species or remote locations, and are increasingly used to survey marine habitats. Marine Protected Areas (MPAs) are a conservation tool used to protect marine species, and regular population assessments can establish if MPAs are effectively facilitating the recovery of endangered species. Sea turtles in the Western Indian Ocean have been historically exploited through trade and by-catch causing a reduction in numbers. Here, UAVs were utilised to assess the population density and distribution of green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles between ocean and lagoon environments in the Chagos Archipelago. Analysis protocols were developed to process UAV imagery, including carapace-measurement techniques, and certainty-classing turtle observations (Definite, Probable or Possible). Along 20 km of coastline, 5.13 km^2 was surveyed across 11 days between July 2019 – February 2021 resulting in a high-certainty estimate of 381 turtles and a low-certainty estimate of 660. Species and life-stage identification implicate Chagos as developmental habitat for immature hawksbill turtles: 78.47% (n = 299/381) of identified definite turtles were immature, of which 66.55% (n = 199/299) were hawksbill. Diego Garcia Ocean Site 1, West sites and Turtle Cove were significant turtle hotspots (high-certainty results: 257.19 individuals/km^2, 146.15 individuals/km^2, and 135.08 individuals/km^2, respectively), while Marina sites were least-dense (0 - 4.87 individuals/km^2). Results for low-certainty data were comparable: 325.27 individuals/km^2 in Diego Garcia Site 1, followed by 309.27 and 292.67 individuals/km^2 in Turtle Cove. Population density decreased significantly with increasing distance from the shore, and decreased with increasing distance from Turtle Cove. Green turtles were smaller (50.33 ± 17.65 cm straight-carapace length, SCL) than hawksbill turtles (53.16 ± 11.17 cm SCL). This study highlights the Chagos Archipelago as developmental habitat for immature turtles, and demonstrates the applicability of UAVs for *in-situ* population monitoring to infer conservation status of marine megafauna.

Key Words: Unmanned Aerial System, drone survey, marine turtle, endangered species, population monitoring

Lay Summary

Understanding the population size and distribution of sea turtles is crucial when working to protect them through Marine Protected Areas (MPAs). The Chagos Archipelago, a collection of islands and atolls in the Indian Ocean, is a nesting site for green and hawksbill turtles and may act as a stepping stone for turtles on oceanic migrations across the Indian Ocean. Turtles have been protected here since the early 1970s, and the waters surrounding the archipelago have been protected since 2010 as an MPA. The MPA contains pristine seagrass meadows and coral reefs, which are foraging grounds for green and hawksbill turtles, respectively. Foraging sites are vital for developing immature turtles, and these so-called 'developmental habitats' are utilised before individuals mature into adulthood. Foraging populations of sea turtles are hard to study as turtles spend a large proportion of time beneath the waters' surface, but aerial surveys provide a means to observe turtles in the environment. Unmanned Aerial Vehicles (UAVs, or drones) can access remote locations to allow observation of species with little disturbance. A birds-eye-view allows turtles to be measured, which can infer the life-stage and species of the individual, and tail length can identify sex, with male tails notably longer. This study utilised UAVs to estimate the population density and understand the distribution of green and hawksbill sea turtles in the Chagos Archipelago. An extensive area of 5.13 km^2 along 20 km of coastline was surveyed across two marine habitats (ocean and lagoon environments) and two islands (Diego Garcia and Nelson's Island). During 122 UAV transects, 660 individual turtles were observed, 381 of which were definite turtles. Species and life-stage identification showed the majority of individuals within the archipelago were immature hawksbill turtles, and significant hotspots occurred in both lagoon and ocean environments, up to 257.19 individuals per km^2, compared to the lowest density where turtles were present at 4.87 individuals/km^2. Population density decreased with increasing distance from the shore and from Turtle Cove. Green turtles were smaller than hawksbill turtles, on average. This study has confirmed the Chagos Archipelago as an important developmental habitat for turtles within the Indian Ocean, and of global importance for the long-term protection and conservation of sea turtles.

Declarations

Statement 1: This work has not previously been accepted in substance for any degree and is not concurrently being submitted in candidature for any degree.

Signed [redacted]

Date 29/09/2021

Statement 2: This thesis is the result of my own investigations, except where otherwise stated, and other sources have been acknowledged below. A bibliography is appended.

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Statement 3: I hereby give consent for this thesis, if accepted, to be made available online in the University's Open Access Repository and for inter-library loan, and for the title and summary to be made available to outside organisations.

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Statement of Expenditure

Student Name: Carina Rees

Student Number: [redacted]

Project Title: Unmanned Aerial Vehicle (UAV) surveys to compare foraging sea turtle density and distribution in two contrasting habitats in the Chagos Archipelago

Category	Item	Description	Cost*
Software	Adobe® Premiere® Pro monthly subscription	Monthly subscription to video-editing software utilised to view videos and extract frames during video analysis 17th May – 17th October @ £16.24 / month	£97.44
Data Storage	5 TB Hard drive (LaCie Rugged mini, STJJ5000400)	Required to share 127 4K video files	£134.45
Equipment	LG Monitor (model 27UL600)	4K ultraHD 27" monitor to allow viewing of 4K survey footage	£331.19
	Asus Desktop (TUF Gaming B460-PLUS)	Custom-made with motherboard and graphics card best-suited for high quality streaming of 4K footage	£1,904.00
Total			**£2,467.08**

*includes VAT and delivery where applicable

I hereby certify that the above information is true and correct to the best of my knowledge

Signed,

[redacted]

Signature (supervisor)

[redacted]

Signature (student)

Statement of Contribution

Contributor Role	Contributor
Conceptualisation	NE, CR
Data Curation	NE, JM, JL, HS
Formal Analysis	CR
Funding Acquisition	NE
Investigation	CR
Methodology	NE, CR
Project Administration	NE
Resources	NE
Software	CR
Supervision	NE
Validation	NE, KS
Visualisation	CR
Writing – Original Draft Preparation	CR
Writing – Review & Editing	NE, KS, CR

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CR - Carina Rees (MRes Student)
JM - Dr Jeanne Mortimer (Data collection and provision)
JL - Dr Jacques-Olivier Laloë (Data collection)
HS - Holly Stokes (Data collection)
KS - Dr Kimberley Stokes (Advisor and reviewer)

Ethics

No ethical issues were highlighted for this study as aerial observation causes little-to-no disturbance to turtles, and all subsequent work was desk-based.

Reference Number: STU_BIOL_172164_020321100602_1

Approval Number: SU-Ethics-Student-030321/3813

Health and Safety

College: College of Science

Location: Home-based learning

Activity: MRes Research Project

Assessment Date: 10/03/2021

Assessor: Dr Nicole Esteban

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
Prolonged Screen Time	Researcher	- Blurry vision - Headaches - Tired or aching eyes	- Taking breaks - Positioned my desk in front of a window to allow me to evert my eyes from the screen regularly				- Adapt brightness when necessary i.e. decrease brightness during darker hours	1	4	4	

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
Sitting down all day	Researcher	- Poor posture during computer analysis could lead to back pain - Legs become weaker due to lack of use	- Proper desk chair to offer full support - Laptop raised to eye level to improve posture - Taking regular breaks, that include walking or other forms of exercise				- Take breaks to stretch - Regularly think about posture, and correct poor posture	1	4	4	
Lone working	Researcher	- Mental health could suffer due to long hours alone	- Weekly zoom session with research group to discuss progress and general chat - Taking regular breaks - Speaking to friends and family - Walking the dog				- Reach out to others in research team if struggling or need help	1	2	2	

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List of Abbreviations

AGL	Above Ground Level
AIC	Akaike Information Criterion
CCL	Curved Carapace Length
CM	*Chelonia mydas*
DIC	Difference In Count
EI	*Eretmochelys imbricata*
GLM	Generalised Linear Model
GSD	Ground Sampling Distance
HW	High Water
LW	Low Water
L:W	Length-to-Width ratio
MPA	Marine Protected Area
MRR	Mark-Release-Recapture
PSR	Primary Sex Ratio
SCL	Straight Carapace Length
SCW	Straight Carapace Width
SE	Southern Equatorial (ocean current)
SLD	Straight-Line Distance
SWIO	South-West Indian Ocean
UAV	Unmanned Aerial Vehicle
WIO	Western Indian Ocean

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For Nigel.

Introduction

Sea Turtle Foraging Behaviour and Global Status

As an air-breathing migratory species, sea turtles spend a large proportion of their time submerged, limiting the opportunities for observation at the surface (Hochscheid and Wilson, 1999). Sea turtles typically nest and forage in geographically discrete locations and can undergo long-distance transoceanic migrations seasonally (Limpus et al., 1992; Meylan et al., 2011). Their large oceanic home range makes observation *in-situ* challenging therefore surveys are concentrated in key nesting and foraging sites. Turtles can migrate up to thousands of kilometres to foraging sites (Hays et al., 2020a; Limpus et al., 1992), and therefore individuals in foraging grounds can comprise nesting populations from several genetically-distinct subpopulations. Conservation of key foraging sites can therefore influence the longevity of turtle populations across large geographical ranges.

Turtle diet and geographical location are interlinked: in tropical waters, green turtles (*Chelonia mydas)* are herbivorous grazers feeding on seagrass and macroalgae (Stokes et al., 2019), while in more temperate regions, diet mainly comprises animal matter (Esteban et al., 2020); hawksbill turtles (*Eretmochelys imbricata)* are omnivorous, feeding primarily on sponges (spongivorous), supplemented by anthozoans, molluscs and vegetation (Stringell et al., 2016; von Brandis et al., 2014). Foraging needs subsequently lead them to neritic waters where seagrass meadows and coral reefs thrive (Hays et al., 2018; Troëng et al., 2005), and their foraging plays a key role in maintaining healthy ecosystems: hawksbill spongivory can control sponge populations which benefit coral reefs competing for space (León and Bjorndal, 2002); and green turtle grazing of seagrass meadows can minimise the impact of eutrophication (Christianen et al., 2012) without impacting seagrass biodiversity (Hearne et al., 2019). Sympatric existence of sea turtles is possible due to their minimal diet overlap, which is unchanged through all life-stages (Stringell et al., 2016).

After hatching from nesting beaches, hatchling turtles utilise ocean currents to depart from neritic waters to open-ocean environments (Carr et al., 1978). After the so-called ‘lost years’ where exact turtle location and behaviour is not fully understood, the developmental habitat hypothesis suggests turtles then reside in typically immature-dominated neritic habitats (e.g. Meylan et al., 2011). This benthic developmental stage was first hypothesised by Carr et al. (1978), and is believed to be where turtles complete development before recruitment into adulthood (Luschi et al., 2003). There is evidence for both immature-only and shared immature-adult neritic foraging grounds (e.g. Limpus and Reed, 1985; Meylan et al., 2011) so further investigation into life-stage space-use can increase understanding of ontogenetic habitat shifts.

It is vital to study sea turtle migration, nesting and foraging ecology in order to focus conservation efforts: six of the seven species of sea turtles are listed as at least Vulnerable, with two species (hawksbill, and kemps ridley, *Lepidochelys kempii*) listed as Critically Endangered (Mortimer and Donnelly, 2008; Wibbels and Bevan, 2019). Their global status is a result of anthropogenic threats such as exploitation for shell or meat, poaching of eggs on nesting beaches, habitat degradation i.e. nesting beach loss through disturbance and coastal development, plastic pollution, and fishing bycatch (Mazaris et al., 2009; Mees et al., 2009; Schuyler et al., 2014; Wenban-Smith and Carter, 2016; Whiting and Koch, 2006; Witherington et al., 2011). In the Western Indian Ocean (WIO), historical exploitation and increasing bycatch have led to their decline, and illicit capture still continues within the region. Across villages in Madagascar, fishermen illegally captured between 10,000 - 16,000 sea turtles in 12 months from 2006 - 2007 (Humber et al., 2011). Large scale fisheries also cause significant damage: gillnet fisheries cover approximately 300,000 km^2 in the South-West Indian Ocean (SWIO) and account for the highest bycatch rates of any fishing method (Mellet, 2015): between 2000 - 2011, gillnet fishing caught an average of 40,264 sea turtles annually in the SWIO region, leading to a total 29,964 known mortalities (Mellet, 2015). Gill net fishery bycatch is responsible for 77% of the sea turtles caught annually in the SWIO, with prawn trawl and beach seines comprising the remainder (18% and 5%, respectively, 52,370 individuals in total, Mellet, 2015). Of the five species found within the WIO, green and hawksbill turtles are the most common (Bourjea et al., 2008), and are Endangered and Critically Endangered, respectively (Mortimer and Donnelly, 2008; Seminoff, 2004). Continued monitoring of populations is therefore critical to show trends of sea turtle populations over time, to assess decline or recovery dynamics and efficacy of conservation intervention.

Recovery of sea turtle populations across global sites (e.g. Florida, Ehrhart et al., 2014; South Atlantic, Weber et al., 2014; see Chaloupka et al., 2014 for global summary) is a result of long-term continued protection, with the population status assessed only after sustained monitoring periods (Mazaris et al., 2017). Understanding the use of foraging sites is crucial when implementing conservation as key foraging sites can sustain transoceanic nesting populations (Hays et al., 2020a) thus can impact turtles from distinct geographic regions. The movements and migrations of sea turtles can be better understood with the aid of satellite telemetry: green turtles can migrate thousands of kilometres to foraging grounds despite suitable local habitats (e.g. Limpus et al., 1992; Read et al., 2014), and show strong fidelity to both foraging and nesting sites (Meylan et al., 2010; Mortimer and Portier, 1989; Shimada et al., 2020); and there is evidence of similar migrations (> 1000 km) of hawksbill turtles in the Indian Ocean (e.g. Fossette et al., 2021; Whiting and Koch, 2006). Utilising satellite telemetry gives an insight to the location of and variation in sea turtle movements (Hays et al., 2020a), and can better inform researchers about foraging migrations, but can also give insight to fine-scale movements within foraging grounds (e.g. Hays et al., 2021b).

Population Density and Turtle Identification

Knowing the population size, density and spatiotemporal distribution of a species is crucial in assessment of their conservation status, and frequent assessment can show trends over time, allowing evaluation of conservation interventions. Population estimates can provide evidence of efficacy of protection for future conservation planning. For population assessments to successfully estimate size, density or distribution of marine species, techniques which reduce bias and improve precision must be employed.

Population estimates for sea turtles are generally based on the number of nesting individuals, using either the number of tracks on known nesting beaches or the total number of clutches laid (e.g. Mortimer et al., 2020; Witherington et al., 2009). These metrics act as useful indicators of the number of gravid females to assess change in nesting populations across time. Nesting-based surveys can be completed at a relatively low cost, dependant on location and available research staff. However, evidence from satellite tracking of green turtles in the Chagos Archipelago, WIO, shows that clutch frequency i.e. the number of nests laid by a gravid female in one season (Frazier and Richardson, 1985) can be underestimated by a factor of two, leading to a potentially over-estimated population size (Esteban et al., 2017), and surveying nesting females only overlooks male, sub-adult and immature demographics. Omitting non-female demographics from surveys results in a large proportion of the population unaccounted for, thus population estimates inaccurate. Mark-Release-Recapture (MRR) studies (e.g. Hodge, 2004; Dunstan et al., 2020) and in-water surveys conducted by divers or snorkellers (e.g. Maitz, 2011) can estimate populations while encompassing all demographics, but observational bias can occur during difficult observation from boats or in-water.

Population density, measured by the number of individuals per square kilometre, is a common metric to deduce turtle population size without an extensive survey of all individuals and environments. Moreover, population size alone tells us little of the spatiotemporal distribution of turtles, while density estimates are comparable across space and time. We cannot assume that populations are evenly distributed throughout a given area or habitat so population density can identify species hotspots i.e. high-aggregation sites, potentially for foraging or breeding. Where species or life-stage identification is possible, trait-specific densities can be calculated, allowing intraspecific comparisons to better understand population composition and therefore conservation status.

The sex of adult turtles can be identified through secondary sex characteristics (Pritchard et al., 1983). Males have a notably longer tail than females, extending past the rear flippers, providing a non-invasive method of determining sex (Casale et al., 2005). Previous research recommends measurement of the distance from the cloaca to the posterior margin of the carapace (Casale et al., 2005), but this requires physical examination of individuals. Where close-proximity is not possible, sex can still be determined visually, although differentiation may be more difficult in sub-adult males (Schofield et al., 2019). Turtle species can also be identified using carapace morphology such as length-to-width ratio, shape and colouration (Pritchard and Mortimer, 1999).

Sea turtles exhibit Temperature-dependant Sex Determination (TSD) by which the nest temperature impacts the Primary Sex Ratio (PSR) i.e. the female-to-male ratio in hatchlings, with warmer environments causing a female-skew and *vice vera* (Santidrián Tomillo and Spotila, 2020). Skewed sex ratios may not negatively impact adult populations, as males are likely to visit breeding grounds more frequently (Hays et al., 2010), however increasing global temperatures risks pushing PSRs closer to single-sex generations. Understanding the Operational Sex Ratio (OSR) of a population i.e. the ratio of sexually-active males to receptive females at any given time (Emlen and Oring, 1977) can inform the reproductive capability of the population and identify populations at risk from anthropogenic climate change.

Turtle Observation Methods

In-situ monitoring of marine megafauna is crucial to infer information on population size, health and behaviour, but observation presents a unique set of challenges due to their elusive nature: diving behaviour results in infrequent surface intervals, limiting the time available for observation at the surface; and long-distance migrations across varied habitats increase difficulty of detections (e.g. sea turtles, Luschi et al., 2006; whales, *Balaenoptera musculus*, Oestreich et al., 2020).

Aerial surveys, such as those conducted by plane or helicopter, are utilised to aid observation of species in marine environments and offer a birds-eye view to identify and observe individuals with little disturbance (Bevan et al., 2016). The perspective achieved provides a greater field-of-view within which to observe species, and the ability to span greater areas when compared to ground-based surveys allows for more time-efficient assessment (e.g. Vermeulen et al., 2013). While improving on boat- or land-based surveys (Hodgson et al., 2018), high costs are incurred, there is an associated risk of injury, and application is not suited to cryptic habitats (Jones et al., 2006; Sasse, 2003; Stringell et al., 2014).

The development of Unmanned Aerial Vehicles (remotely-operated drones, UAVs) has aided assessments where observation of species is required *in-situ*. The use of UAVs has evolved since first studies in the early 2000s (Jones et al., 2006), and UAVs are now recognised as an effective assessment tool. UAVs can either (a) hover over species for identification and observation (e.g. Durban et al., 2015) or (b) follow systematic sampling methods such as line transects to assess an ecosystem or population as a whole (e.g. Vermeulen et al., 2013). Using UAV imagery, researchers can assess various parameters including population density, physical health, and demographic data such as sex and age-class of individuals (Bevan et al., 2016; Schaub et al., 2018; Vermeulen et al., 2013).

Deployment of UAVs within remote and inaccessible areas allows access to previously unsurveyed locations (Sardà-Palomera et al., 2012), and on-board cameras allow data to be recorded remotely, alleviating the need for piloted surveys, reducing risk, cost and workforce required to conduct marine surveys. UAVs can facilitate more accurate detection of target species: aerial photogrammetry i.e. the capture of images from an aircraft, allows for imagery to be stored permanently and viewed multiple times by multiple observers (e.g. Sykora-Bodie et al., 2017); and high manoeuvrability paired with little noise disturbance permits low flight altitude for increased proximity to target species (e.g. Bevan et al., 2016). UAVs have the capacity to track hundreds or thousands of individuals over their lifespan and reduce survey effort by scientists for a much smaller cost (e.g. Liu et al., 2020; for review see Rees et al., 2018) increasing feasibility of regular surveys. Evidence of the increased accessibility for scientific research is shown via the abundance of studies utilising UAVs for species observation, together with the increased diversity of marine fauna studied (dugongs, *Dugong dugon*, Hodgson et al., 2013; elasmobranchs, Kiszka et al., 2016; penguins, Liu et al., 2020; seabirds, *Larus fuscus*, Rush et al., 2018).

UAVs were first used for sea turtle research in 2012, over seagrass meadows in the WIO, where a population estimate for green turtles was conducted using a mini fixed-wing UAV (Ballorain et al., 2014). UAV surveys of turtles have since been conducted in Mexico, Hawaii and Australia, studying species abundance, identifying courtship behaviour and estimating nesting population size, respectively (Bevan et al., 2016; Brooke et al., 2015; Dunstan et al., 2020). Aerial surveys utilising UAVs also ensure surveys include a range of demographics including males and immature turtles that are omitted from track- or clutch-count surveys, improving accuracy of population estimates. However, while UAV surveys aid observation of sea turtles, research utilising UAVs are subject to biases as there is limited availability to observe turtles at the surface, leaving uncertainty in the accuracy of total counts or densities. The broad range of research and improvements on traditional sea turtle population estimates demonstrates the diversity of the potential application of UAVs, as well as a global shift to UAV technology from previously used aerial techniques (Rees et al., 2018).

The Chagos Archipelago

The Chagos Archipelago (hereinafter termed Chagos) is a collection of islands and atolls in the WIO where turtles are known to reside. The archipelago is comprised of 55 islands across five atolls: Diego Garcia, Egmont, Peros Banhos, Salomon and Great Chagos Bank. During the early 20th century when Chagos was populated, exploitation of sea turtles was common place: from 1904 to 1915, 4,070 kg of hawksbill turtle shell was exported from Chagos to Mauritius (Frazier, 1980; Stoddart, 1971), and turtle meat and eggs were openly traded (Wenban-Smith and Carter, 2016). Nesting numbers decreased significantly, and in 1996, populations were estimated at 400 - 800 green and 300 - 700 hawksbill turtles (Mortimer and Day, 1999). Until 2009, long-line and purse seine fisheries remained in Chagos, leading to incidental capture or entanglement of non-target species (Mees et al., 2009), which turtles were frequently subject to. In 2010, a 550,000 km^2 no-take Marine Protected Area (MPA) surrounding Chagos was established, making it one of the largest MPAs in the world (Sheppard et al., 2012). Evidence of the MPA's success can be seen in nest-count studies, where from 2011 to 2018, green and hawksbill annual nesting increased up to five and nine times, respectively, compared to their frequency in 1996 (Mortimer et al., 2020).

Chagos provides rich foraging habitats for turtle species: satellite tracking of green turtles revealed pristine seagrass meadows within the Great Chagos Bank, the largest atoll within the archipelago (Esteban et al., 2018); and a 2015 survey of coral reefs confirmed Chagos as one of the most diverse coral habitats in the world, with 58 coral genera identified, covering 42% of the archipelago extent (Carlton et al., 2015).

Chagos is a long-standing nesting sanctuary for both green and hawksbill turtles and supports foraging populations within the wider WIO (Hays et al., 2020b; Mortimer et al., 2020). Satellite tracking data has revealed migratory routes of green turtles travelling between nesting grounds in Chagos to foraging grounds across the WIO, including Maldives, Seychelles, Madagascar, Somalia, and Mozambique, the latter being the longest known migration of a green sea turtle at over 4,000 km (Hays et al., 2020a). The majority of tracked individuals (n = 28/36) were estimated to spend 9.8% of their adult life within the boundaries of the MPA, while seven individuals, tracked for minimum three months, did not leave the MPA but remained on foraging grounds surrounding

Chagos (Hays et al., 2020a, 2020b). Diego Garcia, the largest island in the archipelago, provides protected foraging sites for immature turtles (Hays et al., 2021a). The beaches and shallow waters of the Chagos MPA are thought to be fundamental in supporting sea turtle populations throughout the WIO. As Chagos is a key foraging ground for turtles across the Indian Ocean, understanding the density and distribution of the foraging population can elucidate the importance of Chagos for populations across the wider WIO.

Aims and Objectives

Aerial surveys allow for observation of all demographics of turtle populations (female, male and immature) and can be utilised in Chagos to estimate density and distribution of turtles within the MPA. UAV surveys conducted in Chagos aimed to investigate: (1) the population density of green and hawksbill turtles within Chagos using systematic UAV transects; (2) the distribution of demographics between environments i.e. identify the life-stage and species of individuals based on carapace measurement, and subsequently compare trait-dependent use of ocean and lagoon environments, as well as islands (Nelson's Island and Diego Garcia); and (3) further assess the utility of UAVs and image analysis techniques for sea turtle identification and assessment. Understanding the density and distribution of sea turtles in the Chagos Archipelago can better inform researchers and conservation efforts within the wider WIO region.

Methods

Study Site and Species

The Chagos Archipelago (4.71 - 7.72°S, 70.72 - 72.79°E) is located in the WIO (Figure 1), approximately 2000 km east of the Seychelles. It's comprised of 55 islands and atolls, including the largest atoll structure worldwide, the Great Chagos Bank. The archipelago lies within a MPA spanning 550,000 km^2 (Sheppard et al., 2012). Habitats are varied: surrounding islands, shallow reef flats are followed by deep oceanic reefs (> 30 m), and lagoon environments occur within atoll structures, with varied depths.

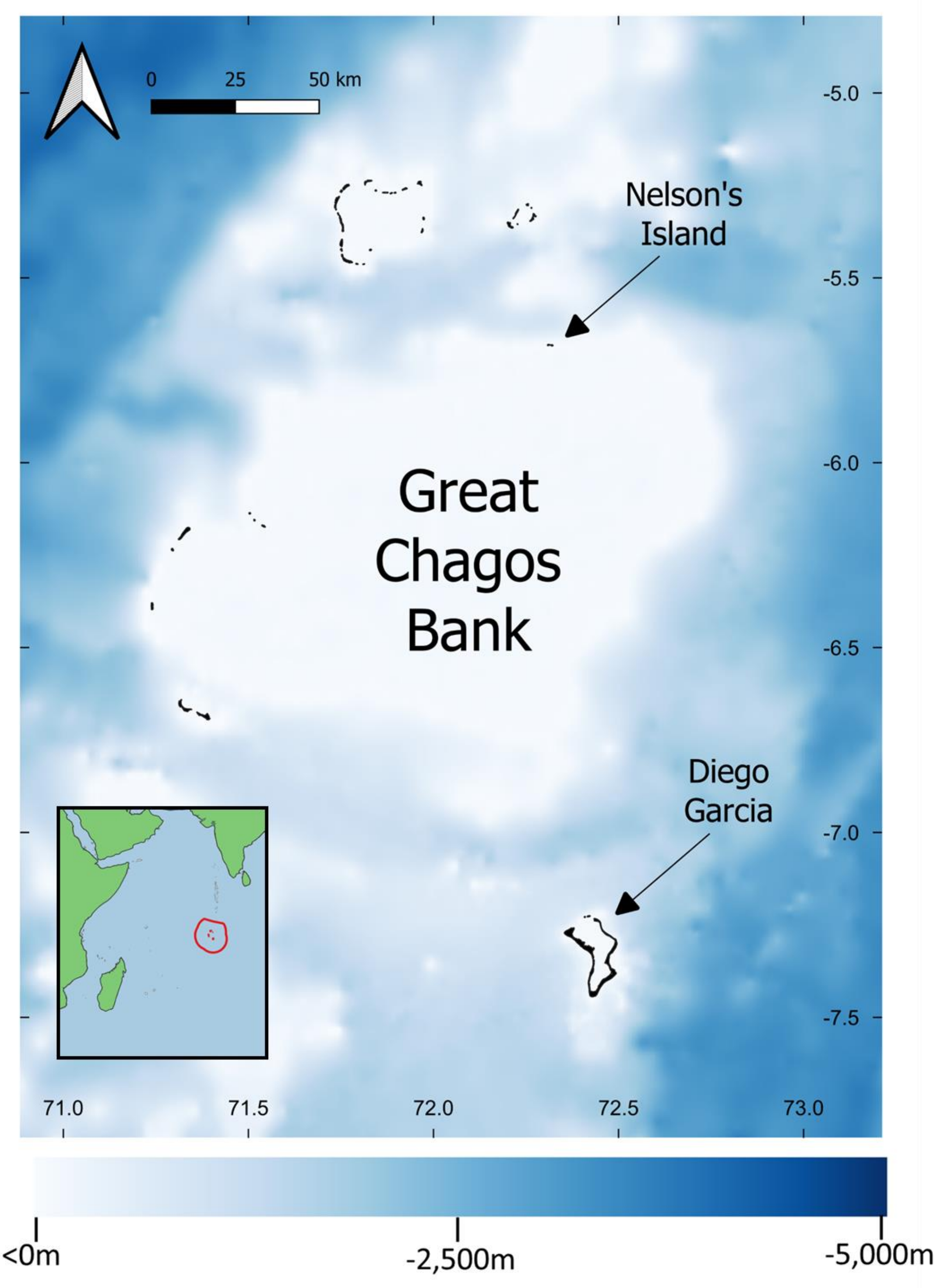

Figure 1. The Chagos Archipelago, with inset map to show position in larger West Indian Ocean. Red outline shows boundary of Exclusive Economic Zone, which is the full extent of the Marine Protected Area. Islands shown in black. Arrows indicate survey locations: Diego Garcia Atoll and Nelson's Island on the northern rim of the Great Chagos Bank Atoll. Bathymetry source: GEBCO (2021); Exclusive Economic Zone boundary source: Marineregions.org (Flanders Marine Institute, 2021); Island shapefiles: GADM (Global Administrative Areas, 2018).

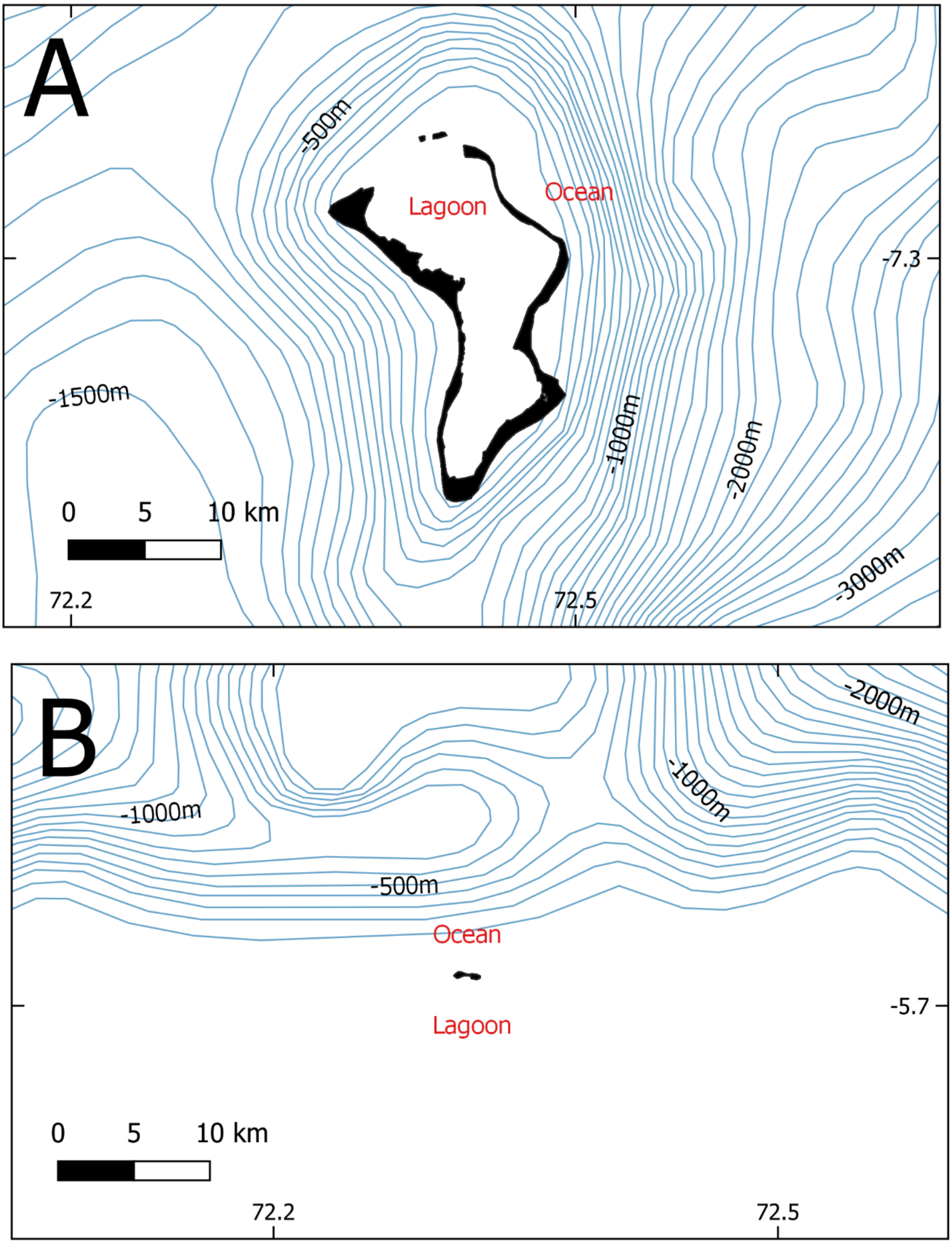

Figure 2. UAV surveys took place in two contrasting environments: ocean sites (oceanside of atoll islands) and in the lagoon (sheltered by the island). The bathymetry maps of A) Diego Garcia and B) Nelson's Island indicate comparative depth of the two environments. Nelson's Island is centrally located on the wide northern rim of the Great Chagos Bank and the slope of the seabed is shallower. Islands shown in black, 100 m depth contour lines in blue. Bathymetry source: GEBCO (2021).

Diego Garcia (7.31^{o}S, 72.42^{o}E) is an islanded atoll with an interior semi-enclosed lagoon, and channel leading to the exterior ocean environment (Figure 2). The exterior ocean depth increases sharply and reaches approximately 5000 m, while the small lagoon environment reaches a maximum depth of 31 m (Sheppard, 2016). It is the largest and only inhabited island within the archipelago. Nelson's Island (5.68^{o}S, 72.31^{o}E) is a small outer island on the northern-edge of the Great Chagos Bank atoll, with deep oceanic environment to the north, and a shallower open lagoon environment to the south (Figure 2).

Both green and hawksbill turtles utilise the Chagos Archipelago as a nesting and foraging ground (Mortimer et al., 2020). Nesting seasonality differs between species: green turtles nest year-round with peaks during the austral winter (June - August), while hawksbill turtles nest within the austral summer only (December – February, Mortimer et al., 2020). Foraging occurs year-round for both species, with the Chagos Archipelago highlighted as an important foraging area for green turtles due to extensive sea grass meadows (Esteban et al., 2018). Turtle Cove, a tidal creek within the Diego Garcia lagoon, has been previously identified as a hotspot for immature hawksbill turtles (Mortimer and Day, 1999).

Survey Design

UAV surveys were conducted systematically around both Diego Garcia and Nelson's Island and followed established UAV survey protocols. One kilometre transects were flown parallel to the shore, at increasing distances (50 m, 150 m, 250 m, 350 m, 450 m). Transect sites were selected in order to compare ocean and lagoon environments. Diego Garcia had four ocean transect sites and 14 lagoon sites (Figure 3 and 4). Nelson's Island had two transect sites, on the oceanside (north) and lagoon-side (south) coasts (Figure 5). Unbalanced survey design was representative of island size (Table 1): Diego Garcia has an extensive oceanside coastline (approximately 59 km) so four ocean sites were selected for a comprehensive survey, and Diego Garcia's lagoon (coastline approximately 63 km) has been identified as an important foraging ground for immature hawksbill turtles (Mortimer and Day, 1999) so transects were conducted in 14 sites to cover the full extent of the lagoon; Nelson's Island is approximately 1.8 km in length therefore only one transect was viable on each coast. Survey locations were spaced at minimum 4 km intervals on the oceanside of Diego Garcia providing a buffer to limit re-sight of individuals (Bevan et al., 2016), as well as maximise extent of surveyed coastline (16 km out of approximately 59 km). Survey locations were also limited by accessibility to the coastline.

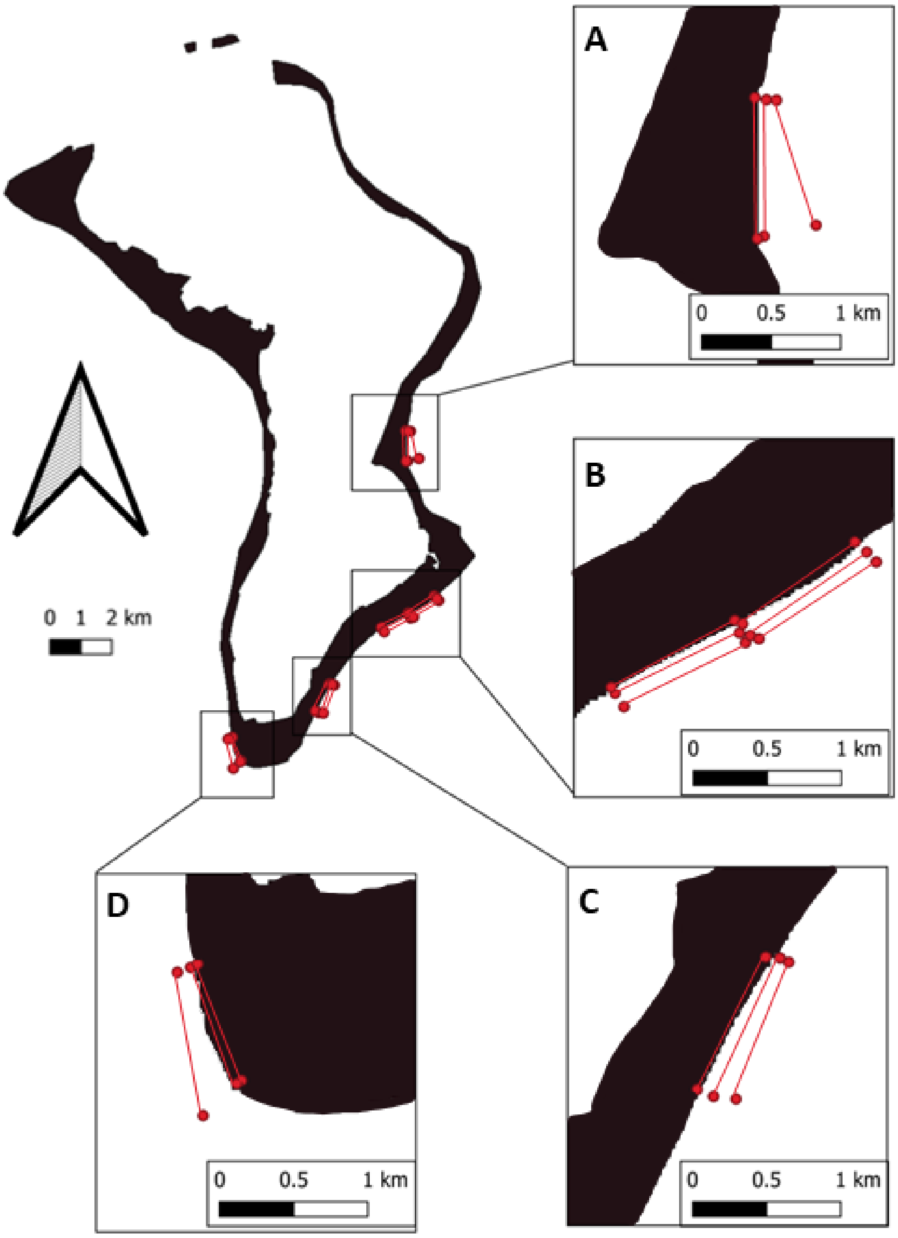

Figure 3. Oceanside transect locations on Diego Garcia. A) Site 1, B) Site 2, C) Site 3, and D) Site 4. Transects at Site 2 comprise of two 1 km transects. Only one repeat is shown. Coordinates shown in Figures 1 and 2A. Island shapefile source: GADM (Global Administrative Areas, 2018).

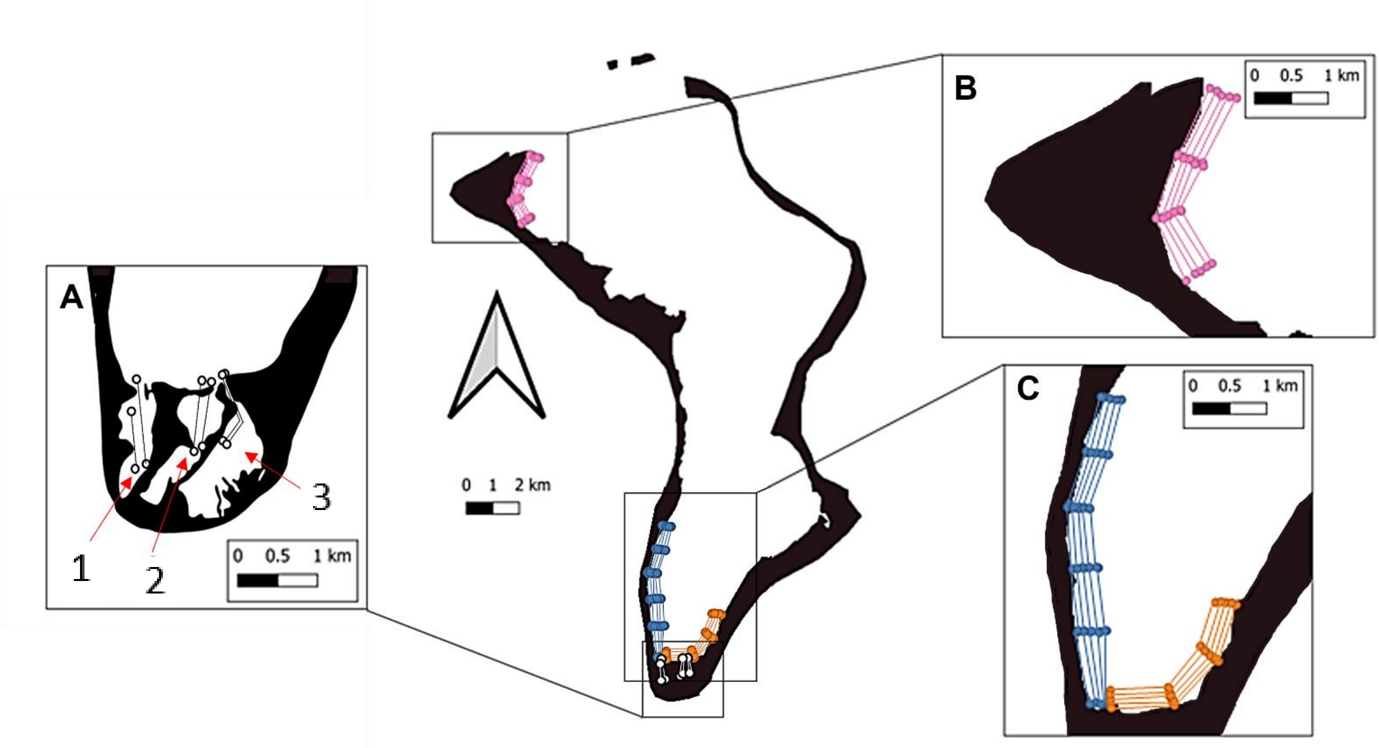

Figure 4. Lagoon-side transect locations on Diego Garcia: A) Turtle Cove, where 1 - 3 represent the three distinct zones (TC9, 10, 11); B) Marina North, Centre and South shown in pink (M1, 2, 3); and C) West shown in blue (W4, 5, 6, 7,8), with West 4 most-northernly, and East shown in orange (E12, 13, 14), with East 12 most-southernly. Coordinates shown in Figures 1 and 2A. Island shapefile source: GADM (Global Administrative Areas, 2018).

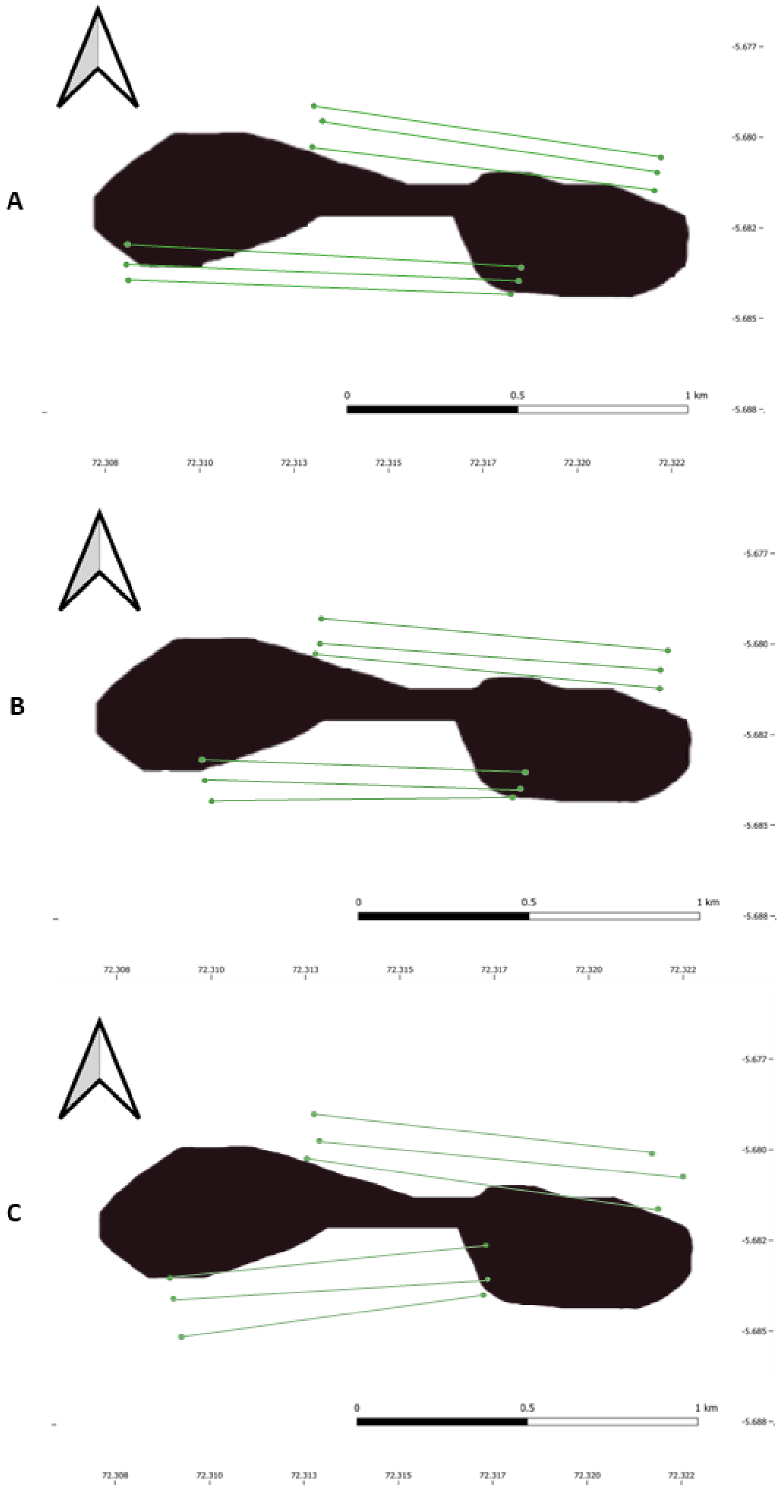

Figure 5. Transect locations on the oceanside (north, NI.O) and lagoon-side (south, NI.L) of Nelson's Island, Great Chagos Bank. All three repeats are shown highlighting intra-repeat variability in transects: A) repeat 1, B) repeat 2, and C) repeat 3. Island shapefile source: GADM (Global Administrative Areas, 2018).

Table 1. Geographical information on survey sites Diego Garcia and Nelson's Island, comparing coastline length and lagoon type. Coastline data measured manually on Google Earth.

Atoll	Island	Total Coastline (km)	Total Land Area (km^2)	Oceanic Coastline (km)	Lagoon Coastline (km)	Lagoon Type	Coordinates
Diego Garcia	Diego Garcia	121.58	31.83	58.89	62.69	Semi-enclosed	7.31^{o}S, 72.42^{o}E
Great Chagos Bank	Nelson's Island	3.71	0.35	1.81	1.90	Open	5.68^{o}S, 72.31^{o}E

Transect length of 1 km was selected based on: (1) the ability to maintain visual line-of-sight of the UAV at all times, to ensure safe flight operation, following UAV flight regulations (Goebel et al., 2015; The UK Civil Aviation Authority, 2021); (2) the optimal locations for UAV surveys limiting the distance available for straight transect lines, with 1 km selected as a suitable maximum; and (3) the battery life of the UAV and therefore the maximum flight time possible at the chosen flight speed. At Diego Garcia Ocean Site 2, two kilometres of coastline was surveyed, with standardised 1 km transects conducted on each repeat (Figure 3). Parallel transects are an established protocol for UAV sea turtle surveys (e.g. Bevan et al., 2016; Schofield et al., 2017a; Sykora-Bodie et al., 2017) as males tend to swim parallel to the shore (Schofield et al., 2006). Conducting parallel surveys therefore helps to limit the resight of individuals across transect lines. Transects were standardised at 100 m intervals from the coast at 50 m, 150 m and 250 m offshore for Diego Garcia ocean transects and Nelson's Island surveys based on increasing water depth (> 30 m) limiting visibility, and were increased to 350 m and 450 m on the lagoon-side of Diego Garcia (Figure 4) based on the shallow depth profile (< 31 m). Hodgson et al. (2013) spaced UAV transects of dugongs (*Dugong dugon*) at 72 m intervals, based on the field-of-view of the UAV at 500 ft (152.4 m) providing a strip-width of 72 m; while a review by Raoult et al. (2020) found all sea turtle UAV studies included were conducted at intervals of either 100 or 500 m (e.g. Bevan et al., 2016; Schofield et al., 2017b). At the chosen flight altitude of 30 m above ground level (AGL), the UAV field-of-view width was 47.72 m, thus a distance of 50 m was chosen from shore to cover the full extent of the habitat from the shoreline outwards. An interval of 100 m between subsequent transects was chosen to space transects adequately, preventing overlap of transect lines and potential resight of individuals, following established UAV survey protocols (Raoult et al., 2020).

To locate the start point of the first transect, the UAV pilot stood at the centre point of proposed transect. The UAV was flown 50 m from the shore, turned 90° and flown until the Straight-Line Distance (SLD) between the pilot and the UAV was 502.5 m, at which point the UAV was 500 m from the centre point (Figure 6). The UAV was turned 180° to face the direction of travel before the transect began. With the on-board camera recording, the UAV was flown 1000 m, following the edge of the coastline as a reference, until the SLD between pilot and UAV was 502.5 m again, confirming the UAV had travelled 1000 m in distance. The same method was used for each distance from the shore (150 m from shore = 522 m SLD; 250 m from shore = 559 m SLD; 350 m from shore = 612.40 m SLD; and 450 m from shore = 674.50 m SLD). At some locations coastline shape influenced location of pilot for line-of-sight UAV flight operations, however, transect length was not impacted and remained at approximately 1 km.

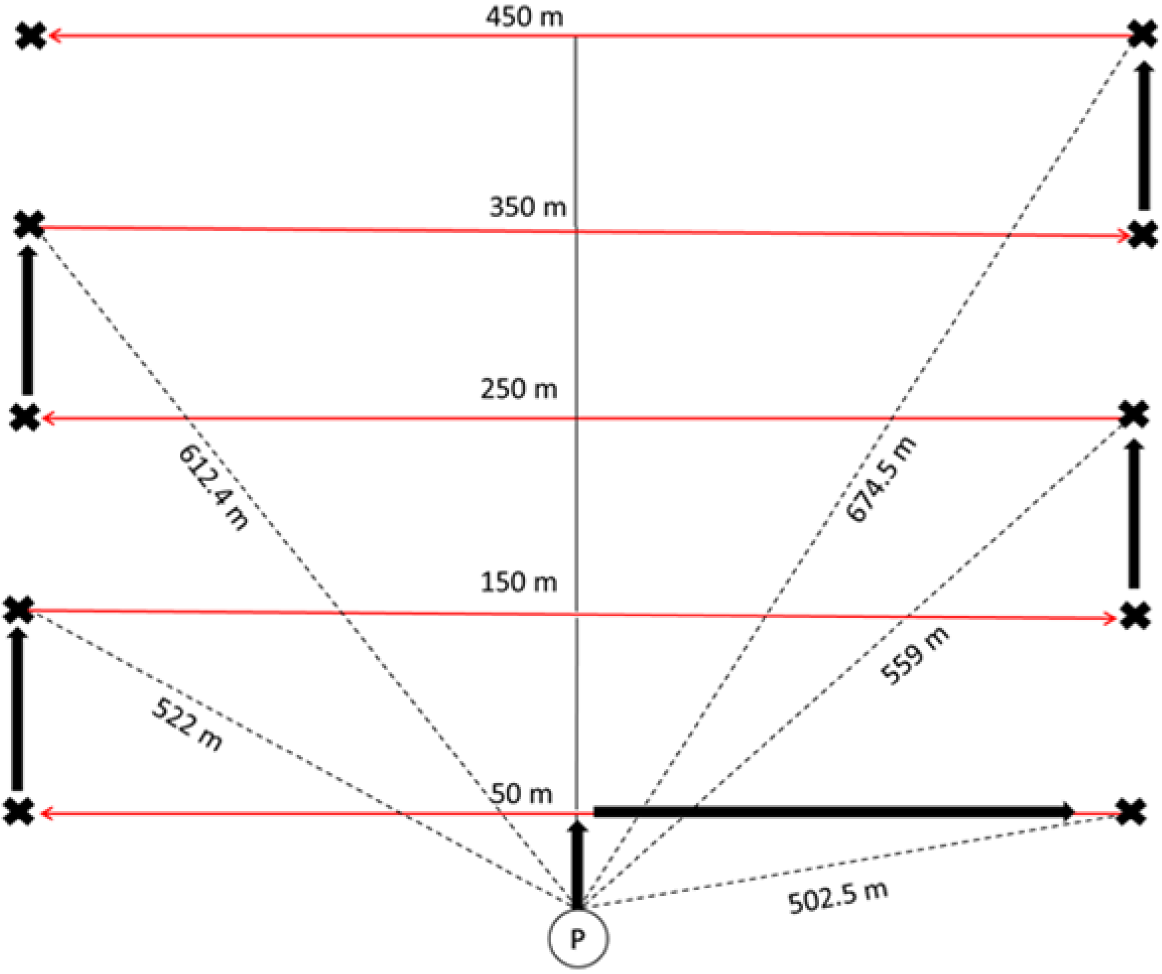

Figure 6. Trigonometry to determine the start point of transects. P is the UAV pilot. Black arrows show movement of UAV between transects. Black crosses mark the start/end of transects. Transects are shown with red arrows pointing in the direction of travel. Dashed lines symbolise the straight-line distance (SLD) required between the pilot and UAV for the correct start point. Picture not to scale.

Transect strip-width depends on altitude of flight and impacts the subsequent field-of-view of the UAV camera (Rees et al., 2018). Previous UAV surveys of marine megafauna have a large range of altitudes (5 m AGL, Bevan et al., 2016; 300 m AGL, Maire et al., 2013) and chosen altitude depends on size of target species and intended use of imagery i.e. simple species counts can be achieved at higher altitudes (e.g. dugongs, *Dugong dugon*, Maire et al., 2013), while photo identification of individuals requires higher resolution imagery and therefore a lower altitude (e.g. killer whales, *Orcinus orca*, Durban et al., 2015; grey seals, *Halichoerus grypus*, Pomeroy et al., 2015). UAV flights were conducted at a chosen survey altitude of 30 m AGL for several reasons: Bevan et al. (2018) reported no behavioural response by turtles to UAV surveys conducted at 30 m AGL, therefore noise disturbance and general UAV presence would not impact turtle behaviour; Schofield et al. (2017a) found 30 m AGL as the maximum altitude where loggerhead turtle (*Caretta caretta)* tails could be reliably distinguished to identify sex; and a lower altitude results in a smaller ground sampling distance (GSD) i.e. the distance between the centre of two adjacent pixels, leading to a higher resolution image and therefore more accurate measurements (Hodgson et al., 2018). A higher survey altitude can increase the survey area (e.g. 50 m AGL provides 90 m transect width, Dunstan et al., 2020). However, higher altitudes result in a decrease in GSD and image resolution, although higher resolution camera equipment can mitigate this (Raoult et al., 2020). While 60 m AGL paired with 100 m intervals between transect lines results in full coverage of the available habitat (Raoult et al., 2020), overlapping can occur leading to potential resight of individuals which may require further image processing (e.g. 90 m AGL, Sykora-Bodie et al., 2017), therefore 30 m AGL is recommended to prevent this (Schofield et al., 2017a). Dr Nicole Esteban conducted preliminary test flights at various altitudes in 2018 and confirmed 30 m AGL as optimal to provide a large field-of-view (47.72 m x 26.84 m) whilst maintaining clear visibility for turtle identification and measurement (Esteban, pers. comm.).

UAV surveys were repeated on three subsequent days as (1) weather conditions (sun glare, precipitation, wind) and sea state can impact the availability of turtles to be observed or the possibility of flights being conducted, so multiple repeats can account for this spatiotemporal change in state, (2) high winds or battery failure can cause UAV operations to be suspended, and potential errors in imagery-recording could prevent surveys, and (3) taking repeat surveys allows more reliable conclusions to be made as variation in data is accounted for.

Surveys were conducted between daylight hours of 07:00 – 19:30, with flight time following the tidal cycle so surveys were conducted during the same tidal state. Flights were only conducted in optimal weather conditions i.e. no precipitation, low winds. Flight operations were manually controlled by N. Esteban to follow the curvature of the coastline, maintaining the edge of the field-of-view on the shoreline to maximise available area surveyed (similar to Kelaher et al., 2019). The UAV on-board camera was directed to nadir i.e. 90° downfacing and 720p footage was live-streamed to the UAV controller providing a first-person-view of the survey, allowing the UAV pilot to adjust flight course when necessary. A small time-lag between the UAV position and the footage viewed on the controller resulted in the UAV diverting from the chosen flight path, sometimes over unavailable habitat such as beach or exposed rocks, which had to be accounted for during image analysis. Strong winds also impacted the ability of the UAV to sustain a direct forward motion and caused some deviation from the desired flight path (Bevan et al., 2015).

UAV speed was fixed at 5 metres per second (m/s) to balance the needs of extracting single frames from video footage for turtle measurement whilst minimising flight time (one battery can provide only 20 minutes of flight time, Autel Robotics, 2021). When covering larger survey areas, studies have flown UAVs at faster speeds (e.g. 12 m/s, Schofield et al., 2017a) but for 1 km transects, ~5 m/s is in line with other UAV surveys (e.g. 1000 m, 5 m/s, Dunstan et al., 2020; 1000 m and 700m, 4 m/s, Varela et al., 2019). UAV speed can be impacted by (1) high winds increasing either UAV velocity or drag exerted on it, or (2) obstacles (namely birds) causing the UAV to stop. For obstacle avoidance to be activated, the UAV speed is then limited to a maximum of 10 m/s (dependent on UAV make and model).

Metadata

Various metadata were collected during flights based on metrics recorded by other UAV sea turtle surveys (Hodgson et al., 2018; Lauriano et al., 2011; Schofield et al., 2017a; Sykora-Bodie et al., 2017). This included dates, start and end coordinates and times for take-off and landing. During image analysis, all timings and dates were checked to ensure accurate notation. Wind speed was collected using an anemometer and measured in metres per second (m/s). Wind speed was recorded at ground level and not 30 m AGL so could be unrepresentative of true wind speed exerted on the UAV during surveys. Where wind speed was not collected (Nelson's Island), Weather Underground (Weather Underground, 2021) was used to access historical weather data for Diego Garcia to approximate. To ensure the intended survey design was achieved, UAV travel speed and flight altitude were recorded for each flight. Direction of travel was noted as this impacted sun glare and therefore visibility, and some transects were flown in the opposite direction than planned to limit this. Tidal state during time of survey was noted i.e. high water (HW) or low water (LW). Where not noted, tide tables for Diego Garcia provided by N. Esteban were used. HW or LW was assigned to surveys if they were within three hours of the high tide or low tide, respectively. Some days e.g. 08/02/2021 had only one high tide so N/A was noted when survey time was outside of the three-hour period. Duration of flight was noted too: when surveys exceeded five minutes, the UAV automatically created a second video file, and these files were reviewed together in the first repeat of image analysis.

UAV Model and Regulations

A portable, quadcopter UAV equipped with an integrated camera was used for aerial surveys (Autel Robotics EVO™). Multirotor-UAVs provide good manoeuvrability for manually flown transects; fixed-wing UAVs have a larger range and battery life (and therefore flight time) but require constant forward motion and a larger take-off site (Raoult et al., 2020; Rees et al., 2018). The Autel Robotics EVO™ is a small, lightweight multi-rotor UAV with camera able to record in 4K resolution and 30 frames per second (fps). The on-board camera is fitted onto a separately controlled gimbal and can be controlled independently to the UAV. Video footage was recorded as a .MOV file and was stored on an external microSD card. Rechargeable batteries allowed for a maximum 20-minute flight time, with each survey (three transects) requiring between one and three batteries. The UAV pilot ensured multiple spare batteries were available to allow for high winds or obstacles increasing total survey time. A return-to-home feature ensured the UAV returned to the take-off point if connection to the controller was lost. During surveys, line-of-sight had to be maintained: the EVO™ is bright orange in colour, and an assistant pilot used binoculars to maintain sight at all times. The UAV was launched from the beach on a take-off-and-landing platform and directed to the transect start point, calculated using the aforementioned trigonometry using the SLD between the pilot and UAV (see Figure 6).

UAV flights were conducted by an authorised pilot (N. Esteban) licensed with Permission for Commercial Operations from the UK Civil Aviation Authority. An assistant pilot was present for all flights to record data, monitor the environment and birds in vicinity of the UAV, and maintain line-of-sight with the UAV (Dr Jeanne Mortimer, Dr Jacques-Olivier Laloë, Holly Stokes). Radio communications were maintained with Air Traffic Controllers prior-to and during UAV operations. All work was approved by Swansea University Ethics Committee and the British Indian Ocean Territory Administration of the UK Foreign, Commonwealth and Development Office. The study was endorsed through research permits (0009SE18, 0004SE19, 0006SE19, 00001SE21) from the Commissioner’s Representative for BIOT and research complied with all relevant local and national legislation.

Image Processing

Analysis Training and Familiarisation

Analysis training was undertaken to develop observational skills: example survey videos were viewed simultaneously over a Zoom call with N. Esteban to help identify turtles, and to aid in methodology development. Videos were slowed down to 0.25 x speed using VLC player (VideoLAN, 2021) to aid observation and therefore improve accuracy of turtle counts.

Turtles were identified using the characteristic shape of carapace and flippers. When objects were identified as potential turtles, the footage was moved frame-by-frame to observe if any movement occurred. This can be challenging when sea state and wind speed impact the movement of the water, obscuring anything below. Therefore turtles were categorised based on certainty: 'Definite' turtles were clear and obvious turtles, determined by identification of the carapace and flippers, and where movement has potentially occurred; 'Probable' turtles were turtle-like shape of carapace and flippers that contrasts with the surroundings, but potentially no movement has occurred; and 'Possible' turtles were turtle-like shapes, but no movement or clear carapace was observed (Figure 7). Probable and Possible turtles were differentiated based on presence or absence of flippers, as well as location i.e. if definite turtles were observed nearby.

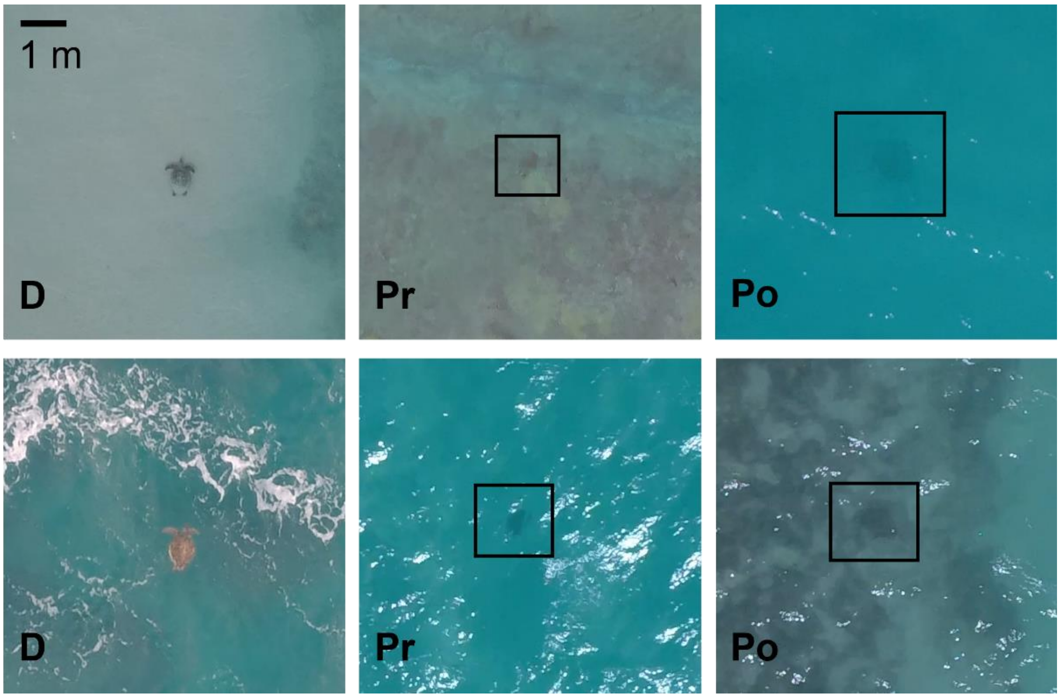

Figure 7. Examples of turtles identified with different certainty levels: D is definite; Pr is probable; Po is possible. A black square surrounds some turtles to aid identification. Pictures are all true-to-size from UAV imagery, one metre scale bar applies to all images.

A subset of videos (n = 6) provided by N. Esteban were viewed, a turtle count was conducted, and the results compared with eight observers of varying observational skills (seven non-experienced, one experienced) to identify if turtle counts were subject to variation between observers. Inter-observer variation was calculated following methodology outlined in Giuffrida et al. (2018), where each observers' results were compared to one reference observer, identified as the most experienced and therefore the most accurate. Practice videos were viewed before and after image analysis to see if precision improved with experience so intra-observer variation could be assessed. Intra-observer variation was not assessed for the reference observer due to unavailability for a blind repeat survey.

Video Analysis Software

Research was undertaken to find software best-suited to analysis. Software required would ideally be able to (1) provide the time code and frame number of any given frame, (2) move frame-by-frame through footage, (3) enable the user to adjust playback speed to allow for viewing in slow-motion to help observational accuracy and (4) extract individual frames, with optional file formats, so a high-quality image could be utilised for further analysis.

Initially, UAV footage was viewed in VLC media player® (VideoLAN, 2021), and although it provided a clear image, the frame number could not be displayed. Seven free media players (Table 2) were downloaded and trialled as potential software for image analysis, but none met all four ideal requirements. QuickTime Player® (Apple, 2021) did fulfil each ideal characteristic, however did not function correctly on Windows as an Apple product. Adobe Premiere Pro® (Adobe, 2021), a subscription-based software, was trialled and met the requirements, although introduced a novel issue - changing the playback speed altered the frame number. Playback speed therefore could not be altered as a result but moving frame-by-frame (by pressing the arrow keys) was sufficient to view footage at a slower speed. Adobe Premiere Pro® was decided as best suited for the research needs and a rolling monthly subscription was purchased.

Table 2. Characteristics of software trialled for image analysis. Tick or cross symbolises Yes or No, respectively. When not a clear Yes or No, additional information is given

Software	**Frame Number?**	**Move Frame-by-Frame?**	**Change playback speed?**	**Extract Frame?**
VLC media player	✗	✓	✓	✓
Quick Time Player	✓	✓	50% only	✓
GOM Player	✗	Forward only	✓	✓
SM Player	✗	Forwards only	✗	✓
Virtual Dub	✓	✓	✓	Copy to clipboard only
MPC-HC	✗	✓	✓	✓
Pot Player	✓	✓	Slow motion only	Copy to clipboard only
DJV	✓	✓	✓	✗
Adobe Premiere Pro	✓	✓	✓	✓

UAV Calibration

To allow the measurement of turtles using the UAV, calibration flights were conducted to calculate the number of pixels per known-distance. Calibration flights were conducted at the Swansea University Sports Field, complying with all UK aviation regulations (The UK Civil Aviation Authority, 2021). A 50 m tape measure was laid down with the UAV hovering above at the chosen survey altitude of 30 m AGL. Images were taken in 4K, ensuring the tape measure was in line with the UAV. In ImageJ (Rasband, 2021), an open-source image analysis tool, images were input and a line tool used to measure the number of pixels comprising a given distance. Measurement was carried out for 30 m in length and then divided to determine the number of pixels per metre. Measurement was repeated three times, resulting in a mean of 80.48 pixels per metre. This is equivalent to a ground sampling distance (GSD) of 1.24 cm/pixel (a decrease in GSD represents an increase in image resolution therefore a small GSD is optimal, Hodgson et al., 2018). This information was then utilised to measure turtles, calculate the total area of the field-of-view of the UAV, and measure the total available area within the transect. ImageJ was also used to estimate the unavailable area due to glare, shadow, and white water in images, measured as a percentage cover.

Image Analysis

Data was received from N. Esteban on a hard drive including all video files alongside metadata. Metadata records were matched with each file, and the time code was compared to ensure start time of each survey was recorded correctly, in local time (UTC+6). Several data were recorded directly into a spreadsheet: the number of turtles and certainty of each individual (definite, probable, or possible); size of turtle, measured as straight carapace length (SCL) and straight carapace width (SCW), provided the carapace edge is clear for accurate measurement; turtle sex, where possible, by identification of tail extending past the rear flippers; and metadata including turbidity measured in a scale (1 - 4), and percentage cover of glare, shadow and wave swell. SCL is the length of the turtle's carapace from nuchal scute to supracaudal scute i.e. the most posterior marginal scute (Wyneken, 2001). SCW is the width of the turtle's carapace, measuring the widest part of the carapace from the edge of one marginal scute to another (Eckert et al., 1999). Turtle sex was differentiated utilising the secondary sex characteristic of tail length (such as Schofield et el., 2017a, see Appendix Figure 1), but only for individuals above the smallest nesting size (67.5 cm SCL for hawksbill, 85 cm SCL for green) as to not wrongly assign the sex of immature turtles whose tail length can vary. Glare, shadow and wave swell were all measured using the polygon tool in ImageJ (Rasband, 2021) to calculate percentage cover (see Appendix Figure 2), and turbidity was noted following a numerical system outlined in Hodgson et al. (2013) (see Appendix Figure 3) and were adapted as follows:

1. Shallow clear water with bottom visible
2. Shallow water with bottom obscured by turbidity
3. Deep water with bottom visible but unclear
4. Deep water with bottom not visible

A custom-built high-performance desktop equipped with an Intel® B460 (LGA 1200) ATX motherboard and high-quality integrated graphics card was purchased (ASUS TUF Gaming B460-PLUS), alongside a 4K ultraHD monitor (LG 27” 4K monitor, model 27UL600), to allow for optimal image quality for turtle observation and analysis.

UAV video files were processed in Adobe Premiere Pro® (Adobe, 2021) to count individuals and extract images for turtle measurement. Footage was viewed at full speed, but frequently stopped to search for turtles. Once a turtle was identified, the file was moved frame-by-frame to find the optimal frame for carapace measurement. The frame was then extracted as a .TIFF file and named using the following structure: video file name, the frame number and the time e.g. MAX_0003_W5_250.801.0026 for file name MAX_0003_W5_250 (West 5, 250m from shore), frame number 801, and time 00:26. This .TIFF file was then edited in Windows Paint® (Microsoft, 2021) to circle each turtle to aid observation when reviewing images later in analysis. Lettering was also added to denote the certainty of the observation: no lettering assumed turtles were definite, PROB for probable turtles, and POSS for possible. Editing the image did not impact the resolution: a comparison was done using two screen captures of the same frame, one edited in the aforementioned manner and one not, and measurements taken from images resulted in the same mean SCL, and 0.66 cm difference in mean SCW. Turtle identification and frame extraction was completed for the whole video file, then the images used for data input. During this process, images were opened in ImageJ (Rasband, 2021) for measurement of (a) turtle SCL and SCW (see Appendix Figure 4) and (b) area measurement of glare, shadow and wave swell. In data input, each turtle was assigned an ID comprised of the location, the repeat, the distance from shore and the number turtle i.e. DG.O1.2.50.1 was Diego Garcia Ocean Site 1, repeat 2, 50 m from shore, turtle number 1. The SCL and SCW of the turtle, where the carapace margin was clear, was measured three times utilising the number of pixels per metre determined by calibration flights (80.48 pixels/m) and the mean calculated. The presence of a tail was also noted by a simple yes/no field and marked as unclear if not visible.

The 127 video files were viewed by a single observer, and then repeated blind and in random order to limit observational bias. After both repeats were completed, results were validated by comparing turtles in repeat 1 and 2 (see Appendix). Repeat 2 was regarded as the most accurate as the observer had more experience when this repeat was carried out, thus all turtles for repeat 2 were accepted. Where counts differed, images were compared: turtles observed in the first repeat, not counted in the second repeat, were either accepted or rejected based on certainty of the observer, and video files were sometimes viewed (in addition to still images) to aid the decision.

Life-Stage Characterisation Methodology Development

Species Identification

To identify species, the utility of length-to-width (L:W) ratio of the carapace (using the mean SCL and SCW, respectively) was investigated. Turtle carapace morphometrics differ between species and can be used for species identification (Pritchard and Mortimer, 1999). Data on green and hawksbill size were provided by Dr Jeanne Mortimer for turtles residing within Turtle Cove in the Diego Garcia lagoon (green, n = 18; hawksbill, n = 75), all of which were immature. Due to small sample size of green turtles, data were supplemented with immature turtle measurements from Seychelles (n = 80) as populations are genetically linked (Mortimer and Broderick, 1999). The L:W ratio was calculated for all individuals by dividing SCL by SCW: mean L:W ratio was 1.28 ± 0.05 standard deviation (SD) for hawksbill turtles (range 1.18 – 1.40), and 1.17 ± 0.04 SD for green turtles (range 0.96 – 1.28). The deviation around the mean for both species were considered, and turtles were assigned as follows: turtles with ratio < 1.18 assigned green; turtles with ratio > 1.23 assigned hawksbill, turtles within the range of 1.18 – 1.23 left unidentified. Whilst theoretically sound, an issue with this methodology was highlighted: in a frame extracted from a Nelson's Island oceanside survey containing seven mating turtles (see Figure 8), five were deemed hawksbill and one green. This was unlikely as (1) the mating behaviour observed should denote all individuals are the same species, and (2) the survey was conducted in July during green mating season, outside hawksbill mating season (Mortimer et al., 2020). Satellite-tracking data provided by N. Esteban showed a green turtle residing in the ocean environment surrounding Nelson's Island on the same date (7th July 2019), therefore there was a high certainty that the mating individuals were green turtles.

Incorrect identification could be due to an immature-biased dataset. Data from J. Mortimer on turtles of known life-stages in the Seychelles (green, immature n = 91, subadult n = 3, adult n = 112; hawksbill, immature n = 195, subadult n = 54, adult n = 48) provided insight into the change of the L:W ratio through-out maturation (Table 3). For immature turtles, the mean L:W ratio for green turtles was 1.17 ± 0.03 (range 1.11 – 1.28), and hawksbill turtles was 1.27 ± 0.04 (range 1.17 – 1.41). This corresponds with our findings of < 1.18 and > 1.23 L:W ratio for green and hawksbill turtles respectively, and is expected due to the immature-bias. However, L:W ratio for adult turtles shifted: 1.29 ± 0.05 (range 1.15 – 1.46) for green turtles and 1.32 ± 0.04 (range 1.23 – 1.43) for hawksbill.

Therefore, L:W ratio conditions were applied based on life-stage (Table 4). No difference in ratios for females and males was observed so the same ratio was applied to both sexes.

Table 3. Length-to-Width (L:W) ratio results for green and hawksbill turtles in Turtle Cove were comparable to immature L:W ratios in the Seychelles. L:W ratios are given (± standard deviation) for different life-stages and sex where possible. Turtle Cove data provided by N. Esteban; Seychelles data provided by J. Mortimer.

Species	Location	Length-to-Width Ratio				
		Adult	Sub-adult	Immature	Female	Male
Green	Turtle Cove	1.17 ± 0.04			N/A	N/A
	Seychelles	1.29 ± 0.05	1.19 ± 0.04	1.17 ± 0.04	1.29 ± 0.05	1.28 ± 0.05
Hawksbill	Turtle Cove	1.28 ± 0.05			N/A	N/A
	Seychelles	1.32 ± 0.04	1.31 ± 0.05	1.27 ± 0.04	1.32 ± 0.05	1.32 ± 0.05

Table 4. Final Length-to-Width (L:W) ratio thresholds for adult and immature turtle species allocation. Based on straight-carapace L:W ratios from green and hawksbill turtles in the Seychelles and Chagos Archipelago.

Life-stage	Length-to-Width Ratio for Species Allocation		
	Green	Hawksbill	Unidentified
Adult	< 1.29	> 1.32	1.29 – 1.32
Immature	< 1.20	> 1.23	1.20 – 1.23

Life-stage Identification

Immature and adult turtles can be differentiated using the smallest observed nesting individuals. Data exists for nesting females in Chagos but is measured as Curved Carapace Length (CCL), and currently there is no published equation for CCL-to-SCL conversion for Indian Ocean sub-populations. Seychelles turtles were therefore used as a proxy for Chagos as they cannot be genetically distinguished (Mortimer and Broderick, 1999). The smallest adult hawksbill was 75 cm SCL so, as the typically smaller species, any individuals < 75 cm should be immature (or sub-adult); the smallest adult green was 87 cm, so therefore any individuals > 87 cm should be adult. However, the largest green immature turtle was 79.30 cm therefore using 75 cm SCL as a cut-off point between adults and immatures results in 98.9% of immature individuals in the Chagos dataset (n = 187/189) falling below the threshold, resulting in only a small margin of error. Sub-adult individuals were not distinguished as (1) only a small sample size (n = 3) of sub-adult green turtles were identified in the Seychelles dataset thus there was little certainty of size and (2) green sub-adults ranged from 69 – 79 cm SCL, and hawksbill sub-adults ranged from 57 – 83.5 cm SCL, therefore no clear threshold could be defined without including immature green or adult hawksbill turtles.

The methodology of L:W ratio to identify species was therefore utilised, but imagery was used to validate species allocation i.e. confirming or rejecting identification based on carapace size and shape, carapace colour, and head shape. A second observer (N. Esteban) aided this validation. Unmeasured individuals (n = 293) were not identified and excluded from statistical analyses. A small number of turtles (n = 12) were identified manually based on visual observation (e.g. Figure 8A).

Secondary sex characteristic of tail length was used to differentiate turtle sex, as males have a notably longer tail (Casale et al., 2005). Sex differentiation by tail length has been previously applied in UAV surveys (e.g. Schofield et al., 2017a) and used a 5 cm threshold (< 5 cm, female, > 5 cm, male) based on previously reported male tail lengths (Casale et al., 2005; Rees et al., 2013). This study applied tail length differentiation for individuals larger than the smallest adult male turtle observed in Chagos (87 cm and 62.5 cm SCL, for green and hawksbill turtles, respectively). Tail length was not measured but males identified if tail clearly extended past the rear flippers.

Population Density Estimates

Survey Area Estimation

To calculate the population density, the area of each transect was estimated. The UAV field of view was 47.72 x 26.84 m, and transect-length was measured using the distance tool in Google Earth (Google, 2021). Transects were flown manually and followed the curvature of the coastline, so in length measurements, the same approach was taken i.e. at each distance away from the shore, the transect followed the curvature of the coastline. When unclear on the specific route flown by the UAV pilot, the corresponding footage was viewed to aid accuracy in length measurements. Sometimes the UAV moved laterally from the start point i.e. to move from unavailable habitat (land), and this was considered when measuring transect length. Each length was measured three times and calculated into a mean. The coordinates for one location (DG.TC12U.1) appeared to differ from the start- and end-points of the video footage when reviewed, therefore the transect length for this survey was measured manually using the video as a reference for the flight path.

Partial areas within transects were deemed ‘unavailable’ for two reasons: (1) habitats were unavailable for sea turtles e.g. land or exposed rocks; or (2) habitats were unavailable for observation e.g. restricted visibility due to sun glare or wave swell (e.g. Sykora-Bodie et al., 2017). ImageJ (Rasband, 2021) was used to measure these areas to subtract from the total transect area to calculate the available transect area.

Initially a random number generator was used to select a random frame from each video, and the total unavailable area then measured accumulatively until the point of inflection i.e. where the data plateaus and collecting more is unlikely to change the result. However, areas where the UAV drifted over land skewed the unavailable area and was unrepresentative of the transect as a whole. An alternative method was devised: the time taken for the transect to move 26.84 m (the length of the field-of-view of the UAV) was calculated at 5.37 seconds or 156.67 frames based on the UAV speed of 5 m/s. Theoretically, an orthomosaic of frames captured every 157 frames would cover all available area of the transect, allowing for the accurate measurement of the total unavailable area. An image was therefore taken every 157 frames from the starting frame, determined manually as when the UAV had a birds-eye view of the survey site, and the transect survey was about to begin i.e. just before the UAV began to move. Once this starting frame was determined, each subsequent frame was determined by adding 157.

The video was played and if there was unavailable area to be measured, the video was moved to the correct frame number and the frame extracted. At the end of the video, if the final frame did not cover the end of the transect, the ending frame was found manually. The ending frame was the last frame before the UAV on-board camera rotates to face the horizon and therefore the last birds-eye-view frame. The frames were saved as .TIFF files and the polygon tool in ImageJ (Rasband, 2021) used to measure the unavailable area. The total unavailable area was summed and subtracted from the total to give the total available area for sea turtle observation, which was then used in population density calculations. As sun glare and wave swell changed as the UAV travelled, frames surrounding the chosen frame were viewed to confirm if the area was truly unavailable.

There were two issues identified with this methodology: UAV speed was not always 5 m/s due to strong winds and obstacles; and lateral movement of the UAV meant within the 5.37 seconds, unavailable area would potentially be missed. To resolve this, either (a) the frame was selected manually to ensure no unavailable area was missed, or (b) the frame frequency was altered i.e. if a frame does not match the previous frame to produce an orthomosaic, the UAV speed is not 5 m/s as a result of high winds or obstacles, therefore the frame frequency can then be updated manually by the observer (e.g. if it took 139 frames to move one field-of-view, the UAV speed was 5.50 m/s). Each video was played to ensure the observer was aware if any area had been missed.

Density Calculations

Population densities were calculated using the total number of turtles within all repeats of a given transect and divided by the total available area of all repeats. Population density was calculated for each transect, measured in individuals per square-kilometre (individual/km^2). Population density was then calculated for each zone: extrapolation to the larger island scale was not possible due to identified hotspots such as Turtle Cove in the Diego Garcia lagoon (Mortimer and Day, 1999). Turtle cove was divided into three zones based on long term satellite tracking and monitoring of the shallow developmental habitat (Hays et al., 2021b; see Figure 4 for zone boundaries). Population densities for specific life-stages and species were also determined.

Statistical Analyses

All statistical tests were carried out using R (version 4.0.3, R Core Team, 2021, see Appendix for code), and utilised the high-certainty, definite-only data set.

Observer Variation

Observer variation was calculated following methodology in Giuffrida et al. (2018), by which observer counts are compared to the counts of a ‘reference observer’ who is deemed the most experienced and therefore accurate, allowing comparisons to be made between experienced observers and non-experienced citizen scientists. When assessing observer variation in turtle counts, descriptive statistics were used: total count, total difference in count; mean difference in count, absolute mean difference in count; mean squared error, and the correlation coefficient. The total counts represent the count of turtles across six videos, whilst mean difference in count and mean squared error address the variance in counts between the same videos. While the total count is easily comparable and may be similar between observers, further analysis provides more information on the spread of the data across videos i.e. two observers with the same total count may have a low correlation coefficient as counts varied between videos.

A Friedman test, a non-parametric repeated measures analysis of variance, was then carried out to compare the difference in turtle counts between non-experienced observers, to assess the variation in observers of the same skills level. This was followed by a Nemenyi *post-hoc* test to make pairwise comparisons.

Intra-observer variation was assessed using a Wilcoxon signed-rank test, a non-parametric test to compare two groups using ranks, differentiated from the Wilcoxon rank-sum test by paired samples. Counts of the same observer before and after >70 hours of image analysis (turtle counting and measuring) were compared to establish if observer experience affects accuracy of turtle counting.

Turtle Size and Environment

Turtle size (straight carapace length) of individuals from the Seychelles and Chagos data sets were compared using a Wilcoxon rank-sum test, separated by species, to ensure turtles from the two distinct locations were comparable in size, justifying the application of L:W ratios from Seychelles individuals to Chagos individuals.

The mean SCL for different species, life-stages and sex were compared. Statistical tests compared the mean SCL between ocean and lagoon environments: as the mean SCL was normally distributed in Diego Garcia, a student's t-test was used; while a small sample size in Nelson's Island resulted in a non-normal distribution and a Wilcoxon rank-sum test was used. Each test was carried out three times, where data was separated by life-stage (immature only, adult only, all individuals). As there was a small sample size of adults, a Wilcoxon rank-sum test was used for Diego Garcia adults as a result of a non-normal distribution, and adult-only comparisons could not be conducted for Nelson's Island. The same analysis was then carried out with data separated by species (green and hawksbill), but not all comparisons could be made as not all demographics were represented in all environments or islands.

Turtle Count and Environment

A generalised linear model (GLM) was carried out to model how the number of turtles was influenced by the environment (ocean and lagoon), as well as by island (Diego Garcia and Nelson's Island) to determine if abundance and therefore distribution of turtles is influenced by environmental factors. A null model was formulated, by which turtle count was tested as a function of a constant, one, to justify the inclusion of parameters. A global model was then generated with additive and interactive effects, and the sub-models derived from it. The dispersion parameter, which informs if the model has overdispersion (i.e. the variance is greater than the mean), was calculated in R (R Core Team, 2021) by dividing residual deviance by degrees of freedom. Optimisation of the error family was determined based on the dispersion parameter. An Akaike

Information Criterion (AIC) then compared different models to identify which variables best explained the difference in turtle counts, with the smallest value representing the model with the best fit. The nesting rule states that inference can be improved by removing models more complex than a nested model with a lower AIC (Harrison et al., 2018), thus this rule was applied in model selection to determine the top model set.

Population Densities

Comparing population densities between environments and islands can identify turtle hotspots within the Chagos MPA and establish trends in turtle distribution. A Wilcoxon rank-sum test was first used to compare the population density of turtles across both islands and environments, separated by species, to compare densities of green and hawksbill turtles. The same test was then used to compare the population density of all individuals across both islands and environments.

Total population density was then compared between all zones using a non-parametric Kruskal-Wallis test, including both islands and environment, to identify general trends in distribution and density of turtles across both environments of Diego Garcia and Nelson's Island. This was followed by a Dunn's *post-hoc* test, utilised as it allows for unequal sample sizes, to identify which sites were significantly different, if any.

As Turtle Cove has been previously identified as a turtle hotspot (Mortimer and Day, 1999), the population density in Turtle Cove was then directly compared to other lagoon sites using a Wilcoxon rank-sum test. The four ocean sites in Diego Garcia were also compared to assess inter-environmental variation using a Kruskal-Wallis and Dunn's *post-hoc* test.

Distance-density relationships were investigated: a Kruskal-Wallis test assessed the impact of distance from shore on total population density (in all sites except Turtle Cove where transects at varied distances from the shore were not possible due to space-limitations); and a simple linear regression investigated the impact of distance from Turtle Cove (measured using Google Earth, Google, 2021) on the total population density within the Diego Garcia lagoon. Distance from the shore and population density was also compared separately for different species and environments.

Finally, a Wilcoxon rank-sum test compared population densities of different species and life-stages, for both lagoon and ocean environments. This was not conducted for Nelson's Island due to small sample size. A Wilcoxon rank-sum test was used for all groups except for the comparison of species-specific population densities in the Diego Garcia ocean environment, where the data were normally distributed, therefore a student's t-test was used.

Results

Surveys were conducted at 20 sites along the ocean and lagoon coastline of two islands (Diego Garcia, n = 18, Nelson's Island, n = 2). A total of 122 transects of 1 km length (Diego Garcia, n = 104; Nelson's Island, n = 18) were conducted across 11 surveys days in three separate months of 2019 and 2021 (Diego Garcia lagoon, three days, December 2019; Diego Garcia ocean, five days, February 2021; Nelson's Island, three days, July 2019). The mean flight time for each 1 km transect was 03:37 minutes ± 0.03 SD (range 00:27 – 04:49 minutes), and a total of 7 hours 40 minutes of video footage was generated. Turtles were observed in 73.8% (n = 90/122) of transects. There was a total of 560 extracted frames with 660 turtles in. Application of a numerical turbidity scale showed the majority of frames had clear, shallow water (Table 5), and environmental conditions, on average, did not exceed 10% of frame area so did not impact observation detrimentally (Table 6).

Table 5. Turbidity scale application showed majority sites had clear visibility. Turbidity scale adapted from Hodgson et al. (2013): 1) shallow clear water with bottom visible; 2) shallow water with bottom obscured by turbidity; 3) deep water with bottom visible but unclear; 4) deep water with bottom not visible. Data shown as number of frames and as a percentage of the total.

Frames	**Turbidity Scale**			
	1	**2**	**3**	**4**
Total Number	345	150	40	25
Percentage (%)	62	27	7	4

Table 6. Mean glare, shadow and wave swell was less than 10% of the total area of frames. Each environmental condition is shown as a percentage cover of each frame. Mean and max are shown.

Environmental Condition	**Percentage Cover (%)**	
	Mean	**Max**
Glare	8	67
Shadow	0.30	39.70
Wave swell	3.60	91.30

Two repeats of image analysis were conducted by a single observer: repeat 1 took 38 hours 21 minutes to complete, resulting in a total of 608 turtles identified; repeat 2 took 28 hours 24 minutes to complete, identifying 589 turtles. Validation, where turtles from repeat 1 were accepted or rejected, took 5 hours 54 minutes to complete, confirming the final total at 660 turtles. Validated data resulted in a higher overall turtle count as turtles were missed in both repeats. Turtle counting and measuring took a total of 72 hours and 39 minutes.

Observer Variation

Following Giuffrida et al. (2018), inter- and intra-observer variation for counts from six randomly-selected transects in Turtle Cove, Diego Garcia was calculated to assess variation between multiple observers of varied experience (Table 7). Observer 1 was the only experienced observer, and Observers 2 – 9a were non-experienced. Observer 9a and Observer 9b were the same individual before and after approximately 70 hours of video analysis, respectively, therefore Observer 9b was deemed an experienced observer. The results of Observer 1 were considered true, but as the total count was estimated once only by Observer 1, the intra-observer variation for could not be assessed. Therefore potential error by the reference observer could not be considered.

Table 7. Comparison between estimates of turtle count in UAV transects in Turtle Cove, Diego Garcia was conducted to assess observer variation. Ten observers provided counts and each observer compared to Observer 1 (experienced, reference observer). Results beside Observer 1 show 100% agreement. Intra-Obs represents the intra-observer variation calculated for Observer 9a and 9b (before and after 70 hours image analysis). Descriptive statistics are total count of individual turtles, total difference in count (DIC), mean DIC, mean absolute DIC (|DIC|), mean squared error (MSE) and the correlation coefficient (R^2). Pairs of observers whose counts differed significantly shown with superscript letters a,b and c.

Observer	Total Count	Total DIC	Mean DIC	Mean |DIC|	MSE	R^2
1	80	0	0	0	0	1
2	68	-12	-2 (2)	2.33 (1.51)	7.33	0.98^{ab}
3	70	-10	-1.67 (3.33)	2.67 (2.42)	12	0.92
4	123	43	7.17 (4.62)	7.17 (4.62)	69.17	0.86^{ac}
5	104	24	4 (6.42)	5.67 (4.68)	50.33	0.71
6	97	17	2.83 (10.65)	6.17 (8.80)	102.50	0.37
7	69	-11	-1.83 (1.94)	1.83 (1.94)	6.50	0.98^{c}
8	90	10	1.67 (1.21)	1.67 (1.21)	4	0.99
9a	110	30	5 (6.23)	6.33 (4.55)	57.33	0.79^{b}
9b	71	-9	-1.50 (3.02)	2.17 (2.48)	9.83	0.96
Intra-Obs	N/A	-39	-6.50 (4.81)	6.50 (4.81)	61.50	0.88

Total counts for six videos varied widely (68 – 123 turtles). The correlation coefficient (R^2) relates to the correlation of counts compared with the reference observer (1 = optimal). For non-experienced observers, R^2 ranged from 0.37 – 0.99 showing a large variation in counts. Note that the largest difference in count did not necessarily equate to the lowest correlation coefficient. Five observers (Observer 2, 3, 7, 8 and 9b) had an R^2 value over 0.9 showing strong correlation with the reference observer.

A Friedman test was carried out to compare difference in turtle counts between non-experienced observers to assess if there was variation between observers of the same skill level. There was a highly significant difference between counts ($X^2(7) = 27.60$, $p < 0.01$). Nemenyi *post-hoc* tests were carried out to make pairwise comparisons, with significant differences between Observer 2 and 4 ($p = 0.01$), 2 and 9 ($p < 0.05$) and 4 and 7 ($p < 0.05$). All other pairwise comparisons were not significant. As only three out of a total 28 (10.71%) pairwise comparisons were significantly different, variation between observers of the same skill level was minimal.

Comparing Observer 9a and 9b using a Wilcoxon signed-rank test showed a significant difference between counts pre- and post-experience ($V = 21$, $p = 0.03$), with a reduction in Difference In Count (DIC) from 30 to 9, and an increase in the R^2 correlation coefficient from 0.79 to 0.96. This shows observational experience greatly improved accuracy of counts when compared to the reference observer.

Life History Characteristics and Abundance

Final validated data had a total of 660 turtles across a total area of 5.13 km^2 (see Table 8). The final turtle count after validation was larger than repeat 1 or 2 alone as turtles were missed in both repeats. Adding missed turtles to the validated data set resulted in a cumulatively higher total count.

Table 8. Estimates of turtles from UAV transects including demographic characteristics and certainty levels were similar for two repeats. The validated data set was created by comparing repeat 1 to repeat 2, accepting or rejecting turtles that were missed or were categorised as a lower certainty level i.e. possible or probable turtles.

Repeat	Species			Life-stage			Sex			Certainty		
	Green	Hawksbill	Unknown	Adult	Immature	Unknown	Female	Male	Unknown	Definite	Probable	Possible
1	98	182	330	16	287	305	16	8	584	340	86	182
2	103	227	259	17	335	237	18	10	561	363	72	154
Validated	99	250	311	18	348	294	17	8	635	381	89	190

Certainty of turtles improved through analysis: the number of definite turtles increased (repeat 1, n = 340; repeat 2, n = 363) whilst the number of probable and possible turtles decreased (repeat 1, probable, n = 86, possible, n = 182; repeat 2, probable, n = 72, possible, n = 154). The overall total count reduced as in repeat 1, more ‘possible’ turtles were identified as the observer was less confident and competent in comparison to repeat 2. The number of individuals of unknown species, life-stage and sex decreased in repeat 2 compared with repeat 1. In all repeats, the largest subset represented were immature hawksbill turtles. The number of unknown species, life-stage and sex reduced in repeat 2 (unknown species, repeat 1, n = 326, repeat 2, n = 264; unknown life-stage, repeat 1, n = 305, repeat 2, n = 237; sex, repeat 1, n = 563, repeat 2, n = 529) coinciding with the decrease in total turtles observed (repeat 1, n = 608, repeat 2, n = 589).

Turtles were only measured when the carapace margin could be clearly seen (Figure 8). Turtles were not measured for several reasons: unclear carapace from high turbidity, glare, or wave swell, or turtles resting at greater depths; carapace obstructed from view by overhanging rock, tree, or another turtle; or the carapace was out of the field-of-view of the UAV. These issues also meant species was unidentified. Not all measured turtles could be identified by sex as either (a) the tail was not visible, or (b) turtles were smaller than 62.50 cm and 85 cm cut-off for hawksbill and green turtles, respectively. In repeat 1, 50.65% (n = 308/608) of turtles were measured, in repeat 2, 60.10% (n = 354/589) were measured, and in the validated data, 55.61% (n = 367/660) were measured. The increase in the number of measured individuals (n = 308, 354, 367, for repeat 1, 2 and validated data, respectively) reflects the increase in total count for the validated data set due to acceptance of missed turtles.

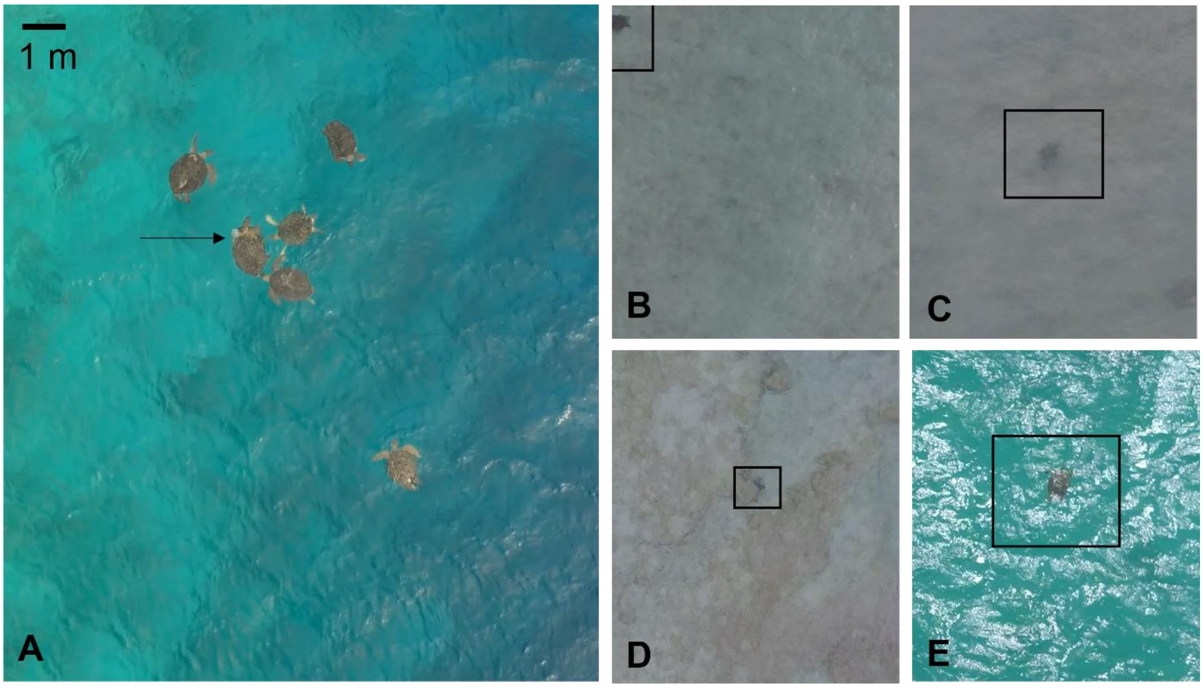

Figure 8. Turtles could not be identified or measured due to a range of environmental and habitat factors. A) Mating pair of green turtles (arrow) surrounded by five males, where female was under the male turtle and could not be measured; B) Turtle was out of the field-of-view of the UAV; C) Turtle carapace margin was unclear due to turbidity; D) Turtle was underneath a rocky overhang; E) Glare on the surface was obscuring the turtle outline. Pictures are all true-to-size from UAV imagery, one metre scale bar applies to all images.

High-certainty Results

The following results utilise the 381 definite turtles from the validated data set, ensuring conclusions are based on certain identifications.

SCL of turtles in the Seychelles (data provided by J. Mortimer) was compared to SCL of turtles in Turtle Cove: SCL of green turtles differed significantly (Wilcox rank-sum test, W = 2890.50, $p < 0.001$) while hawksbill turtles did not. The L:W ratios from the Seychelles dataset were utilised for species differentiation and identified 293 individuals (hawksbill, n = 194; green, n = 99).

Further species validation by N. Esteban for 55 individuals resulted in 72.72% (n = 40) confirmed as the correct species based on carapace morphometrics. The 15 incorrect species were changed (green to hawksbill, n = 12; hawksbill to green, n = 3). Two green individuals were removed due to their position with respect to the UAV camera, with an upward angle meaning SCL measurement could be inaccurate. From inspecting each turtle to confirm species identification, 12 individuals (hawksbill, n = 6; green, n = 6). were assigned based on absolute certainty of observation (Figure 9). This included individuals in mating group of green turtles that could not be measured, an unmeasured individual with clear species appearance, and a turtle with ratio just beyond ID threshold that is clear to be one species (L:W ratio of 1.21, individual DG.O4.2.50.8). Species was confirmed for 303 individuals (hawksbill, n = 209; green, n = 94) included in subsequent analysis. Of the 94 green turtles, nine were adult and 85 immature – only eight adults were assigned by size, the remaining adult was assigned by observation (female in the mating group, Figure 8A). Of the 209 hawksbill turtles, seven were adult, 199 were immature, and three were of unknown life-stage (not measured but assigned by observation). Of the 17 females and 8 males confirmed in the validated data, all were definite turtles and therefore utilised for analyses.

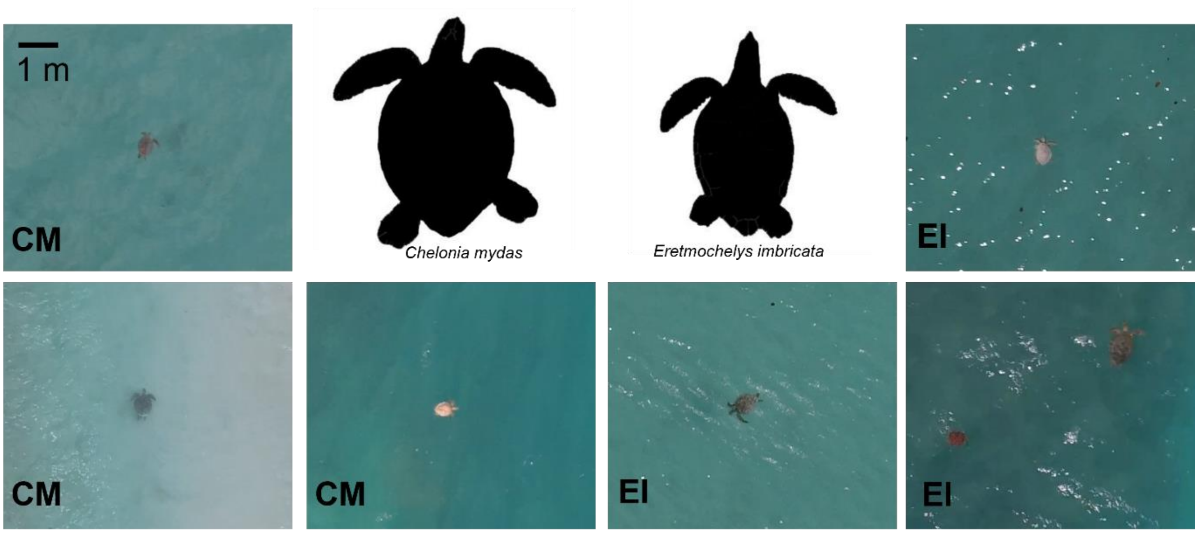

Figure 9. Species identification of green and hawksbill turtles based on carapace morphology. Silhouettes extracted from Pritchard and Mortimer, 1999. CM represent Chelonia mydas*; EI is* Eretmochelys imbricata*. Pictures are all true-to-size from UAV imagery, one metre scale bar applies to all images.*

Size Variation

The mean SCL and standard deviation (±) for different characteristics was highly varied (Table 9): green turtles were smallest of the two species (green, 50.33 ± 17.65 cm SCL, range 29.17 - 113.60 cm; hawksbill, 53.22 ± 11.17 cm SCL, range 29.30 - 86.83 cm); green turtles represented the smallest and the largest individuals observed overall (29.17 cm SCL and 113.60 cm SCL, respectively); and males were the larger than females (males, 95.60 ± 17.96 cm SCL, range 63.33 – 113.60 cm; females, 71.14 ± 5.62 cm SCL, range 63.10 - 81.67 cm). For both species, approximately 60% (green, n = 56; hawksbill, n = 124) were found in Diego Garcia ocean environments, where mean SCL was even smaller for green turtles (46.31 ± 10.63 SCL cm, range 29.17 – 76.30 cm) than hawksbill (53.26 ± 10.64 SCL cm, range 32.33 – 75.73 cm).

Table 9. Mean Straight Carapace Length (SCL) compared for demographic characteristics, immature turtles were smallest and male largest. SCL is shown as mean, ± standard deviation, minimum and maximum. Reported in centimetres (cm). Minimum possible size for females and males was 62.50 cm SCL based on minimum threshold to allow identification by secondary sex characteristic of tail length.

Characteristic	**Number of Turtles**	**Straight Carapace Length (cm)**			
		Mean	**Standard Deviation**	**Minimum**	**Maximum**
Green	94	50.33	17.65	29.17	113.60
Hawksbill	209	53.16	11.17	29.30	86.83
Immature	299	50.27	10.20	29.17	73.03
Adult	17	88.93	13.64	75.33	113.60
Female	17	71.14	5.62	63.10	81.67
Male	8	95.60	17.96	63.33	113.60

Comparing mean SCL between environments on Diego Garcia showed little variation for all individuals: ocean, 50.96 ± 10.96 cm SCL (range 29.17 - 76.30 cm SCL); lagoon, 52.39 ± 11.66 cm SCL (range 31.07 - 86.83 cm SCL). While mean SCL was highly varied between environments in Nelson's Island when all individuals were grouped: ocean, 88.13 ± 31.02 cm SCL (range 32.73 - 113.60 cm SCL); lagoon, 37.76 ± 7.15 cm SCL (range 29.30 - 47.07 cm SCL, Figure 10).

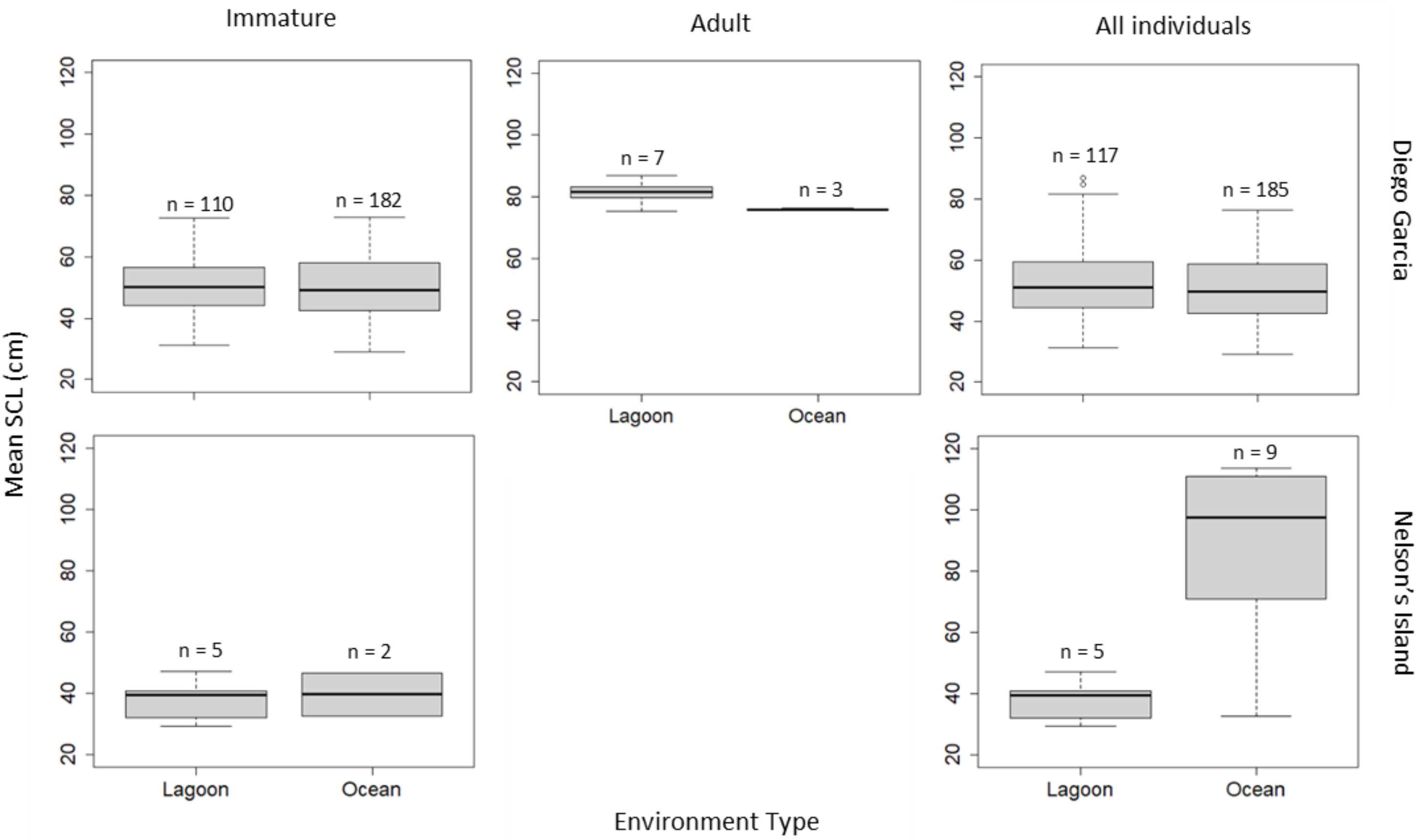

Figure 10. Mean straight carapace length (SCL) for turtles in lagoon and ocean environments of Diego Garcia were not significant, while mean SCL for Nelson's Island differed significantly between environments for all individuals. Turtles were separated by life-stage, showing results for immatures, adults and all individuals.

Mean SCL for Diego Garcia environments was not significant for any groups. There was a significant difference in mean SCL between environments on Nelson's Island for all individuals (Wilcox rank-sum test, $W = 4$, $p < 0.05$). No adults were found on the lagoon-side of Nelson's Island so no comparison could be made. Seven adults were observed on the oceanside of Nelson's Island and potentially were causing bias resulting in the significant result. When looking at immature turtles only, the mean SCL was 39.63 ± 9.76 cm and there was no significant difference between environments.

When analysing data by species, there was no significant difference in mean SCL between any environments for both immature and adult turtles. When all life-stages were grouped, but still separated by species, no significant difference was found. Not all comparisons could be made due to Nelson's Island's small sample size: all green adult turtles were found in the ocean and all green immature in the lagoon; and no hawksbill adults were observed surrounding Nelson's Island.

Population Density and Distribution

Turtle count differed between environments and islands (Table 10). Overall, Diego Garcia had five times the turtle count per square-kilometre area when compared to Nelson's Island (366 turtles within 4.35 km^2 compared with 15 turtles within 0.79 km^2, respectively), and approximately 60% of turtles were observed in the ocean environment.

Table 10. Species and life-stage distribution varied across habitats and islands. Total represents the total number of turtles observed in each site (including unknown species and life-stage) and is not the column total.

Species	**Turtle Count**			
	Diego Garcia		**Nelson's Island**	
	Lagoon	**Ocean**	**Lagoon**	**Ocean**
Green	30	56	1	7
Hawksbill	79	124	4	2
Adult	7	3	0	7
Immature	110	182	5	2
Total	144	222	5	10

Several GLMs were run to investigate the impact of environment and island on the number of turtles observed (Table 11). A negative binomial error family was selected as the poison error structure resulted in overdispersion (dispersion parameter of 9.33 for poison vs 1.55 for negative binomial) and a Type I error (false positive) stating Nelson's Island caused a small but significant decrease on turtle count. A selection rule of delta6 AIC i.e. a difference in AIC of six or less when compared to the best AIC, determined inclusion of sub-models in top model set. The nesting rule meant the interactive model of Environment*Island was not included in the top model set.

Table 11. Generalised Linear Model top model set and inclusion parameters. Optimal dispersion parameter is one, and numbers much larger than one suggest overdispersion. Akaike Information Criterion is shown to highlight top model selection. DeltaAIC (ΔAIC) shows change in AIC compared to the best model. Retained under nesting rule highlights that models that are of highly complexity than the best model with higher AIC are not to be included in top model set to improve inference.

Model	**Dispersion Parameter**	**AIC**	**ΔAIC**	**Retained under nesting rule?**
Environment + Island	1.53	384.24	0	Y
Environment only	1.60	385.22	0.98	Y
Environment * Island	1.55	386.24	2	N
Island only	1.66	389.01	4.77	Y
Null model	1.73	389.59	5.35	Y

With the lowest AIC of 384.24, the additive model best explains the results: both Diego Garcia and ocean environments caused a significant increase in turtle count (Diego Garcia, mean density = 73.27 individuals/km^2, parameter estimate = 1.41 ± 0.17 standard error SE; Ocean environment, mean density = 120 individuals/km^2, parameter estimate = 0.69 ± 0.25 SE). Nelson's island caused a decrease in turtle count (mean density = 18.85 individuals/km^2, parameter estimate = -0.88 ± 0.48 SE), but it was not significant.

For population density calculations, transects were grouped into zones (Table 12). Manual measurement of the available area took 26 hours and 48 minutes, and a total of 4795 frames were viewed, with a mean of 37.82 frames per video (range 1 - 52, mode 37). There were no 'definite' turtles observed in Marina North or Centre (M1 and M2) in the Diego Garcia lagoon. The lowest population density of turtles, where turtles were observed, was 4.45 individuals/km^2 in East 13, and the highest density of 257.19 individuals/km^2 in Diego Garcia Ocean Site 1 (Figure 11). Diego Garcia Ocean Site 1 was the most populous overall but also represented the highest density of both species across islands and habitats (green, 75.64 individuals/km^2; hawksbill, 143.72 individuals/km^2), as well as the most immature turtles (219.37 individuals/km^2). The next three most-dense sites were West 8 at 146.15 individuals/km^2, Turtle Cove 10 at 135.08 individuals/km^2 and Diego Garcia Ocean Site 3 at 132.83 individuals/km^2. For Diego Garcia, the mean density (± SD) in ocean sites was 143.46 ± 84.49 individuals/km^2, and 53.21 ± 55.30 individuals/km^2 for lagoon sites. For Nelson's Island, there was only one ocean and lagoon site due to small island size. While population densities were higher for hawksbill turtles in 65% (n = 13/20) of sites, there was no significant difference between densities of the two species overall when compared using a Wilcoxon rank-sum test.

Table 12. Population density calculations for each survey zone highlighted turtle hotspots. Densities separated into total population density and densities for life-stage (unknown, adult, immature) and species (unknown, green, hawksbill). Total count is all turtles observed in all transects and all repeats for each zone. Total area surveyed includes all transect repeats i.e. the total area of three repeats of three transects. Total population density is total count divided by total area and is measured in individuals per square-kilometre (individuals/km^2). Population densities specific to different traits are calculated in the same manner utilising total counts. Mean straight carapace length (SCL) is shown in centimetres (±) the standard deviation.

Island	Environment	Location Code	Count	Total Area Surveyed (km^2)	Population Density (individuals/km^2)							Mean SCL (cm)
					Total	Unknown Life-stage	Adult	Immature	Unknown Species	Green	Hawksbill	
NI	Ocean	NI.O	10	0.40	24.89	2.49	17.43	4.98	2.49	17.43	4.98	88.13 (31.02)
NI	Lagoon	NI.L	5	0.39	12.80	0	0	12.80	0	2.56	10.24	37.76 (7.15)
DG	Ocean	DG.O1	102	0.40	257.19	30.26	7.56	219.37	37.82	75.64	143.72	53.33 (11.69)
DG	Ocean	DG.O2	18	0.34	52.85	14.68	0	38.17	14.68	11.74	26.42	51.91 (10.09)
DG	Ocean	DG.O3	53	0.40	132.83	22.56	0	110.27	27.57	35.09	70.17	49.21 (10.42)
DG	Ocean	DG.O4	49	0.37	130.97	29.40	0	101.57	29.40	21.38	80.19	47.07 (8.75)
DG	Lagoon	M1	0	0.23	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A
DG	Lagoon	M2	0	0.19	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A
DG	Lagoon	M3	1	0.21	4.87	0	0	4.87	0	4.87	0	40.4
DG	Lagoon	W4	3	0.22	13.70	0	4.57	9.13	0	0	13.70	62.47 (16.60)
DG	Lagoon	W5	5	0.21	23.83	4.77	0	19.06	4.77	4.77	14.30	60.92 (10.95)

Island	Environment	Location Code	Count	Total Surveyed Area (km^2)	Population Density (individuals/km^2)							Mean SCL (cm)
					Total	Unknown Life-stage	Adult	Immature	Unknown Species	Green	Hawksbill	
DG	Lagoon	W6	21	0.23	91.50	8.71	4.36	78.43	13.07	8.71	69.71	50.35 (12.17)
DG	Lagoon	W7	20	0.24	83.61	16.72	12.54	54.34	16.72	20.90	45.98	58.64 (13.68)
DG	Lagoon	W8	40	0.27	146.15	14.61	3.65	127.88	25.58	29.23	91.34	51.48 (9.72)
DG	Lagoon	TC9	5	0.07	75.96	45.58	0	30.39	45.58	0	30.39	52.45 (4.22)
DG	Lagoon	TC10	18	0.13	135.08	15.01	0	120.07	22.51	30.02	82.55	48.11 (12.15)
DG	Lagoon	TC11	22	0.17	130.85	59.48	0	71.37	65.42	29.74	35.69	51.21 (8.79)
DG	Lagoon	E12	6	0.24	25.51	4.25	17.01	4.25	12.76	12.76	0	53.73 (15.90)
DG	Lagoon	E13	1	0.22	4.45	0	0	4.45	0	4.45	0	57.13
DG	Lagoon	E14	2	0.21	9.43	0	0	9.43	0	0	9.43	47.72 (10.68)

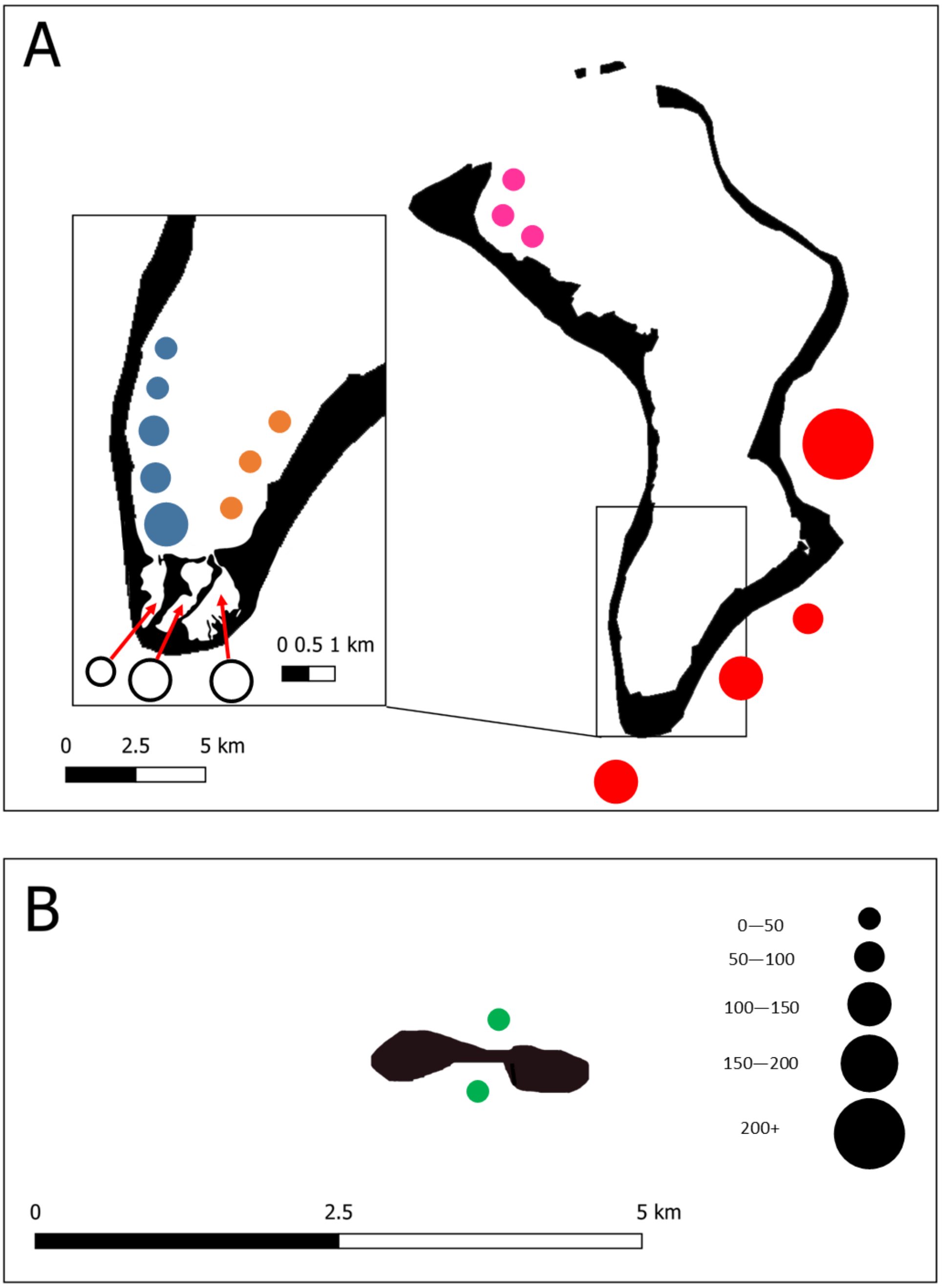

Figure 11. Population density map of (A) Diego Garcia and (B) Nelson's Island. Circles increase with size with bins of population density measured as individuals per km^2. Colour coding is as follows: red, Diego Garcia ocean sites; pink, Marina; blue, West; orange, East; white circle with black outline, Turtle Cove; green, Nelson's Island.

For statistical analysis, a Wilcoxon rank-sum test compared the population density between environments for each island. There was no significant difference between lagoon and ocean population densities for both islands, Diego Garcia only, or Nelson's Island only.

Population density of each zone was then compared to identify more general trends in distribution and density of sea turtles (Figure 12). A Kruskal-Wallis test comparing population density of each zone found no overall significant difference between any zones. Dunn's Multiple Comparison *post-hoc* test was used to make pairwise comparisons between zones and confirmed none differed significantly.

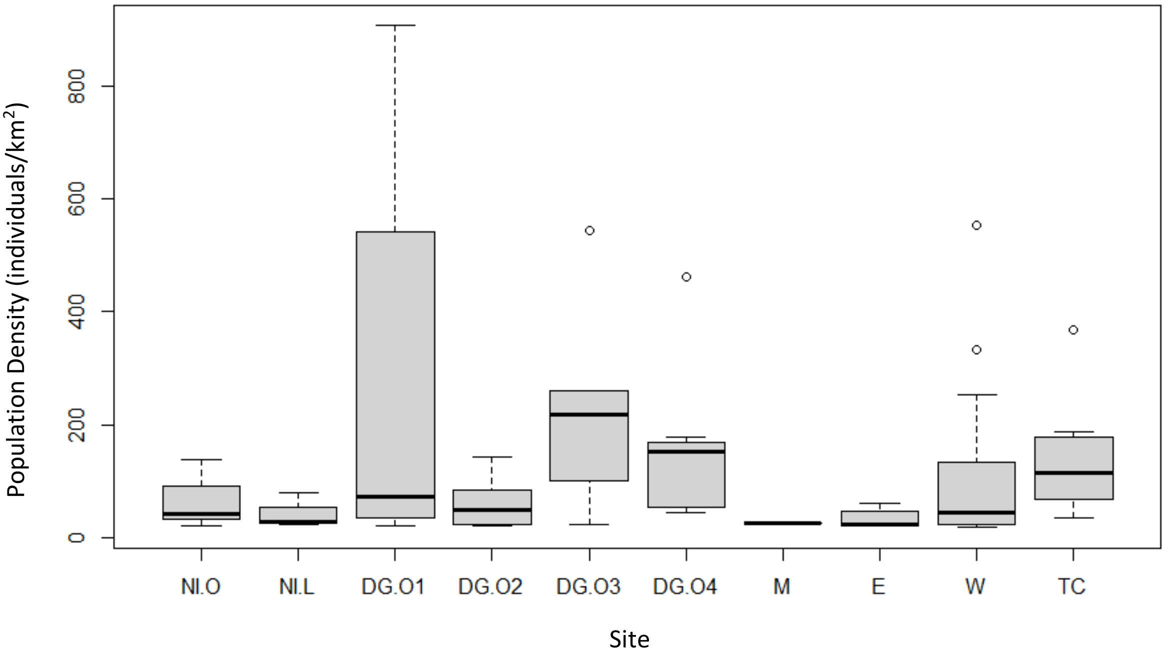

Figure 12. Population density did not differ significantly between sites. Site codes are as follows: Nelson's Island, NI.O, oceanside; NI.L, lagoon-side; Diego Garcia, DG.O 1 - 4, Ocean Sites 1 - 4; M, Marina; E, East; W, West; and TC, Turtle Cove. Population density is in individuals per square-kilometre (individuals/km^2)

Further analysis compared specific zones: Turtle Cove had significantly higher population densities than other lagoon sites in Diego Garcia ($W = 70$, $p < 0.05$); when comparing the four Diego Garcia ocean sites, a Kruskal-Wallis test found no significant difference between sites.

A Kruskal-Wallis test analysed the relationship between the population density and the distance from the shoreline (Figure 13). This included all zones except Turtle Cove where space-limitations meant only one transect was possible. As distance from shore increased, population density significantly decreased ($X^2(4) = 26.08$, $p = 0.01$). When separated by species and environment, the same significant decrease in population density occurred with increasing distance from shore (green, $X^2(4) = 16.16$, $p < 0.01$; hawksbill, $X^2(4) = 10.99$, $p < 0.05$; ocean, $X^2(2) = 15.75$, $p < 0.01$; lagoon, $X^2(4) = 16.68$, $p < 0.01$).

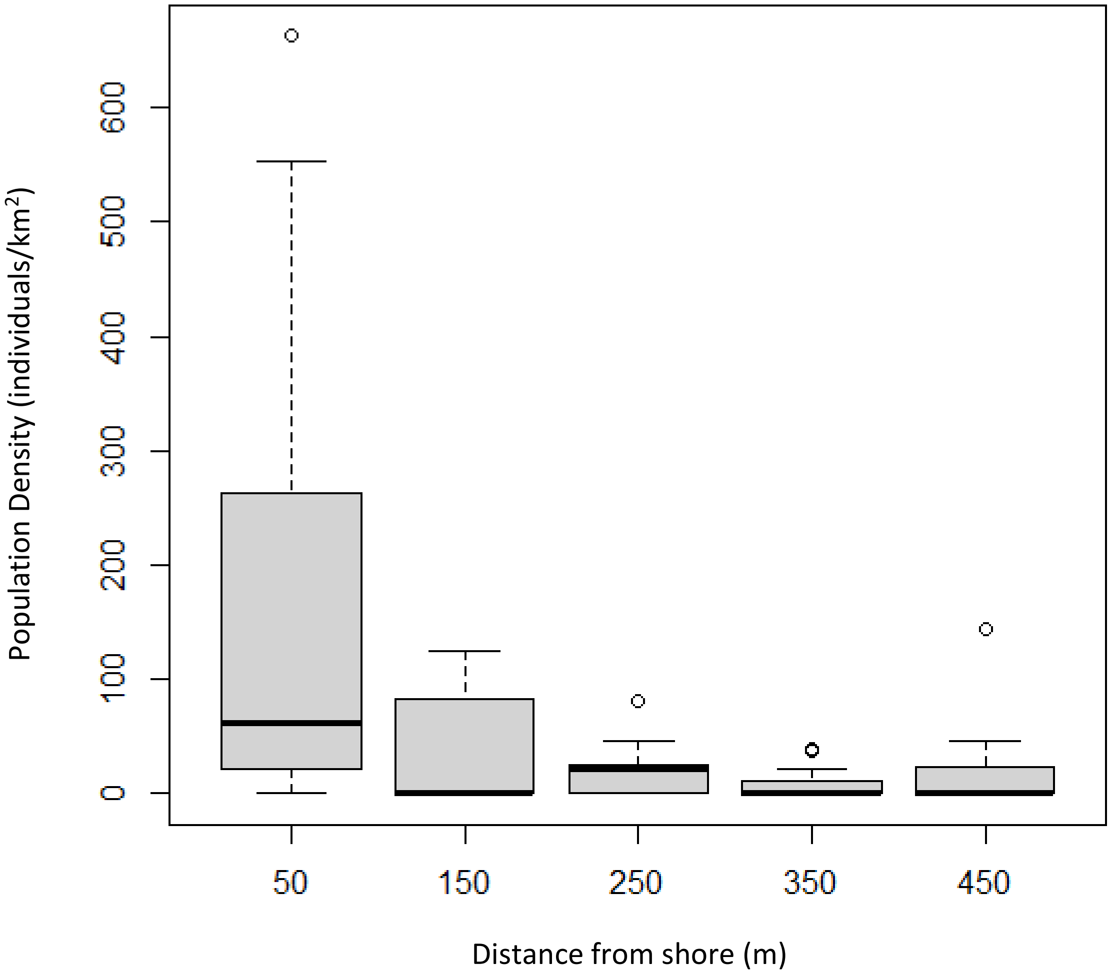

Figure 13. Population density decreased as distance from the shore increased. Distance is in metres (m); population density is in individuals per square-kilometre (individuals/km^2). Sample size at each distance was: n = 13 at 50 m; n = 8 at 150 m; n = 10 at 250 m; n = 3 at 350 m; and n = 5 at 450 m.

A distance-density relationship was also investigated within the lagoon: the atoll is managed as a nature reserve, and Turtle Cove has been highlighted as a key foraging ground for immature hawksbill turtles (Mortimer and Day, 1999). A simple linear regression was used to evaluate the relationship between population density and distance from Turtle Cove (Figure 14), and while there was a decrease in population density as distance from Turtle Cove increased, it was not significant.

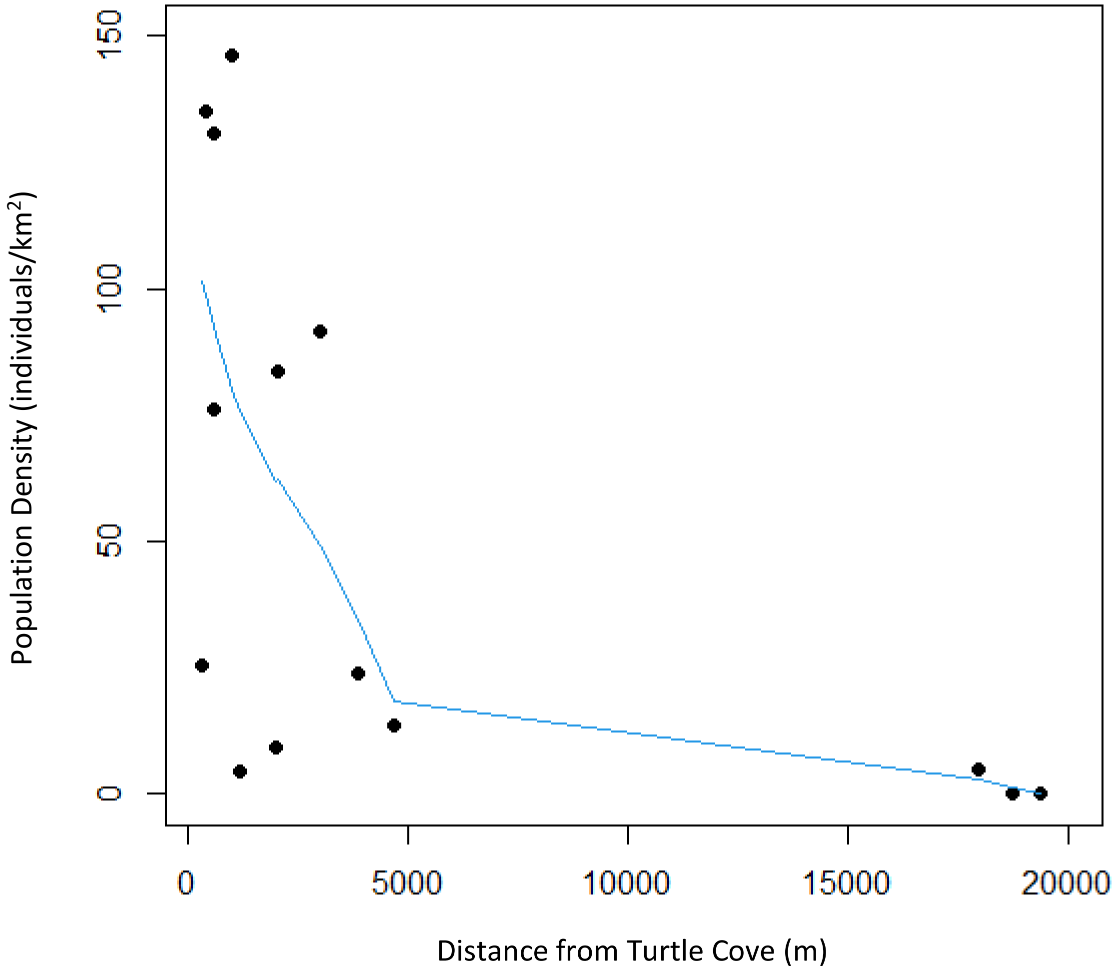

Figure 14. As distance from turtle cove increased, the total population density per lagoon zone (n = 14) decreased, but it was not significant. No data was collected between 5000 – 18000 m. Scatterplot fitted with LOWESS (Locally Weighted Scatterplot Smoothing) line to highlight exponential decrease in population density as distance increases to 5000 m. Distance is in metres (m); population density is in individuals per square-kilometre (individuals/km^2).

Population densities were then compared by species and life-stage (Figure 15). This could only be completed for Diego Garcia as small sample size meant not all demographics were observed in Nelson's Island environments. Population densities differed significantly between life-stages in both lagoon (Wilcoxon rank-sum test, W = 13, $p < 0.001$) and ocean environments (W = 0, $p < 0.05$), while there was no significant difference between species.

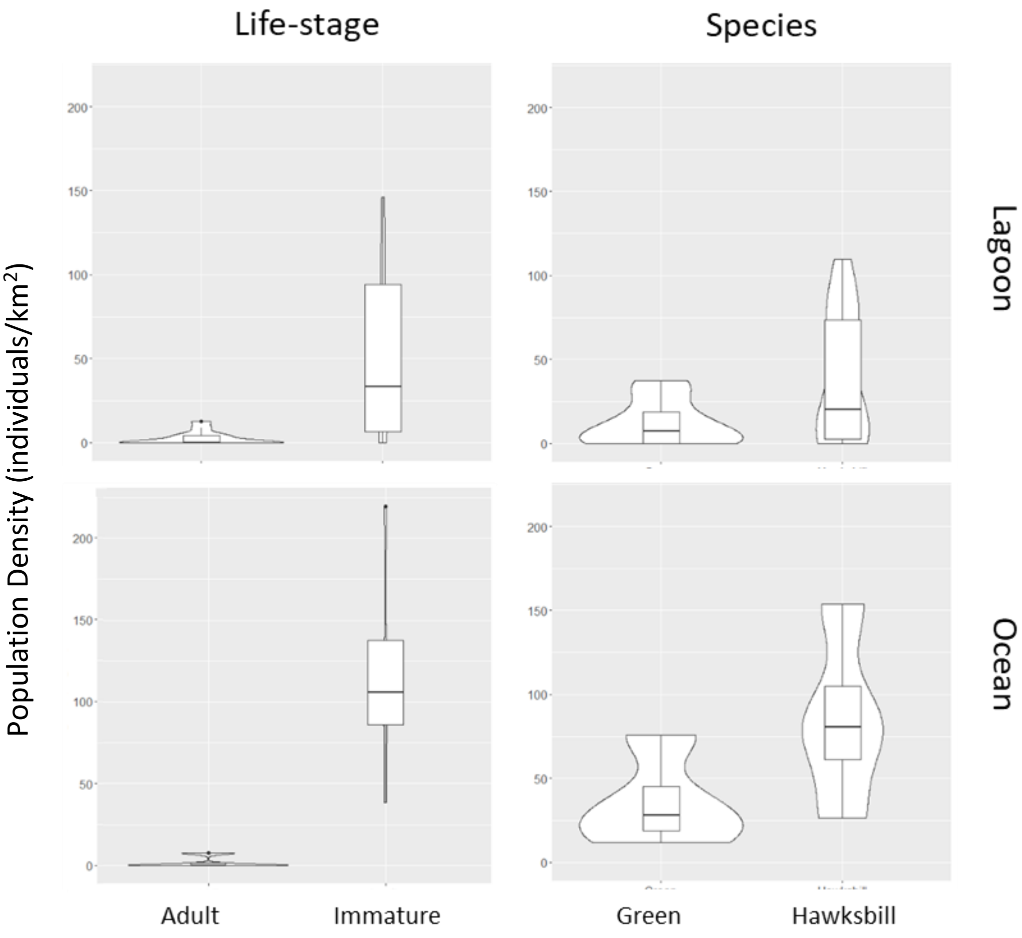

Figure 15. Population density differed significantly between environments when separated by life-stage but not species in Diego Garcia. Nelson's Island could not be visualised due to lack of observation of some demographics. Violin plots show the distribution of data. Population density is in individuals per square-kilometre (individuals/km^2).

Low-certainty Results

When utilising low-certainty results i.e. all definite, probable and possible turtles, the outcome of analyses differed (see Appendix for full results and figures). While the relationship between distance from shore and population density remained significant, there was also a significant relationship between distance from Turtle Cove and population density (linear regression, $F_{(1-12)} = 6.48$, $p < 0.05$).

Results of mean SCL comparisons between environments and islands were similar, except for a significant difference in the mean SCL of adults in Diego Garcia (Wilcoxon rank-sum test, $W = 38$, $p < 0.05$), a result that was not significant for high-certainty data.

Population densities differed: overall population density was much higher i.e. Diego Garcia Ocean Site 1 had 325.27 individuals/km^2 for low-certainty data compared with 257.19 individuals/km^2 for high-certainty data; and the most-populous sites changed, after Diego Garcia Ocean Site 1, the next three most-populous sites were all three coves of Turtle Cove (309.27 individuals/km^2 in TC11, 292.67 individuals/km^2 in TC10, and 258.28 individuals/km^2 in TC9) as opposed to West 8, followed by Turtle Cove 10, and Diego Garcia Ocean Site 3 in high-certainty data (146.15 individuals/km^2, 135.08 individuals/km^2, and 132.83 individuals/km^2, respectively). There were no sites in the low-certainty data set where no turtles were observed, and the lowest-density site remained in the Marina (M1, 8.60 individuals/km^2). Environment and island still had a significant impact on the number of turtles, with ocean environments and Diego Garcia having a significant increasing effect, and Nelson's Island a significant decreasing effect.

Comparisons of population density between sites showed no significant difference when using high-certainty data, but low-certainty data highlighted significant differences in population densities between five pairs of sites: a Kruskal-Wallis pairwise comparison for Diego Garcia ocean sites found a significant difference between densities in Site 2 and 4 ($p < 0.05$); and a Kruskal-Wallis test also identified a significant difference between zones ($X^2(6)= 23.64$, $p<0.01$), with a Dunn's Multiple Comparison *post-hoc* test showing differences between four pairs of zones - Marina and Turtle Cove ($p < 0.01$), Marina and West ($p < 0.01$); Marina and Diego Garcia ocean sites ($p < 0.01$); and Diego Garcia ocean sites and East ($p < 0.05$). All other sites did not differ significantly.

Discussion

Population Density and Distribution

The highest density of green and hawksbill turtles occurred at the south-eastern oceanside of Diego Garcia. As Diego Garcia Ocean Site 1 is on the central-eastern edge of the island, high densities may be associated with the pull of ocean currents: the South Equatorial (SE) current flows westwardly across the northern Indian Ocean (Chen et al., 2014; Jensen et al., 2020), and turtles may utilise this current as means to conserve energy, driving migratory turtles to foraging sites in the Chagos Archipelago. The archipelago's protected oceans contain highly diverse and extensive coral reefs (Carlton et al., 2015), which turtles utilise as a resting and foraging site, and potentially as protection from predators (Musick and Limpus, 1997). Other population density studies within SWIO MPAs found the highest density of turtles coincided with the geomorphology of the coast, with higher densities in coral reef zones compared to sandy or rocky zones (Jean et al., 2010). The near-shore habitat of reef flat may therefore explain the high aggregation of turtles. As DG.O1 was majority immature, these findings could highlight east Diego Garcia oceanside as a developmental habitat for immature turtles across the WIO.

When utilising high-certainty data, the next two most-populous sites were both within Diego Garcia lagoon: sites West 8 and Turtle Cove 10. W8 and TC10 are approximately 1 km apart, at the southern-most point of the lagoon, approximately 20 km straight-line-distance from the lagoon opening at the north. Results were similar for low-certainty data, with TC11 and TC10 as the next most-populous sites. High population densities in the lagoon may be explained by the predator-avoidance hypothesis (Lima and Dill, 1990), by which species distribution and behaviour is influenced by predation-risk. For example, green turtles in Shark Bay, Australia, select microhabitats in a condition-dependant manner due to tiger shark (*Galeocerdo cuvier*) predation-risk (Heithaus et al., 2007); and deep dive-behaviours observed in migratory green turtles may be undertaken to reduce susceptibility to visual predators (Hays et al., 2001). Individuals must weigh up the risks and benefits associated with remaining in sheltered habitats compared to open water habitats, where there is a trade-off between risk of predation and the benefits of foraging (Lima and Dill, 1990). As a long-lived prey species turtles may be more risk-averse during more vulnerable periods (during nesting or when immature) to ensure successful recruitment to adulthood (Heithaus et al., 2007): during the inter-nesting interval, green turtles in the Eastern Indian Ocean utilised a relatively small area when compared with foraging movements (Fossette et al., 2021); and immature hawksbill turtles in Puerto Rico select habitats based on habitat-utility i.e. stony coral reefs to provide shelter, rather than forage-availability (Rincon-Diaz et al., 2011). Antipredator behaviour is vital for immature individuals where smaller body size increases vulnerability to predation (Heithaus, 2013), and oceanic ‘lost years’ may be predator-avoidance response to typically predator-dense neritic waters (Bolten, 2003).

The three least-dense sites, where turtles were present, were East 13, Marina 3 and East 14 for high-certainty data and Marina 1, West 4 and Marina 3 for low-certainty data. As humans can disturb turtles or contribute to a large proportion of sea turtle mortalities through fisheries bycatch or injury from boats (Bourjea et al., 2008), the Marina zones of the Diego Garcia lagoon perhaps leave turtles vulnerable. This is possibly represented in our findings as no turtles were observed in Marina 1 and Marina 2. However, there is evidence from foraging grounds in Honduras that boat traffic within

MPAs does not impact hawksbill behaviour or distribution (Wright et al., 2020) so similar assessment within Chagos could help assess if boat traffic is a contributary factor to the low turtle density. Low population densities in East and West zones is surprising due to the close-proximity to highly-dense Turtle Cove (between 300 – 2000 m). West sites, at a larger distance from Turtle Cove (1000 – 4600 m) had much higher densities in the high-certainty data when compared to East sites. Perhaps from the entrance at the north of the lagoon, more turtles will pass through West zones to reach Turtle Cove based on the morphology of the island, with less travelling further to East sites. Further investigation into fine-scale distribution within Diego Garcia lagoon may help understand this disparity.

Diego Garcia's inner lagoon may be a developmental habitat to facilitate successful recruitment of immature turtles to adulthood. Turtle Cove is a tidal creek, and both Turtle Cove and West sites are sandy lagoon environments, therefore have low benthic cover (such as corals, sponges or algae) providing limited prey forage items. Satellite-tracking of immature turtles within Turtle Cove for approximately seven months found 78.26% (n = 18/23) remained within a small home range of 1 km^2 (95% utilisation distribution), while two individuals relocated only a short distance to the oceanside of Diego Garcia and the remaining three left Diego Garcia (Hays et al., 2021b). This highlights a trade-off between forage-availability and risk of predation. This shows high fidelity of immature turtles to Turtle Cove, concurring with our findings of Turtle Cove as a highly-dense aggregation site for both green and hawksbill turtles, and a possible key developmental habitat for immature turtles within the archipelago.

Diego Garcia had relatively high total densities in comparison with Nelson's Island. Variation could be explained by island size and location, as Nelson's Island is a narrow, isolated island with approximately two kilometres of coastline compared to approximately 120 km coastline of Diego Garcia, however Diego Garcia had more turtles per kilometre overall. Nelson's Island is part of a larger atoll, the Great Chagos Bank, with other islands dotted around its edge to the south-west, so perhaps turtles have a low fidelity to individual islands across large atolls. Nelson's Island's lagoon is also an open environment meaning turtles could easily enter and disperse, unlike Diego Garcia's semi-enclosed lagoon.

Population densities are typically estimated for nesting populations due to feasibility of assessment, therefore there is little comparable data for foraging populations. One study investigated the foraging hawksbill density in the Seychelles and found 3.95 turtles per hectare, equivalent to 395 individuals/km^2, similar to our highest reported density of 325.27 individuals/km^2 when analysing the low-certainty data (von Brandis, 2010). This similarly between Chagos and Seychelles turtle population contributes to the idea that these turtles form one sub-population as they cannot be genetically differentiated (Mortimer and Broderick, 1999). The close proximity of the Seychelles and Chagos allows turtles migration between foraging and nesting grounds on the two archipelagos (Hays et al., 2020b), and both archipelagos are clearly instrumental in the success of green and hawksbill turtles in the WIO. Further estimations of the foraging population density in the WIO are needed to understand the density and distribution of foraging sea turtles in the wider Indian Ocean.

Compared to nesting population densities in the SWIO, relatively high densities were observed in Chagos: for green and hawksbill turtles, Mauritius had a maximum density of 0.88 individuals/km^2 (Reyne et al., 2014); and neighbouring Reunion Island reported 1.44 individuals/km^2 (Jean et al., 2010), however both studies acknowledge generally low levels of nesting. Other countries within the SWIO have estimated turtle population size rather than density (e.g. Bourjea et al., 2015; West, 2017), but none based on foraging populations. Nest or nesting female counts can be used as a proxy for population size and therefore density, but further *in-situ* monitoring is needed.

Global sea turtle densities vary greatly: in the Belizean Barrier Reef, most recent estimates of foraging hawksbill turtles were 62.68 individuals/km^2 (Strindberg et al., 2016); while in the Pacific Islands, in-water green turtle densities across 53 sites, thus representing the whole population, were reported at a maximum of 0.072 individual/km^2 (Becker et al., 2019). Counts of four species in southeast Florida across 22,000 km had similarly low densities of 0.64 individuals/km^2 (Bovery and Wyneken, 2015). While not all studies compare foraging populations only, this study highlights Chagos as a relatively high-density foraging site, thus inferring how vital the MPA is for turtle populations across the WIO.

Temporal changes in sea turtle density and distribution can occur in nesting areas, where the number of males, females and different life-stages changes dependant on the season (Bovery and Wyneken, 2015). As known-nesting sites, densities of turtles on the oceanside of Diego Garcia and Nelson's Island could be subject to temporal changes as turtles undergo breeding and nesting. UAV surveys of Diego Garcia oceanside (where breeding turtles would be located) were conducted outside of peak green or hawksbill nesting, whilst UAV surveys of Nelson's Island were conducted at peak green turtle nesting season (Mortimer et al., 2020). Further comparison of population density across time i.e. during peak hawksbill nesting season, could infer if any temporal change in population composition occurs.

Green, hawksbill and immature turtles were observed in the highest aggregations at south-eastern Diego Garcia oceanside, while the highest density of adult turtles was on the oceanside of Nelson's Island. During Nelson's Island oceanside surveys, the UAV opportunistically captured a group of mating turtles in survey footage (see Figure 8), the only adults observed surrounding Nelson's Island. Nelson's Island's oceanside bathymetry has a steep depth profile and may be more suited to adult diving preferences: green turtles in the SWIO show diel variation in diving, ranging from 2 – 10 m depth (Ballorain et al., 2013). Habitats vary in predation risk and foraging quality, and for adults who are less susceptible to predation than immature turtles (Bjorndal et al., 2003; Heithaus et al., 2007), habitat selection is driven by potential forage. As the Great Chagos Bank atoll contains pristine seagrass meadows (Hays et al., 2018), adults may remain in the vicinity of the high-quality forage, resting at depths between grazing. Variation in adult turtle count between sites may have been biased by timing of surveys as Nelson's Island was surveyed during peak green nesting season (Mortimer et al., 2020). Perhaps habitat-type or bathymetry were also influencing the proportion of adults, however, as only 17 were observed in total, drawing conclusions is unreliable.

Immature hawksbill turtles were the majority demographic represented in surveys, in line with previous observations within the archipelago (Mortimer and Day, 1999), highlighting Chagos as a key developmental habitat for hawksbill turtles throughout the WIO. High numbers of immature turtles in Chagos influence nesting population success in countries across the WIO as immature turtle within the Diego Garcia lagoon have been tracked to nesting sites across six countries, up to 4,000 km away (Hays et al., 2020a). Only seven individuals tracked from Turtle Cove remained within the Chagos MPA, meaning 20% (n = 7/36) remained within the Chagos Archipelago until tracking ceased while 80% migrated to other sites. This correlates with our findings as only a small number of adults were observed (high-certainty data, n = 18/381) representing just 4.72% of the total population, suggesting that foraging immature turtles in Chagos support adult nesting populations in geographically distinct locations. Adults may return to foraging sites here, and high fidelity has been observed in long-term tracking studies (Schofield et al., 2010; Shimada et al., 2020; Siegwalt et al., 2020), so further assessments through annual satellite tracking could inform temporal change in life-stage use.

Immigration, emigration and mortality rates impact turtle abundance, as well as survival rates of immature turtles into adults. Estimating immigration/emigration rates and survival probability could help understand what is causing change, if any, in abundance (e.g. Bjorndal et al., 2005). Long-term assessment of populations in Chagos could evaluate temporal changes in abundance of each life-stage, and further understanding of life-stage space-use in the WIO.

Green turtle aggregations were less-dense than hawksbill, possibly due to larger home ranges (Christiansen et al., 2017) or as coral reefs, which comprise the near-shore habitat, are sub-optimal foraging grounds compared to seagrass meadows within the Great Chagos Bank (Esteban et al., 2018). However, low population densities of green turtles can be beneficial as it allows for faster growth rates in immature turtles (Bjorndal et al., 2000), perhaps due to lack of competition for resources.

Density-distance investigations showed that population density decreased significantly as distance from the shore increased across all environments. Population density was more varied at 450 m from shore compared with 350 m from shore, perhaps due to a high count of eight individuals in high-density West 8 zone (the maximum count for 350 was two in W7 and W8). Evidence from Australia shows green turtles typically rest at depths < 8 m during diurnal-diving (Hazel et al., 2009; Thomson et al., 2012), while in the SWIO, green turtles fitted with time-depth recorders (n = 21) in waters surrounding Mayotte had a mean dive depth of 3.30 m, with 82.60% of dives < 4 m (Ballorain et al., 2013). Immature-only depth-analysis of 49 green turtles across five islands (Europa, Glorieuses, Juan de Nova, La Reunion and Mayotte) found mean dive depth was 1.50 m (Chambault et al., 2020). Hawksbill turtles typically dive deeper: on the eastern coast of Australia, approximately 33% (n = 12/36) of satellite-tracked adult hawksbill turtles were observed foraging in < 10 m depth across median 188 days, while 17% were observed foraging at unusually deep sites (> 20 m, Fossette et al., 2021); and in the Caribbean, time-depth recorders attached to five immature hawksbill turtles reported mean dive depths of 8 – 10 m (van Dam and Diez, 1997). For both green and hawksbill turtles, evidence shows shallower depth-profiles for immature individuals, in line with our findings. However, turtle proximity to the shore, assessed for immature turtles across five islands in the SWIO, was shown to change temporally (Chambault et al., 2020): while one island reported individuals frequenting near-shore habitats more often during the day when compared with nocturnal activity, the remaining four sites showed the opposite (Chambault et al., 2020). Behavioural plasticity is clear, and further research comparing diurnal and nocturnal space-use in near-shore habitats of Chagos could further understanding of spatiotemporal change in turtle distribution.

Distance also had an effect on population densities within the Diego Garcia lagoon, where densities decreased exponentially with increasing distance from Turtle Cove, but it was not significant. This distance-density relationship may be demonstrating a ‘spill-over effect’ from a highly-dense turtle hotspot (Hays et al., 2021b). The spill over effect is typically associated with marine fisheries benefiting from the export of species from MPAs (Rowley, 1994) but could be applied in general to the increase in density as a result of protection. Overspill from highly-dense Turtle Cove could therefore explain the high density of turtles seen in neighbouring survey locations West and East zones. Marina is approximately 18 km from Turtle Cove and had the lowest population density in the lagoon. However, as sites East 13 and 14 represented two of the three least-dense sites, this effect may not be solely due to spill-over from protected areas, and other environmental factors may be contributing. Hays et al. (2021b) found majority of turtles satellite-tracked within Turtle Cove had a small home range of one square-kilometre, thus could explain low densities in within the larger area. As previously mentioned, the route from lagoon-entrance to Turtle Cove may lead more turtles to pass through West sites as opposed to East, and further satellite-tracking studies within the lagoon could better understanding. No data were recorded between 5000 and 18000 m from Turtle Cove, as surveys were limited by habitat accessibility and time restraints, so more surveys are needed within this zone to draw confident conclusions.

Size Variation

Green turtles were smaller on average than hawksbill turtles observed during UAV surveys despite green turtles being typically larger (green, max. 120 cm SCL; hawksbill, max. 90 cm SCL; Pritchard and Mortimer, 1999). Perhaps the waters of the Chagos MPA are primary habitats for young immature green turtles leaving the pelagic nursery phase and entering the later immature developmental habitat (Musick and Limpus, 1997) hence explaining the presence of smaller green individuals. As smaller population densities allow for faster somatic growth (Bjorndal et al., 2000), research into growth rates in Chagos could improve understanding of life-stage habitat-use for green turtles.

Mean SCL on Nelson’s Island differed significantly: oceanside had the largest overall SCL of all environments and islands while the lagoon-side had the smallest. Nelson’s Island lagoon environment is an open lagoon characterised by a shallow extended reef flat. No adults were observed in the lagoon environment thus demonstrating its potential role as a developmental habitat. Conversely, the oceanside of Nelson's Island was the most adult-dense zone, and a large group of mating turtles was observed. As habitat-type, bathymetry and season are postulated to drive adult distribution (Ballorain et al., 2013; Bovery and Wyneken, 2015), perhaps life-stage use is a better measure of ontogenetic habitat-shifts.

Males were the largest of the sexes, contrasting with other studies where females were typically larger (green turtles, Godley et al., 2002; green and hawksbill turtles, Omeyer et al., 2017). Lower population densities allow for faster growth (Bjorndal et al., 2000), however, this does not explain the intraspecific difference. In the Seychelles, females were bigger than males for both green and hawksbill turtles (Mortimer, pers. comms.). Similar sexual dimorphism, where males were larger, has been found in olive ridley turtles in the Republic of Congo (Girard et al., 2021), but the small sample size observed here (females, n = 17; males, n = 8) results in a level of uncertainty in findings. Further investigation of sex-specific growth-rates and carapace measurements could improve understanding of sexual dimorphism in WIO sub-populations.

Limitations in Demographic Allocation

Species identification was based on the L:W ratio of the carapace, utilising SCL data from genetically-linked turtle populations in the Seychelles (Mortimer and Broderick, 1999). A significant difference between Chagos and Seychelles turtles SCL was expected as Turtle Cove data was immature-only while Seychelles data comprised three life-stages (adult, sub-adult, immature). Hawksbill turtle SCL in Chagos was not significantly different to Seychelles individuals, possibly as 66% (n = 195/297) of Seychelles turtles were immature. Validation of species-identification had 75% accuracy so a margin of error may have been introduced, however each identified turtle was reviewed to limit this. Validation is crucial when allocating species in this manner as L:W ratios can be impacted by several factors: the angle of the turtle in regard to the UAV; movements of the water which can morph the size and shape of the carapace; and the clarity of the carapace edge for measurement (e.g. Bevan et al., 2016). Changing the assigned species of a small group of individuals is subjective but highlights the importance of validation, repeat measurements, and methodology that balances needs of the researcher i.e. a UAV flight altitude selected based on research focus. Utilising characteristics of the carapace and head proved a useful metric to aid validation of assigned turtle species. CCL data were available for turtles in Chagos, however only SCL measurements were achievable based on the aerial point-of-view. CCL-to-SCL equations exist for specific oceans and species (green turtles, North Atlantic Ocean, Goshe et al., 2010; hawksbill turtles, Caribbean Sea, Hawkes et al., 2014; green turtles, North Pacific Ocean, Tanaka, 2009), but no such equation is available for the Indian Ocean sub-populations of green or hawksbill turtles. To improve certainty in future aerial surveys that attempt species allocation, data sets with both CCL and SCL should be utilised to calculate CCL-to-SCL conversion equations.

Comparison of mean SCL across islands and habitats confirms the Chagos sea turtle population is dominated by immature individuals. However, life-stage was assigned on a 75 cm SCL threshold, based on the SCL of the smallest observed nesting individual (Esteban, pers. comm.), and this fixed threshold may mean sub-adult individuals could be wrongly assigned. The size of sub-adult green and hawksbill turtles has intra- and inter-specific variation: Seychelles data provided by J. Mortimer showed green sub-adults (n = 3) ranged from 69 - 79 cm SCL, and hawksbill sub-adults (n = 54) ranged from 57 - 83.5 cm SCL. Setting a threshold for all turtles when the species is unknown would cause incorrect allocation of life-stage i.e. a 70 – 80 cm threshold, which would contain green and hawksbill sub-adult turtles, would certainly include adult hawksbill turtles, whose maximum size is approximately 90 cm SCL (Pritchard and Mortimer, 1999). Life-stage allocation subsequently determines the L:W ratio applied to identify species therefore sub-adults were not categorised in this study to limit error in identification. In Atlantic green populations, Phillips et al. (2021) determined size-at-maturity based on two standard deviations below the mean nesting female size to include pre-nesting adults, although error may be introduced as adult males are typically smaller than females (Godley et al., 2002; Omeyer et al., 2017). Based on mean SCL of female green turtles in the Seychelles (Mortimer, pers. comms.), this methodology would assign adults from 94.30 cm SCL (mean SCL 103.70 ± 4.70 cm), this would introduce errors as there are recorded nesting individuals of a smaller size e.g. 92.40 cm SCL. More data on specific size-at-maturity in the Indian Ocean will improve demographic allocation using UAV surveys.

Turtle sex could only be identified for individuals larger than the smallest nesting size. This resulted in a relatively small sample size (females, n = 17; males, n = 8). However, 80% of the identified females were hawksbill, and 75% of males were green, thus we cannot draw conclusions on the operational sex ratio.

Observer Variation

Observer variation analysis proved experience-effect on accuracy of counts: the same individual showed a significant increase in count accuracy after approximately 70 hours of turtle-observation experience, showing a smaller difference in count when compared to the reference observer, as well as an increased correlation coefficient. While non-experienced observers showed a large variation in counts for individual survey videos, this was not translated into the final turtle counts and overall observers had a strong positive correlation with the reference observer, highlighting that citizen-science projects that involve non-experienced observers can still successfully estimate counts, agreeing with the findings of Giuffrida et al. (2018).

One limitation of observer analysis was the utilised methodology: Observer 1 and Observer 9b utilised a 'definite-only' methodology where turtles were only counted when certain; however, Observer 9a utilised the 'definite/probable/possible' methodology that was defined for this research, which may explain the change in the DIC values. Studies utilising known-population sizes (e.g. Hodgson et al., 2018) could better assess observer variation for turtles *in-situ*.

Low-certainty and High-certainty data

Utilising high-certainty definite-only observations allows for confidence in conclusions but results in conservative estimates of population density. Environmental factors (turbidity, glare, water depth) all impact the certainty of observations so conducting UAV surveys in optimal weather conditions can positively impact results by reducing uncertainty. The change in population density observed here concurs with another study utilising certainty-allocation for UAV-based turtle observation, with high-certainty and low-certainty population densities estimated at 227 ± 80 individuals/km^2 and 365 ± 140 individuals/km^2, respectively (Sykora-Bodie et al., 2017).

The dataset utilised impacted the outcome of analyses, with changes observed for comparisons of population densities between sites, as well as the relationship between density and distance from Turtle Cove. While outcomes of statistical tests and therefore confidence in findings varied, the same overall trends were observed. Comparisons highlight the importance of appropriate UAV survey protocols dependant on target species and research-focus. For example, optimal flight altitude: UAV surveys of killer whales (*Orcinus orca*) were able to identify individuals when operating at 35 – 40 m AGL (Durban et al., 2015), while surveys of penguins in Antarctica, a comparatively smaller species, operated flights at a similar altitude (30 m AGL) to maximise survey area (Liu et al., 2020). Optimal protocols are therefore dependent on research-focus and should be developed independently, considering previously highlighted advantages and limitations (see Fiori et al., 2017; Raoult et al., 2020 for review).

UAV survey design

While UAVs are a cost-effective and risk-averse alternative to traditional aerial surveys (Fiori et al., 2017; Rees et al., 2018), some limitations occur based on their operation and available functions. Software on the Autel EVO™ UAV (Autel Robotics, 2021) did not allow for input of coordinates to programme transect locations pre-survey. Other UAV models have improved functions e.g. DJI® UAV models allow for return to previously-visited points using the complementary GO app (Bevan et al., 2016; Wang, 2021), a useful feature between battery-changes. Waypoints could be added but only manually using the touch screen, and relied on a stable Wi-Fi connection which was unavailable in remote field locations. Transect-length could therefore only be calculated using the straight-line distance between the UAV and controller using trigonometry, and could not consider the curvature of the coastline. While this effect was minimised by the pilot tracking the coastline, transects were often < 1 km in length. Following the coastline in this manner achieved coverage of the maximum available area, but included some unavailable area as a result i.e. land or exposed rocky areas. Due to a small lag between the UAV and the live-streamed video on the controller, this was unnoticed for a number of seconds and was then quickly corrected. This unavailable area, as well as areas unobservable due to sun glare, shadow or wave swell, had to be subtracted from the total area which added to the time-cost of post-survey processing.

To calculate the total area, transects were measured in Google Earth (Google, 2021), following the curvature of the coastline between the start and end coordinates. However, this method therefore cannot account for the UAV diverting from the chosen path due to high winds or obstacles. When unsure of the exact flight path, the survey footage was viewed, emphasising the value of video-recorded surveys (Raoult et al., 2018). When calculating the unavailable area using the orthomosaic-approach, as the UAV speed was subject to environmental influences, using 5 m/s to calculate the frame frequency did not provide an accurate orthomosaic. Frame frequency was often determined manually, but changed systematically in increments of 0.25 m/s. This process was critical to ensure all unavailable area was removed to provide accurate density estimates, but introduced subjectivity. This reiterated the importance of optimal weather conditions during UAV flights to reduce time-cost of additional analysis post-survey.

One limitation of aerial surveys of marine-dwelling species is the difficulty to observe individuals beneath the surface. As diving-species, sea turtles spend approximately 80 - 90% of their time below the surface (Hazel et al., 2009; Howell et al., 2010; van Dam and Diez, 1997). The availability of object to be detected by the observer i.e. the availability bias, subsequently impacts species counts, especially in marine ecosystems where depth, sea state and glare can all impact the ability to observe target species (Marsh and Sinclair, 1989). Many studies account for this availability bias (e.g. Barco et al., 2018; Pollock et al., 2006; Sykora-Bodie et al., 2017) utilising depth-surface dive behaviour, resulting in higher population estimates. For example, Sykora-Bodie et al. (2017) utilised olive ridley (*Lepidochelys olivacea*) diving behaviour to account for availability bias during a mass-nesting event in Costa Rica, resulting in an increase from 227 ± 80 individuals/km^2 to 1299 ± 458 individuals/km^2. Secchi disk-like experiments have also been used to identify specific depths at which species become unavailable for detection (Fuentes et al., 2015; Pollock et al., 2006), but require sufficient time and equipment in the field prior to surveys.

The availability bias greatly depends on the depth of the survey site: here, each frame was assigned 1 – 4 on a turbidity scale adapted from Hodgson et al. (2013), with 89% (n = 495/560) assigned 1 - 2 where habitats were shallow. Therefore only 11% of frames had an unclear sea floor and were subject to availability bias so it was not calculated. Perception bias also occurs, where an object that is available for detection is not perceived by the observer (Marsh and Sinclair, 1989), but repeat viewing and validation should reduce this.

Conclusion

This study demonstrates the importance of the Chagos Archipelago as a developmental habitat for a high density of sea turtles, providing shelter to rest and foraging habitats. Diego Garcia and Nelson's Island had high population densities when compared to other sites within the SWIO (Jean et al., 2010; Reyne et al., 2014), and globally (Becker et al., 2019; Bovery and Wyneken, 2015) and therefore the area is a key site for turtle conservation. This highlights the success of the Chagos MPA as means to conserve endangered turtles.

Population densities separated by life-stage and species highlighted the eastern coast of Diego Garcia as the most turtle-dense survey site: as a neritic habitat rich in coral, turtles migrating with the South Equatorial ocean current may reside there due to rich foraging grounds and reef structures (Carlton et al., 2015; Esteban et al., 2018), and is likely acting as a stepping stone for turtles migrating across the Indian Ocean (Sheppard et al., 2012). Immature hawksbill turtles comprised the majority of identified individuals, demonstrating Chagos as an important developmental habitat. Only a small number of adults were observed, the majority on the oceanside of Nelson's Island during peak green turtle breeding season.

The high numbers of turtles observed in this study confirmed the applicability of UAV surveys to population estimates of foraging sea turtle populations. Further to this research, UAVs could be utilised to estimate the population size of green and hawksbill turtles across the Chagos Archipelago, for example using integrated mark-release-recapture survey approaches (e.g. Dunstan et al., 2020). The ability of UAVs to span large areas in a limited time can improve feasibility of long-term monitoring of marine populations (Fiori et al., 2017). Repeat viewing of imagery allows observer variation to be assessed and can aid species- and sex-allocation for analyses. Permanently-stored footage could also be utilised for further analysis in future. UAV surveys could be instrumental in the long-term monitoring of sea turtle populations *in-situ* and should be utilised where possible.

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