NELSON MANDELA
UNIVERSITY

Department of Zoology

Insights into the relative abundance, demographics and behaviour of sea turtles along the east coast of South Africa

Natalie Aida dos Santos

Submitted in fulfilment of the requirements for the degree of Master of Science in the Faculty of Science at the Nelson Mandela University

December 2023

Supervisor: Prof. Ronel Nel

Co-supervisor: Dr. Diane Le Gouvello

Declaration by candidate

Name: Natalie Aida dos Santos

Student number: 217939848

Qualification: MSc (Zoology)

Title of project: Insights into the relative abundance, demographics and behaviour of sea turtles along the east coast of South Africa

In accordance with Rule G5.11.4, I hereby declare that the above-mentioned thesis is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

Signature: NA dos Santos

Date: 24 August 2023

NELSON MANDELA
UNIVERSITY

Permission to submit final copies of thesis to the assessment and graduation office

Faculty: Science

Department: Zoology

I, (surname and initials of supervisor) Nel R.

and (surname and initials of co-supervisor) Le Gouvello D. Z. M.

the supervisor and co-supervisor respectively

for (surname and initials of candidate) dos Santos N. A. (student number) 217939848

a candidate for the (full description of qualification) degree of Master of Science

with a thesis entitled (full title of thesis): Insights into the relative abundance, demographics and behaviour of sea turtles along the east coast of South Africa

It is hereby certified that the proposed amendments to the thesis have been affected and that **permission is granted to the candidate to submit** the final bound copies of her thesis to the examination office.

Prof. Ronel Nel
Supervisor

10 November 2023
Date

Dr. Diane Le Gouvello
Co-supervisor

10 November 2023
Date

Table of Contents

Summary

Sea turtles are ecologically important species that have endured a history of overexploitation. Combined with their long, complex life cycles and ongoing anthropogenic pressures, they remain conservation-dependent. Conservation efforts worldwide focus on sea turtle nesting beach protection, however, comprehensive management strategies require an understanding of their lives at sea which are often spent in distant waters. This understanding is hindered by the relative challenges of in-water studies. South Africa has also focused research and conservation efforts on nesting adult female loggerheads (*Caretta caretta*) and leatherbacks (*Dermochelys coriacea*), largely overlooking the species or age classes remaining at sea. Green turtles (*Chelonia mydas*), hawksbills (*Eretmochelys imbricata*) and non-breeding loggerheads are frequently stranded and rehabilitated by aquaria, and observed by recreational divers on reefs, suggesting year-round residency along the country's entire seaboard. Recent technological advancements in photo-identification methods for sea turtles, underwater photography and internet connectivity allowing even recreational divers to become citizen scientists now place us on the verge of an exciting opportunity to unravel the cryptic in-water biology of these species.

The overall aim of this study was to conduct the first assessment of relative abundance, demographics, distribution, and behaviour of sea turtles on reefs within the iSimangaliso and Aliwal Shoal Marine Protected Areas (MPAs) on the east coast of South Africa. A robust photo-identification database was established from research dives (supplemented by voluntourism), citizen science contributions and opportunistic sightings over a two-year period.

From 1057 sightings in the two MPAs, a total of 227 individual sea turtles were identified constituting three species (green turtles: n = 120; hawksbills: n = 46; loggerheads: n = 61). Their relative abundance was proportional to the overall sizes of the South West Indian Ocean (SWIO) populations (green turtles > hawksbills > loggerheads > leatherbacks). However, sightings per unit effort (SPUE) showed that loggerheads were more prevalent than hawksbills in iSimangaliso, likely due to its proximity to this loggerhead rookery. Reefs supported mixed size aggregations with juvenile to adult-sized green turtles (straight carapace lengths, SCLs of 44.9–99.2 cm), whilst hawksbills were mostly juveniles or subadults (SCL range: 37.4–73.4 cm) and loggerheads were mostly adult-sized (SCL range: 66.9–81 cm). Adult sex ratios were slightly female-biased but not significantly different from 1:1. The longest minimum residence periods recorded for individual subadult green and hawksbill turtles (676 and 675 days respectively) and adult-sized loggerheads (621 days) were suggestive of residency. Resident sea turtle activities were typical; they were observed foraging, resting, cleaning and interacting year-round, whilst only loggerheads and leatherbacks were observed in breeding behaviour (e.g., patrolling and mating) just after the seasonal arrival of transient individuals.

This study thus reveals that the east coast of South Africa hosts regionally important resident and transient sea turtle aggregations with some of the highest SPUE results recorded for the region. This first attempt at monitoring foraging grounds using a variety of techniques and stakeholder groups can serve as the baseline assessment for future work and the foundation for a long-term in-water monitoring programme, allowing for expansion along the entire coastline.

Key words: photo-identification, citizen science, paired-laser photogrammetry, relative abundance, spatial distribution, residency, behaviour, in-water observation, foraging grounds, sea turtles

Acknowledgements

I would like to express a leatherback-sized thanks to Prof. Ronel Nel for entrusting me the wonderful opportunity to undertake this research, for generously imparting your superb insights on matters extending beyond the realm of sea turtles, and for always challenging me to give my utmost best. Merci beaucoup to Dr. Diane Le Gouvello for your valuable input and support throughout this study, for your quiet leadership by example and for the many insightful French lessons. I am very grateful to both of you for your patience, encouragement and expert guidance on this journey.

I am very grateful to Grant Smith (Sharklife Conservation Group) for your extensive dedication to data collection, in-kind support and warm hospitality on field trips to Sodwana Bay. Many thanks to conservation authorities, iSimangaliso Wetland Park and Ezemvelo KZN Wildlife, for allowing us to conduct research in iSimangaliso, and to Anton Cloete for advising on the safest way to carry out diving-related fieldwork.

I wish to extend my thanks to the Nelson Mandela University and National Research Foundation (NRF) for generous scholarships that made this research endeavour possible, and to the NRF for the research grant to Prof. Nel that covered some fieldwork expenses. A sincere thanks goes to Linda Ness (Linda Ness Photography) for financial support that allowed us to keep getting out to sea before we received fieldwork funding, and for your continued support today. I am also sincerely grateful to everyone who donated to initial project running costs. Thanks also go to the Western Indian Ocean Marine Science Association (WIOMSA) for a travel grant to present this research at the 12th WIOMSA Scientific Symposium in Gqeberha, South Africa.

A great white shark-sized thanks to Cassie Weinberg (Wetu Safaris) and Emil and Travis Pirzenthal (Aliwal Shoal Adventures) for your in-kind support and memorable trips to Aliwal Shoal. This thanks extends to the Sharklife research assistants, Samantha Kruger, Candice Parkes and Romain Allemann, for your tireless data entry efforts, unfailing enthusiasm and support. I am also grateful to the dedicated citizen scientists who contributed to this work, especially Alexandra Torborg, Emma Tomkins and Jamie Lynn Marais. A big thanks also goes to Nina Faure-Beaulieu, Jessica Williams, Michaela King, Michelle Carpenter and Stephanie Venables for your statistics and map-making advice, and to Prof. Nel's team of fellow 'turtle trotters' for the support.

My heartfelt gratitude goes to my family and friends for their support throughout this journey. To Michael Tarr, for your support in and out of the water, and for machining the ultimate paired-laser photogrammetry rig. To Andy Coetzee, for being a significant mentor in my life, for sharing your

deep appreciation of nature with me, for always keeping me fuelled with candy, condensed milk and country music, and for the countless pep talks when hours behind the computer exceeded those spent underwater. My last special thanks go to Dexter who was by my side almost every step of the way, both under my desk and out at sea.

One of many wonderful memories on Aliwal Shoal with the most frequently sighted male loggerhead, Donny Parton, indulged in a lengthy siphonophore feast near the surface. Photographer[1]: Andy Coetzee.

---

[1] Unless otherwise stated, photographs in this thesis are my own and gathered throughout the course of this study. Permission was granted to use photographic contributions by others and credit is given where due.

Ethics statement

Sea turtles were always approached as cautiously as possible underwater to minimise disturbance. Both Human (including citizen science data) and Animal ethical clearance was obtained for this study from the Nelson Mandela University (reference numbers: **H21-SCI-ZOO-002**, **A21-SCI-ZOO-008**). A research agreement entitled "iSimangaliso Wetland Park Sea Turtle Assessment: To describe the ecology and population dynamics of non-nesting sea turtles" allowed the study to be conducted in the iSimangaliso Wetland Park and Marine Protected Area (iSimangaliso) with assisted data collection from Sharklife Conservation Group's (Sharklife's) volunteer tourism programme in Sodwana Bay. A permit from the Department of Forestry, Fisheries and Environment - Oceans and Coasts permitted pilot observations made in iSimangaliso in 2020 (permit number: **RES2021/14**). To ensure personal safety and liability whilst conducting field work (free diving or SCUBA diving), diving only took place with recreational service providers or Sharklife within the limits of personal recreational qualifications and whilst covered by DAN-SA diving insurance. Some morphometric data included in this study was obtained by capturing sea turtles on SCUBA for another study, with animal ethical clearance obtained from Nelson Mandela University (**A21-SCI-ZOO-009**).

Chapter 1: General Introduction

1.1 Overexploitation of ecologically important species

Human activities are undoubtedly the strongest drivers of change in marine biodiversity, which has undergone a rapid decline globally over the past few centuries (Jackson 1997; Jackson *et al.* 2001; Sala and Knowlton 2006). Global marine biodiversity loss has been exacerbated by the overexploitation of ecologically important marine megafauna such as sea turtles, sirenians, cetaceans and elasmobranchs, whose current populations are a fraction of the millions they once were (Bertram and Bertram 1973; Jackson 1997; Malakoff 1997; Pandolfi *et al.* 2003; Roman and Palumbi 2003). Their local removal has severely compromised the overall structure, functioning and resilience of marine ecosystems, impacting the stability of food web dynamics (Estes *et al.* 1989) and the productivity of fisheries (Pauly *et al.* 1998).

The history of overexploitation for sea turtle meat, shell and eggs spans centuries (Frazier 1980; Jackson 1997; Malakoff 1997). Coupled with their longevity and slow maturity that render them more vulnerable to overharvesting (Musick and Limpus 1997), there have been considerable sea turtle population declines globally (Frazier 1980; Jackson 1997; Malakoff 1997). For example, historic accounts indicate there were once tens of millions of green turtles (*Chelonia mydas*) in the Caribbean, whose meat and eggs sustained colonists and slaves during intense exploration periods (Carr 1954; Parsons 1962; Jackson 1997). Caribbean green turtle populations were overharvested by the early 1800s and some nesting populations became locally extinct (Lagueux 2001), with little sign of recovery until recently (e.g., Troëng and Rankin 2005). Historic accounts from the South West Indian Ocean (SWIO), report at least 200–300 nesting female green turtles *per night* on Assumption Island, Seychelles, in the early 1900s (Hornell 1927). Green turtles from Seychelles Islands were severely overexploited to produce a variety of goods, most importantly calipee (a gelatinous substance found beneath the shell), used by Europeans for turtle soup (Hornell 1927; Stoddart 1971; Frazier 1974). At least 232,942 kg of calipee was produced in Seychelles over 61 years (1907–1968), equivalent to an estimated 113,845 slaughtered green turtles (Stoddart 1984). Hawksbill turtles (*Eretmochelys imbricata*) were also overharvested on a large scale for their shell, used to make ornamental combs, bracelets, and other objects in the tortoiseshell (bekko) trade (Hornell 1927; Mortimer 1984). An estimated 42,727 kg of hawksbill shell was exported from Seychelles Islands over 33 years (1893–1925), primarily to Japan (Hornell 1927). There are very few historic records of past human-use or abundance of sea turtles in South Africa, but evidence from the Sibudu Cave in KwaZulu-Natal (KZN) suggests that the history of humans and sea turtles goes as far back as the Middle Stone Age (Plug 2004). One anecdotal account indicates that sea turtles were once sold in Durban, KZN, and reports hundreds if not thousands of green turtles in the uMzimkhulu River alone (lower KZN) 156 years ago (Turner 1867 as cited in Child 1980); numbers which certainly do not exist today.

Sea turtles fulfil unique ecological roles in marine ecosystems through the large amount of plants and animals they consume and intense physical and biological disturbance they cause (Jackson 1997; McClenachan *et al.* 2006). Green turtles consume large amounts of algae and seagrasses, and in doing so enhance benthic diversity by cropping over-abundant species and stimulating seagrass bed growth (Jackson 1997; Jackson *et al.* 2001; McClenachan *et al.* 2006). Hawksbills also maintain benthic biodiversity by controlling fast-growing sponge populations that compete with corals for space (León and Bjorndal 2002). The loss of green turtles and hawksbills has been recognised as one of the first steps in the serial collapse of Caribbean marine ecosystems, now dominated by seagrass monocultures and small fishes, due to dramatic reductions and qualitative changes in seagrass grazing, sponge predation, productivity to adjacent ecosystems and food web structure (Jackson 1997; Jackson *et al.* 2001; McClenachan *et al.* 2006). In addition to their ecological importance, sea turtles are also valued in human societies for traditional use, cultural and religious practices, education, ecotourism, and symbolic representation of the marine environment (Campbell 2003; Frazier 2005). Severe population declines are not only a concern for sea turtles themselves, but for overall marine ecosystems and socio-ecological systems. Thus, all sea turtle species are conservation-dependent irrespective of the current population size.

1.2 Conservation complexities

Sea turtle monitoring and conservation efforts are challenged by their long, complex life cycles and broad geographic ranges that require international agreements and cooperation for transboundary management strategies (Shillinger *et al.* 2008; Runge *et al.* 2014). Immediately after hatching, sea turtles are dispersed offshore by active swimming (Putman *et al.* 2012; Putman and Mansfield 2015) and passive drifting with ocean currents (Carr 1978; Carr 1987; Luschi *et al.* 2003; Hays *et al.* 2010), and remain in oceanic sea surface habitats for many years (Musick and Limpus 1997). Most species, as larger juveniles, recruit to neritic developmental foraging grounds shared by multiple rookeries (population overlap) and frequented solely by juveniles or shared with adults (Musick and Limpus 1997; Bowen *et al.* 2005). Immature sea turtles shift developmental foraging grounds as they mature, and adults use separate breeding and foraging grounds (Carr 1978; Musick and Limpus 1997). Adult females exhibit natal philopatry, returning to natal rookeries to breed (Meylan *et al.* 1990), and adult males are also philopatric to courtship areas near natal rookeries but male-mediated gene flow is suspected to occur through opportunistic mating by males during migration (FitzSimmons *et al.* 1997). Population overlap in developmental habitats may pose a conservation risk because anthropogenic threats could potentially affect future generations of multiple populations (Bowen *et al.* 2005). Similarly, natal philopatry, despite providing advantages for finding mates and locating favourable breeding habitats (Hendry *et al.* 2004), makes rookeries vulnerable to anthropogenic threats in unprotected areas (e.g., Huxley 1999).

In addition to these complexities, sea turtle populations have been overexploited over so many human generations, often with little historic documentation, that scientists tend to use current population levels (or those from only a few generations before) as the baseline to measure population change against (Jackson 1997; Bjorndal and Bolten 2003). This “shifting baseline syndrome” (Pauly 1995) undermines the magnitude of biodiversity already lost and indirectly undermines population recovery efforts. Whilst sea turtle population trends over time should be assessed against pre-European abundances, these historical baselines are likely inappropriate to base recovery targets for current sea turtle populations on, because current marine ecosystems may be too altered to sustain them (Bjorndal and Bolten 2003). Therefore, recovery targets should be set to population abundances at which sea turtles fulfil their ecological functions, which will also promote ecosystem resilience and recovery (Bjorndal and Bolten 2003; McClenachan *et al.* 2006). The past and present ecological roles of sea turtles are thus a global research priority (Hamann *et al.* 2010) but before we can begin to understand these roles in local marine ecosystems, we need to gather basic information on the in-water abundance, demographics, spatial distribution, and behaviour of sea turtle populations that is largely lacking globally.

1.3 Disconnect between land and sea

Despite sea turtles spending most of their lives in the ocean, data collection for most studies have been conducted on the beach where nesting females and hatchlings are easily accessible, as in-water studies are relatively far more challenging due to their resource- and labour-intensive nature, difficulty of locating animals, and often unpredictable sea conditions (Eckert *et al.* 1999). Historically, sea turtle population assessments have been based on nesting trends such as the number of nesting females which comprise only a small portion of the complex life cycles of sea turtles, reflect recruitment a generation ago, and ignore the immature, male and non-breeding female portions of populations (Bjorndal and Bolten 2000; Bjorndal *et al.* 2005). In-water monitoring may detect changes in juvenile abundance (e.g., from overharvesting), offering an early indication of population decline given the slow maturity of sea turtles (Musick and Limpus 1997; Tucek *et al.* 2014). By the time declines are reflected as fewer females on nesting beaches, it may be too late to take conservation action to mitigate them (Mortimer 1984; Bjorndal *et al.* 2005). Although the study of nesting trends is critical and recent studies have shown that the protection of nesting females and eggs has remarkably increased nesting trends in some areas (e.g., Chaloupka *et al.* 2008; Mortimer *et al.* 2011; Weber *et al.* 2014), the effects of population recovery on developmental foraging grounds remain largely unknown without in-water monitoring (van der Zee *et al.* 2019). This knowledge is not only important to assess conservation efficacy but also to ensure that developmental habitat quality and quantity are not negatively affected by overconsumption (e.g., Fourqurean *et al.* 2010), increased intraspecific competition for resources, and habitat collapse (Christianen *et al.* 2014). To adequately protect both adult breeding grounds and developmental foraging grounds, the interactions between nesting trends at rookeries and recruitment, population dynamics and ecology at foraging grounds needs to be understood (van der Zee *et al.* 2019). The data gained by in-water studies are thus critical for effective species-specific management and conservation action (Bjorndal and Bolten 2000; Bjorndal *et al.* 2005).

The recognition of the necessity for in-water studies gained momentum among scientists in the 1980s and 90s, creating a growing awareness and urgency for such work (Bjorndal and Bolten 2000). Early methods for in-water studies included aerial and ship transects (e.g., Braun and Epperly 1996), catch per unit effort (CPUE) in entanglement nets (e.g., Shaver 1994), and capture-mark-recaptures (CMRs) using boat pursuit, free diving or SCUBA diving where sea turtles are usually marked with uniquely coded flipper tags (e.g., Chaloupka and Limpus 2001). These in-water methods have allowed scientists to determine species composition, relative abundance or abundance estimates, residency, site fidelity, size classes, growth rates and sex ratios of sea turtles on foraging grounds (e.g., León and Diez 1999; Chaloupka and Limpus 2001) and thus develop a more complete understanding of their fundamental biology and ecology throughout their life cycle.

Technological advancements have improved in-water methods significantly by reducing the need for time-consuming, labour-intensive physical capture and marking that causes stress to animals. Photographic-identification (photo-ID) uses unique natural markings that are stable over time to identify individuals (Würsig and Jefferson 1990), such as spot patterns on whale sharks (Meekan *et al.* 2006), ventral markings on manta rays (Deakos 2010) and dorsal fin shapes of great white sharks (Anderson *et al.* 2011). The discovery of unique postocular scute patterns on sea turtles (Bennett and Keuper-Bennett 2001) has resulted in the proliferation of photo-ID in sea turtle research as a non-invasive CMR technique, sometimes referred to as a 'sight-resight' technique. Photo-ID has allowed scientists to collect data even from recreational diver's photographs of sea turtles in a form of citizen science, where members of the public gather scientific information in large quantities over broad areas (Bhattacharjee 2005). Paired-laser photogrammetry is another relatively new technique that allows divers to measure sea turtles from a distance underwater by projecting two laser beams set at a known distance apart (essentially a scale) onto their carapace (dorsal shell) (e.g., Araujo *et al.* 2019). These methods have revolutionized sea turtle research, offering more efficient and non-invasive ways to gather valuable data and making it an opportune time to conduct such studies. More details on these methods are provided in subsequent chapters.

1.4 Sea turtles of the SWIO

According to the 'Nairobi Convention', the SWIO encompasses countries on the east African continental coastline from Somalia to South Africa as well as the islands and island groups of Chagos Archipelago, Seychelles, Mauritius, Réunion, Madagascar, Comoros, Mayotte, and the French Scattered Islands (Îles Éparses) which include Europa, Bassas da India, Juan de Nova, Glorieuses and Tromelin. Five of the world's seven sea turtle species occur in the SWIO, namely the green turtle (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*) and olive ridley (*Lepidochelys olivacea*). Categorised as per the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, globally green turtles are Endangered (Seminoff 2004), hawksbills are Critically Endangered (Mortimer and Donnelly 2008) and loggerheads, leatherbacks and olive ridleys are Vulnerable (Abreu-Grobois and Plotkin 2008; Wallace *et al.* 2013b; Casale and Tucker 2015). However, the highly migratory nature and complex life cycles of sea turtles have resulted in significant genetic and ecological variations in populations across regions, which have thus been categorised into regional management units (RMUs) based on their distinct genetics, distribution, movement and demography (Wallace *et al.* 2010). RMUs represent designated geographic areas used for targeted management and conservation efforts that address the specific threats faced by each sea turtle population within its respective region. In the SWIO RMU, loggerheads are Near Threatened (Nel and Casale 2015), leatherbacks are Critically Endangered (Wallace *et al.* 2013a), and green turtles, hawksbills and olive ridleys have not yet been regionally assessed. A broad overview of current knowledge on SWIO sea turtle populations is provided below.

Nesting

The SWIO hosts nesting green turtles throughout its range whilst hawksbills mainly nest in the tropical north. Loggerheads and leatherbacks nest in the subtropical south and scattered olive ridley nesting occurs throughout the north and middle of the region. The SWIO hosts globally important nesting grounds for green turtles which are found on most of the islands and island groups and along the east African coastline from Somalia to northern Mozambique (Hughes 1973; Frazier 1975; Seminoff 2004, Fig. 1.1). The combined green turtle RMU is estimated to be very large at > 10 000 adult nesting females per year, with the Comoros, Îles Éparses and Seychelles hosting the largest of these stocks (Lauret-Stepler *et al.* 2007). Hawksbill nesting grounds are also found on many of the SWIO islands and island groups but to a lesser extent than those of green turtles, as well as the east African coastline from Somalia to northern Mozambique (Mortimer and Donnelly 2008, Fig. 1.1). The combined hawksbill RMU is estimated to be large with 2000–3000 adult nesting females per year, with Seychelles, Madagascar and Chagos Archipelago hosting a significant portion of these stocks (Mortimer and Donnelly 2008; Mortimer *et al.* 2020). The largest loggerhead and leatherback rookeries in the SWIO are both found on the northeastern coastline of South Africa and southern Mozambique (Nel *et al.* 2013a; Pereira *et al.* 2014), with low, unquantified nesting activity of both species in south-east Madagascar (van der Elst *et al.* 2012; Humber *et al.* 2016) (Fig. 1.1). Both RMUs are considered small, with fewer than 1000 nesting female loggerheads and about 70 nesting female leatherbacks per year (Nel *et al.* 2013a). Olive Ridley nesting in the SWIO has only occurred in rare cases in Kenya, Mozambique, South Africa and Madagascar (Hughes 1972; Okemwa *et al.* 2004; Costa *et al.* 2007; Humber *et al.* 2016). According to estimated numbers of nesting females per year, green turtles (Cm) are the most abundant species in the SWIO followed by hawksbills (Ei), loggerheads (Cc), leatherbacks (Dc) and olive ridleys (Lo). Thus Cm > Ei > Cc > Dc > Lo in terms of abundance (abbreviations used again in this study).

Post-nesting and juvenile migrations

Satellite tracking studies of post-nesting adult female green turtle migrations from Îles Éparses, Comoros and Mayotte have highlighted the importance of the east African coastline (particularly Tanzania, Kenya and Mozambique) and west coast of Madagascar as regionally important foraging grounds for this species (Bourjea *et al.* 2013; Dalleau *et al.* 2019). There have been relatively few studies on adult female hawksbill post-nesting migrations from the SWIO, but a few have been tracked to foraging grounds off Tanzania and Madagascar (J. Mortimer unpubl. data) and many have stayed relatively close to breeding grounds near Seychelles Banks (Mortimer and Balazs 2000) and Chagos Archipelago (Hays *et al.* 2022).

The east African coastline also hosts important developmental foraging grounds for juvenile sea turtles from SWIO islands, with ocean currents playing an important role in their migration and distribution (Jensen *et al.* 2020). As such, stranded and bycaught juvenile green turtles in South Africa were shown to have originated from Îles Éparses and Ascension Island (central Atlantic Ocean) and stranded juvenile hawksbills were shown to have originated from Seychelles Islands (Hickman 2017). Juvenile hawksbills have also been tracked via flipper tag recoveries from Seychelles to Kenya and northern Mozambique (von Brandis *et al.* 2017).

Post-nesting adult female loggerheads mostly migrate from South African breeding grounds to foraging grounds in southern Mozambique and to a lesser extent, Madagascar and the Atlantic Ocean (Hughes 1973; Harris *et al.* 2018). Post-nesting adult female leatherbacks mostly migrate from South Africa to foraging grounds in the Mozambique Channel whilst others head into the southern Indian and Atlantic Oceans (Hughes 1973; Robinson *et al.* 2016; Harris *et al.* 2018).

Juvenile loggerheads and leatherbacks are rarely seen in the SWIO, but satellite tracking of a few fisheries bycaught juvenile loggerheads from Reunion Island revealed that most went to the North West Indian Ocean (NWIO) RMU and few went to Madagascar and the southern Indian Ocean (Bousquet *et al.* 2020), suggesting the SWIO is used as a migratory corridor by juveniles of this species. Similarly, two fisheries bycaught olive ridley juveniles (also rare in SWIO waters) were tracked from Reunion Island to the NWIO RMU and the southern Indian Ocean (Bousquet *et al.* 2020). An overview of post-nesting and juvenile sea turtle migrations in the SWIO is shown in Figure 1.1.

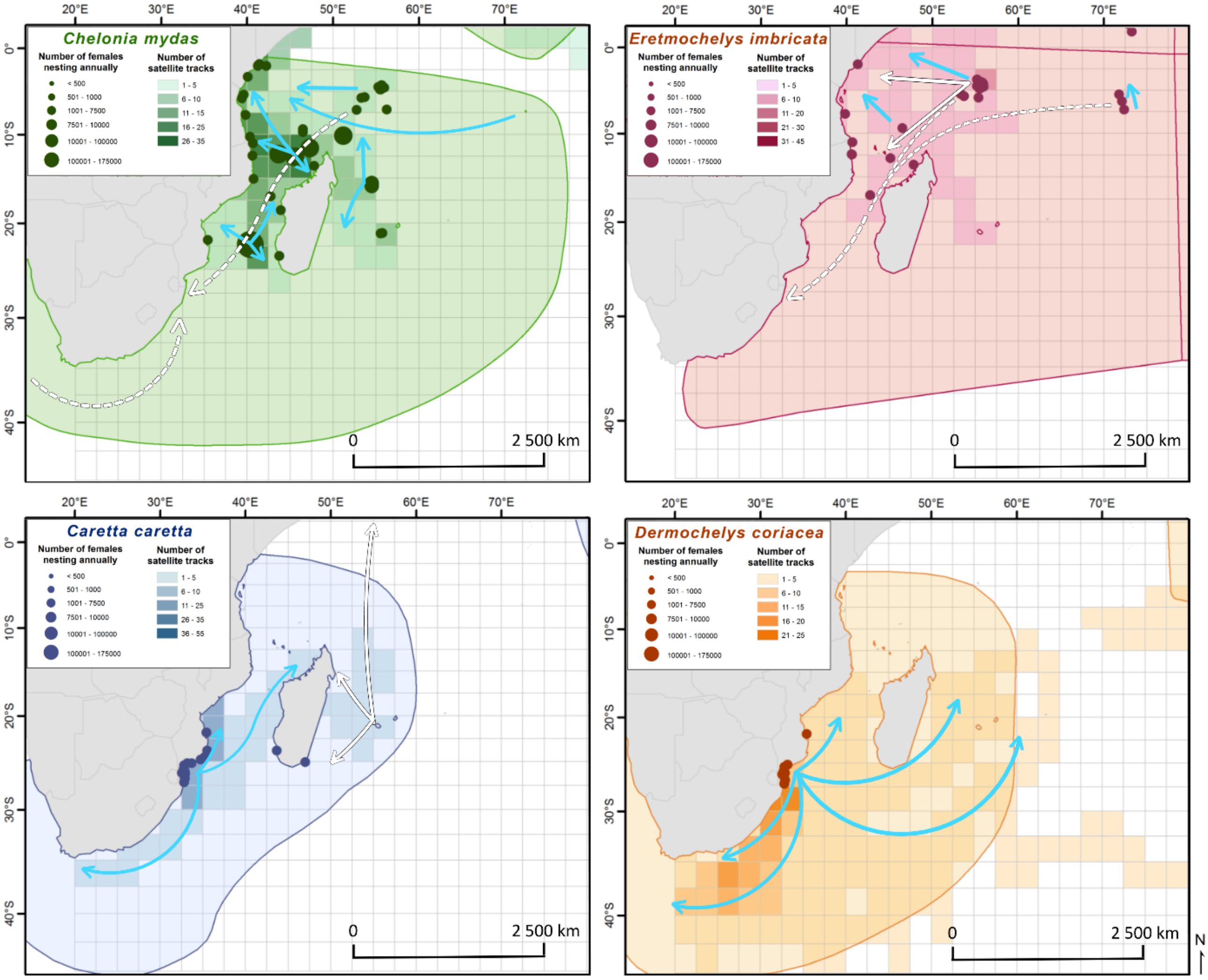


Figure 1.1 Distribution of sea turtles across SWIO RMUs (shaded areas) according to nesting grounds (circles) and satellite track distributions (squares) adapted from Nel *et al.* (2013b). Blue arrows indicate direction of post-nesting adult female migration to foraging grounds (as per Bourjea *et al.* 2013; Harris *et al.* 2018; Hays *et al.* 2020; Hays *et al.* 2022; J. Mortimer unpubl. data). White arrows indicate direction of juvenile migrations to foraging grounds (as per von Brandis *et al.* 2017; Bousquet *et al.* 2020). Broken white arrows indicate juvenile migration to developmental foraging grounds off South Africa based on genetic information (Hickman 2017; R. Nel unpubl. data).

Foraging grounds

The shelf areas off east Africa and SWIO islands host extensive coral reefs and seagrass beds which are ideal foraging grounds for sea turtles (Gullström *et al.* 2002). Sea turtles in Seychelles, Mayotte and South Africa have been shown to have similar diets to those in other regions (green turtles: seagrasses and algae, hawksbills: sponges and other benthic invertebrates, loggerheads: benthic molluscs, crustaceans and echinoderms, leatherbacks: gelatinous zooplankton) (Hughes 1973; Ballorain *et al.* 2010; von Brandis 2010; Robinson *et al.* 2016; Rambaran 2020). Olive ridleys in the

NWIO (closest studied population) have also been shown to have similar diets to those in other regions (benthic molluscs and crustaceans; Behera *et al.* 2015).

The few in-water studies on SWIO foraging sea turtles have confirmed that species composition and sizes on foraging grounds support satellite tracking and genetic data; island foraging grounds host mainly green turtles (juveniles to adults) (Taquet *et al.* 2006; Ballorain *et al.* 2010; Chassagneux *et al.* 2013; Stokes *et al.* 2023) and hawksbills (mostly juveniles but adults observed too) (von Brandis 2010; Stokes *et al.* 2023), while the east African reefs and seagrass beds host these as well as subadult and adult loggerheads and leatherbacks (Zanre 2005; Fulanda *et al.* 2007; Brazier *et al.* 2012; Williams *et al.* 2017; Rambaran 2020) (see Appendix 1.1 for recorded size classes of sea turtles on SWIO foraging grounds).

In-water abundance, relative abundance, and density estimates are scarce and vary widely (as shown in Appendix 1.2), but foraging grounds at SWIO islands generally have higher estimates than those on the east African coastline (Fulanda *et al.* 2007; Ballorain *et al.* 2010; von Brandis 2010; Brazier *et al.* 2012; Reyne *et al.* 2017; Williams *et al.* 2017; Stokes *et al.* 2023). However, aerial surveys and observations from recreational divers suggest a higher abundance of green turtles, hawksbills and loggerheads on east African foraging grounds than currently recognised (Wamukoya *et al.* 1996; Muir 2005; Provancha and Stolen 2008; R. Nel pers. comm.).

Both juvenile and adult green turtles and hawksbills on foraging grounds in Chagos Archipelago, Seychelles, Mozambique and South Africa generally have small home ranges and strong site fidelity with extended residence periods (von Brandis 2010; Williams *et al.* 2017; Rambaran 2020; Hays *et al.* 2021) but there is very little information regarding loggerheads who are likely resident foragers on the east African coastline too. The distribution of foraging grounds and in-water abundance, population structure and ecology of sea turtles is considered a significant data gap not only for the entire region but globally and has thus been highlighted as a priority research area (Eckert *et al.* 1999; Hamann *et al.* 2010; Rees *et al.* 2016; Wildermann *et al.* 2018; Dalleau *et al.* 2020; van de Geer *et al.* 2022).

Threats and conservation

Declines in sea turtle populations have led to conservation efforts in the SWIO since the 1960s which have included nesting beach protection (e.g., Lauret-Stepler *et al.* 2007), fisheries bycatch regulations (e.g., Fennessy *et al.* 2008), establishment of marine protected areas (MPAs) (e.g., Hays *et al.* 2021), and protection in every country/territory under numerous local, national, and international legislations (Dalleau *et al.* 2020). Population recoveries have occurred in a few well-protected areas, such as on Aldabra Atoll, Seychelles, where green turtles have shown a 500–800% increase in egg clutches during 40 years of complete protection since 1968 (Mortimer *et al.* 2011).

South Africa has the longest running nesting beach monitoring and protection programme in the SWIO, and one of the longest in the world, which was initiated in 1963 by the Natal Parks Board (now Ezemvelo KZN Wildlife) to protect declining loggerhead and leatherback populations as a result of overharvesting in the early 1900s (Hughes 1973; Nel *et al.* 2013a). Successful protection has been demonstrated by the dramatic increase in number of loggerhead nests from ~ 250 to > 1700 per year in a 13 km index area, but the number of leatherback nests in the same area initially increased from ~ 10 to 70 per year then stabilised (Nel *et al.* 2013a). The leatherback population is relatively well-protected on nesting beaches, so it is suspected that in-water threats such as fisheries bycatch are hindering recovery efforts (Nel *et al.* 2013a). The MPA encompassing loggerhead and leatherback nesting beaches, known as iSimangaliso, had an offshore and longshore expansion in 2019 largely motivated by the extensive internesting movements of leatherbacks as shown by Harris *et al*. (2015). However, it is likely too soon to see the effects of this additional protection and challenges still lay ahead as the future of nesting beaches may be compromised by socio-political pressures including land claims, dune mining, illegal harvesting and fishing, and proposed economic developments (R. Nel, pers. comm.).

1.5 Rationale and thesis outline

Across the SWIO, efforts to manage and conserve these ecologically important, conservation-dependent species are hindered by a lack of basic knowledge and empirical data on their lives at sea, where they spend almost all their time. South Africa too has focused research effort on adult female loggerheads and leatherbacks on nesting beaches, with little research investment into the green turtles, hawksbills and loggerheads that are suspected to forage along the country's entire seaboard. Despite the challenges of in-water studies, recent advances position us on the verge of an extraordinary opportunity to learn about sea turtles frequenting reefs protected in two MPAs on the east coast of South Africa. Each is situated in a distinct geographic region and renowned as a world-class diving destination in which sea turtles are regularly sighted; the iSimangaliso MPA in a transition zone between tropical and subtropical waters, and the Aliwal Shoal MPA in subtropical waters. There is significant research potential to use in-water studies here to conduct the first investigation into sea turtle species composition, relative abundance, size distribution, sex ratios, spatial distribution, residency, site fidelity, seasonality, behaviour and human disturbance, which is not only fundamental for a more complete understanding of basic biology and ecology but may also inform species-specific management and conservation strategies. There also lies a valuable opportunity to harness the potential of citizen science among enthusiastic recreational divers and fishermen to supplement data collection and evaluate the potential of a sustainable, long-term in-water sea turtle monitoring programme.

The overall aim of this study is to conduct the first in-water assessment of relative abundance, demographics, distribution, and behaviour of sea turtles on reefs along the east coast of South Africa. This study will also serve as the baseline assessment for future work and establish the foundation for a new long-term in-water monitoring programme.

The thesis is outlined as follows:

This chapter (Chapter 1) introduces sea turtles as ecologically important, conservation-dependent species whose conservation is hindered by a lack of basic knowledge in their primary habitat and gives a broad overview of the current state of knowledge and gaps in the SWIO.

Chapter 2 investigates the relative abundance, demographics (size distribution and sex ratios) and spatial distribution (local distribution, residency and site fidelity) among sea turtle species in the iSimangaliso and Aliwal Shoal MPAs using a photo-ID dataset collected by timed research surveys (supplemented by voluntourism), citizen scientists and opportunistic sightings. It is hypothesised that 1) relative abundance will be proportional to the nesting female abundance in the SWIO (Cm > Ei > Cc > Dc > Lo); 2) the size classes of non-nesting species (green turtles and hawksbills) will be dominated by juveniles, and size classes of nesting species (loggerheads and leatherbacks) will be dominated by adults; but that 3) adult sex ratios will be balanced (1 male: 1 female) for all species; and 4) juveniles of all species will have longer residence periods than adults.

Building on these findings, Chapter 3 investigates spatiotemporal behaviour of sea turtles *in situ* on reefs within the two MPAs on the east coast of South Africa using the photo-ID dataset described above coupled with behavioural observations and environmental data. It is hypothesised that 1) there will be seasonal changes in the relative abundance of transient nesting species/individuals (loggerheads and leatherbacks) but not resident foraging species/individuals (green turtles, hawksbills and non-breeding loggerheads); 2) behaviour will be reflective of life history stage i.e., resident species/individuals will be observed foraging year-round (in both MPAs) but transient adults will be observed courting and mating in iSimangaliso at the start of the nesting season; 3) sea turtle sightings will be affected by a combination of temporal, environmental, and oceanographic variables; and 4) sea turtles on frequently dived reefs will be more prone to human disturbance and thus have smaller flight initiation distances and a higher prevalence of boat strike injuries than those on less frequented reefs.

Chapter 4 concludes the thesis with a summary of key findings and their relevance, as well as recommendations for a long-term in-water sea turtle monitoring programme and further research.

1.6 References

Abreu-Grobois, A. and Plotkin, P. (2008). *Lepidochelys olivacea.* The IUCN Red List of Threatened Species 2008: e.T11534A3292503.

Anderson, S. D., Chapple, T. K., Jorgensen, S. J., Klimley, A. P. and Block, B. A. (2011). Long-term individual identification and site fidelity of white sharks, *Carcharodon carcharias*, off California using dorsal fins. *Marine Biology,* 158, pp. 1233-1237

Araujo, G., Legaspi, C. G., Ferber, S., Murray, R., Burdett, K., Grundy, S., Labaja, J., Snow, S., Yaptinchay, A. and Ponzo, A. (2019). In-water methods reveal population dynamics of a green turtle *Chelonia mydas* foraging aggregation in the Philippines. *Endangered Species Research,* 40, pp. 207-218

Ballorain, K., Ciccione, S., Bourjea, J., Grizel, H., Enstipp, M. and Georges, J.-Y. (2010). Habitat use of a multispecific seagrass meadow by green turtles *Chelonia mydas* at Mayotte Island. *Marine Biology,* 157(12), pp. 2581-2590

Behera, S., Tripathy, B., Sivakumar, K. and Choudhury, B. Stomach contents of olive ridley turtles (*Lepidochelys olivacea*) occurring in Gahirmatha, Odisha coast of India. *Proceedings of the Zoological Society*: Springer, 91-95.

Bennett, P. and Keuper-Bennett, U. (2001). The use of subjective patterns in green turtle profiles to find matches in an image database. Proceedings of the 21st Annual Symposium on Sea Turtle Biology and Conservation. 2005. Coyne, M. & R.D. Clark (Comps.). NOAA Tech Memo NMFS-SEFSC-528. pp. 115-116

Bertram, G. and Bertram, C. R. (1973). The modern Sirenia: their distribution and status. *Biological Journal of the Linnean Society,* 5(4), pp. 297-338

Bhattacharjee, Y. 2005. Citizen scientists supplement work of Cornell researchers. American Association for the Advancement of Science.

Bjorndal, K. A. and Bolten, A. B. (2000). Proceedings of a Workshop on Assessing Abundance and Trends for In-Water Sea Turtle Populations, held at the Archie Carr Center for Sea Turtle Research University of Florida, Gainesville, Florida, 24-26 March 2000.

Bjorndal, K. A. and Bolten, A. B. (2003). From ghosts to key species: restoring sea turtle populations to fulfill their ecological roles. *Marine Turtle Newsletter,* 100(100), pp. 16-21

Bjorndal, K. A., Bolten, A. B. and Chaloupka, M. Y. (2005). Evaluating trends in abundance of immature green turtles, *Chelonia mydas*, in the greater Caribbean. *Ecological Applications,* 15(1), pp. 304-314

Bourjea, J., Ciccione, S. and Dalleau, M. (2013). DYMITILE–DYnamique MIgratoire des Tortues marines nidifiant dans les ILEs françaises de l'Océan Indien.

Bousquet, O., Dalleau, M., Bocquet, M., Gaspar, P., Bielli, S., Ciccione, S., Remy, E. and Vidard, A. (2020). Sea Turtles for Ocean Research and Monitoring: Overview and Initial Results of the STORM Project in the Southwest Indian Ocean. *Frontiers in Marine Science,* 7

Bowen, B. W., Bass, A. L., Soares, L. and Toonen, R. J. (2005). Conservation implications of complex population structure: lessons from the loggerhead turtle (*Caretta caretta*). *Mol Ecol,* 14(8), pp. 2389-402

Braun, J. and Epperly, S. P. (1996). Aerial surveys for sea turtles in southern Georgia waters, June 1991. *Gulf of Mexico Science,* 14(1), pp. 8

Brazier, W., Nel, R., Cliff, G. and Dudley, S. (2012). Impact of protective shark nets on sea turtles in KwaZulu-Natal, South Africa, 1981–2008. *African Journal of Marine Science,* 34(2), pp. 249-257

Campbell, L. M. (2003). Challenges for interdisciplinary sea turtle research: perspectives of a social scientist. *Marine Turtle Newsletter,* 100, pp. 28-32

Carr, A. F. (1954). The passing of the fleet. *AIBS Bulletin,* 4(5), pp. 17-19

Carr, A. F. (1987). New perspectives on the pelagic stage of sea turtle development. *Conservation Biology,* 1(2), pp. 103-121

Carr, A. F., Carr, M.H. and Meylan, A.B. (1978). The ecology and migrations of sea turtles. 7, The West Caribbean green turtle colony. *Bulletin of the AMNH,* v. 162

Casale, P. and Tucker, A. (2015). *Caretta caretta.* The IUCN Red List of Threatened Species 2015: e. T3897A83157651.

Chaloupka, M., Bjorndal, K. A., Balazs, G. H., Bolten, A. B., Ehrhart, L. M., Limpus, C. J., Suganuma, H., Troëng, S. and Yamaguchi, M. (2008). Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Global Ecology and Biogeography,* 17(2), pp. 297-304

Chaloupka, M. and Limpus, C. (2001). Trends in the abundance of sea turtles resident in southern Great Barrier Reef waters. *Biological Conservation,* 102(3), pp. 235-249

Chassagneux, A., Jean, C., Bourjea, J. and Ciccione, S. (2013). Unraveling behavioral patterns of foraging hawksbill and green turtles using photo-identification. *Marine Turtle Newsletter,* (137), pp. 1

Child, D. (1980) *Portrait of a Pioneer: The Letters of Sidney Turner from South Africa, 1864-1901.* Macmillan South Africa.

Christianen, M. J., Herman, P. M., Bouma, T. J., Lamers, L. P., van Katwijk, M. M., van der Heide, T., Mumby, P. J., Silliman, B. R., Engelhard, S. L., van de Kerk, M., Kiswara, W. and van de Koppel, J. (2014). Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. *Proc Biol Sci,* 281(1777), pp. 20132890

Costa, A., Motta, H., Pereira, M. A., Videira, E. J., Louro, C. M. and João, J. (2007). Marine Turtles in Mozambique: towards an effective conservation and management program. *Marine Turtle Newsletter,* 117, pp. 1-3

Dalleau, M., Bourjea, J. and Nel, R. (2020). Sea Turtles in the East Africa and the West Indian Ocean Region. *MTSG Annual Regional Report,*

Dalleau, M., Kramer-Schadt, S., Gangat, Y., Bourjea, J., Lajoie, G. and Grimm, V. (2019). Modeling the emergence of migratory corridors and foraging hot spots of the green sea turtle. *Ecol Evol,* 9(18), pp. 10317-10342

Deakos, M. H. (2010). Paired-laser photogrammetry as a simple and accurate system for measuring the body size of free-ranging manta rays *Manta alfredi*. *Aquatic Biology,* 10(1), pp. 1-10

Eckert, K., Bjorndal, K., Abreu-Grobois, F. and Donnelly, M. (1999). Priorities for research in foraging habitats. *Research and management techniques for the conservation of sea turtles,* 4, pp. 12-18

Estes, J. A., Duggins, D. O. and Rathbun, G. B. (1989). The ecology of extinctions in kelp forest communities. *Conservation Biology,* 3(3), pp. 252-264

Fennessy, S., Vincent, X., Budeba, Y., Mueni, E. and Gove, D. (2008). An update on initiatives to reduce prawn trawl bycatch in the western Indian Ocean. *Western Indian Ocean Journal of Marine Science,* 7(2)

FitzSimmons, N. N., Limpus, C. J., Norman, J. A., Goldizen, A. R., Miller, J. D. and Moritz, C. (1997). Philopatry of male marine turtles inferred from mitochondrial DNA markers. *Proceedings of the National Academy of Sciences,* 94(16), pp. 8912-8917

Fourqurean, J. W., Manuel, S., Coates, K. A., Kenworthy, W. J. and Smith, S. R. (2010). Effects of excluding sea turtle herbivores from a seagrass bed: Overgrazing may have led to loss of seagrass meadows in Bermuda. *Marine Ecology Progress Series,* 419, pp. 223-232

Frazier, J. (1974). Sea turtles in Seychelles. *Biological Conservation,* 6(1), pp. 71-73

Frazier, J. (1975). Marine turtles of the western Indian Ocean. *Oryx,* 13(2), pp. 164-175

Frazier, J. (1980). Exploitation of marine turtles in the Indian Ocean. *Human Ecology,* 8, pp. 329-370

Frazier, J. (2005). Marine turtles: the role of flagship species in interactions between people and the sea. *Mast*.

Fulanda, B., Ohtomi, J., Mueni, E., Nzuki, S., Muasa, J., Muthama, C. and Hossain, Y. (2007). A preliminary assessment of the green sea turtle *Chelonia mydas* population and its foraging grounds in Kilifi Creek, Kenya. *South Pacific Studies,* 28, pp. 31-41

Gullström, M., de la Torre Castro, M., Bandeira, S. O., Björk, M., Dahlberg, M., Kautsky, N., Rönnbäck, P. and Öhman, M. C. (2002). Seagrass Ecosystems in the Western Indian Ocean. *AMBIO: A Journal of the Human Environment,* 31(7), pp. 588-596

Hamann, M., Godfrey, M. H., Seminoff, J. A., Arthur, K., Barata, P. C. R., Bjorndal, K. A., Bolten, A. B., Broderick, A. C., Campbell, L. M., Carreras, C., Casale, P., Chaloupka, M., Chan, S. K. F., Coyne, M. S., Crowder, L. B., Diez, C. E., Dutton, P. H., Epperly, S. P., FitzSimmons, N. N., Formia, A., Girondot, M., Hays, G. C., Cheng, I. S., Kaska, Y., Lewison, R., Mortimer, J. A., Nichols, W. J., Reina, R. D., Shanker, K., Spotila, J. R., Tomás, J., Wallace, B. P., Work, T. M., Zbinden, J. and Godley, B. J. (2010). Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endangered Species Research,* 11(3), pp. 245-269

Harris, L. R., Nel, R., Oosthuizen, H., Meÿer, M., Kotze, D., Anders, D., McCue, S. and Bachoo, S. (2018). Managing conflicts between economic activities and threatened migratory marine species toward creating a multiobjective blue economy. *Conservation Biology,* 32(2), pp. 411-423

Harris, L. R., Nel, R., Oosthuizen, H., Meyer, M., Kotze, D., Anders, D., McCue, S. and Bachoo, S. (2015). Paper-efficient multi-species conservation and management are not always field-effective: The status and future of Western Indian Ocean leatherbacks. *Biological Conservation,* 191, pp. 383-390

Hays, G. C., Atchison-Balmond, N., Cerritelli, G., Laloe, J. O., Luschi, P., Mortimer, J. A., Rattray, A. and Esteban, N. (2022). Travel routes to remote ocean targets reveal the map sense resolution for a marine migrant. *J R Soc Interface,* 19(190), pp. 20210859

Hays, G. C., Cerritelli, G., Esteban, N., Rattray, A. and Luschi, P. (2020). Open Ocean Reorientation and Challenges of Island Finding by Sea Turtles during Long-Distance Migration. *Curr Biol,* 30(16), pp. 3236-3242 e3

Hays, G. C., Fossette, S., Katselidis, K. A., Mariani, P. and Schofield, G. (2010). Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. *J R Soc Interface,* 7(50), pp. 1319-27

Hays, G. C., Mortimer, J. A., Rattray, A., Shimada, T. and Esteban, N. (2021). High accuracy tracking reveals how small conservation areas can protect marine megafauna. *Ecological Applications,* 31(7), pp. e02418

Hendry, A. P., Castric, V., Kinnison, M. T., Quinn, T. P., Hendry, A. and Stearns, S. (2004). The evolution of philopatry and dispersal. *Evolution illuminated: salmon and their relatives*, pp. 52-91

Hickman, S. (2017) The genetic diversity and home populations of immature loggerhead (*Caretta caretta*), green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles frequenting South African waters. Honours thesis, Nelson Mandela University

Hornell, J. (1927) *The turtle fisheries of the Seychelles Islands.* HM Stationery Office.

Hughes, G. R. (1972). The olive ridley sea-turtle (*Lepidochelys olivacea*) in South-east Africa. *Biological Conservation,* 4(2), pp. 128-134

Hughes, G. R. (1973) The sea turtles of South East Africa.

Humber, F., Godley, B. J., Nicolas, T., Raynaud, O., Pichon, F. and Broderick, A. (2016). Placing Madagascar's marine turtle populations in a regional context using community-based monitoring. *Oryx,* 51(3), pp. 542-553

Huxley, R. (1999). Historical overview of marine turtle exploitation, Ascension Island, South Atlantic. *Marine Turtle Newsletter,* 84, pp. 7-9

Jackson, J. B. (1997). Reefs since columbus. *Coral Reefs,* 16, pp. S23-S32

Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science,* 293(5530), pp. 629-37

Jensen, M. P., Dalleau, M., Gaspar, P., Lalire, M., Jean, C., Ciccione, S., Mortimer, J. A., Quillard, M., Taquet, C., Wamukota, A., Leroux, G. and Bourjea, J. (2020). Seascape Genetics and the Spatial Ecology of Juvenile Green Turtles. *Genes (Basel),* 11(3)

Lagueux, C. J. (2001). Status and distribution of the green turtle, , in the Wider Caribbean Region. *Marine Turtle Conservation in the Wider Caribbean Region-A Dialogue for Effective Regional Management, Santo Domingo, Dominican Republic*, pp. 32-35

Lauret-Stepler, M., Bourjea, J., Roos, D., Pelletier, D., Ryan, P., Ciccione, S. and Grizel, H. (2007). Reproductive seasonality and trend of *Chelonia mydas* in the SW Indian Ocean: a 20 yr study based on track counts. *Endangered Species Research,* 3(2), pp. 217-227

León, Y. M. and Bjorndal, K. A. (2002). Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. *Marine Ecology Progress Series,* 245, pp. 249-258

León, Y. M. and Diez, C. E. (1999). Population structure of hawksbill turtles on a foraging ground in the Dominican Republic. *Chelonian Conservation and Biology,* 3(2), pp. 230-236

Luschi, P., Hays, G. C. and Papi, F. (2003). A review of long-distance movements by marine turtles, and the possible role of ocean currents. *Oikos,* 103(2), pp. 293-302

Malakoff, D. (1997). Extinction on the High Seas. *Science,* 277(5325), pp. 486-488

McClenachan, L., Jackson, J. B. and Newman, M. J. (2006). Conservation implications of historic sea turtle nesting beach loss. *Frontiers in Ecology and the Environment,* 4(6), pp. 290-296

Meekan, M. G., Bradshaw, C. J., Press, M., McLean, C., Richards, A., Quasnichka, S. and Taylor, J. G. (2006). Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. *Marine Ecology Progress Series,* 319, pp. 275-285

Meylan, A. B., Bowen, B. W. and Avise, J. C. (1990). A genetic test of the natal homing versus social facilitation models for green turtle migration. *Science,* 248(4956), pp. 724-727

Mortimer, J. A. (1984) *Marine Turtles in the Republic of the Seychelles: Status and Management: Report on Project 1809 (1981-1984).* IUCN.

Mortimer, J. A. and Balazs, G. H. Post-nesting migrations of hawksbill turtles in the granitic Seychelles and implications for conservation. *HJ Kalb and T. Wibbels, comps. Proceedings of the 19th Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-443*, 22-26.

Mortimer, J. A. and Donnelly, M. (2008). *Eretmochelys imbricata.* The IUCN Red List of Threatened Species 2008. e. T8005A12881238.

Mortimer, J. A., Esteban, N., Guzman, A. N. and Hays, G. C. (2020). Estimates of marine turtle nesting populations in the south-west Indian Ocean indicate the importance of the Chagos Archipelago. *Oryx,* 54(3), pp. 332-343

Mortimer, J. A., Von Brandis, R. G., Liljevik, A., Chapman, R. and Collie, J. (2011). Fall and rise of nesting green turtles (*Chelonia mydas*) at Aldabra Atoll, Seychelles: positive response to four decades of protection (1968–2008). *Chelonian Conservation and Biology,* 10(2), pp. 165-176

Muir, C. (2005). The status of marine turtles in the United Republic of Tanzania, East Africa. *Sea sense (Tanzania Turtle & Dugong Conservation Programme),* 35

Musick, J. A. and Limpus, C. J. (1997) Habitat utilization and migration in juvenile sea turtles, *The Biology of Sea Turtles, Volume I*: CRC Press, pp. 137-163.

Nel, R. and Casale, P. (2015). *Caretta caretta* (South West Indian Ocean Subpopulation). The IUCN Red List of Threatened Species 2015: e.T84199475A84199755.

Nel, R., Punt, A. E. and Hughes, G. R. (2013a). Are coastal protected areas always effective in achieving population recovery for nesting sea turtles? *PLoS One,* 8(5), pp. e63525

Nel, R., Wanless, R., Angel, A., Mellet, B. and Harris, L. (2013b). Ecological Risk Assessment and Productivity-Susceptibility Analysis of sea turtles overlapping with fisheries in the IOTC region. Unpublished report to the IOTC and IOSEA Marine Turtle MoU.

Okemwa, G. M., Nzuki, S. and Mueni, E. M. (2004). The status and conservation of sea turtles in Kenya.

Pandolfi, J. M., Bradbury, R. H., Sala, E., Hughes, T. P., Bjorndal, K. A., Cooke, R. G., McArdle, D., McClenachan, L., Newman, M. J., Paredes, G., Warner, R. R. and Jackson, J. B. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science,* 301(5635), pp. 955-8

Parsons, J. J. (1962). The green turtle and man.

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in ecology & evolution,* 10(10), pp. 430

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres Jr, F. (1998). Fishing down marine food webs. *Science,* 279(5352), pp. 860-863

Pereira, M., Fernandes, R., Videira, E., Louro, C. and Gonçalves, P. (2014). Celebrating 20 years of marine turtle tagging and monitoring in southern Mozambique. *African Sea Turtle Newsletter,* 2, pp. 31-33

Plug, I. (2004). Resource exploitation: animal use during the Middle Stone Age at Sibudu cave, KwaZulu-Natal: Sibudu cave. *South African Journal of Science,* 100(3), pp. 151-158

Provancha, J. and Stolen, E. (2008). Dugong aerial survey report, May 25–29, 2008. *Bazaruto Archipelago National Park, Inhambane Province, Mozambique. Final report for WWF. Dynamac Corporation Kennedy Space Center, FL, USA,* 29

Putman, N. F. and Mansfield, K. L. (2015). Direct evidence of swimming demonstrates active dispersal in the sea turtle "lost years". *Current Biology,* 25(9), pp. 1221-7

Putman, N. F., Scott, R., Verley, P., Marsh, R. and Hays, G. C. (2012). Natal site and offshore swimming influence fitness and long-distance ocean transport in young sea turtles. *Marine Biology,* 159(10), pp. 2117-2126

Rambaran, R. (2020) Defining the potential ecological roles of three sea turtle species (*Caretta caretta*, *Chelonia mydas* and *Eretmochelys imbricata*) along the Eastern seaboard of South Africa. Masters thesis, Nelson Mandela Metropolitan University

Rees, A. F., Alfaro-Shigueto, J., Barata, P. C. R., Bjorndal, K. A., Bolten, A. B., Bourjea, J., Broderick, A. C., Campbell, L. M., Cardona, L., Carreras, C., Casale, P., Ceriani, S. A., Dutton, P. H., Eguchi, T., Formia, A., Fuentes, M., Fuller, W. J., Girondot, M., Godfrey, M. H., Hamann, M., Hart, K. M., Hays, G. C., Hochscheid, S., Kaska, Y., Jensen, M. P., Mangel, J. C., Mortimer, J. A., Naro-Maciel, E., Ng, C. K. Y., Nichols, W. J., Phillott, A. D., Reina, R. D., Revuelta, O., Schofield, G., Seminoff, J. A., Shanker, K., Tomás, J., van de Merwe, J. P., Van Houtan, K. S., Vander Zanden, H. B., Wallace, B. P., Wedemeyer-Strombel, K. R., Work, T. M. and Godley, B. J. (2016). Are we working towards global research priorities for management and conservation of sea turtles? *Endangered Species Research,* 31, pp. 337-382

Reyne, M., Webster, I. and Huggins, A. (2017). A preliminary study on the sea turtle density in Mauritius. *Mar. Turt. Newsl,* 152, pp. 5-8

Robinson, N. J., Morreale, S. J., Nel, R. and Paladino, F. V. (2016). Coastal leatherback turtles reveal conservation hotspot. *Sci Rep,* 6, pp. 37851

Roman, J. and Palumbi, S. R. (2003). Whales before whaling in the North Atlantic. *Science,* 301(5632), pp. 508-510

Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G. and Fuller, R. A. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment,* 12(7), pp. 395-402

Sala, E. and Knowlton, N. (2006). Global Marine Biodiversity Trends. *Annual Review of Environment and Resources,* 31(1), pp. 93-122

Seminoff, J. A. (2004). *Chelonia mydas.* The IUCN Red List of Threatened Species 2004: e.T4615A11037468.

Shaver, D. J. (1994). Relative abundance, temporal patterns, and growth of sea turtles at the Mansfield Channel, Texas. *Journal of Herpetology*, pp. 491-497

Shillinger, G. L., Palacios, D. M., Bailey, H., Bograd, S. J., Swithenbank, A. M., Gaspar, P., Wallace, B. P., Spotila, J. R., Paladino, F. V., Piedra, R., Eckert, S. A. and Block, B. A. (2008). Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biol,* 6(7), pp. e171

Stoddart, D. R. (1971). Settlement, development and conservation of Aldabra. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences,* 260(836), pp. 611-628

Stoddart, D. R. (1984). Impact of man in the Seychelles.

Stokes, H. J., Mortimer, J. A., Laloë, J. O., Hays, G. C. and Esteban, N. (2023). Synergistic use of UAV surveys, satellite tracking data, and mark-recapture to estimate abundance of elusive species. *Ecosphere,* 14(3)

Taquet, C., Taquet, M., Dempster, T., Soria, M., Ciccione, S., Roos, D. and Dagorn, L. (2006). Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. *Marine Ecology Progress Series,* 306, pp. 295-302

Troëng, S. and Rankin, E. (2005). Long-term conservation efforts contribute to positive green turtle *Chelonia mydas* nesting trend at Tortuguero, Costa Rica. *Biological Conservation,* 121(1), pp. 111-116

Tucek, J., Nel, R., Girondot, M. and Hughes, G. (2014). Age-size relationship at reproduction of South African female loggerhead turtles *Caretta caretta*. *Endangered Species Research,* 23(2), pp. 167-175

van de Geer, C. H., Bourjea, J., Broderick, A. C., Dalleau, M., Fernandes, R. S., Harris, L. R., Inteca, G. E., Kiponda, F. K., Louro, C. M. M., Mortimer, J. A., Msangameno, D., Mwasi, L. D., Nel, R., Okemwa, G. M., Olendo, M., Pereira, M. A. M., Rees, A. F., Silva, I., Singh, S., West, L., Williams, J. L. and Godley, B. J. (2022). Marine turtles of the African east coast: current knowledge and priorities for conservation and research. *Endangered Species Research,* 47, pp. 297-331

van der Elst, R., Fennessy, S., Everett, B., Mackay, F., Floros, C., Schleyer, M., Kiszka, J., Bourjea, J. and Wanless, R. (2012). Mainstreaming biodiversity in fisheries management: a retrospective analysis of existing data on vulnerable organisms in the South West Indian Ocean. *Report prepared for the South West Indian Ocean Fisheries Project (SWIOFP). Oceanographic Research Institute, Durban, South Africa,*

van der Zee, J. P., Christianen, M. J. A., Nava, M., Velez-Zuazo, X., Hao, W., Berube, M., van Lavieren, H., Hiwat, M., Berzins, R., Chevalier, J., Chevallier, D., Lankester, M. C., Bjorndal, K. A., Bolten, A. B., Becking, L. E. and Palsboll, P. J. (2019). Population recovery changes population composition at a major southern Caribbean juvenile developmental habitat for the green turtle, *Chelonia mydas*. *Sci Rep,* 9(1), pp. 14392

von Brandis, R. G. (2010) The Ecology of Foraging Hawksbill Turtles (*Eretmochelys imbricata*) at D'Arros Island and St. Joseph Atoll in the Seychelles, Western Indian Ocean. Doctoral thesis, Tshwane University of Technology

von Brandis, R. G., Mortimer, J. A., Van De Geer, C. and Lea, J. S. (2017). A long migratory record for a small post-pelagic hawksbill. *Mar. Turt. Newsl,* 152, pp. 13-15

Wallace, B. P., DiMatteo, A. D., Hurley, B. J., Finkbeiner, E. M., Bolten, A. B., Chaloupka, M. Y., Hutchinson, B. J., Abreu-Grobois, F. A., Amorocho, D., Bjorndal, K. A., Bourjea, J., Bowen, B. W., Duenas, R. B., Casale, P., Choudhury, B. C., Costa, A., Dutton, P. H., Fallabrino, A., Girard, A., Girondot, M., Godfrey, M. H., Hamann, M., Lopez-Mendilaharsu, M., Marcovaldi, M. A., Mortimer, J. A., Musick, J. A., Nel, R., Pilcher, N. J., Seminoff, J. A., Troeng, S., Witherington, B. and Mast, R. B. (2010). Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS One,* 5(12), pp. e15465

Wallace, B. P., Tiwari, M. and Girondot, M. (2013a). *Dermochelys coriacea* (South West Indian Ocean subpopulation). The IUCN Red List of Threatened Species 2013: e.T46967863A46967866.

Wallace, B. P., Tiwari, M. and Girondot, M. (2013b). *Dermochelys coriacea*. The IUCN Red List of Threatened Species 2013: e.T6494A43526147.

Wamukoya, G., Mirangi, J., Ottichillo, W., Cockroft, V. and Salm, R. (1996). Report on the Marine aerial survey marine mammals, sea turtles, sharks and rays.

Weber, S. B., Weber, N., Ellick, J., Avery, A., Frauenstein, R., Godley, B. J., Sim, J., Williams, N. and Broderick, A. C. (2014). Recovery of the South Atlantic's largest green turtle nesting population. *Biodiversity and Conservation,* 23(12), pp. 3005-3018

Wildermann, N. E., Gredzens, C., Avens, L., Barrios-Garrido, H. A., Bell, I., Blumenthal, J., Bolten, A. B., Braun McNeill, J., Casale, P., Di Domenico, M., Domit, C., Epperly, S. P., Godfrey, M. H., Godley, B. J., González-Carman, V., Hamann, M., Hart, K. M., Ishihara, T., Mansfield, K. L., Metz, T. L., Miller, J. D., Pilcher, N. J., Read, M. A., Sasso, C., Seminoff, J. A., Seney, E. E., Willard, A. S., Tomás, J., Vélez-Rubio, G. M., Ware, M., Williams, J. L., Wyneken, J. and Fuentes, M. (2018). Informing research priorities for immature sea turtles through expert elicitation. *Endangered Species Research,* 37, pp. 55-76

Williams, J. L., Pierce, S. J., Rohner, C. A., Fuentes, M. M. and Hamann, M. (2017). Spatial distribution and residency of green and loggerhead sea turtles using coastal reef habitats in southern Mozambique. *Frontiers in Marine Science,* 3, pp. 288

Würsig, B. and Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. Report of the International Whaling Commission. (Special Issue 12), pp. 43

Zanre, R. (2005). Report on Watamu Turtle Watch's sea turtle bycatch release programme, Watamu, Kenya. Local Ocean Conservation, Watamu, Kenya.

1.7 Appendix

Appendix 1.1 Size classes of sea turtles on SWIO foraging grounds. Cm: green turtle; Ei: hawksbill; Cc: loggerhead; Dc: leatherback; n: sample size; SCL: straight carapace length; CCL: curved carapace length; NR: not reported; KZNSB: KwaZulu-Natal Sharks Board. Approximate conversion factor from SCL to CCL = 1.1 (von Brandis 2010).

Species	**Location**	**Study period**	**Method**	**n**	**SCL or CCL range (cm)**	**Mean ± SD SCL or CCL (cm)**	**Notes**	**Reference**
Cm	Turtle Cove, Diego Garcia, Chagos Archipelago	1996-2021	In-water captures	35	SCL: ± 35-57	NR	All juveniles	Stokes *et al*. 2023
Cm	N'Gouja Bay, Mayotte Island	2003	In-water captures	8	CCL: 70-109	CCL: 94.1 ± 11.6	All subadults and adults	Taquet *et al*. 2006
Cm	N'Gouja Bay, Mayotte Island	2004-2005	In-water captures	7 22	CCL: 39-58.5 CCL: 83-105	CCL: 48.9 ± 2.4 CCL: 94.5 ± 2.5	Distinguished between 'small' (< 80 cm CCL) and 'large' (> 80 cm CCL) individuals. Mostly large individuals.	Ballorain *et al*. 2010
Cm	Kilifi Creek, Kenya	2004-2005	In-water captures	64	CCL: 45-105	CCL: 69 ± 17	Mostly juveniles and subadults	Fulanda *et al*. 2007
Cm	Kenya	1998-2004	Caught in traditional fisheries bycatch	1169	CCL: 4.5-111.5	CCL: 45.7 ± 10.5	Mostly juveniles	Zanre 2005
Cm	Praia do Tofo, southern Mozambique	2011-2015	In-water sightings	218	CCL: 30-140*	CCL: 60 ± 20	Mostly juveniles and subadults	Williams *et al*. 2017
Cm	KZN coastline	1981-2008	KZNSB bycatch	318	CCL: 30-130	NR	Mostly subadults (n = ± 75 at 80 cm CCL)	Brazier *et al*. 2012
Cm	KZN coastline	2007-2016	KZNSB bycatch	13	CCL: 39.7-107.2 SCL: 33.9-84	CCL: 62.6 ± 19.7 SCL: 62 ± 14.2	Mostly subadults	Rambaran 2020
Cm	Sodwana Bay, South Africa	2013	In-water captures	5	CCL: 60.9-98.4	76.9 ± 17.2	Mostly subadults	Rambaran 2020
Ei	Turtle Cove, Diego Garcia, Chagos Archipelago	1996-2021	In-water captures	227	SCL: 29.7-75.8	SCL: 46.9 ± 9.5	Mostly juveniles, some subadults	Stokes *et al*. 2023
Ei	D'Arros Island, Seychelles	2006-2009	In-water captures In-water sightings	40 16	CCL: 32-85 CCL: 30-90*	CCL: 49 ± 14.3 CCL: 54.1 ± 14.2	Mostly juveniles (only n = 4 adults > 75 cm CCL, all males) Mostly juveniles	von Brandis 2010
Ei	Kenya	1998-2004	Caught in traditional fisheries bycatch	250	CCL: 3.9-85.4	CCL: 36.1 ± 16	Mostly juveniles	Zanre 2005
Ei	Praia do Tofo, southern Mozambique	2011-2015	In-water sightings	47	CCL: 30-115*	CCL: 60 ± 20	Mostly juveniles and subadults	Williams *et al*. 2017
Ei	KZN coastline	2007-2016	KZNSB bycatch	2	CCL: 37.2-48 SCL: 32.1-46.2	CCL: 42.6 ± 7.6 SCL: 39.2 ± 10	All juveniles	Rambaran 2020
Ei	Sodwana Bay, South Africa	2013	In-water captures	3	CCL: 44.6-80.6	68.9 ± 15.6	Juveniles and subadults	Rambaran 2020
Cc	Kenya	1998-2004	Caught in traditional fisheries bycatch	3	CCL: 68.5-96.8	CCL: 78.8	Mostly adults	Zanre 2005
Cc	Praia do Tofo, southern Mozambique	2011-2015	In-water sightings	324	CCL: 45-130*	CCL: 80 ± 20	Mostly adults	Williams *et al*. 2017
Cc	KZN coastline	1981-2008	KZNSB bycatch	986	CCL: 45-105	NR	Mostly subadults (n = ± 220 at 80 cm CCL)	Brazier *et al*. 2012
Cc	KZN coastline	2007-2016	KZNSB bycatch	27	CCL: 69.4-89.9 SCL: 68-86	CCL: 79.4 ± 6.3 SCL: 76.4 ± 5.3	Subadults and adults	Rambaran 2020
Dc	Praia do Tofo, southern Mozambique	2011-2015	In-water sightings	12	CCL: 60-200*	NR	Mostly adults	Williams *et al*. 2017
Dc	KZN coastline	1981-2008	KZNSB bycatch	124	CCL: 80-180	NR	Mostly adults (n = ± 26 at 150 cm CCL)	Brazier *et al*. 2012

*visual in-water estimates

Appendix 1.2 In-water relative abundance, abundance, and density estimates of sea turtles on SWIO foraging grounds. Cm: green turtle; Ei: hawksbill; Cc: loggerhead; Dc: leatherback; CMR: Capture-mark-recapture; UAV: uncrewed aerial vehicle; SPUE: Sightings per unit effort; CPUE: Catch per unit effort; KZNSB: KwaZulu-Natal Sharks Board; NR: not reported; n: sample size.

Species	**Location**	**Study period**	**Habitat**	**Method**	**Study site abundance (total number of individuals)**	**Relative abundance**	**Density (turtles/km^2)**	**Study site area (km^2)**	**Reference**
Cm	Turtle Cove, Diego Garcia, Chagos Archipelago	1996-2021	Shallow rocky tidal creeks, algae	CMR, UAV	31	NR	**24** (high water) - **45** (low water)	1.28 (high water) - 0.68 (low water)	Stokes *et al.* 2023
Cm	N'Gouja Bay, Mayotte Island	2004-2005	Seagrass meadows	CMR, snorkel surveys	NR	NR	23.9 x 10^{-4} ± 10^{-4} turtles/m^2 = **2.39 x 10^{-9} turtles/km^2**	~ 0.13	Ballorain *et al.* 2010
Cm	Kilifi Creek, Kenya	2004-2005	Seagrass beds and coral reef	CMR, dive surveys	NR	NR but 66 sightings, ± 80 hr survey time (4 hr at sea for 20 days) = **~ 0.83 turtles/hour**	NR but 66 sightings in ± 1.5km^2 = **~ 4.4 turtles/km^2**	~ 1.5	Fulanda *et al.* 2007
Cm	Praia do Tofo, southern Mozambique	2011-2015	Rocky reef, low hard coral diversity	SPUE, photo-ID, citizen science	22	0.15 turtles/hour (n = 157, h = 1055)	NR	~ 400	Williams *et al.* 2017
Cm	KZN coastline	1981-2008	Neritic zone	CPUE (KZNSB bycatch)	NR	0.32 turtles/km of net/yr (n = 334)	NR	NR but ~ 44 km coastline	Brazier *et al.* 2012
Cm and Ei	Mahebourg Bay, Mauritius	2013-2014	Coral reef	Boat transects	5 (95% CI: 1-21)	NR	0.20*	25	Reyne *et al.* 2017
Cm and Ei	North Mauritius	2013-2014	Coral reef	Boat transects	7 (95% CI: 4-13)	NR	0.40*	17	Reyne *et al.* 2017
Cm and Ei	Grand Bay-Port Louis, Mauritius	2013-2014	Coral reef	Boat transects	70 (95% CI: 42-116)	NR	0.88*	80	Reyne *et al.* 2017
Ei	Turtle Cove, Diego Garcia, Chagos Archipelago	1996-2021	Shallow rocky tidal creeks, algae	CMR, UAV	308 (95% CI: 258-358)	NR	**241** (high water) - **454** (low water)	1.28 (high water) - 0.68 (low water)	Stokes *et al.* 2023
Ei	Chalet platform reef, D'Arros Island, Seychelles	2006-2009	Coral reef	SPUE, photo-ID	16	4.2 turtles/hour (n = 827, h = 178)	Based on mean sightings: 3.95 turtles/ha = **0.04 turtles/km^2** Based on minimum density: 9 turtles/ha = **0.09 turtles/km^2**	~ 0.01	von Brandis 2010
Ei	Reef flat, D'Arros Island, Seychelles	2006-2009	Shallow reef flat encircling island	CMR	35	2.1 turtles/hour (n = 32, h = 15)	0.17 turtles/ha = **1.7 x 10^{-3} turtles/km^2**	~ 0.15	von Brandis 2010
Cc	Praia do Tofo, southern Mozambique	2011-2015	Rocky reef, low hard coral diversity	SPUE, photo-ID, citizen science	42	0.2 turtles/hour (n = 210, h = 1055)	NR	~ 400	Williams *et al.* 2017
Cc	KZN coastline	1981-2008	Neritic zone	CPUE (KZNSB bycatch)	NR	1.11 turtles/km of net/yr (n = 1146)	NR	NR but ~ 44 km coastline	Brazier *et al.* 2012
Dc	KZN coastline	1981-2008	Neritic zone	CPUE (KZNSB bycatch)	NR	0.14 turtles/km of net/yr (n = 150)	NR	NR but ~ 44 km coastline	Brazier *et al.* 2012

Chapter 2: The relative abundance, demographics and distribution of sea turtles on reefs along the east coast of South Africa

2.1 Abstract

South Africa holds a significant portion of the SWIO loggerhead and leatherback populations underpinned by long-term research and conservation efforts on nesting beaches, yet the in-water lives of these species and non-nesting green and hawksbill turtles in adjacent neritic habitats remains cryptic. This study provides the first in-water estimates of relative abundance, demographics and spatial distribution of sea turtles in two MPAs (iSimangaliso and Aliwal Shoal) on the east coast of South Africa. Over a two-year period, a total of 1057 sea turtle sightings were recorded from timed research surveys (supplemented by voluntourism), citizen science contributions and opportunistic sightings in the two MPAs, from which 227 individual sea turtles were photo-identified (green turtles: n = 120; hawksbills: n = 46; loggerheads: n = 61). Mean (± SD) sightings per unit effort (SPUE) from timed research surveys was highest for green turtles at all sites (iSimangaliso: 2.2 ± 4.47 turtles/hour, n = 263; Aliwal Shoal: 1.2 ± 1.98 turtles/hour, n = 60). Hawksbills had a higher mean SPUE at Aliwal Shoal (0.8 ± 1.35 turtles/hour, n = 48) than iSimangaliso (0.2 ± 1.20 turtles/hour, n = 32) whilst loggerheads had similar mean SPUEs (iSimangaliso: 0.5 ± 1.54 turtles/hour, n = 65; Aliwal Shoal: 0.5 ± 1.16 turtles/hour, n = 36). Reefs support aggregations of mixed size classes; green turtles ranged from juveniles to adult-sized with SCLs of 44.9–99.2 cm, hawksbills were mostly juveniles or subadults (SCL range: 37.4–73.4 cm) and loggerheads were mostly adult-sized (SCL range: 66.9–81 cm). The adult sex ratios of green turtles and loggerheads were slightly female-biased but not significantly different from 1:1. The longest minimum residence periods recorded to date for individual subadult green and hawksbill turtles (676 and 675 days respectively) and adult-sized loggerheads (621 days) were highly indicative of residency. Green turtles, hawksbills and loggerheads displayed strong site fidelity with individuals resighted up to 19, 10 and 11 times respectively on the same reef over the two-year study period. Citizen science data were particularly useful in revealing a wider distribution of sea turtles along the entire South African coastline than currently recognised. This study highlights the importance of SWIO rookery output in influencing neritic habitats along the east coast of South Africa and provides novel insights into in-water sea turtle biology for understudied populations that may inform effective species-specific management and conservation strategies.

2.2 Introduction

Studying individuals in a population is essential to all ecological studies. Almost all global sea turtle research has been underpinned by the use of flipper tags to identify individuals (Balazs 1999), particularly on nesting beaches where they are easily accessible (e.g., Hughes 1973), but also on foraging grounds where they spend most of their time (e.g., Bjorndal *et al.* 2005). Identifying individuals not only allows for population abundance estimates to be made (e.g., Chaloupka and Limpus 2001), but coupled with records of location and size, allows the history of individual sea turtles to be retraced with each recapture. This provides valuable information on aspects such as internesting intervals within a nesting season and breeding remigration intervals (e.g., Hughes 1973), oceanic movements (e.g., von Brandis *et al.* 2017) and growth rates (e.g., Le Gouvello *et al.* 2020). Given the challenges associated with such capture-mark-recapture (CMR) studies at sea relative to nesting beaches (i.e., the difficulty of locating animals, resource- and labour-intensive nature, and stress of physical capture; Eckert *et al.* 1999), as well as flipper tag loss (Mrosovsky 1976), knowledge of sea turtles on foraging grounds is limited globally (Bjorndal and Bolten 2000).

These challenges, however, have been significantly reduced by the relatively recent discovery of unique postocular scutes of sea turtles that allow individuals to be photo-IDed (Bennett and Keuper-Bennett 2001), eliminating the need for physical capture. The postocular scute patterns of sea turtles have displayed stability over several years (e.g., Reisser *et al.* 2008; Dunbar *et al.* 2014) with the longest study to date finding no significant pattern changes on wild juvenile and adult-sized green turtles over 11 years (Carpentier *et al.* 2016). These features are easily photographed whilst free diving or SCUBA diving with minimal disturbance to animals. The use of photo-ID to gather information on sea turtle abundance, growth rates, movements, residency, site fidelity and home ranges on foraging grounds has thus proliferated worldwide and shown great successes (e.g., von Brandis 2010; Chassagneux *et al.* 2013; Williams *et al.* 2017; Araujo *et al.* 2019).

Since photo-ID for sea turtles requires only an underwater camera and minimal instructions (just that a clear photograph of each facial profile needs to be obtained), recreational divers can easily photo-ID sea turtles and thus contribute to scientific research (Williams *et al.* 2015). Citizen science provides significant benefits to scientific research through cost-effective large-scale data collection over broad areas and long time periods (Montagna *et al.* 2017). What may make citizen science particularly successful to sea turtle research is that the intrinsic charismatic nature of these animals naturally attracts recreational divers to reefs to photograph them. The success of citizen science in sea turtle research has already been demonstrated worldwide (e.g., Bell *et al.* 2008; Williams *et al.*

2015; Mancini and Elsadek 2019; Hanna *et al.* 2021) and has not only contributed to increased knowledge but has also fostered a greater awareness and appreciation for marine animals and ecosystems by members of the public (Jean *et al.* 2010). Recent advancements in the availability and quality of waterproof action cameras, internet and technology that partially automates the photo-ID process have further made it easier for researchers and citizen scientists to collect data over large scales and areas (Read and Jean 2021). This has resulted in large-scale databases such as the 'Internet of Turtles' (http://iot.wildbook.org/; Berger-Wolf *et al*. 2017) which, over time, are likely to fill large knowledge gaps that exist for sea turtles on foraging grounds globally.

The northeastern coastline of South Africa supports a significant portion of the largest SWIO loggerhead and leatherback rookeries, which have been the focus of almost six decades of robust research and successful conservation efforts (Nel *et al.* 2013a). However, little is known about the in-water lives of these species. Even less is known about non-nesting green and hawksbill turtles that are known to frequent these waters based on historic anecdotal records (Turner 1867 as cited in Child 1980), bycatch in KZN Sharks Board (KZNSB) bather protection nets (Brazier *et al.* 2012), anecdotal reports from recreational divers and fishermen (R. Nel, pers. comm.), and a recent satellite tracking study indicating their residency in Sodwana Bay, northern KZN (Rambaran 2020).

Genetic analyses have, however, indicated that locally stranded and bycaught juvenile green turtles originate from Îles Éparses and Ascension Island, and juvenile hawksbills originate from Seychelles (Hickman 2017), which supports evidence that SWIO rookery size and hatchling dispersal via ocean currents influences the composition of east African foraging grounds (Jensen *et al.* 2020). It is thus suspected that local sea turtle relative abundance is proportional to the rookeries they come from, and that size class distribution follows that of regional foraging grounds where mixed green turtle aggregations (Fulanda *et al.* 2007; Ballorain *et al.* 2010; Williams *et al.* 2017), immature hawksbills (von Brandis 2010; Williams *et al.* 2017) and adult loggerheads (Williams *et al.* 2017) are present.

There is a significant research opportunity to use in-water methods to study sea turtles on the east coast of South Africa for the first time whilst taking advantage of recreational divers (citizen scientists) and voluntourism (Campbell and Smith 2006) through a non-government organisation (Sharklife) in local world-renowned diving destinations. This may provide novel insight into the cryptic in-water lives of sea turtles in local neritic habitats which may fill significant knowledge gaps and inform effective species-specific management and conservation strategies (Hamann *et al.* 2010; Rees *et al.* 2016; Wildermann *et al.* 2018; van de Geer *et al.* 2022).

This chapter thus aims to provide the first estimates of in-water relative abundance, demographics and spatial distribution of sea turtles on the east coast of South Africa. The objectives are to describe and compare the relative abundance, size distribution, sex ratios, local distribution, residency and site fidelity among sea turtle species in the iSimangaliso and Aliwal Shoal MPAs using a photo-ID dataset collected by timed research surveys (supplemented by voluntourism), citizen scientists and opportunistic sightings. It is hypothesised that 1) relative abundance will be proportional to the nesting female abundance in the SWIO (Cm > Ei > Cc > Dc > Lo); 2) the size classes of non-nesting species (green turtles and hawksbills) will be dominated by juveniles, and size classes of nesting species (loggerheads and leatherbacks) will be dominated by adults; but that 3) adult sex ratios will be balanced (1 male: 1 female) for all species; and 4) juveniles of all species will have longer residence periods than adults.

2.3 Materials and methods

2.3.1 Study sites

Sea turtle populations on the KZN coastline on the east coast of South Africa (Fig. 2.1), were assessed over a two-year period from September 2020 to August 2022. There are two marine ecoregions along this coastline, namely the Delagoa ecoregion extending from Cape Vidal (northern KZN coast) northwards to Mozambique and Natal ecoregion extending from Cape Vidal southwards to the Eastern Cape (Sink *et al.* 2019, Fig. 2.1). The Delagoa ecoregion is characterised by warm, clear oligotrophic waters resulting from the Agulhas current, narrow continental shelf and absence of riverine input (Porter *et al.* 2017). It is considered a transition zone between subtropical and tropical coastal waters where flourishing coral communities on top of fossilised dunes do not form accretive coral reefs (Schleyer and Porter 2018). The Natal ecoregion is considered a subtropical region (Sink *et al.* 2019) characterised by higher turbidity and riverine input (De Lecea *et al.* 2013) with algal-dominated reefs.

The humid subtropical climate on the KZN coastline (Hunter 1988) and warm water temperatures make it an ideal area for year-round diving. Recreational divers frequent reefs in two MPAs within these ecoregions, namely the iSimangaliso MPA in northern KZN (mostly Delagoa ecoregion), where water temperatures range from 21–31 °C, and the Aliwal Shoal MPA in southern KZN (Natal ecoregion) where water temperatures range from 19–28°C (Fig. 2.1). Reefs within these MPAs were chosen as study sites (Fig. 2.1) due to their representation of each distinct ecoregion, ease of access, and regular sea turtle sighting reports by recreational divers. Consistent sampling throughout the two-year study period was occasionally limited by weather and practical constraints.

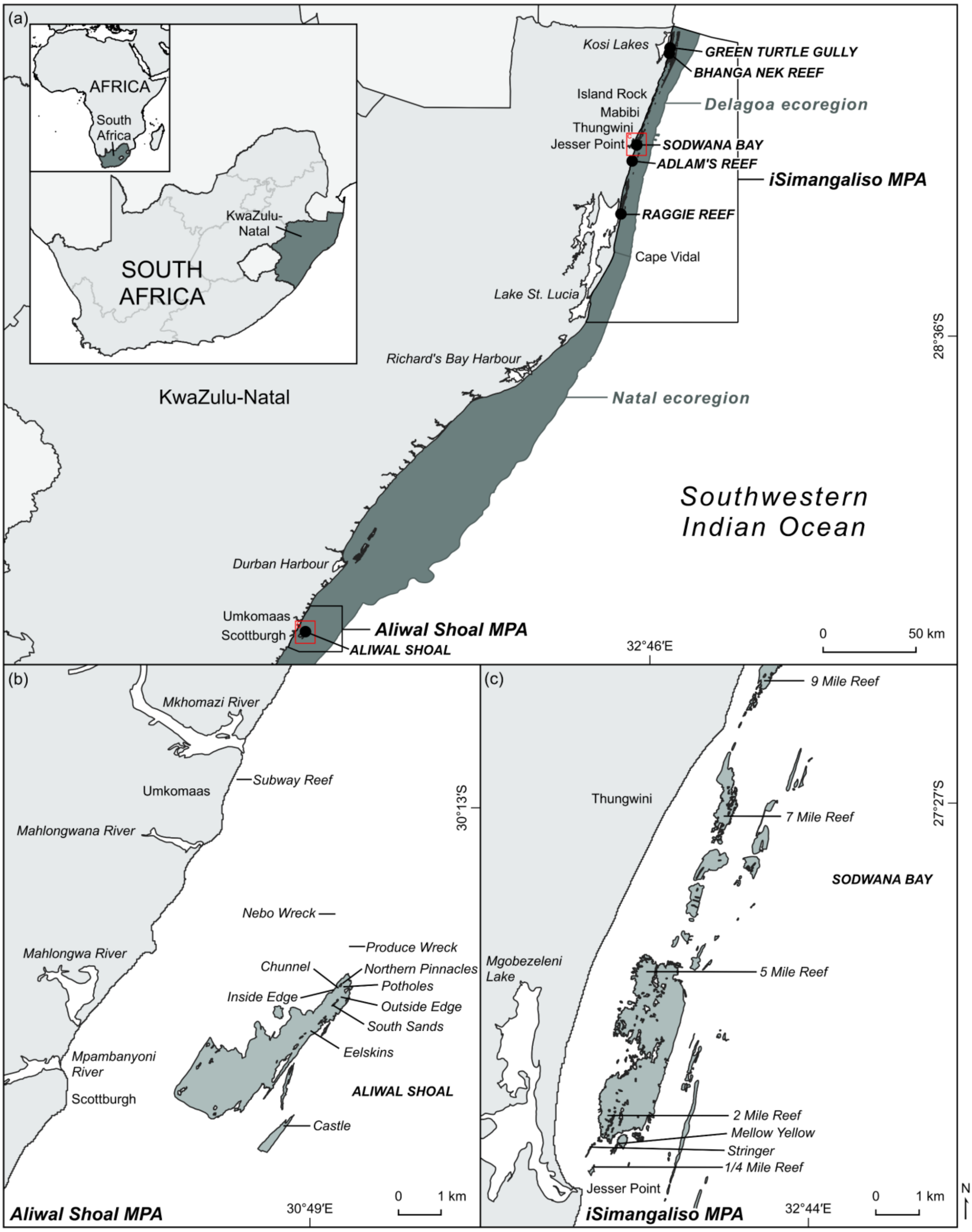


Figure 2.1 (a) Map of KwaZulu-Natal (KZN) on the east coast of South Africa showing the Delagoa and Natal marine ecoregions (dark grey) split at Cape Vidal. Study sites (marked by black circles) in the iSimangaliso MPA are situated within the Delagoa ecoregion and the Aliwal Shoal MPA is situated within the Natal ecoregion. Detailed maps of the two most frequently dived study sites in each MPA, (b) Aliwal Shoal and (c) Sodwana Bay are shown. Scales differ between maps.

iSimangaliso MPA

Scheduled sampling in iSimangaliso took place at Sodwana Bay and Raggie Reef, with three other sites sampled opportunistically; Green Turtle Gully, Bhanga Nek Reef and Adlam's Reef. Green Turtle Gully was the northernmost study site in the MPA, located ~ 14 km south of Mozambique (Fig. 2.1a). This small site (~ 0.02 km^2) consists of a series of subtidal sandy gullies in shallow rock pools (± 0.5–5 m depth, Fig. 2.2a, b) and was sampled opportunistically on spring low tide at night over January and February 2022 (2.5 total hours). The site has been visited every summer since 2019 and is often frequented by sea turtles (pers. obs.). Human disturbance is extremely low with only a few local fishermen using the rocks as a platform to fish deeper waters at low tide (pers. obs.).

Bhanga Nek Reef, situated ~ 3.5 km south of Green Turtle Gully (Fig. 2.1a), is a small (~ 0.07 km^2) rocky reef off Bhanga Nek beach with a shallow flat section (± 4 m depth) covered in algae, encrusting sponges and zoanthids (Fig. 2.2c), and a slightly deeper section (± 8 m depth) with scattered reef and boulders (Fig. 2.2d). This reef was sampled opportunistically over December 2021 and January and February 2022 (3.3 total hours) but has been visited every summer by sea turtle researchers who frequently observe turtles (pers. obs.). The reef is only minimally disturbed by humans in summer when a few recreational fishermen and snorkelers are in the area (pers. obs.).

Sodwana Bay to the south lies close to iSimangaliso's centre (Fig. 2.1a) and consists of an aeolianite reef complex running north-east parallel to the coast from Jesser Point (Anderson *et al.* 2005) (Fig. 2.1c). The reefs vary in topography and depth (± 5–35 m depth) and are covered in a thin veneer of hard and soft corals, sponges and algae (Ramsay and Mason 1990) (Fig. 2.2e). Reefs are named according to their distance north from Jesser Point, the boat launch site: Quarter Mile (~ 1.49 x 10^{-3} km^2), Two Mile (~ 1.9 km^2), Five Mile (~ 2.5 km^2), Seven Mile (~ 0.005 km^2) and Nine Mile (~ 0.6 km^2) (Fig. 2.1c). Over the two-year study period, reefs were sampled almost daily (weather-permitting) by Sharklife alongside elasmobranch surveys (126.6 total hours) with the highest effort near Quarter Mile and Two Mile reefs. As an internationally renowned diving destination, Sodwana Bay has high levels of human disturbance and frequent sea turtle sighting reports by recreational divers.

Adlam's Reef, situated ~ 9 km south of Jesser Point (Fig. 2.1a), is a flat, algal-dominated rocky reef (± 8–12 m depth, ~ 0.03 km^2) interspersed between sand channels and seagrass beds (Fig. 2.2f). Adlam's Reef was sampled opportunistically over March and June 2021 and January–March 2022 (3.2 total hours). The reef is frequented by green turtles (pers. obs.) and is minimally disturbed by humans.

Raggie Reef was the southernmost reef sampled in iSimangaliso, situated ~ 40 km south of Jesser Point in a long-term sanctuary zone (Fig. 2.1a). It is typical of Sodwana Bay reefs (Fig. 2.2g) but in pristine condition due to decades of protection restricting all human activities. The northernmost reef section and sand-reef interface (± 11–13 m, ~ 0.02 km^2) was sampled weekly (weather-permitting) by Sharklife over the two-year study period (59.9 total hours). A Remote Underwater Video (RUV) system (Fig. 2.2h) monitors elasmobranchs here and frequently captures sea turtle footage. Raggie Reef has no human disturbance other than weekly monitoring surveys by Sharklife.

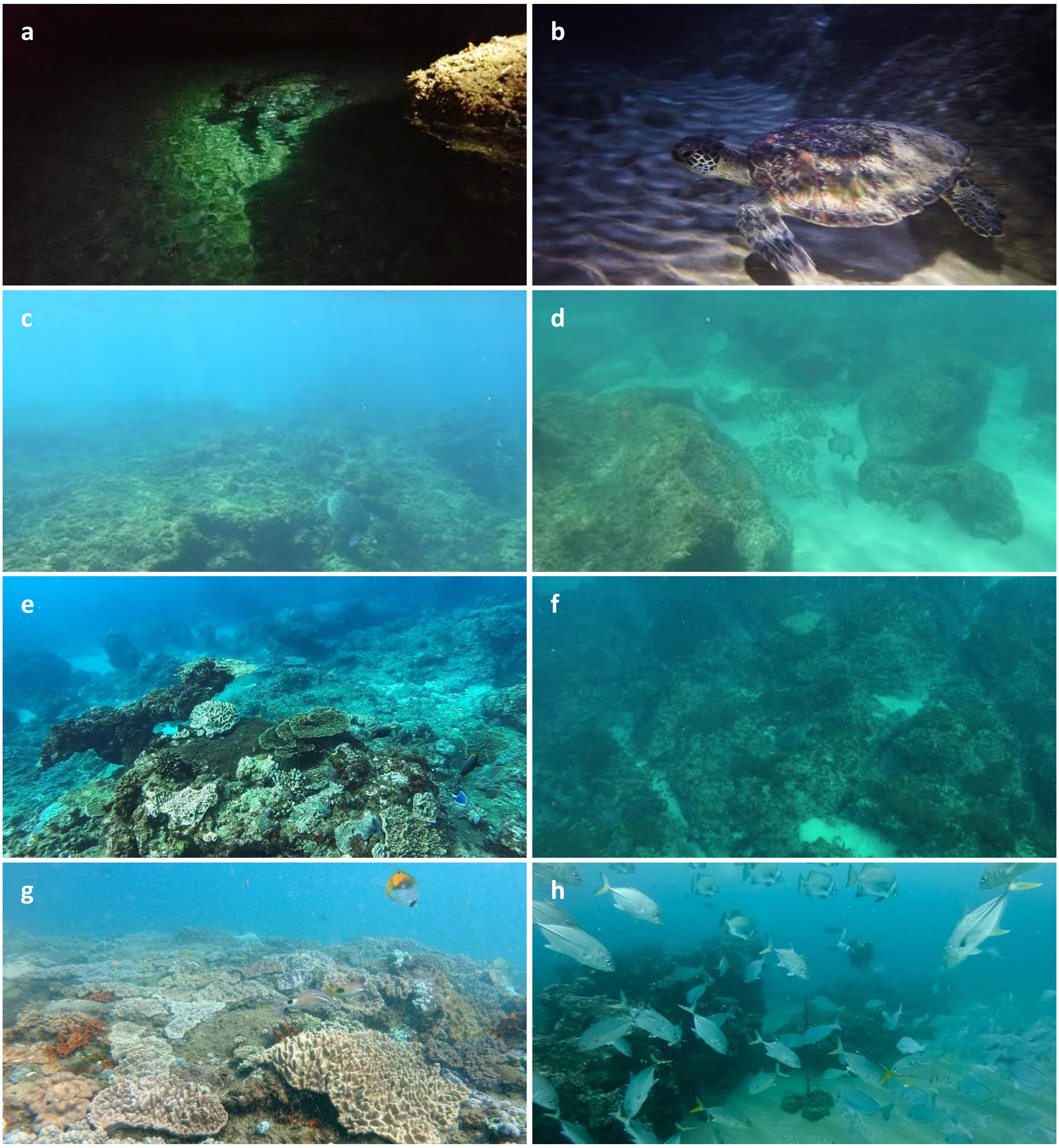


Figure 2.2 Study sites in iSimangaliso. (a) Green Turtle Gully above and (b) below the water; (c) Bhanga Nek Reef's shallow section and (d) deeper section; (e) typical Sodwana Bay reef; (f) Adlam's scattered reef; (g) Raggie Reef epibenthos and (h) sand-reef interface with RUV system. Photographer: Grant Smith (f).

Aliwal Shoal MPA

Aliwal Shoal reef lies roughly four kilometres offshore of Umkomaas on the southern KZN coastline and consists primarily of aeolianite reef running north-east parallel to the coast (Bosman *et al.* 2005) (Figure 2.1a, b). This reef has very rugose topography with shallow pinnacle ridges (Fig. 2.3a) and deep reef slopes (± 5–35 m depth) (Fig. 2.3b). Sampling focused on the shallow northern section (± 5–22 m depth, ~ 2.1 km^2) but the total area of reef is > 5.6 km^2 (Bosman *et al.* 2005). This shallow northern section is algal-dominated but also hosts a high diversity of sponges and some hard and soft corals (Fig. 2.3a, b) (Olbers *et al.* 2009). Aliwal Shoal was sampled almost weekly (weather-permitting) over the two-year study period (69.4 total hours). Being the other internationally renowned diving destination on the KZN coastline, the reef experiences high levels of human disturbance and recreational divers frequently report sea turtle sightings.

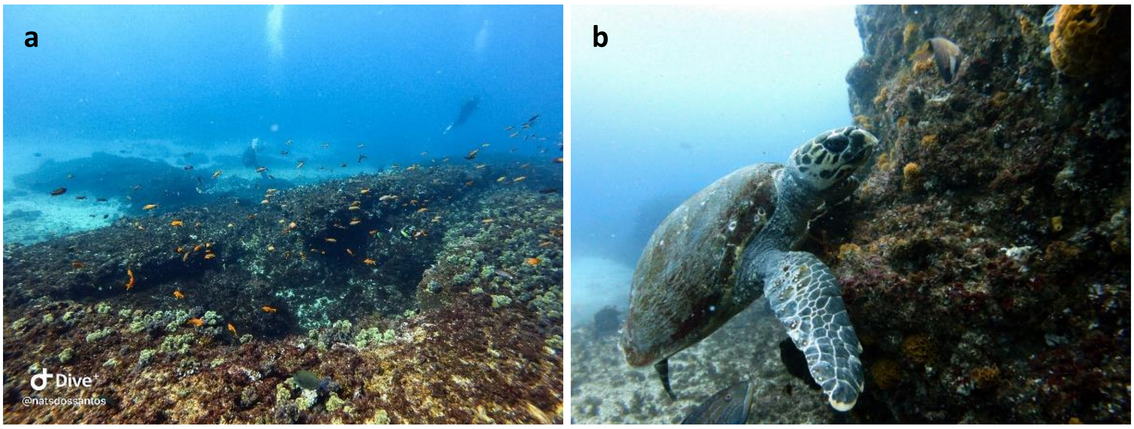


Figure 2.3 Aliwal Shoal study site. Algal-dominated (a) shallow reef near pinnacle ridges and (b) reef slope.

2.3.2 In-water data collection

Timed research surveys

Timed research surveys were undertaken and supplemented by Sharklife voluntourism surveys, citizen science contributions and opportunistic sightings. Timed searches, measured from entering to exiting the water in minutes, were conducted on study sites by one or two trained observers who searched for sea turtles at a relatively constant rate whilst freediving or SCUBA diving. Dives took place in the morning or early afternoon depending on weather conditions. When a sea turtle was encountered, the species was identified (see Appendix 2.1 for identification guide), time was recorded and a camera (GoPro HERO6 Black/Olympus Tough TG-6 in Sea Frogs waterproof housing) was used to capture photos of both the unique left and right postocular scutes whenever possible to allow individuals to be identified (Fig. 2.4) as per Schofield *et al*. (2008). Photos of the carapace and any other unique characteristics were also taken as other identifying features. Observers were trained to approach sea turtles slowly from alongside whenever possible to minimise disturbance.

Figure 2.4 Observer photographing a green turtle's right postocular scutes from alongside with minimal disturbance to the animal. Photographer: Grant Smith.

The straight carapace length (SCL in cm, notch to tip, Appendix 2.1) was visually estimated and categorised as juvenile (<60 cm), subadult (60–80 cm: hawksbills and loggerheads; 60–90 cm: green turtles), or adult-sized (adult)[1] (>80 cm: hawksbills and loggerheads; >90 cm: green turtles; >140 cm: leatherbacks) based on global and regional literature (Hughes 1973; Chaloupka and Limpus 2001; Casale *et al.* 2005; Avens and Snover 2013; Stokes *et al.* 2023; see Appendix 1.1 for regional literature summary and Fig. 2.5 for examples of observed size classes). Observers used their own known body lengths when swimming beside animals to assist with visual SCL estimation (e.g., length from fingertips to elbow ~ 40 cm; see diagram in Appendix 2.2). The sex of adult-sized sea turtles was visually determined based on the presence of secondary sexual characteristics in males (Wibbels 1999; Casale *et al.* 2005), namely a large tail extending past the hind flippers (Fig. 2.5d, j, l). The sex of immature sea turtles cannot be determined visually. The presence or absence of flipper tags on sea turtles was also recorded on each encounter. On each survey, the date, location, start time and duration (minutes) were recorded irrespective of sea turtle sightings for effort calculations.

---

[1] Please note that adult-sized sea turtles are occasionally referred to as adults in this study, but sexual maturity was not confirmed. Sea turtles reach sexual maturity at a variety of sizes based on various factors influencing growth rates and life stage durations (Avens and Snover 2013).

Figure 2.5 Examples of observed size classes and sex of green turtles (a–d), hawksbills (e–g), loggerheads (h–j) and leatherbacks (k, l) on the east coast of South Africa in the two-year study period. Size classes were based on visual SCL (cm) estimates (juveniles: <60; subadult hawksbills and loggerheads: 60-80; subadult green turtles: 60-90; adult-sized hawksbills and loggerheads: >80; adult-sized green turtles: >90; adult-sized leatherbacks: >140) as per regional and global literature. Adult-sized sea turtle sex was determined by tail length. No adult male hawksbills, juvenile loggerheads or immature leatherbacks were observed in the two-year study period. Photographers: Michael Tarr (f, h), Samantha Kruger (i, j) and Sharklife (k, l).

Since observers may overestimate sea turtle size due to light refraction making objects appear larger and closer, a subsample of sea turtles at each site was measured using paired-laser photogrammetry for comparison to visual estimates. Using a design and methods adapted from Deakos (2010) and Rohner *et al*. (2011), a paired-laser photogrammetry rig consisting of a steel bracket mounting two green lasers (OceanCo Shark Lasers) 50 cm apart in parallel with an underwater camera (Olympus Tough TG-6 in Sea Frogs waterproof housing) was custom-made (Fig. 2.6a). The rig was pointed perpendicular to sea turtle carapaces underwater from ~ 2–4 m away (Fig. 2.6b) to project parallel beams of light onto them, creating a 50 cm scale bar visible in photographs (Fig. 2.6c) which allowed SCL to be extrapolated digitally. The steel bracket allowed each laser to be adjusted both vertically and horizontally to achieve precise parallel alignment. The rig was calibrated on land before each dive by lining up the laser beams on two points 50 cm apart from two, five and eight metres away with > 0.2 cm accuracy (as adapted from Deakos 2010; Rohner *et al.* 2011).

Whilst paired-laser photogrammetry is minimally invasive in comparison to the physical capture of sea turtles for morphometric measurements, free-swimming sea turtles had to be approached from above rather than alongside, which usually causes disturbance (pers. obs.). The observer therefore positioned the bulk of their body above and slightly behind each sea turtle's head to minimise disturbance whilst measuring them (Fig. 2.6b). Sea turtles were never 'chased' if they showed signs of disturbance like increased swimming speed. Lasers were also never pointed into the eyes of any animals and turned off when not in use during dives. Paired-laser photogrammetry measurements were supplemented by SCL measurements using callipers when sea turtles were caught at Sodwana Bay and Green Turtle Gully for other studies.

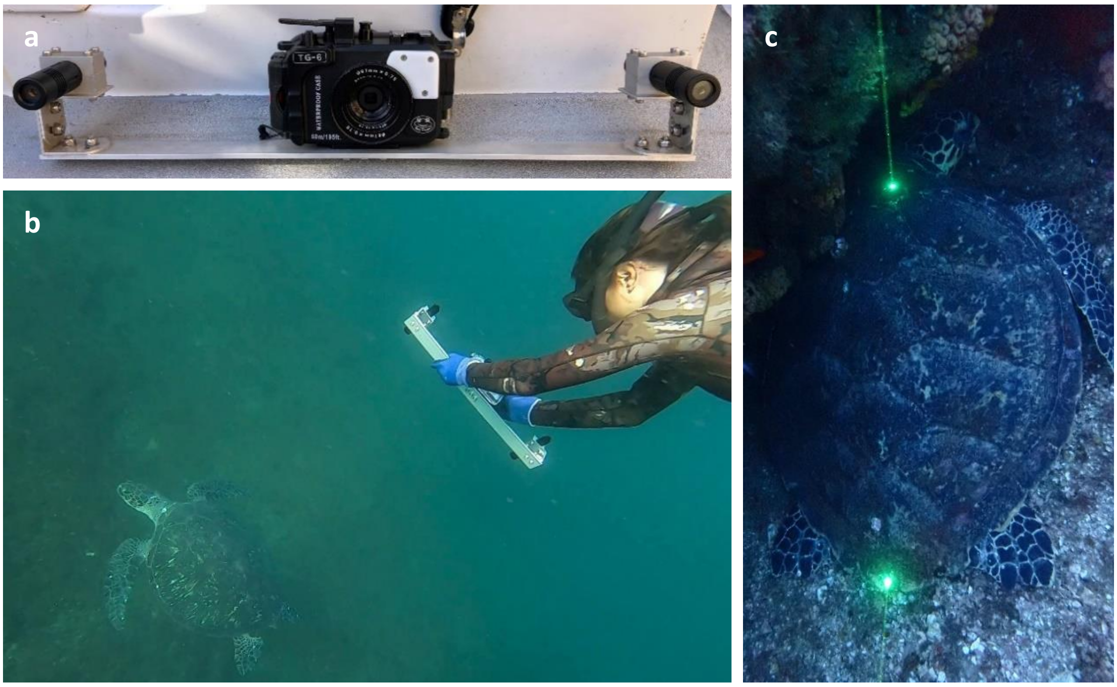


Figure 2.6 (a) The custom-made paired-laser photogrammetry rig with lasers mounted in parallel with an underwater camera housing. (b) Using paired-laser photogrammetry to measure sea turtle SCL underwater with minimal disturbance. (c) Laser points projected onto the carapace of a juvenile hawksbill from which an SCL measurement can be digitally obtained. Photographer: Michael Tarr (b).

Citizen science

Public presentations at dive centres and word of mouth were used to encourage recreational divers and fishermen to share information about sea turtle sightings through citizen science (see Appendix 2.2) to supplement data collected on timed research surveys. Citizen scientists were required to report mandatory information via email, instant messaging applications or social media, namely the date, time and location of sightings and photos of the left and right postocular scutes and carapace. Data contributions from citizen scientists were not accepted without footage for a single researcher (myself) to verify species, size class and sex, as recommended by Williams *et al*. (2015).

Opportunistic sightings

Sea turtles that were sighted on the surface from boats travelling to or from reefs for timed research surveys were considered opportunistic sightings where species and size class were recorded and photo-IDs taken whenever possible. Footage of sea turtles captured on RUVs (e.g., Fig. 2.7c) used primarily to monitor elasmobranchs on Raggie Reef (and occasionally Seven Mile Reef and Quarter Mile Reef in Sodwana Bay) was also included in the study. The RUV system, designed by Sharklife, consisted of two GoPro cameras placed perpendicular to one another (for wider field of view) and two batteries mounted on a steel frame anchored to the benthos (Fig. 2.7a, b). The batteries allowed the RUV to capture photos every few seconds for about a week.

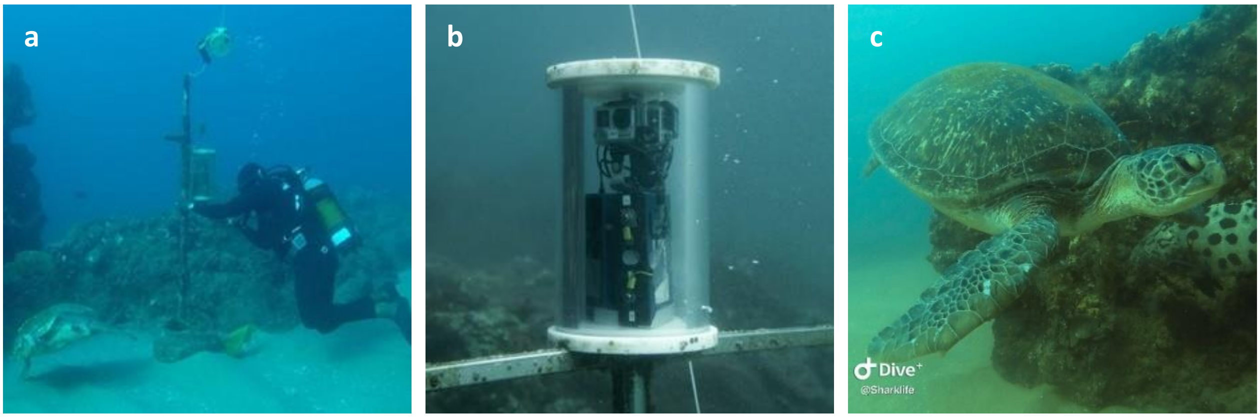


Figure 2.7 (a) The RUV system anchored on Raggie Reef; (b) close-up of the cameras and batteries in the RUV system; (c) example of RUV footage capturing a green turtle on Raggie Reef, allowing this individual to be photo-IDed. Photographer: Sharklife (b).

Baited RUV (BRUV) systems (Fig. 2.8a) are also often deployed in iSimangaliso for elasmobranch research by Sharklife. These BRUVs are deployed on the benthos for an hour at a time and are designed to capture footage of animals attracted by the smell of bait (Fig. 2.8a). Footage of sea turtles investigating BRUVs was also included in this study (e.g., Fig. 2.8b).

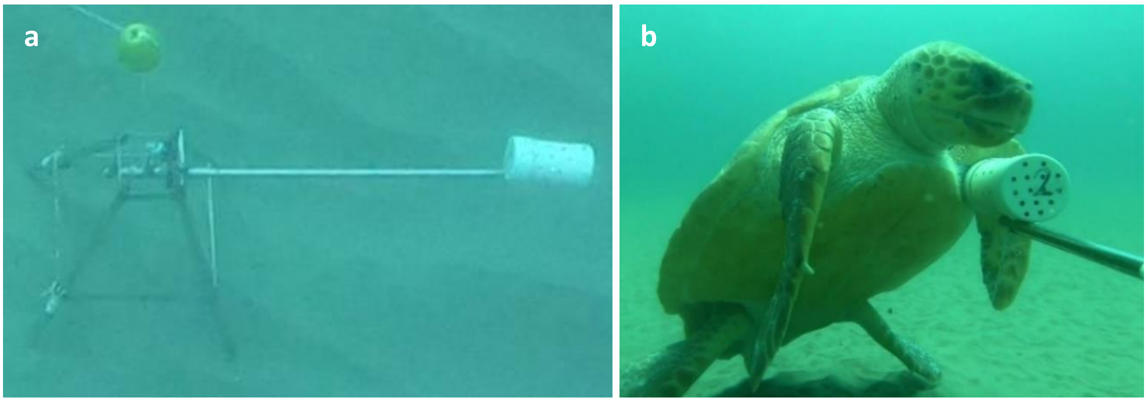


Figure 2.8 (a) The BRUV system consisting of a GoPro camera and bait cannister mounted on a steel frame; (b) example of BRUV footage capturing a loggerhead investigating the bait cannister, allowing this individual to be photo-IDed.

Observer bias considerations

Potential observer biases in species identification, size and detectability have been considered as hard-shelled species are relatively similar in appearance, and smaller individuals may be less visible than larger individuals particularly when cryptically resting in areas such as overhangs and crevices. Observer bias was thus acknowledged and reduced where possible. Observers were trained to be able to discriminate between hard-shelled species on reefs (Fig. 2.9), and if hard-shelled sea turtle sightings were too fleeting or distant to identify to species level, they were recorded as 'hard-shelled' species. Observers were also aware that the smallest individuals observed on reefs had ~ 30 cm SCL, and that sea turtles cryptically rested in the same frequented areas on reefs. Observers carefully inspected these areas to try to avoid undersampling cryptic individuals.

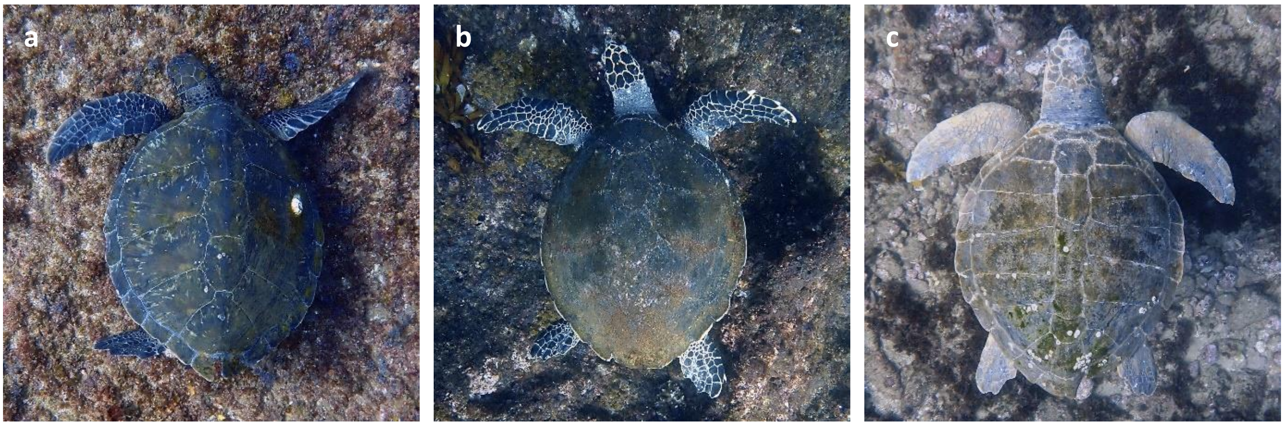


Figure 2.9 Photos of hard-shelled sea turtle species (a: green turtle, b: hawksbill, c: loggerhead) on reefs from above, showing that species are easily discriminated (especially by trained observers). Photographer: Michael Tarr.

2.3.3 Data preparation

Photo-identification of sea turtles

Photos of the unique left and/or right postocular scutes of sea turtles were analysed using a free computer-aided photo-ID application, I^{3}S Pattern (Version 4.02, Den Hartog and Reijns 2014), as per Dunbar *et al*. (2014) and Calmanovici *et al*. (2018). The photo-ID process began with manual placement of three reference points on the sea turtle's face (beak edge, inner edge of eye area and edge of outer scute) and manual outline of the region of interest, i.e., the postocular scutes (Fig. 2.10). The software then used an automatic key point extraction algorithm to generate a unique fingerprint for the annotated image (Fig. 2.10).

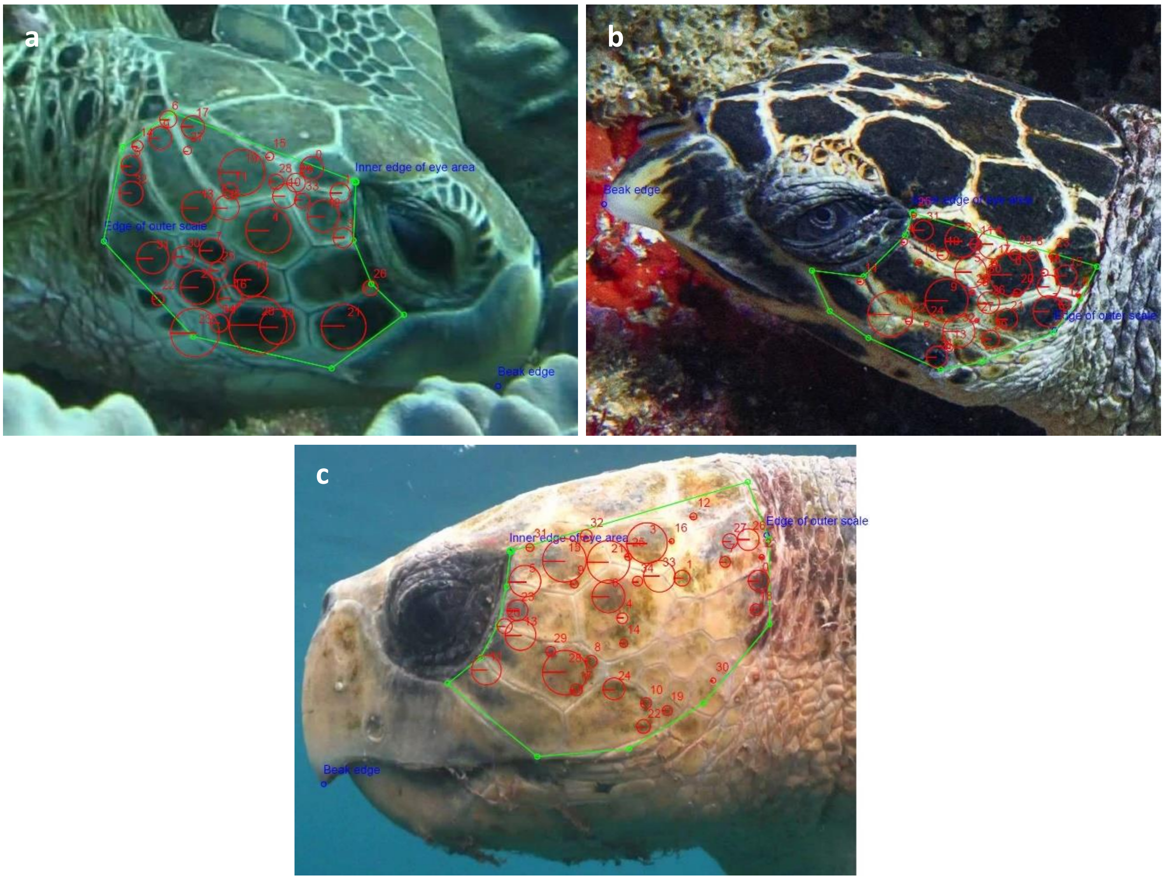


Figure 2.10 Example of I3S Pattern image analysis of a (a) green turtle, (b) hawksbill and (c) loggerhead using standardised reference points (blue; beak edge, inner edge of eye area and edge of outer scute), region of interest (green; postocular scutes), and an automatic key point extraction algorithm (red). Photographers: Chris Johnston (a), Leila Scheltema (b) and Andy Coetzee (c).

Keywords describing species, sex, view (left or right facial profile) and location were manually added to the image to limit the search as specified (e.g., only left profiles of male loggerheads in Sodwana Bay). The software then automatically compared the image of the unknown individual to specified/all images in the identification database and presented a ranked list of best matched individuals. The final match between an unknown and known individual, or addition of a new individual to the identification database if no matching profiles existed, was determined manually. Thus, I^3S Pattern essentially created a short, manageable list of possible matches for unknown individuals to manually choose from, eliminating the need to compare a photo to hundreds of others. The identification database consisted of identified individuals and their resighting records (see Appendix 2.3 for examples of individual resighting records for each species). Where photos were of a bad quality or bad angle, photos of the carapace or other unique characteristics such as injuries, scutes on top of the head or tick lines (lines that project midway through a scute as shown in Appendix 2.3) were manually assessed to confirm identifications. A single researcher (myself) processed all photos using I^3S Pattern and managed the identification database to avoid errors and duplication from various sources of data.

Measurements of sea turtles

The SCL of sea turtles photographed with the paired-laser photogrammetry rig (Fig. 2.6) was extrapolated using ImageJ software (Version 1.53k, Rasband 2012). ImageJ measurement tools were used to manually draw a line between the two laser points projected onto the carapace and set this as a 50 cm scale bar. A line representing SCL was then manually drawn from notch to tip (Fig. 2.11) and automatically estimated to the nearest mm.

Figure 2.11 Example of a loggerhead measured using paired-laser photogrammetry (laser points 50 cm apart circled on carapace) from which an SCL of 67 cm was extrapolated using ImageJ software, confirming this a subadult. Photographer: Michael Tarr.

2.3.4 Statistical analyses

Sightings per unit effort (SPUE) was used as an index of relative abundance, calculated from timed research survey data as the total number of turtle sightings per hour of observational dive time (turtles/hour) (León and Diez 1999; von Brandis 2010; Williams *et al.* 2017). SPUE was also calculated from citizen science data, where the unit of effort was dive trips instead of hours. SPUE was always calculated per dive to obtain a mean value for each study site. Non-parametric Kruskal-Wallis tests (H) were used to assess whether there were significant differences in SPUE of each species among sites as the assumptions of One-Way ANOVAs were not met. These were followed by post-hoc pairwise comparisons using Bonferroni-corrected Dunn's tests to compare significant differences in SPUE of each species among the six sites.

The data from all sampling methods (timed research surveys, citizen science contributions and opportunistic sightings) were combined for all analyses on demographics and spatial distribution as these are independent of effort. The cumulative number of identified individuals on the most consistently surveyed reefs was plotted over time in a discovery curve to show the rate at which individuals were identified. Each paired-laser photogrammetry and calliper measurement was checked whether it fell into the range of SCLs described above to assess the accuracy of visual size class estimates. Binomial tests were used to compare sex ratios to a 1:1 ratio.

Minimum residence periods were estimated as the total number of days between first and last sightings of photo-IDed individuals (Williams *et al.* 2017; Hanna *et al.* 2021). It is possible that individuals may have departed the study area between resightings, but given that sea turtles usually show strong site fidelity and extended residence periods on foraging grounds (e.g., von Brandis 2010; Rambaran 2020; Hays *et al.* 2021), it was assumed that individuals remained in the study area between resighting events over the two-year study period. The mean period (days) between consecutive resightings was used to assess the reliability of inferred minimum residence periods. Site fidelity was inferred from the location of individual resightings. All statistical analyses were conducted using R version 4.2.1 (R Core Team 2022) and RStudio (RStudio Team 2022). Significance was accepted at $p < 0.05$. All spatial distribution maps were made using Quantum GIS version 3.26.3 (QGIS Development Team 2022).

2.4 Results

2.4.1 Relative abundance

Over the two-year study period, a total of 1057 sea turtle sightings were recorded from a combination of timed research surveys (supplemented by voluntourism), citizen scientists and opportunistic sightings in the iSimangaliso and Aliwal Shoal MPAs. Sightings comprised of green turtles (52%, n = 545), hawksbills (20%, n = 208), loggerheads (22%, n = 234), hard-shelled turtles (6%, n = 65) and leatherbacks (<1%, n = 5). Half of all sightings (51%, n = 539) were identified to individual level, resulting in 227 unique individuals (green turtle: 53%, n = 120; hawksbill: 20%, n = 46; loggerhead: 27%, n = 61). No olive ridleys were observed in this study and no leatherbacks were identified to individual level.

Timed research surveys

A total 264.9 hours was spent on timed research surveys across six study sites in the two-year study period. Dive effort was highest at consistently sampled sites (Sodwana Bay: 126.6 hours; Aliwal Shoal: 69.4 hours; Raggie Reef: 59.9 hours), and lowest at opportunistically sampled sites (Green Turtle Gully: 2.5 hours; Bhanga Nek Reef: 3.3 hours; Adlam's Reef: 3.2 hours) (Fig. 2.12). Dive effort was generally highest around summer months (December–March) given the optimal weather conditions this time of year, and lowest at the end of winter/early spring (July–October) when there are fewer good weather days to launch a boat (Fig. 2.12). Dive effort was biased to mornings at iSimangaliso and Aliwal Shoal (n = 251.9 and 140.8 hours respectively) rather than afternoons/evenings (n = 29.5 and 45.1 hours respectively).

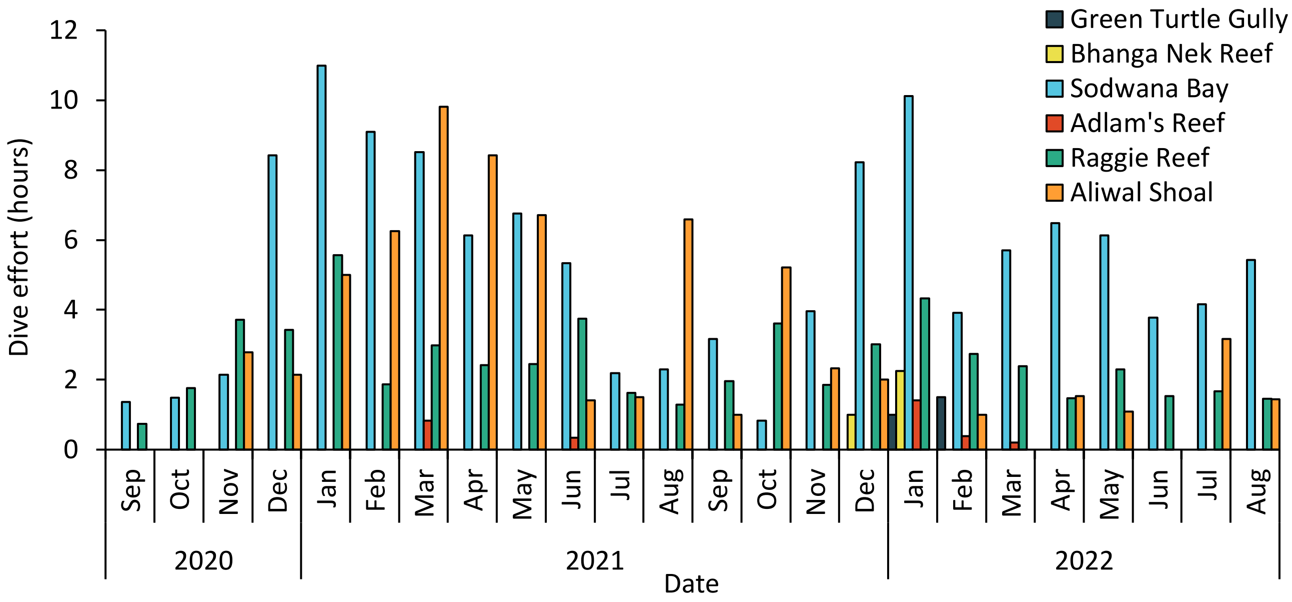


Figure 2.12 Dive effort (hours) during timed research surveys at six study sites over a two-year study period.

A total of 360 sightings of three sea turtle species (green turtles, hawksbills and loggerheads) were made in 195.5 hours underwater (433 timed research surveys) across five study sites in iSimangaliso (Table 2.1). Of these, 177 (49%) were identified to individual level yielding 70 unique individuals (Table 2.1). On Aliwal Shoal, 144 sightings of three sea turtle species (green turtles, hawksbills and loggerheads) were made in 69.4 hours underwater (75 timed research surveys, Table 2.1). Of these, 83 (58%) were identified to individual level yielding 52 unique individuals (Table 2.1). Sea turtles were absent from 225 (52%) timed research surveys in iSimangaliso, and 10 (13%) timed research surveys on Aliwal Shoal.

Table 2.1 Total number of sea turtles sighted and identified among study sites during timed research surveys over a two-year study period. Cm: green turtle; Ei: hawksbill; Cc: loggerhead.

		Total # turtles sighted				**Total # turtles identified to individual level**			**Total # unique individuals**		
Study site	**Total effort (hrs)**	**Cm**	**Ei**	**Cc**	**Hard-shelled**	**Cm**	**Ei**	**Cc**	**Cm**	**Ei**	**Cc**
Green Turtle Gully	2.5	13	0	0	0	12	0	0	6	0	0
Bhanga Nek Reef	3.3	8	1	0	0	2	1	0	2	1	0
Sodwana Bay	126.6	206	23	47	13	113	17	21	31	9	12
Adlam's Reef	3.2	10	0	1	1	0	0	0	0	0	0
Raggie Reef	59.9	26	8	17	2	2	2	7	2	2	5
Total for five iSimangaliso sites	195.5	263	32	65	16	129	20	28	41	12	17
Aliwal Shoal	69.4	60	48	36	14	30	32	21	20	17	15
Total for all sites	264.9	323	80	101	30	159	52	49	61	29	32

On timed research surveys, green turtles had the highest mean SPUE across all study sites in iSimangaliso, ranging from 0.5 turtles/hour (SD 1.24, n = 26) at Raggie Reef to 5.8 turtles/hour (SD 3.90, n = 13) at Green Turtle Gully (Fig. 2.13). Loggerheads had the next highest mean SPUE in iSimangaliso ranging from 0 (no sightings) at Green Turtle Gully and Bhanga Nek Reef to 0.5 turtles/hour (SD 1.65, n = 47) at Sodwana Bay (Fig. 2.13). Hawksbills were the third most abundant species with mean SPUE ranging from 0 (no sightings) at Green Turtle Gully and Adlam's Reef to 0.3 turtles/hour (SD 1.30, n = 23) at Sodwana Bay (Fig. 2.13). When all study sites in iSimangaliso were combined, the same pattern existed where green turtles had the highest SPUE (mean ± SD: 2.2 ± 4.47 turtles/hour, n = 263), followed by loggerheads (mean ± SD: 0.5 ± 1.54 turtles/hour, n = 65), and then hawksbills (mean ± SD: 0.2 ± 1.20 turtles/hour, n = 32) (Appendix 2.4). Thus, the pattern of relative abundance from timed research surveys in iSimangaliso is green turtles > loggerheads > hawksbills (Fig. 2.13).

On Aliwal Shoal, green turtles had the highest SPUE (mean ± SD: 1.2 ± 1.98 turtles/hour, n = 60), followed by hawksbills (mean ± SD: 0.8 ± 1.35 turtles/hour, n = 48) and then loggerheads (mean ± SD: 0.5 ± 1.16 turtles/hour, n = 36) (Fig. 2.13). Thus, green turtles > hawksbills > loggerheads in terms of relative abundance from timed research surveys on Aliwal Shoal (Fig. 2.13). No leatherbacks were seen on any timed research surveys on any of the reefs.

SPUE of each species differed significantly among sites (Kruskal-Wallis tests, green turtles: H = 24.99, df = 5, p < 0.05; hawksbills: H = 65.26, df = 5, p < 0.05; loggerheads: H = 13.19, df = 5, p < 0.05). Dunn's post-hoc tests identified significant differences in green turtle SPUE between Raggie Reef and Green Turtle Gully, Sodwana Bay and Aliwal Shoal (p < 0.05) as well as between Green Turtle Gully and Sodwana Bay (p < 0.05). Dunn's post-hoc tests also identified significant differences in hawksbill SPUE between Aliwal Shoal and Green Turtle Gully, Sodwana Bay, Adlam's Reef and Raggie Reef (p < 0.05), whilst significant differences in loggerhead SPUE were only identified between Aliwal Shoal and Sodwana Bay (p < 0.05). See Appendix 2.4 for all mean SPUE values from timed research surveys.

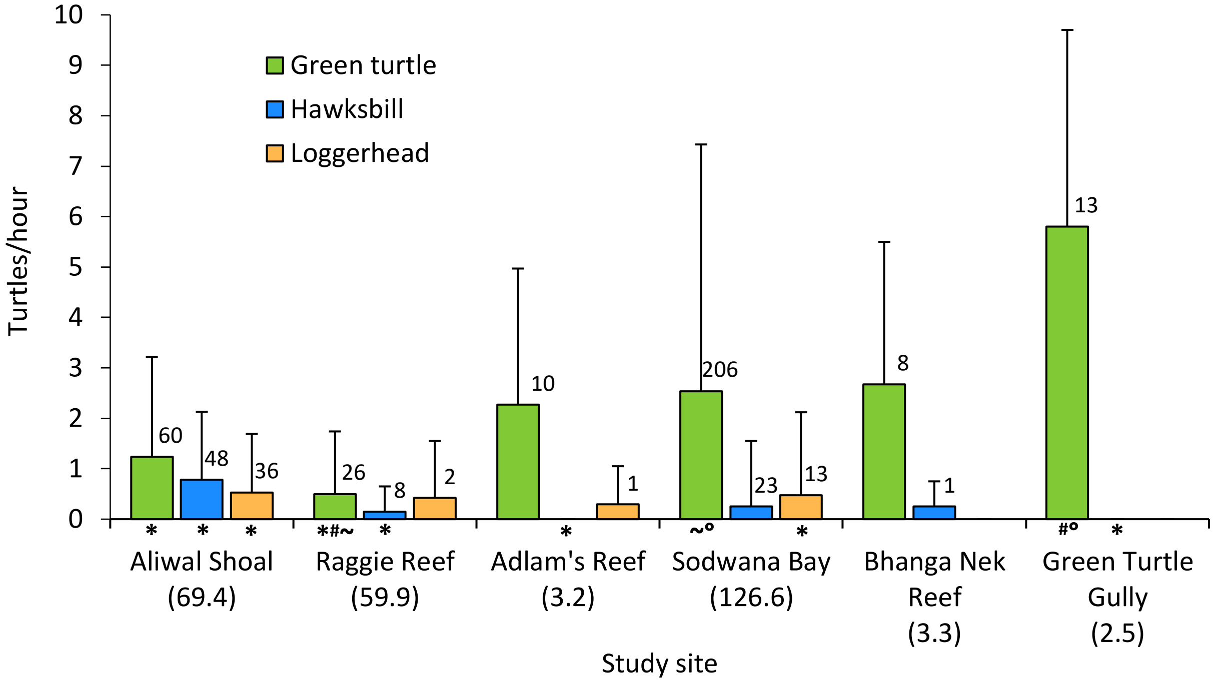


Figure 2.13 Relative abundance of sea turtles as mean number of turtles per hour among study sites from timed research surveys over a two-year study period. Bars represent standard deviation. The total number of sightings is indicated above each column and dive effort (hours) is indicated below each study site. Symbols *, #, °, ~ indicate significant differences in SPUE among species per site.

Citizen science

Citizen scientists only dived two of the six study sites, Sodwana Bay and Aliwal Shoal (Fig. 2.14). Dive effort was highest in summer and autumn (December–May) and lowest in winter and early spring (June–October).

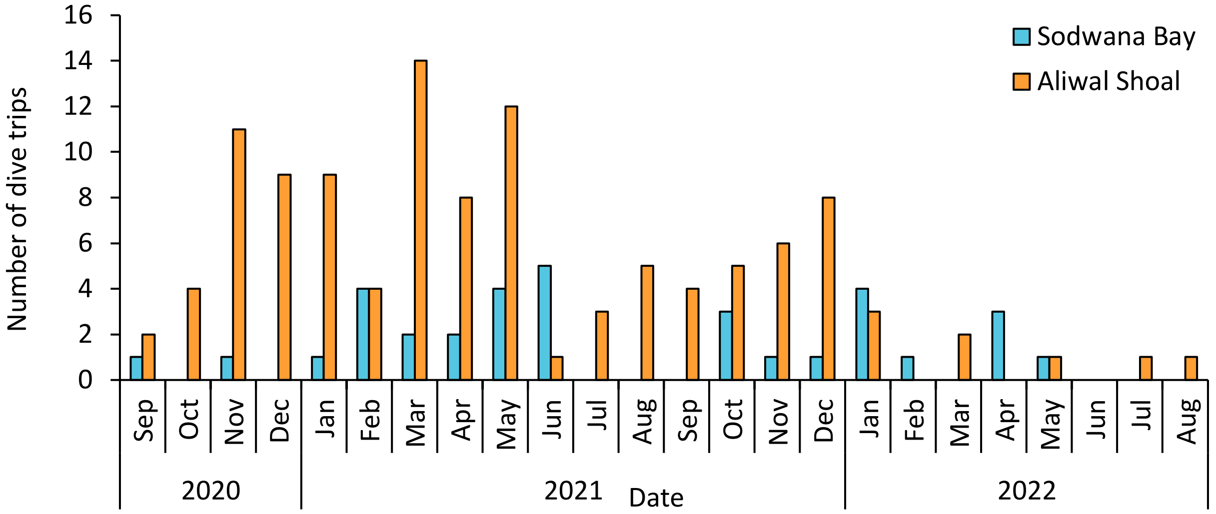


Figure 2.14 Dive effort (number of dive trips) of citizen scientists at two frequently dived study sites over a two-year study period.

In Sodwana Bay, 60 sightings of four sea turtle species (including leatherbacks) were reported by 13 citizen scientists over 34 dive trips (Table 2.2). Of these, 44 (73%) were identified to individual level yielding 27 unique individuals (Table 2.2). On Aliwal Shoal, 177 sightings of three sea turtle species (no leatherbacks) were reported by 30 citizen scientists over 113 dive trips (Table 2.2). Of these, 135 (76%) were identified to individual level yielding 65 unique individuals (Table 2.2).

Table 2.2 Total number of turtles sighted and identified among study sites from citizen science contributions over a two-year study period. Cm: green turtle; Ei: hawksbill; Cc: loggerhead; Dc: leatherback.

		Total # turtles sighted					Total # turtles identified to individual level				Total # unique individuals			
Study site	**Total effort (dive trips)**	**Cm**	**Ei**	**Cc**	**Dc**	**Hard-shelled**	**Cm**	**Ei**	**Cc**	**Dc**	**Cm**	**Ei**	**Cc**	**Dc**
Sodwana Bay	34	33	12	14	1	0	28	9	7	0	17	5	5	0
Aliwal Shoal	113	50	88	39	0	2	37	71	27	0	21	26	18	0
Total	147	83	100	53	1	2	65	80	34	0	38	31	23	0

Similar to results from timed research surveys, citizen science data showed that green turtles in Sodwana Bay had the highest mean SPUE (mean ± SD: 1.0 ± 1.11 turtles/dive trip, n = 33), followed by loggerheads (mean ± SD: 0.4 ± 0.70 turtles/dive trip, n = 14), hawksbills (mean ± SD: 0.4 ± 0.54 turtles/dive trip, n = 12), and lastly leatherbacks (mean ± SD: 0.03 ± 0.17 turtles/dive trip, n = 1) (Fig. 2.15). Thus, the pattern of relative abundance from citizen science data in iSimangaliso is green turtles > loggerheads > hawksbills > leatherbacks (Fig. 2.15).

However, relative abundance of species on Aliwal Shoal differed between citizen science and timed research survey data, as citizen scientists found that hawksbills (mean ± SD: 0.8 ± 0.85 turtles/dive trip, n = 88) were more abundant than green turtles (mean ± SD: 0.4 ± 0.89 turtles/dive trip, n = 50), followed by loggerheads (mean ± SD: 0.4 ± 0.58 turtles/dive trip, n = 39) (Fig. 2.15). Thus, hawksbills > green turtles > loggerheads in terms of relative abundance from citizen science contributions on Aliwal Shoal (Fig. 2.15).

SPUE from citizen science data differed significantly among Sodwana Bay and Aliwal Shoal for green turtles (Kruskal-Wallis test, H = 11.55, df = 1, $p < 0.05$) and hawksbills (H = 7.24, df = 1, $p < 0.05$), but not for loggerheads (H = 0.10, df = 1, $p > 0.05$) and leatherbacks (H = 3.32, df = 1, $p > 0.05$). See Appendix 2.5 for all mean SPUE values from citizen science contributions.

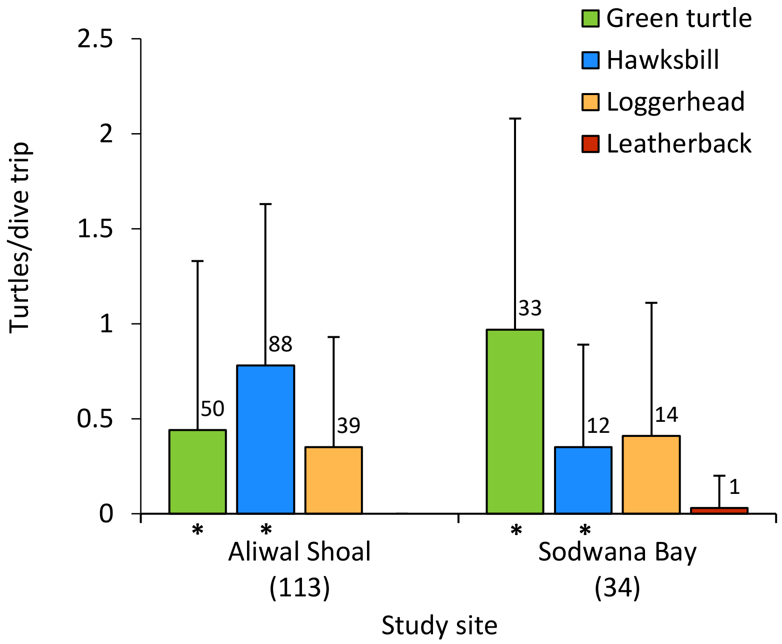


Figure 2.15 Relative abundance of sea turtles as mean number of turtles per dive trip among study sites from citizen science contributions over a two-year study period. Bars represent standard deviation. The total number of sightings is indicated above each column and dive effort (number of dive trips) is indicated below each study site. Symbol * indicates significant differences among species per site.

Opportunistic sightings

A total of 93 sea turtle sightings (green turtle, 27%, n = 25; hawksbill, 13%, n = 12; loggerhead, 25%, n = 23; hard-shelled, 33%, n = 31; leatherback, 2%, n = 2) were sighted from boats on the way to or from study sites in between timed research surveys. Only three of these sightings were identified to individual level as most turtles fled before they could be photographed, and photographs taken from the boat were not clear enough to identify individuals.

RUVs in iSimangaliso captured a total of 174 sightings of three sea turtle species, of which 93 were identified to individual level yielding 63 unique individuals (Table 2.3). BRUVs captured four sea turtle sightings in iSimangaliso (one green turtle, two loggerheads and one hard-shelled turtle) and one of these was identified to individual level.

Table 2.3 Total number of turtles sighted and identified among study sites in iSimangaliso from RUV footage over a two-year study period. Cm: green turtle; Ei: hawksbill; Cc: loggerhead.

	Total # turtles sighted			**Total # turtles identified to individual level**			**Total # unique individuals**		
Study site	**Cm**	**Ei**	**Cc**	**Cm**	**Ei**	**Cc**	**Cm**	**Ei**	**Cc**
Sodwana Bay	22	2	12	10	2	4	10	2	4
Raggie Reef	87	12	39	50	8	19	35	3	9
Total	109	14	51	60	10	23	45	5	13

The data from all sampling methods (timed research surveys, citizen science contributions and opportunistic sightings) are combined for the remaining results to describe patterns per species or individuals as these are independent of effort.

2.4.2 Demographics

Discovery of individuals

Cumulative discovery curves showed that almost 70% of all individual green turtles in Sodwana Bay were identified within the first 10 months of sampling, with the remaining 30% identified throughout the rest of the study period. Individual hawksbills and loggerheads were identified at a slower rate with new identifications after 6 months (Fig. 2.16). Similarly, more than half of all individual green turtles on Raggie Reef were identified within the first six months of sampling, whereas individual hawksbills and loggerheads were identified more steadily throughout the entire sampling period (Fig. 2.16). By contrast, at least 90% of all individual hawksbills and loggerheads on Aliwal Shoal were identified within the first nine months of sampling and only 57% of all individual green turtles were identified by this time (Fig. 2.16).

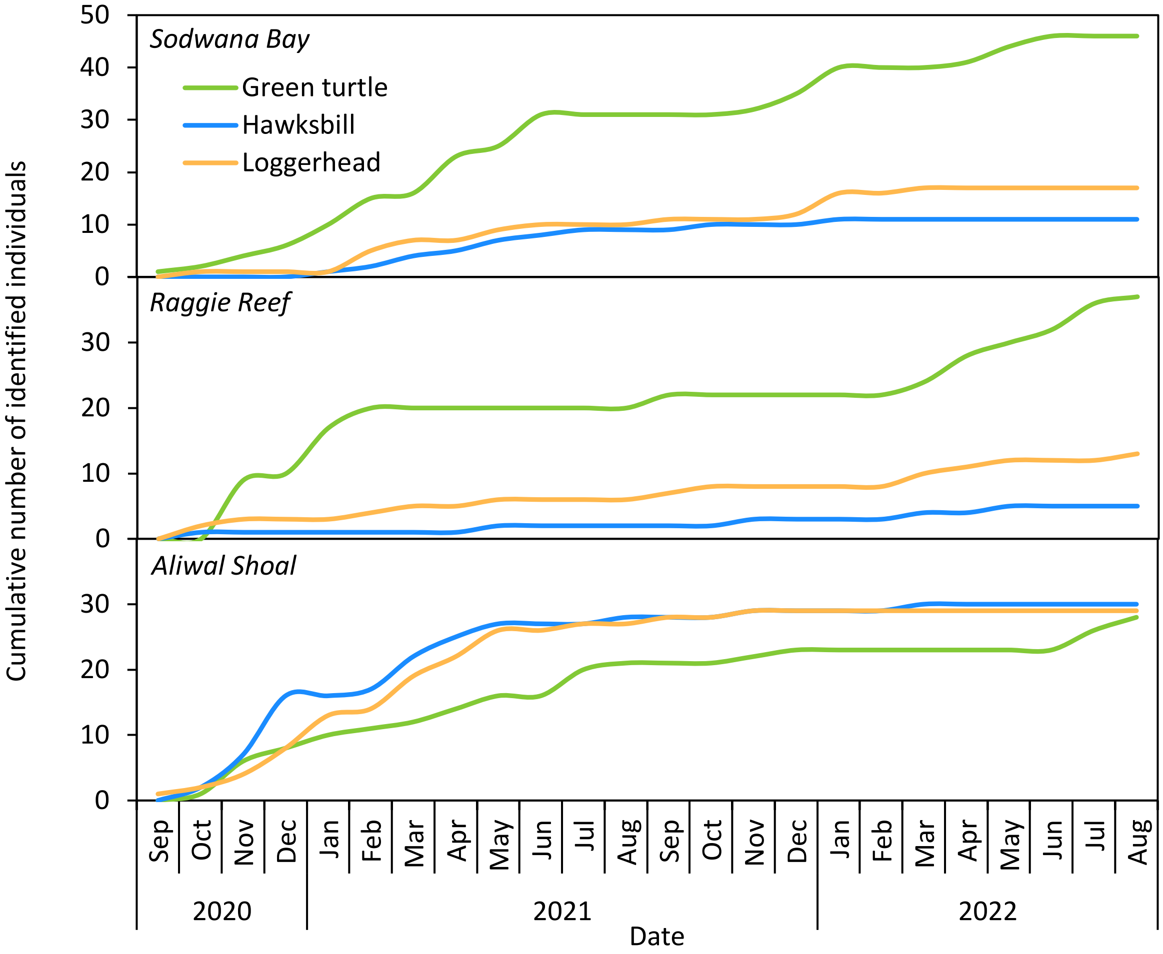


Figure 2.16 Cumulative number of identified individual sea turtles on Sodwana Bay reef complexes (n = 74), Raggie Reef (n = 55) and Aliwal Shoal (n = 87) from timed research surveys, citizen scientists and opportunistic sightings over a two-year study period.

Size and sex of identified individuals

Underwater visual estimates of sea turtle SCLs into size classes were confirmed to be accurate by paired-laser photogrammetry and calliper measurements (Table 2.4). Only three individual green turtles who were visually estimated to be adult-sized (>90 cm) were measured to be 79.8 cm, 83 cm and 86.1 cm (Table 2.4). However, the individual with an SCL of 79.8 cm was a male as indicated by the presence of a long tail extending past the hind flippers, despite having a slightly smaller SCL than approximate size guides suggest. The SCL range of measured individuals (Table 2.4) was 44.9–99.2 cm for green turtles (n = 20), 37.4–73.4 cm for hawksbills (n = 12), and 66.9–81 cm for loggerheads (n = 2).

Table 2.4 Paired-laser photogrammetry and calliper measurements of individual sea turtles that were first visually estimated into size classes underwater. Some individuals were only measured and identified outside the two-year study period. Cm: green turtle; Ei: hawksbill; Cc: loggerhead.

Species	Turtle ID	Visual estimate	Paired-laser photogrammetry (cm)	Calliper (cm)
Cm	SBCm_Deano	Juvenile	-	44.9
Cm	BNCm_Travis	Juvenile	-	47.6
Cm	BNCm_FrankyFourFingers	Juvenile	-	46.8
Cm	ASCm_Linda	Juvenile	52.1	-
Cm	BNCm_Ngubane	Juvenile	-	55.6
Cm	BNCm_Joel	Subadult	-	63.8
Cm	SBCm_Tali	Subadult	-	68.8
Cm	BNCm_Steve	Subadult	-	69.9
Cm	ASCm_Kei	Subadult	76.2	-
Cm	ASCm_Pan	Subadult	82	-
Cm	ASCm_CaptainHook	Subadult	85.1	-
Cm	ASCm_Michy	Subadult	87.3	-
Cm	ASCm_EliudKipchoge	Adult-sized	79.8	-
Cm	ASCm_Bentley	Adult-sized	83	-
Cm	ASCm_Ozzy	Adult-sized	86.1	-
Cm	SBCm_Ntombi	Adult-sized	-	92.3
Cm	ASCm_Louise	Adult-sized	92.4	-
Cm	SBCm_Alex	Adult-sized	-	94.6
Cm	ASCm_Jeff	Adult-sized	97.2	-
Cm	ASCm_Ncami	Adult-sized	99.2	-
Ei	ASEi_Hawky	Juvenile	37.4	-
Ei	ASEi_Christopher	Juvenile	43	-
Ei	SBEi_Steph	Juvenile	-	44.7
Ei	SBEi_BarnacleBrad	Juvenile	-	45
Ei	ASEi_Ron	Juvenile	49.1	-
Ei	ASEi_Redmar	Subadult	54.3	-
Ei	SBEi_Pierre	Subadult	-	56.5
Ei	ASEi_Khandalinyoni	Subadult	57.5	-
Ei	ASEi_Charlie	Subadult	62.7	-
Ei	ASEi_Myrtle	Subadult	63.7	-
Ei	SBEi_KFC	Subadult	-	68.3
Ei	SBEi_Samantha	Subadult	-	73.4
Cc	ASCc_Geremy	Subadult	66.9	-
Cc	ASCc_Shelly	Adult-sized	81	-

Approximate SCL guides used for visual estimates (based on Hughes 1973, Chaloupka and Limpus 2001, Casale *et al*. 2005, Heithaus *et al*. 2005, Avens and Snover 2013, and Stokes *et al*. 2023):
Juvenile: <60 cm (green turtles, hawksbills and loggerheads)

Subadult: 60-80 cm (hawksbills and loggerheads), 60-90 cm (green turtles)

Adult-sized: >80 cm (hawksbills and loggerheads), >90 cm (green turtles)

Based on visual size estimates, 48% (n = 44) of individual green turtles in iSimangaliso were classified as subadults (60-90 cm SCL), 30% (n = 28) were considered adults (>90 cm SCL) and 22% (n = 20) were considered juveniles (<60 cm SCL) (Fig. 2.17). Individual hawksbills in iSimangaliso ranged from <60 – >80 cm SCL but 82% (n = 14) were classified as subadults (60-80 cm SCL) (Fig. 2.17). On Aliwal Shoal, 46% (n = 13) of individual green turtles were classified as subadults (60-90 cm SCL) and 46% (n = 13) were considered adults (>90 cm SCL) (Fig. 2.17). Individual hawksbills on Aliwal Shoal were mostly classified as subadults (73%, n = 22, 60-80 cm SCL) (Fig. 2.17). Individual loggerheads were all classified as adult-sized (>80 cm SCL) at iSimangaliso (n = 32) and Aliwal Shoal (n = 29) (Fig. 2.17). Four subadult-sized loggerheads (60–80 cm SCL) were sighted in iSimangaliso but weren't identified to individual level, and one was identified and measured on Aliwal Shoal outside the study period (Table 2.4). The five unidentified leatherback sightings in iSimangaliso were all classified as adult-sized (>140 cm SCL).

In iSimangaliso, individual adult-sized green turtles (Fig. 2.17) were mostly of unknown sex, but more females (32%, n = 9) were recorded than males (11% male, n = 3). Individual adult-sized green turtles on Aliwal Shoal (Fig. 2.17) were mostly females (62% female, n = 8 and 31% male, n = 4). Adult-sized loggerheads were dominated by females (Fig. 2.17) both in iSimangaliso (53% female, n = 17 and 31% male, n =10) and on Aliwal Shoal (62% female, n = 18 and 28% male, n =8). All individual adult-sized hawksbills observed were female; no males were observed in the study (Fig. 2.17). Out of the five unidentified adult-sized leatherbacks in iSimangaliso, two were female, two were male and one was of unknown sex. Even though sex ratios of individually identified green turtles and loggerheads were female-biased, they were not significantly different from 1:1 (binomial tests, all $p > 0.05$). However, the sex ratio of individually identified adult-sized hawksbills was significantly different from 1:1 (binomial test, $p < 0.05$).

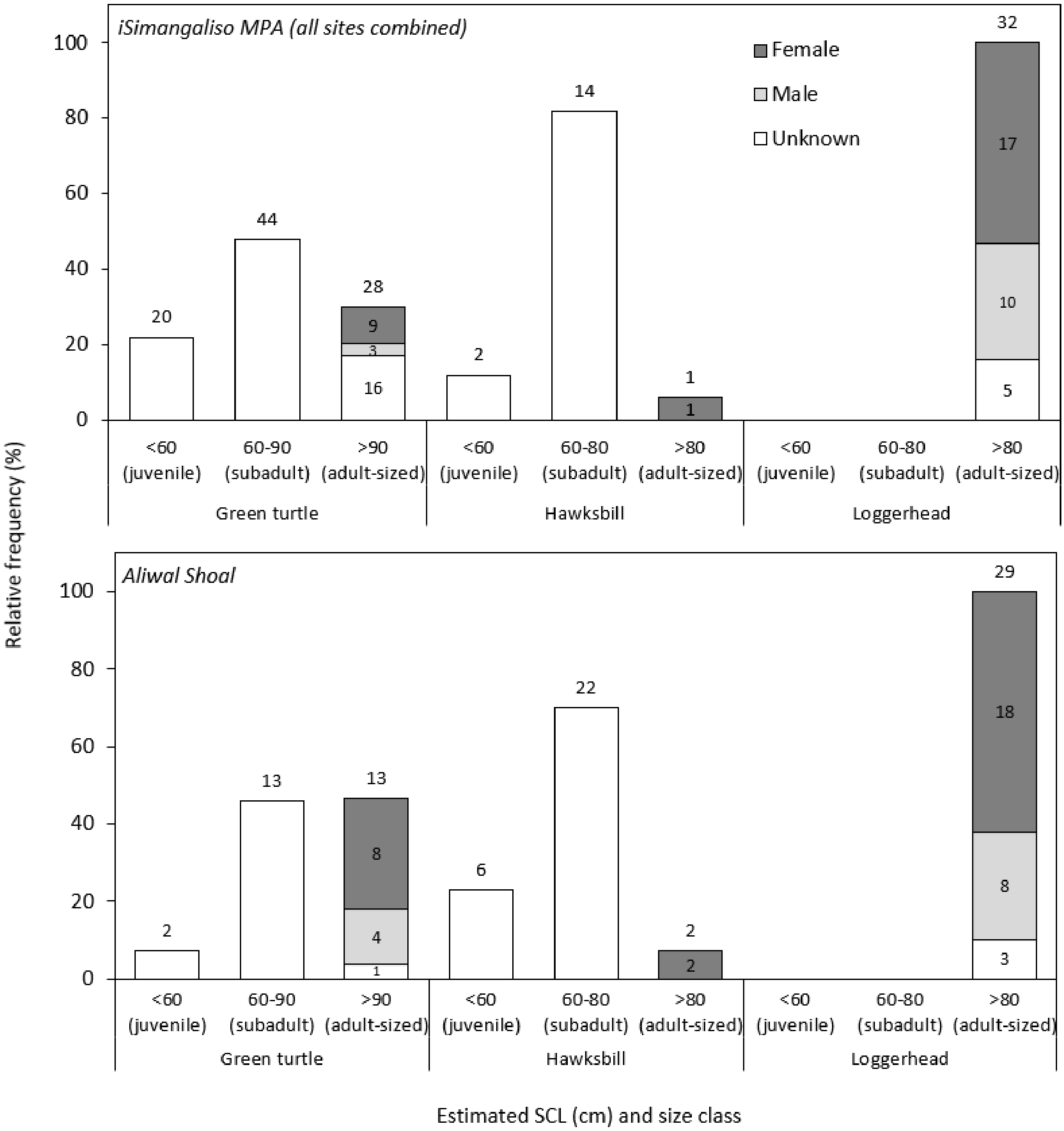


Figure 2.17 Relative frequency of individually identified sea turtles per size class (estimated SCL in cm) and sex in iSimangaliso (all sites combined) (n = 141) and Aliwal Shoal (n = 87) from timed research surveys, citizen scientists and opportunistic sightings over a two-year study period. Actual frequencies are above each bar and inside adult-sized bars.

Only two of the 1057 sea turtles sighted within the iSimangaliso and Aliwal Shoal MPAs in the two-year study period were observed with flipper tags. These individuals (adult-sized female green turtles) were not tagged on nesting beaches, they were captured on SCUBA in Sodwana Bay for satellite tagging purposes in 2013 (Rambaran 2020). The only individuals observed with flipper tags applied on nesting beaches were three adult female loggerheads; either observed at study sites outside the study period (Fig. 2.18a) or outside study sites within the study period (Fig. 2.18b, c).

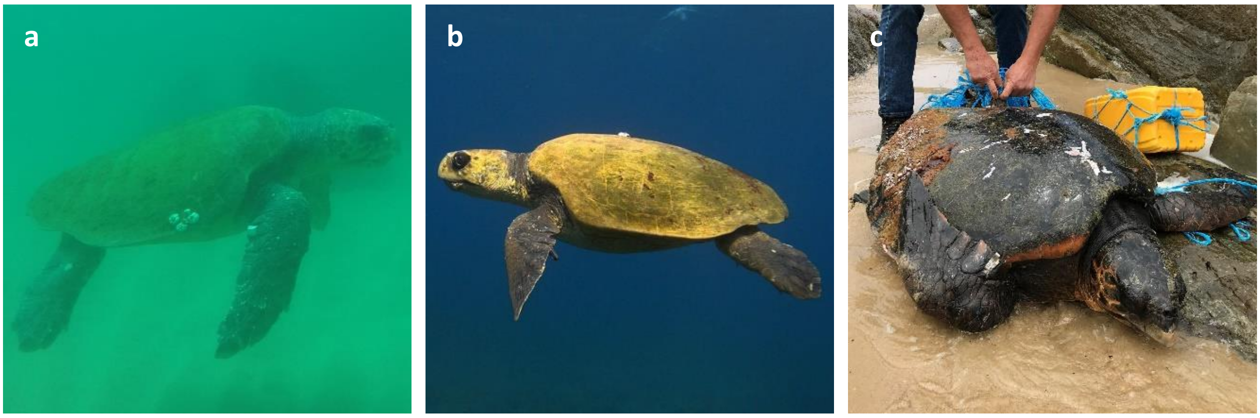


Figure 2.18 Adult female loggerheads observed with flipper tags applied on nesting beaches. (a) Individual captured on RUV on Quarter Mile Reef (Sodwana Bay) in January 2020 (outside study period, within study area) with indiscernible tag number; (b) individual reported by a citizen scientist off Ponta Techobanine, southern Mozambique, in November 2020 (within study period, outside study area) who attempted to nest at Bhanga Nek in 2016 (tag # ZA0657B); (c) individual captured by a citizen scientist at sea off the Tsitsikamma National Park, Eastern Cape in November 2020 and disentangled from plastic (within study period, outside study area) who attempted to nest in Mozambique in 2019 (tag # MZ2802). Photographers: Sharklife (a), Beth Neale (b) and Charles de la Harpe (c).

2.4.3 Distribution

Local distribution

Even though public engagement was focused to the east coast of South Africa, citizen scientists reported sea turtle sightings across the entire country in the two-year study period (n = 116 outside of the studied MPAs). Recreational divers, commercial divers and fishermen reported green turtle, hawksbill and loggerhead sightings in other areas of the KZN coastline including KZN's Richard's Bay harbour and Durban harbour (n = 11; e.g., Fig. 2.19a). Recreational divers and fishermen also reported sightings of green turtles, loggerheads and leatherbacks in coastal waters off the Eastern Cape (n = 28; e.g., Fig. 2.19b–d), particularly over the annual Sardine Run when diving and fishing effort was highest. There were also anecdotal reports of green turtles frequenting estuaries in the upper Eastern Cape, and line fishermen landing sea turtle catches in Algoa Bay, Gqeberha (R. Nel, pers. comm). In the Western Cape, a wildlife photographer frequently reported green turtle aggregations of ~ 50 individuals year-round and > 100 individuals in summer months on suspected shallow water foraging grounds in the De Hoop MPA (e.g., Fig. 2.19e). Recreational divers also infrequently reported green turtles, hawksbills and loggerheads at inshore reefs and kelp forests in False Bay (Pringle Bay, Glencairn Beach and Long Beach; e.g., Fig. 2.19f), as well as Granger Bay off Cape Town (n = 4).

Figure 2.19 Examples of the wide distribution of sea turtles reported by citizen scientists outside the study area. (a) Green turtle in Richard's Bay harbour; (b–c) loggerheads ~ 1.5 km off Coffee Bay and Mbolompo Point, Eastern Cape; (d) adult-sized female leatherback ~ 3 km off Mbashe River Mouth, Eastern Cape, who was satellite tagged on Bhanga Nek beach whilst nesting seven months earlier; (e) green turtle off Skipskop Point in De Hoop MPA; (f) hawksbill seen off Glencairn Beach and Pringle Bay (either side of False Bay, Western Cape) six months apart. Photographers: Michael Tarr (a), Jean Tresfon (b, e), Andy Coetzee (c, d) and Lisa Beasley (f).

Green, hawksbill and loggerhead sea turtles were sighted along most of the coastline within the iSimangaliso (n = 637) and Aliwal Shoal (n = 320) MPAs (Fig. 2.20a and 2.21a respectively), essentially wherever we sampled. Many of these sightings weren't identified to individual level. Leatherbacks (n = 5) were only sighted in shallow inshore waters of iSimangaliso off Island Rock, Sodwana Bay, Red Sands and Cape Vidal (never on reefs) (Fig. 2.20a).

The local distribution of identified individuals varied according to species and size class. Individuals at the two northernmost study sites in iSimangaliso, Green Turtle Gully and Bhanga Nek Reef (n = 10), were mostly juvenile green turtles (n = 6) (Fig. 2.20b, c). At other study sites in iSimangaliso, identified individuals (n = 127) comprised a variety of species and size classes but were dominated by subadult green turtles (n = 42), adult-sized loggerheads (n = 29) and adult-sized green turtles (n = 27) (Fig. 2.20d–g). Individual hawksbills (n = 16) had a very scattered distribution throughout iSimangaliso (Fig. 2.20b–g). The study sites with the most identified individuals in iSimangaliso were

Quarter Mile Reef (n = 45, Fig. 2.20f) and Raggie Reef (n = 53, Fig. 2.20g) where dive effort was highest.

By contrast, identified individuals on Aliwal Shoal (n = 84) had a much more even species distribution (green turtles, n = 28; hawksbills, n = 31; loggerheads, n = 29; Fig. 2.21b) than in iSimangaliso (Fig. 2.20b–g). Individuals were mostly adult-sized loggerheads (n = 29) and subadult hawksbills (n = 21) (Fig. 2.21b). Most identified individuals were on the shallow northern section of Aliwal Shoal where dive effort was highest (Fig. 2.21b).

Despite there being more adult-sized female individuals than males, there was no noticeable difference in the distribution of sex among identified individuals on any study sites as males (except male hawksbills) and females were generally observed at all sites (Fig. 2.20b–g; 2.21b).

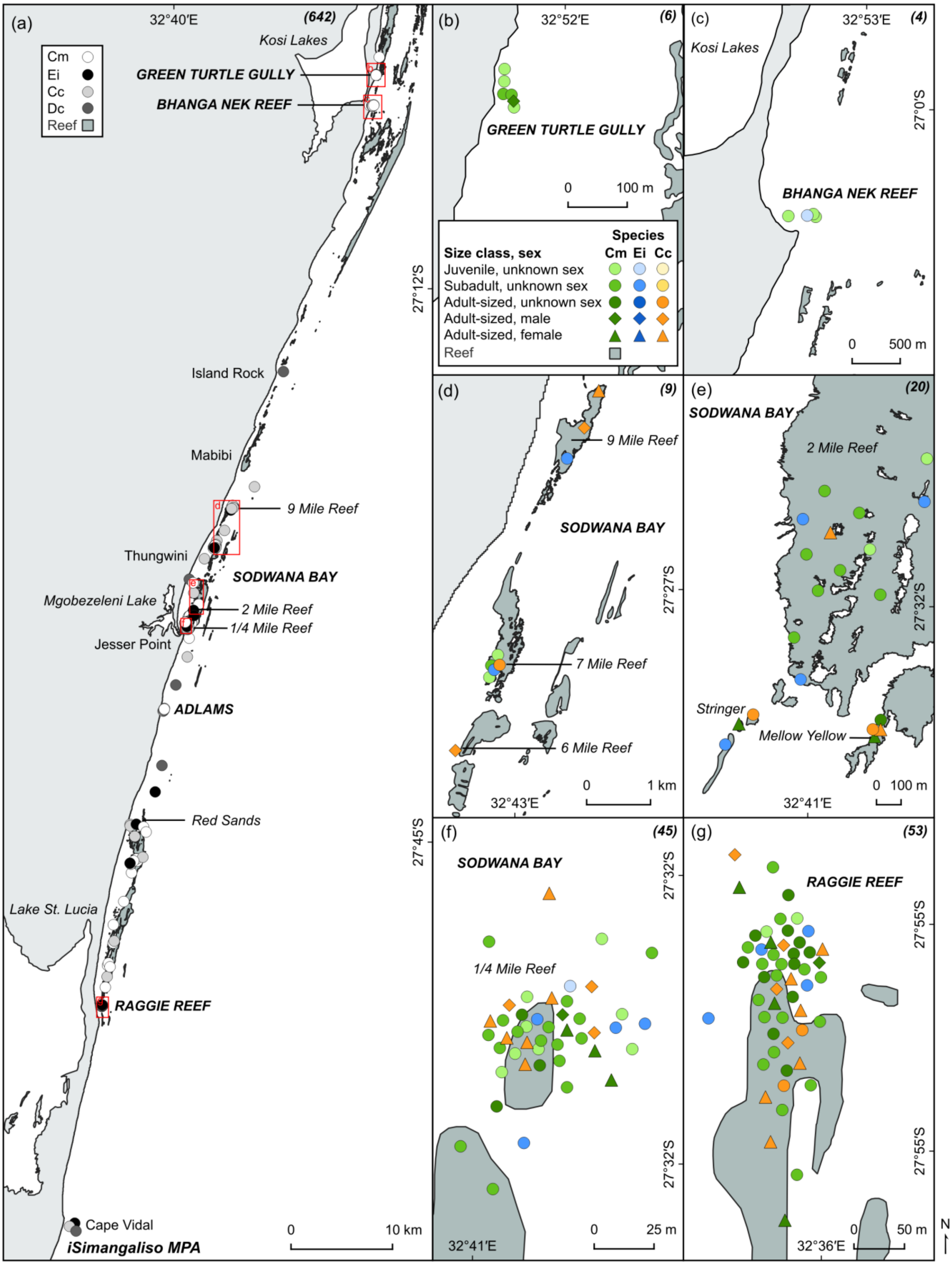


Figure 2.20 (a) Map of all sightings of green turtles (Cm), hawksbills (Ei), loggerheads (Cc) and leatherbacks (Dc) in iSimangaliso. Number of sightings in parentheses (in the top right corner). Individuals were not discerned. (b–g) Map of individuals classed by size and sex on reef complexes within iSimangaliso. Number of individuals in parentheses. Data on both maps were collected by timed research surveys, citizen scientists and opportunistic sightings over a two-year study period. Scales differ between maps.

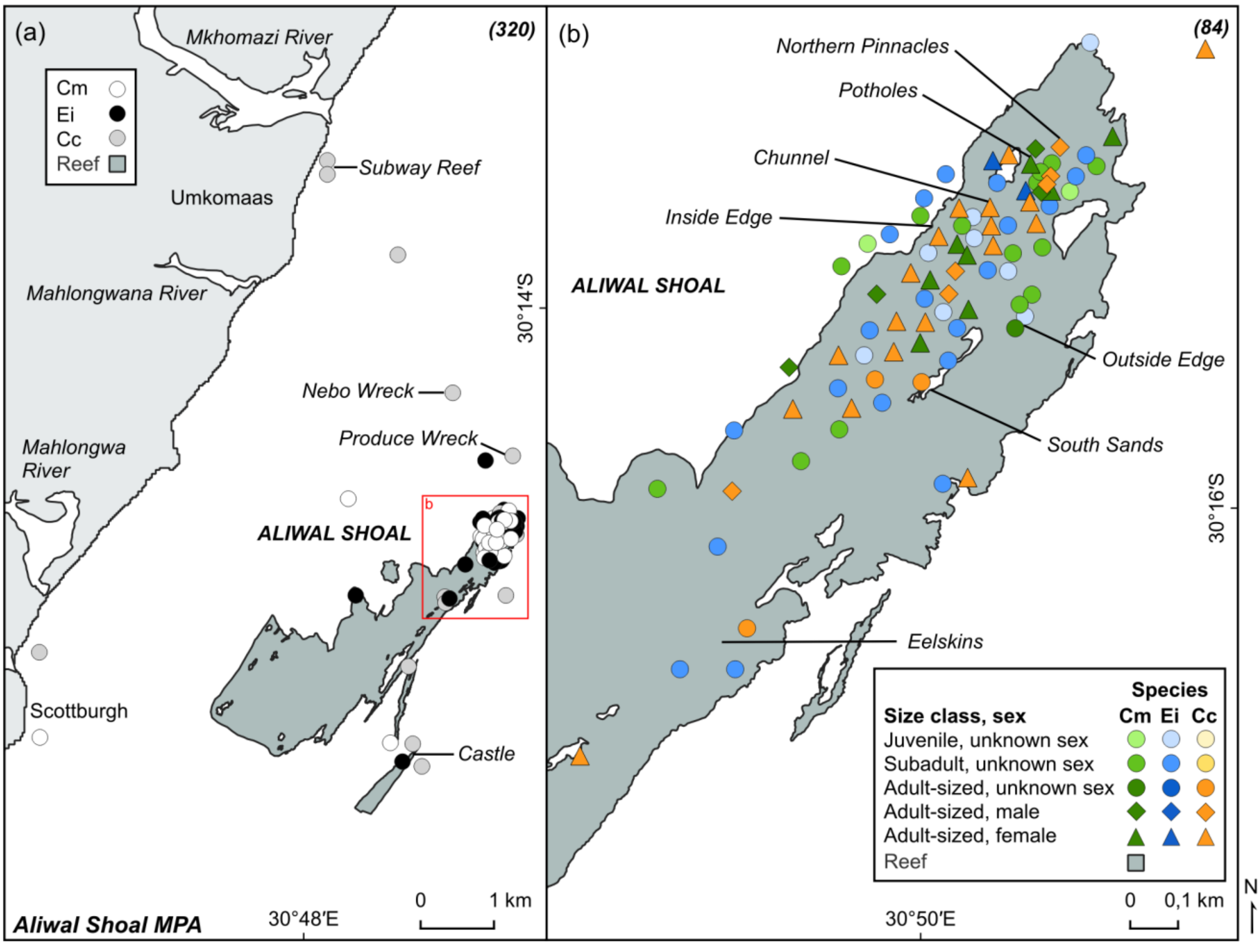


Figure 2.21 (a) Map of all sightings of green turtles (Cm), hawksbills (Ei) and loggerheads (Cc) in the Aliwal Shoal MPA. Number of sightings in parentheses (in the top right corner). Individuals were not discerned. (b) Map of individuals classed by size and sex on Aliwal Shoal. Number of individuals in parentheses. Data on both maps were collected by timed research surveys, citizen scientists and opportunistic sightings over a two-year period. Scales differ between maps.

Residency

Across all sites where individual sea turtles were identified (all except Adlam's Reef), 65% (n = 78) of the 120 individual green turtles were only seen once and 35% (n = 42) were resighted at least once, whereas 37% (n = 17) of the 46 individual hawksbills were only seen once and 63% (n = 29) were resighted at least once (Fig 2.22). Of the 61 individual loggerheads, 70% (n = 43) were only seen once and 30% (n = 18) were resighted at least once (Fig. 2.22). The maximum number of resightings of an individual juvenile green and hawksbill turtle was nine and seven respectively, and individual subadult green and hawksbill turtles were resighted a maximum of 19 and ten times respectively (Fig. 2.22). The maximum number of resightings of an individual adult-sized green turtle, hawksbill and loggerhead was 14, two and 11 respectively (Fig. 2.22).

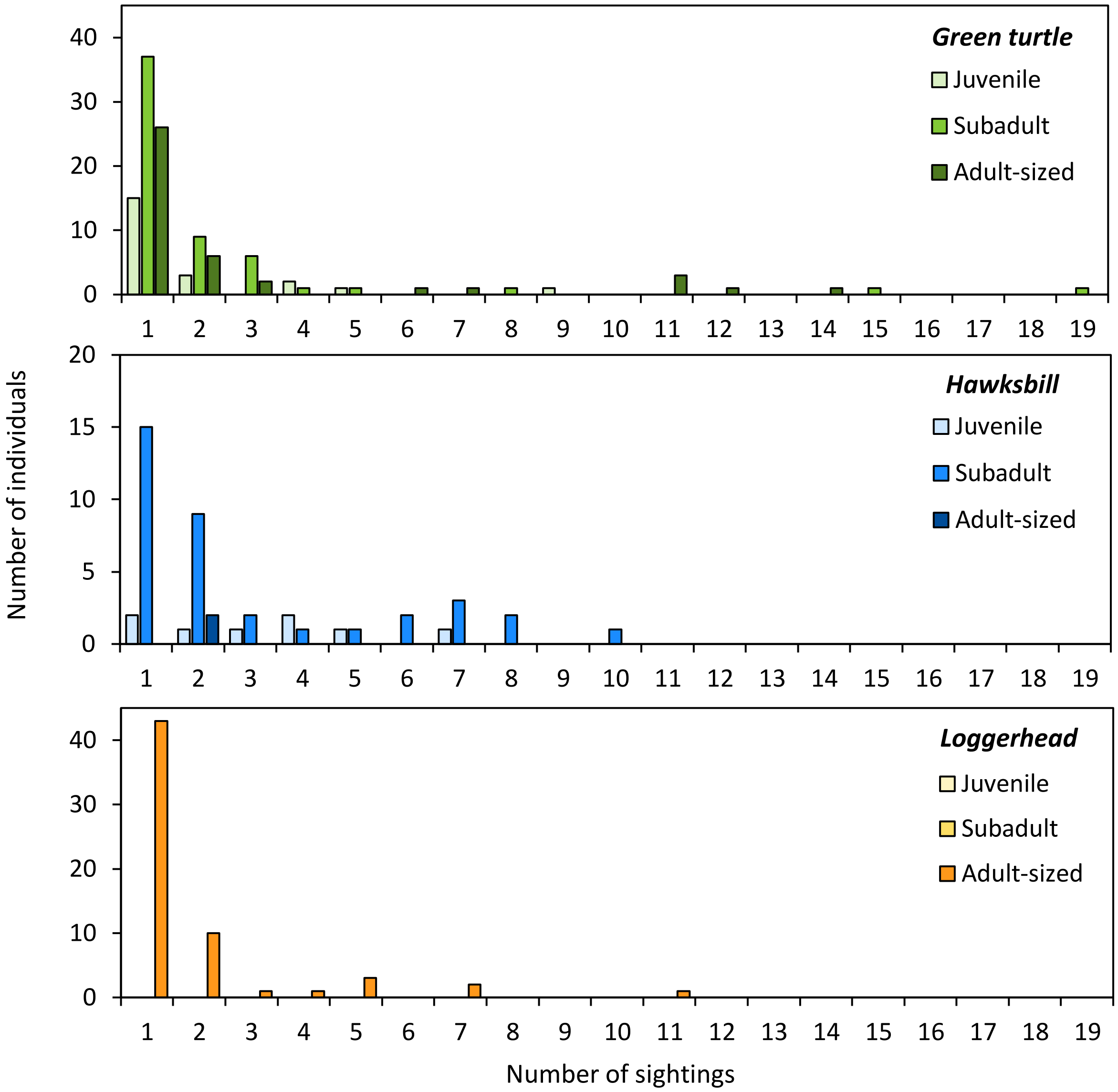


Figure 2.22 Total number of sighting occasions of each individually identified green turtle (n = 120), hawksbill (n = 46) and loggerhead (n = 61) across Green Turtle Gully, Bhanga Nek Reef, Sodwana Bay, Raggie Reef and Aliwal Shoal from timed research surveys, citizen scientists and opportunistic sightings over a two-year study period.

The longest minimum residence periods to date (days between first and last sightings) of individuals per species was 676 days for a subadult green turtle, 675 days for a subadult hawksbill, and 621 days for an adult-sized male loggerhead (Table 2.5). Juvenile green and hawksbill turtles both had the shortest mean periods between consecutive resightings of all size classes per species (51 and 134 days respectively; Table 2.5). Adult-sized loggerheads also had a short mean period between consecutive resightings (67 days; Table 2.5). The two adult-sized female green turtles who were flipper-tagged in Sodwana Bay in 2013 (Rambaran 2020) were still present here in this study and were thus resighted ~ eight and nine years apart, despite possible short-term departures for breeding migrations.

Table 2.5 Longest minimum residence periods to date (days between first and last sightings) and mean periods between consecutive resightings (days) of photo-IDed individuals grouped by size class at all sites over a two-year study period. Grey shaded values are the longest per species. Cm: green turtle; Ei: hawksbill; Cc: loggerhead.

	Longest minimum residence period (days)			Mean period between consecutive resightings (days)		
Size class	**Cm**	**Ei**	**Cc**	**Cm**	**Ei**	**Cc**
Juvenile	543	616	-	51	134	-
Subadult	676	675	-	159	142	-
Adult-sized	545	350	621	135	191	67

Site fidelity

Out of the 89 individuals that were resighted at least once in the study period, most (99%, n = 88) demonstrated a high degree of site fidelity to specific reef complexes. Individuals were seldom resighted on other reef complexes unless they were < 1 km apart, as in the southern section of Sodwana Bay (Fig. 2.23a, c, f). Individuals were also resighted < 1 km apart on different parts of Aliwal Shoal (Fig. 2.23b, d, g). Even these movements of ~ 1 km over a two-year study period are indicative of strong site fidelity. On Aliwal Shoal, subadult hawksbills were resighted on different parts of the reef much more so than green turtles and loggerheads, who showed a high degree of site fidelity to the shallow northern part of the reef (Fig. 2.23b, d, g). Many individuals were only sighted once (n = 138), and thus may have been transient to the area. The movement of one transient individual, an adult-sized female hawksbill (> 80 cm SCL), was tracked over a distance of > 350 km (Fig. 2.23e). This individual was first sighted on Aliwal Shoal on 11 October 2021 and then resighted exactly one month later on Raggie Reef in iSimangaliso (Fig. 2.23e), then never seen again.

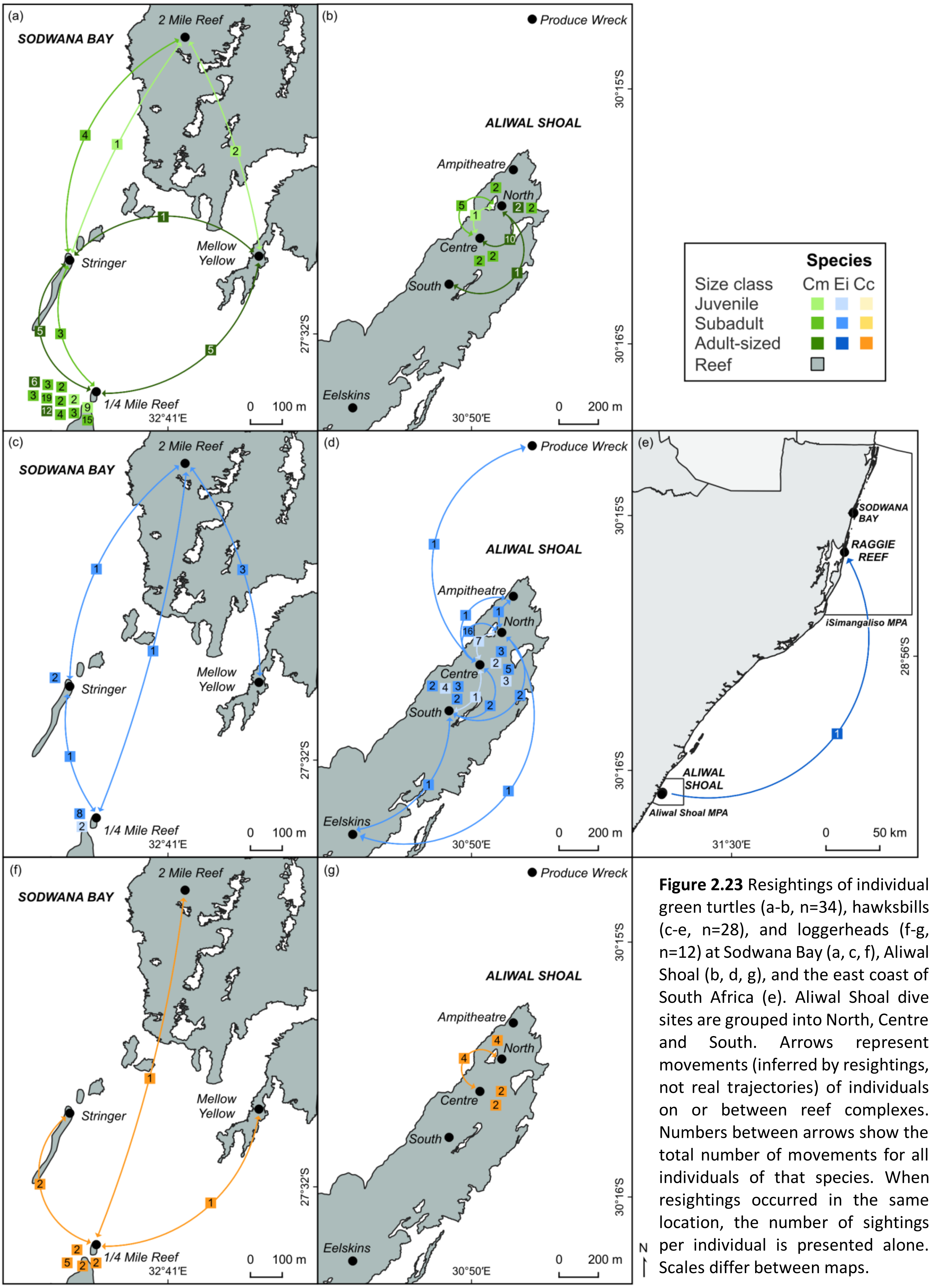


Figure 2.23 Resightings of individual green turtles (a-b, n=34), hawksbills (c-e, n=28), and loggerheads (f-g, n=12) at Sodwana Bay (a, c, f), Aliwal Shoal (b, d, g), and the east coast of South Africa (e). Aliwal Shoal dive sites are grouped into North, Centre and South. Arrows represent movements (inferred by resightings, not real trajectories) of individuals on or between reef complexes. Numbers between arrows show the total number of movements for all individuals of that species. When resightings occurred in the same location, the number of sightings per individual is presented alone. Scales differ between maps.

2.5 Discussion

This chapter investigated the relative abundance, demographics (size distribution and sex ratios) and spatial distribution (local distribution, residency and site fidelity) among sea turtle species in the iSimangaliso and Aliwal Shoal MPAs on the east coast of South Africa. It was hypothesised that 1) relative abundance will be proportional to the nesting female abundance in the SWIO (Cm > Ei > Cc > Dc > Lo); 2) the size classes of non-nesting species (green turtles and hawksbills) will be dominated by juveniles, and size classes of nesting species (loggerheads and leatherbacks) will be dominated by adults; but that 3) adult sex ratios will be balanced (1 male: 1 female) for all species; and 4) juveniles of all species will have longer residence periods than adults.

Relative abundance

The first hypothesis, which proposed that relative abundance will be proportional to the nesting female abundance in the SWIO (Cm > Ei > Cc > Dc > Lo), was supported on Aliwal Shoal but not in iSimangaliso, where loggerheads had a higher relative abundance than hawksbills (Cm > Cc > Ei > Dc). Even though the nesting female hawksbill abundance in the SWIO (2000–3000 nesting females/year; Mortimer and Donnelly 2008) is greater than that of loggerheads (< 1000 nesting females/year; Nel *et al.* 2013a), the major SWIO loggerhead rookery shared by South Africa and Mozambique is much closer to reefs sampled in this study than major SWIO hawksbill rookeries in Seychelles, Madagascar and Chagos Archipelago (Mortimer and Donnelly 2008; Mortimer *et al.* 2020). Local rookery output may thus be driving the higher relative abundance of loggerheads than hawksbills in iSimangaliso. The sheer magnitude of SWIO green turtle rookeries (> 10 000 nesting females/year; Lauret-Stepler *et al.* 2007) was particularly highlighted in this study's results where green turtles had a consistently higher mean SPUE over all other species across all study sites, and discovery curves showed that sampling saturation was reached for individual hawksbills and loggerheads early in the study but never for green turtle individuals, indicating that they were sampled incompletely.

Green turtles on the nearest studied neritic foraging grounds in Praia do Tofo, southern Mozambique (~ 450 km north of iSimangaliso) were sighted at a mean rate of 0.15 turtles/hour (n = 157 in 1055 hours; Williams *et al.* 2017), which was lower than all surveyed sites in this study (range: 0.5 turtles/hour, SD 1.24, n = 26 at Raggie Reef to 5.8 turtles/hour, SD 3.90, n = 13 at Green Turtle Gully). Green turtle SPUE in seagrass meadow and coral reef habitats in Kilifi Creek, Kenya (0.8 turtles/hour, n = 66 in ~ 80 hours; Fulanda *et al.* 2007), was also lower than mean green turtle

SPUE for all but one sampled site in this study (Raggie Reef: 0.5 turtles/hour, SD 1.24, n = 26; range for other sites: 2.3 turtles/hour, SD 4.47, n = 10 to 5.8 turtles/hour, SD 3.90, n = 13). Reefs on the east coast of South Africa are similar to those in southern Mozambique, described as primarily rocky reefs with low hard coral diversity ranging from 11–33 m depth (Williams *et al.* 2017). However, the higher relative abundance of green turtles in this study may have been related to the shallower depths sampled as most sites were < 20 m deep, where sea turtles are more frequently observed (e.g., Jean *et al.* 2010; pers. obs.), whereas the mean depth of all surveyed sites in southern Mozambique was 18 m (Williams *et al.* 2017).

Hawksbills were also sighted less frequently in southern Mozambique, where there were only 12 sightings over four years (SPUE not reported; Williams *et al.* 2017) compared to 208 hawksbill sightings in two years in this study. These results may also be influenced by habitat and depth differences, but given their extreme disparity, may perhaps be more a result of the successful long-term conservation afforded to sea turtles in South African waters (e.g., Marine Living Resources Act of No. 18 of 1998) who face significantly fewer threats of bycatch and illegal trade than those in Mozambique (Williams *et al.* 2019) as well as Kenya and many of the other SWIO countries (Zanre 2005; Bourjea *et al.* 2008). Hawksbill SPUE in neritic habitats of D’Arros Island, Seychelles, ranged from 0.3 turtles/hour (n = 2 in 12.5 hours) on deep reef slopes (20–30 m depth) to 4.2 turtles/hour (n = 827 in 178 hours) on shallow platform reefs (5–16 m depth) (von Brandis 2010). Mean hawksbill SPUE in this study (iSimangaliso: 0.2 turtles/hour, SD 1.2, n = 32; Aliwal Shoal: 0.8 turtles/hour, SD 1.35, n = 48) fell within the range reported by von Brandis (2010) in Seychelles which is likely a result of the distance of South African foraging grounds from major SWIO hawksbill rookeries as mentioned above, as well as differences between the tropical and subtropical habitats.

Loggerheads were the most frequently observed sea turtle species in southern Mozambique (0.2 turtles/hour, n = 210 in 1055 hours; Williams *et al.* 2017), but there were still fewer loggerheads observed there than four out of six surveyed sites in this study (SPUE range (mean ± SD): 0–0.5 ± 1.65 turtles/hour, n = 47). Few sightings of leatherbacks in this study (n = 5 in two years) were consistent with findings of Williams *et al*. (2017) in southern Mozambique (n = 2 sightings in four years). Leatherback presence in low numbers is likely due to the small nearby rookery size (< 100 nesting females/year; Nel *et al.* 2013a) as well as their primarily oceanic lifestyle whereby they only return to coastal waters to reproduce (Hughes 1996; Harris *et al.* 2015); this offshore behaviour also makes them more susceptible to industrial longline fisheries (Petersen *et al.* 2009).

These findings indicate that the relative abundance of sea turtles in the iSimangaliso and Aliwal Shoal MPAs appears to be higher than that of other east African foraging grounds, for example in southern Mozambique (Williams et al. 2017) and Kenya (Fulanda et al. 2007), but lower than SWIO island foraging grounds such as those in Seychelles (von Brandis 2010). Variation in relative abundance is likely influenced by local differences in habitat (rocky reef, coral reef or seagrass meadows and depth thereof), threats and conservation measures. The findings also highlight the importance of SWIO rookery size and distance in the dispersal and composition of sea turtles across foraging grounds on the east African coastline.

Size distribution

The second hypothesis, which predicted that size classes of non-nesting species (green turtles and hawksbills) will be dominated by juveniles, and size classes of nesting species (loggerheads and leatherbacks) will be dominated by adults, was supported. Size class distribution results were consistent with local KZNSB bycatch from 1998 to 2021 of juvenile, subadult and adult green turtles (CCL range: 40–130 cm) but mostly subadults (70–80 cm CCL), as well as juvenile hawksbills (30–60 cm CCL), subadult and adult loggerheads (70–100 cm CCL) and adult leatherbacks (110–160 cm CCL) (Brazier *et al.* 2012; KZNSB unpubl. data).

Given the broad size range of green turtles (44.9–99.2 cm SCL) measured in this study, neritic habitats on the east coast of South Africa may be considered mixed green turtle foraging grounds (comprising of both immature and adult turtles), like those in southern Mozambique (CCL range 30–140 cm; Williams *et al*. 2017), Kenya (CCL range: 45–105 cm; Fulanda *et al*. 2007) and Mayotte Island (CCL range: 70–109 cm; Taquet *et al*. 2006 and 39–105 cm; Ballorain *et al*. 2010). The minimum size of measured green turtles in this study (44.9 cm SCL) suggests that they recruit into neritic habitats on the east coast of South Africa at a similar size to those in Kenya (45 cm CCL; Fulanda *et al*. 2007) and Mayotte Island (39 cm CCL; Ballorain *et al*. 2010). The limited size range of hawksbills (37.4–73.4 cm SCL) indicates that local neritic habitats are developmental (juvenile) foraging grounds for hawksbills, like those in Seychelles (CCL range: 32–85 cm; von Brandis 2010) and Chagos Archipelago (SCL range: 29.7–75.8 cm; Stokes *et al*. 2023). Hawksbills (minimum SCL: 37.4 cm) recruit into local neritic habitats at a slightly larger size to those in Seychelles (32 cm CCL; von Brandis 2010) and Chagos Archipelago (29.7 cm; Stokes *et al*. 2023). These findings suggest that neritic habitats on the east coast of South Africa are a regionally important developmental area for green turtles and hawksbills (Nel *et al.* 2013b). The limited size range of loggerheads (66.9–81 cm SCL) indicates that local neritic habitats are adult foraging grounds for loggerheads like those in Kenya (CCL range: 68.5–96.8 cm, Zanre 2005). Loggerheads (minimum SCL: 66.9 cm) recruit into local neritic habitats at a similar size to those in southern Mozambique (70 cm CCL; Williams *et al*. 2017).

Sex ratios

The third hypothesis, which stated that adult sex ratios will be balanced (1 male: 1 female) for all species, was not supported. Even though sex ratios of individually identified adult-sized green turtles and loggerheads did not deviate significantly from 1:1 (binomial test, all $p > 0.05$), adult-sized individuals of both species were dominated by females (green turtles: $n = 17$ females, $n = 7$ males; loggerheads: $n = 35$ females, $n = 18$ males), and no adult male hawksbills were observed in the study. KZNSB catches from 1981 to 2008 also reported more adult female green turtles ($n = 16$) than males ($n = 12$), but more adult male loggerheads ($n = 128$) than females ($n = 93$), and more adult male hawksbills ($n = 2$) than females ($n = 1$) (Brazier *et al*. 2012). Information on sex ratios at SWIO foraging grounds is limited but hatchling sex ratios based on sand temperature have been studied at the Ascension Island green turtle rookery, one of the sources of stranded green turtles on the KZN coastline (Hickman 2017), revealing female-biased hatchling production (Godley *et al.* 2002). This trend has been observed in 15 of 15 records from green turtle populations globally and in 28 of 29 records from loggerhead populations globally (Hays *et al.* 2014). Female-biased adult sex ratios on foraging grounds stocked by these rookeries are thus not surprising. Similar results were found on foraging grounds off western Australia, where adult green turtles had a strong female-biased sex ratio (~ 3:1) whilst adult loggerhead sex ratios were slightly female-biased but did not deviate significantly from 1:1 (Heithaus *et al.* 2005). These results may underscore the prevalent female-biased sex ratios among sea turtles across species and regions, which has been shown to be accounted for by more frequent breeding by male sea turtles than females (Hays *et al.* 2014).

Local distribution

Even though green turtles, hawksbills and loggerheads were found along the entire east coast of South Africa (and the country), and were each present practically everywhere we sampled, there were many more hawksbills on Aliwal Shoal than in the iSimangaliso MPA. This was indicated by both mean SPUE (Aliwal Shoal: 0.8 turtles/hour, SD 1.35, $n = 48$; iSimangaliso: 0.23 turtles/hour, SD 1.2, $n = 32$) and the number of individuals identified ($n = 30$ on Aliwal Shoal and $n = 16$ in iSimangaliso), despite the area sampled on Aliwal Shoal (~ 2.1 km^2) being half the size of the total area sampled in iSimangaliso (~ 5.2 km^2). These findings may possibly be due to a relatively higher availability of the hawksbill's preferred food source, predominantly sponges (León and Bjorndal 2002; Rambaran 2020), which they were often seen foraging on (as shown in Chapter 3). The higher occurrence of hawksbills on Aliwal Shoal may also be driven by the reef's higher structural complexity from its rugose topography, as Rincon-Diaz *et al*. (2011) showed that the type and complexity of reef structures (likely related to sheltering) played a more important role in the spatial variability of hawksbill abundance than food availability.

The high occurrence and wide distribution of hawksbills in this study (e.g., Fig. 2.19f) was, however, surprising given that hawksbill catches in KZNSB nets have historically been low (only 3% of total catch from 1981 to 2008; Brazier *et al*. 2012), and that this species has a more equatorial nesting range (Hughes 1973; Bowen and Karl 2007). The results of this study thus add to the growing body of evidence that hawksbills have a wider distribution than previously known.

Residency

The fourth hypothesis, which predicted that juveniles of all species will have longer residence periods than adults, was supported for green and hawksbill turtles. This hypothesis was based on knowledge that immature individuals tend to have long residence periods on neritic foraging grounds (e.g., von Brandis 2010; Rambaran 2020; Hays *et al.* 2021), whereas adult individuals may depart neritic foraging grounds seasonally for breeding migrations (e.g., Schofield *et al.* 2010). The longest minimum residence period to date (days between first and last sightings) of 676 days was indeed recorded for a subadult green turtle, whilst the longest minimum residence period for an adult-sized green turtle was 545 days. Juvenile green turtles also had the shortest mean period between consecutive resightings (51 days, year-round) strongly indicating that they did not depart the study area between resightings, whereas adult-sized green turtles had a mean period of 135 days between consecutive resightings. The two adult-sized female green turtles identified via flipper tags in 2013 (Rambaran 2020) and resighted about eight and nine years later in this study are likely to have departed the study area for seasonal breeding migrations given that this species is known to nest every three years in the SWIO (Bourjea *et al.* 2007a). Thus, even though immature green turtles may have longer residence periods in local neritic habitats than adults, adults who depart seasonally for breeding migrations may still be considered residents due to their strong site fidelity.

The second longest minimum residence period to date of 675 days was recorded for a subadult hawksbill, almost double the longest minimum residence period for an adult-sized hawksbill (350 days). Adult-sized hawksbills also had extended intervals between consecutive resightings, averaging 191 days, suggesting that they are transient to the study area. Only two adult-sized hawksbills (4% of all individual hawksbills) were seen in the entire two-year study period, indicating their infrequent presence along the east coast of South Africa. This rarity and transient nature was further supported by the stranding of an adult-sized female hawksbill at Yzerfontein on the west coast who was satellite tracked upon rehabilitation and release in 2013 to the northeast coast of Madagascar (Two Oceans Aquarium unpubl. data). The > 350 km migration of one of the adult-sized female hawksbills in this study, from Aliwal Shoal to Raggie Reef, further supports their transient nature along this coastline and suggests its potential utilisation as a migratory pathway for adults of this species.

The fourth hypothesis of juvenile residence was not supported for loggerhead and leatherback turtles as no juveniles of either species were found on any study sites. Satellite tracks of post-nesting adult female loggerheads and leatherbacks from iSimangaliso indicate that all individuals migrate to foraging grounds away from the South African coast, indicating they are not resident but transient to the area (Harris *et al.* 2018). Sea turtles are known to have separate foraging and breeding grounds worldwide and undertake long migrations between them (Carr 1978; Musick and Limpus 1997). Whilst the lack of leatherback sightings on reefs in this study confirm the transient nature of leatherbacks on the east coast of South Africa, the longest minimum residence period to date recorded for adult-sized loggerheads (621 days, by an adult-sized male which we know so little about) was in fact highly indicative of residency, and the short mean period between consecutive resightings of adult-sized loggerheads (67 days, year-round) strongly indicates that they did not depart the study area between resightings.

These results suggest that adult loggerheads in local neritic habitats are resident year-round, and are thus different individuals to those that nest seasonally on iSimangaliso beaches. Genetic analyses have in fact shown that stranded and bycaught subadult and adult loggerheads in South Africa originate from the North West Atlantic, Mediterranean and South African rookeries (Hickman 2017), thus perhaps residents originate from the rookeries afar. None of the adult-sized female loggerheads observed on sampled reefs in the study period were flipper tagged, further indicating that they do not nest here. Only one flipper tagged loggerhead was recorded on Quarter Mile Reef before this study began, indicating that it is rare for breeding females to spend internesting periods on these reefs. Williams *et al*. (2017) recorded a longest minimum residence period of 532 days for an adult loggerhead, also indicating their residency in southern Mozambique.

These results support those of Rambaran (2020), who found that both immature and adult-sized green turtles and immature hawksbills in Sodwana Bay were highly resident from satellite tracking data. The findings also add to this body of knowledge that adult-sized loggerheads in iSimangaliso are also highly resident, and that all three species are resident on Aliwal Shoal too, and that adult-sized hawksbills are transient to the area.

Site fidelity

The high number of individual resighting events on the exact same reef (e.g., 19 resightings of an individual subadult green turtle on Quarter Mile Reef) was highly indicative of strong site fidelity, supporting results of Rambaran (2020). Strong site fidelity was also shown by immature green turtles in southern Mozambique where individuals were resighted between 13 and 19 times on the same reef over the four-year study period (Williams *et al*. 2017). Immature green and hawksbill turtles, as well as adult-sized loggerheads also showed strong site fidelity to Aliwal Shoal but movement networks indicated that they were not resighted on one part of the reef for periods as extensive as those observed in Sodwana Bay, likely because Aliwal Shoal is one large and continuous foraging area whereas reef complexes in Sodwana Bay are separated and distinct. Juvenile hawksbills also showed very strong site fidelity to one reef off D'Arros Island, Seychelles, being resighted between 8 and 123 times over a four-year period (von Brandis 2010).

Citizen science

Given that citizen science data showed similar trends in relative abundance to timed research survey data, it was considered an extremely useful and valuable method to supplement research data. The slight discrepancy between citizen science data and research data on Aliwal Shoal, where the relative abundance of hawksbills was recorded to be higher than green turtles, was likely due to the way recreational divers approach sea turtles – often not as cautiously as researchers (pers. obs.) – limiting their sightings of timid individuals. Hawksbills on these frequently dived reefs seem to be more habituated to recreational divers than green turtles (pers. obs.).

Citizen science data was particularly useful in revealing a wider distribution of sea turtles along the entire South African coastline than currently recognised, demonstrating one of its main advantages of collecting data over broad scales cost-effectively. Chassagneux *et al*. (2013) and Williams *et al*. (2015) also found citizen science to be a useful tool to learn about in-water sea turtle species composition, size and distribution and to raise conservation awareness among divers.

Study limitations and future research improvements

Even though abundance estimates, morphometric measurements and fine-scale movements of individuals are usually obtained from physical CMR methods and remote technologies (e.g., Rambaran 2020; Stokes *et al*. 2023), this study demonstrated that baseline information on the number of individual sea turtles and morphometrics, movements, residency, and site fidelity thereof can be obtained via inexpensive in-water photo-ID and paired-laser photogrammetry techniques. However, it is acknowledged that small and cryptic (hiding) sea turtle individuals may have been undersampled due to perception and availability biases, whereby observers may have missed animals and animals may not have been available for detection due to their own characteristics or various environmental conditions (Marsh and Sinclair 1989). It would thus be useful in future to develop and use techniques to quantify in-water perception and availability biases as has been done for e.g., aerial surveys of marine mammals (Pollock *et al.* 2006). The timid nature of some sea turtle individuals, particularly at study sites less frequented by humans, contributed to these biases as it limited our ability to photo-ID all individuals present each time. Consequently, none of the 11 sea turtles seen on Adlam's Reef were photo-IDed at all, and timed research survey results only gathered n = 51 sightings which allowed for ten identifications to individual level to be made on Raggie Reef, whereas RUV footage captured n = 138 sightings which allowed for 77 identifications to individual level to be made here when humans were not present. Future in-water studies may thus benefit by an adaptive sampling approach, for example (as per this study), by using RUVs with a simple, cost-effective design to supplement data collected by divers on reefs that are not frequently dived.

Loggerhead photo-IDs were also limited by their minimal postocular scute melanisation, which is much darker and clearer in green and hawksbill turtles. Similarly, Williams *et al*. (2017) found that loggerheads had the fewest usable photos (52%), compared to green turtles (78%) and hawksbills (86%). It is thus highly recommended to use photos of the carapace, scutes on top of the head and any unique features such as injuries or tick lines to aid individual identification where postocular scutes may be unclear, as done in this study and suggested by Schofield *et al*. (2008) and Hall and McNeill (2013).

Another recommendation, going forward, is to always prioritise one side of the face (left usually standard) when photographing sea turtles to minimise the chance of mistaking one individual with only a single documented facial profile for two distinct individuals. According to Chassagneux *et al*.

(2013), a computer-assisted sea turtle identification system known as TORtues marines du Sud-Ouest de l'Océan Indien – Marine Turtles of the SWIO (TORSOOI; https://torsooi.com/), separates identifications into complete (both left and right facial profiles photographed) and single (only one facial profile photographed) in their database and only includes individuals with complete identifications in study analyses. This may be a better approach going forward to avoid one individual photographed from opposite sides on different occasions mistakenly identified as two individuals.

It is also important to acknowledge the limitations of citizen science data, as citizen scientists did not time their search effort (hence dive trips were used instead of hours), and often only submitted data on days they saw sea turtles, not reporting days where zero sightings were made. This may lead to overestimates of SPUE as the effort expended on dive trips where sea turtles were absent was not accounted for. Despite being similar to timed research survey data, it is recommended to make use of citizen science data not for estimates of in-water relative abundance but to gather data on individual identifications, resightings, spatial distribution, movements, residency and site fidelity.

2.6 Conclusion

This is the first study to investigate the relative abundance, demographics and distribution of sea turtles on reefs along the east coast of South Africa using in-water methods. A robust photo-ID database of individual sea turtles in the iSimangaliso and Aliwal Shoal MPAs (n = 227) was established coupled with information on size, sex, resighting events and spatial distribution over a two-year period. Findings suggested that reefs in these MPAs host some of the highest sea turtle SPUE results recorded for the region, and highlighted the influence of local differences in habitat, threats, conservation measures and rookery size and distance from foraging grounds on their species composition and abundance.

Size distribution results confirm that neritic habitats on the east coast of South Africa are a regionally important developmental area for immature green turtles and hawksbills but also host adult-sized green turtles (thus mixed green turtle aggregations) and adult-sized loggerheads, which have slightly female-biased sex ratios based on visual estimates. Results also indicate that green turtles (juveniles to adult-sized), immature hawksbills and adult-sized loggerheads are highly resident and show strong site fidelity in the iSimangaliso and Aliwal Shoal MPAs, with the presence of transient individuals of all species suggesting that coastal waters are also used as a migratory pathway. With the aid of citizen science, we may have potentially recorded the longest migration of an individual sea turtle (adult-sized female hawksbill) using photo-ID (>350 km).

Citizen science was demonstrated as a particularly useful tool to collect data over broad scales cost-effectively. Citizen science reports from other parts of the South African coastline suggest a much broader distribution of sea turtles than currently recognised and highlight significant future research opportunities in seemingly high-density areas, such as estuaries in the upper Eastern Cape and the shallow-water green turtle foraging hotspot in De Hoop MPA, Western Cape.

These findings provide novel insight into resident sea turtle populations along the east coast of South Africa and form the baseline against which to assess future trends. They also serve as the foundation on which a long-term in-water monitoring programme will be established using research surveys supplemented by ongoing voluntourism and citizen science contributions, which will further add to the growing body of in-water sea turtle knowledge and may be used to inform effective species-specific management and conservation strategies.

Spatiotemporal patterns in sea turtle abundance and behaviour are analysed in Chapter 3 to understand when and how sea turtles utilise inshore habitats on the east coast of South Africa.

2.7 References

Anderson, R. J., McKune, C., Bolton, J. J., Declerck, O. and Tronchin, E. (2005). Patterns in subtidal seaweed communities on coral-dominated reefs at Sodwana Bay on the KwaZulu-Natal coast, South Africa. *African Journal of Marine Science,* 27(3), pp. 529-537

Araujo, G., Legaspi, C. G., Ferber, S., Murray, R., Burdett, K., Grundy, S., Labaja, J., Snow, S., Yaptinchay, A. and Ponzo, A. (2019). In-water methods reveal population dynamics of a green turtle *Chelonia mydas* foraging aggregation in the Philippines. *Endangered Species Research,* 40, pp. 207-218

Avens, L. and Snover, M. L. (2013). Age and Age Estimation in Sea Turtles. In: Wyneken, J., Lohmann, K. J., and Musick, J. A. 2013. The Biology of Sea Turtles. 3, pp. 97-134

Balazs, G. H. (1999). Factors to consider in the tagging of sea turtles. In: Eckert, K.L., Bjorndal, K., Abreu-Grobois, F.A. and Donnelly, M. (1999) Research and management techniques for the conservation of sea turtles.

Ballorain, K., Ciccione, S., Bourjea, J., Grizel, H., Enstipp, M. and Georges, J.-Y. (2010). Habitat use of a multispecific seagrass meadow by green turtles *Chelonia mydas* at Mayotte Island. *Marine Biology,* 157(12), pp. 2581-2590

Bell, C. D., Blumenthal, J. M., Austin, T. J., Ebanks-Petrie, G., Broderick, A. C. and Godley, B. J. (2008). Harnessing recreational divers for the collection of sea turtle data around the Cayman Islands. *Tourism in Marine Environments,* 5(4), pp. 245-257

Bennett, P. and Keuper-Bennett, U. (2001). The use of subjective patterns in green turtle profiles to find matches in an image database. Proceedings of the 21st Annual Symposium on Sea Turtle Biology and Conservation. 2005. Coyne, M. & R.D. Clark (Comps.). NOAA Tech Memo NMFS-SEFSC-528. pp. 115-116

Berger-Wolf, T. Y., Rubenstein, D. I., Stewart, C. V., Holmberg, J. A., Parham, J., Menon, S., Crall, J., Van Oast, J., Kiciman, E. and Joppa, L. (2017). Wildbook: Crowdsourcing, computer vision, and data science for conservation. *arXiv preprint arXiv:1710.08880,*

Bjorndal, K. A. and Bolten, A. B. (2000). Proceedings of a Workshop on Assessing Abundance and Trends for In-Water Sea Turtle Populations, held at the Archie Carr Center for Sea Turtle Research University of Florida, Gainesville, Florida, 24-26 March 2000.

Bjorndal, K. A., Bolten, A. B. and Chaloupka, M. Y. (2005). Evaluating trends in abundance of immature green turtles, *Chelonia mydas*, in the greater Caribbean. *Ecological Applications,* 15(1), pp. 304-314

Bosman, C., Uken, R. and Smith, A. (2005). The bathymetry of the Aliwal Shoal, Scottburgh, South Africa. *South African Journal of Science,* 101(5), pp. 255-257

Bourjea, J., Frappier, J., Quillard, M., Ciccione, S., Roos, D., Hughes, G. and Grizel, H. (2007a). Mayotte Island: another important green turtle nesting site in the southwest Indian Ocean. *Endangered Species Research,* 3, pp. 273-282

Bourjea, J., Nel, R., Jiddawi, N., Koonjul, M. and Bianchi, G. (2008). Sea turtle bycatch in the West Indian Ocean: review, recommendations and research priorities. *Western Indian Ocean Journal of Marine Science,* 7(2), pp. 137-150

Bowen, B. W. and Karl, S. (2007). Population genetics and phylogeography of sea turtles. *Molecular ecology,* 16(23), pp. 4886-4907

Brazier, W., Nel, R., Cliff, G. and Dudley, S. (2012). Impact of protective shark nets on sea turtles in KwaZulu-Natal, South Africa, 1981–2008. *African Journal of Marine Science,* 34(2), pp. 249-257

Calmanovici, B., Waayers, D., Reisser, J., Clifton, J. and Proietti, M. (2018). I^{3}S Pattern as a mark-recapture tool to identify captured and free-swimming sea turtles: an assessment. *Marine Ecology Progress Series,* 589, pp. 263-268

Campbell, L. M. and Smith, C. (2006). What makes them pay? Values of volunteer tourists working for sea turtle conservation. *Environ Manage,* 38(1), pp. 84-98

Carpentier, A. S., Jean, C., Barret, M., Chassagneux, A. and Ciccione, S. (2016). Stability of facial scale patterns on green sea turtles *Chelonia mydas* over time: a validation for the use of a photo-identification method. *Journal of Experimental Marine Biology and Ecology,* 476, pp. 15-21

Carr, A. F., Carr, M.H. and Meylan, A.B. (1978). The ecology and migrations of sea turtles. 7, The West Caribbean green turtle colony. *Bulletin of the AMNH,* v. 162

Casale, P., Freggi, D., Basso, R. and Argano, R. (2005). Size at male maturity, sexing methods and adult sex ratio in loggerhead turtles (*Caretta caretta*) from Italian waters investigated through tail measurements. *The Herpetological Journal,* 15(3), pp. 145-148

Chaloupka, M. and Limpus, C. (2001). Trends in the abundance of sea turtles resident in southern Great Barrier Reef waters. *Biological Conservation,* 102(3), pp. 235-249

Chassagneux, A., Jean, C., Bourjea, J. and Ciccione, S. (2013). Unraveling behavioral patterns of foraging hawksbill and green turtles using photo-identification. *Marine Turtle Newsletter,* (137), pp. 1

Child, D. (1980) *Portrait of a Pioneer: The Letters of Sidney Turner from South Africa, 1864-1901.* Macmillan South Africa.

De Lecea, A., Fennessy, S. and Smit, A. (2013). Processes controlling the benthic food web of a mesotrophic bight (KwaZulu-Natal, South Africa) revealed by stable isotope analysis. *Marine Ecology Progress Series,* 484, pp. 97-114

Deakos, M. H. (2010). Paired-laser photogrammetry as a simple and accurate system for measuring the body size of free-ranging manta rays *Manta alfredi*. *Aquatic Biology,* 10(1), pp. 1-10

Den Hartog, J. and Reijns, R. (2014). Interactive Individual Identification System (I^{3}S) Pattern Manual. Version 4.02. https://reijns.com/i3s/.

Dunbar, S., Ito, H., Bahjri, K., Dehom, S. and Salinas, L. (2014). Recognition of juvenile hawksbills *Eretmochelys imbricata* through face scale digitization and automated searching. *Endangered Species Research,* 26(2), pp. 137-146

Eckert, K., Bjorndal, K., Abreu-Grobois, F. and Donnelly, M. (1999). Priorities for research in foraging habitats. *Research and management techniques for the conservation of sea turtles,* 4, pp. 12-18

Fulanda, B., Ohtomi, J., Mueni, E., Nzuki, S., Muasa, J., Muthama, C. and Hossain, Y. (2007). A preliminary assessment of the green sea turtle *Chelonia mydas* population and its foraging grounds in Kilifi Creek, Kenya. *South Pacific Studies,* 28, pp. 31-41

Godley, B., Broderick, A., Glen, F. and Hays, G. (2002). Temperature-dependent sex determination of Ascension Island green turtles. *Marine Ecology Progress Series,* 226, pp. 115-124

Hall, A. G. and McNeill, J. B. (2013). Inferring sea turtle recapture rates using photographic identification. *Herpetological Review,* 44(4), pp. 561-569

Hamann, M., Godfrey, M. H., Seminoff, J. A., Arthur, K., Barata, P. C. R., Bjorndal, K. A., Bolten, A. B., Broderick, A. C., Campbell, L. M., Carreras, C., Casale, P., Chaloupka, M., Chan, S. K. F., Coyne, M. S., Crowder, L. B., Diez, C. E., Dutton, P. H., Epperly, S. P., FitzSimmons, N. N., Formia, A., Girondot, M., Hays, G. C., Cheng, I. S., Kaska, Y., Lewison, R., Mortimer, J. A., Nichols, W. J., Reina, R. D., Shanker, K., Spotila, J. R., Tomás, J., Wallace, B. P., Work, T. M., Zbinden, J. and Godley, B. J. (2010). Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endangered Species Research,* 11(3), pp. 245-269

Hanna, M. E., Chandler, E. M., Semmens, B. X., Eguchi, T., Lemons, G. E. and Seminoff, J. A. (2021). Citizen-sourced sightings and underwater photography reveal novel insights about green sea turtle distribution and ecology in southern California. *Frontiers in Marine Science,* 8, pp. 671061

Harris, L. R., Nel, R., Oosthuizen, H., Meÿer, M., Kotze, D., Anders, D., McCue, S. and Bachoo, S. (2018). Managing conflicts between economic activities and threatened migratory marine species toward creating a multiobjective blue economy. *Conservation Biology,* 32(2), pp. 411-423

Harris, L. R., Nel, R., Oosthuizen, H., Meyer, M., Kotze, D., Anders, D., McCue, S. and Bachoo, S. (2015). Paper-efficient multi-species conservation and management are not always field-effective: The status and future of Western Indian Ocean leatherbacks. *Biological Conservation,* 191, pp. 383-390

Hays, G. C., Mazaris, A. D. and Schofield, G. (2014). Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science,* 1, pp. 43

Hays, G. C., Mortimer, J. A., Rattray, A., Shimada, T. and Esteban, N. (2021). High accuracy tracking reveals how small conservation areas can protect marine megafauna. *Ecological Applications,* 31(7), pp. e02418

Heithaus, M. R., Frid, A., Wirsing, A. J., Bejder, L. and Dill, L. M. (2005). Biology of sea turtles under risk from tiger sharks at a foraging ground. *Marine Ecology Progress Series,* 288, pp. 285-294

Hickman, S. (2017) The genetic diversity and home populations of immature loggerhead (*Caretta caretta*), green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles frequenting South African waters. Honours thesis, Nelson Mandela University

Hughes, G. (1996). Nesting of the Leatherback Turtle (*Dermochelys coriacea*) in Tongaland, KwaZulu-Natal, South Africa, 1963-1995. *Chelonian Conservation and Biology,* 2(2), pp. 153-158

Hughes, G. R. (1973) The sea turtles of South East Africa.

Hunter, I. T. (1988). Climate and weather off Natal. In: E.H. Schumann, (Ed.), Coastal Ocean Studies off Natal, South Africa. *Lecture Notes on Coastal and Estuarine Studies,* 26, pp. 101-130

Jean, C., Ciccione, S., Talma, E., Ballorain, K. and Bourjea, J. (2010). Photo-identification method for green and hawksbill turtles-First results from Reunion. *Indian ocean turtle NewsLeTTER,* 11, pp. 8-13

Jensen, M. P., Dalleau, M., Gaspar, P., Lalire, M., Jean, C., Ciccione, S., Mortimer, J. A., Quillard, M., Taquet, C., Wamukota, A., Leroux, G. and Bourjea, J. (2020). Seascape Genetics and the Spatial Ecology of Juvenile Green Turtles. *Genes (Basel),* 11(3)

Lauret-Stepler, M., Bourjea, J., Roos, D., Pelletier, D., Ryan, P., Ciccione, S. and Grizel, H. (2007). Reproductive seasonality and trend of *Chelonia mydas* in the SW Indian Ocean: a 20 yr study based on track counts. *Endangered Species Research,* 3(2), pp. 217-227

Le Gouvello, D. Z., Girondot, M., Bachoo, S. and Nel, R. (2020). The good and bad news of long-term monitoring: An increase in abundance but decreased body size suggests reduced potential fitness in nesting sea turtles. *Marine Biology,* 167, pp. 1-12

León, Y. M. and Bjorndal, K. A. (2002). Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. *Marine Ecology Progress Series,* 245, pp. 249-258

León, Y. M. and Diez, C. E. (1999). Population structure of hawksbill turtles on a foraging ground in the Dominican Republic. *Chelonian Conservation and Biology,* 3(2), pp. 230-236

Mancini, A. and Elsadek, I. M. (2019). The Role of Citizen Science in Monitoring Megafauna of the Red Sea. *Oceanographic and Biological Aspects of the Red Sea*, pp. 507-519

Marsh, H. and Sinclair, D. F. (1989). Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *The Journal of wildlife management*, pp. 1017-1024

Montagna, M., Taher, A. and Mancini, A. (2017). Combining citizen science and photo identification to monitor a key green turtle feeding ground in the southern Egyptian Red Sea. *African Sea Turtle Newsletter,* 7, pp. 8-15

Mortimer, J. A. and Donnelly, M. (2008). *Eretmochelys imbricata.* The IUCN Red List of Threatened Species 2008. e. T8005A12881238.

Mortimer, J. A., Esteban, N., Guzman, A. N. and Hays, G. C. (2020). Estimates of marine turtle nesting populations in the south-west Indian Ocean indicate the importance of the Chagos Archipelago. *Oryx,* 54(3), pp. 332-343

Mrosovsky, N. (1976). The tag loss problem. *Marine Turtle Newsletter,* 1, pp. 3-4

Musick, J. A. and Limpus, C. J. (1997) Habitat utilization and migration in juvenile sea turtles, *The Biology of Sea Turtles, Volume I*: CRC Press, pp. 137-163.

Nel, R., Punt, A. E. and Hughes, G. R. (2013a). Are coastal protected areas always effective in achieving population recovery for nesting sea turtles? *PLoS One,* 8(5), pp. e63525

Nel, R., Wanless, R., Angel, A., Mellet, B. and Harris, L. (2013b). Ecological Risk Assessment and Productivity-Susceptibility Analysis of sea turtles overlapping with fisheries in the IOTC region. Unpublished report to the IOTC and IOSEA Marine Turtle MoU.

Olbers, J. M., Celliers, L. and Schleyer, M. H. (2009). Zonation of benthic communities on the subtropical Aliwal Shoal, Durban, KwaZulu-Natal, South Africa. *African Zoology,* 44(1), pp. 8-23

Petersen, S. L., Honig, M. B., Ryan, P. G., Nel, R. and Underhill, L. G. (2009). Turtle bycatch in the pelagic longline fishery off southern Africa. *African Journal of Marine Science,* 31(1), pp. 87-96

Pollock, K. H., Marsh, H. D., Lawler, I. R. and Alldredge, M. W. (2006). Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. *The Journal of wildlife management,* 70(1), pp. 255-262

Porter, S. N., Branch, G. M. and Sink, K. J. (2017). Changes in shallow-reef community composition along environmental gradients on the East African coast. *Marine Biology,* 164(5), pp. 101

QGIS Development Team (2022). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

R Core Team (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Rambaran, R. (2020) Defining the potential ecological roles of three sea turtle species (*Caretta caretta*, *Chelonia mydas* and *Eretmochelys imbricata*) along the Eastern seaboard of South Africa. Masters thesis, Nelson Mandela Metropolitan University

Ramsay, P. and Mason, T. (1990). Development of a type zoning model for Zululand coral reefs, Sodwana Bay, South Africa. *Journal of Coastal Research*, pp. 829-852

Rasband, W. S. (2012). ImageJ: Image processing and analysis in Java. Astrophysics Source Code Library, pp.ascl-1206. https://imagej.nih.gov/ij/.

Read, T. and Jean, C. (2021). Using social media and photo-identification for sea turtles of new caledonia. *Marine Turtle Newsletter,* 162, pp. 25-29

Rees, A. F., Alfaro-Shigueto, J., Barata, P. C. R., Bjorndal, K. A., Bolten, A. B., Bourjea, J., Broderick, A. C., Campbell, L. M., Cardona, L., Carreras, C., Casale, P., Ceriani, S. A., Dutton, P. H., Eguchi, T., Formia, A., Fuentes, M., Fuller, W. J., Girondot, M., Godfrey, M. H., Hamann, M., Hart, K. M., Hays, G. C., Hochscheid, S., Kaska, Y., Jensen, M. P., Mangel, J. C., Mortimer, J. A., Naro-Maciel, E., Ng, C. K. Y., Nichols, W. J., Phillott, A. D., Reina, R. D., Revuelta, O., Schofield, G., Seminoff, J. A., Shanker, K., Tomás, J., van de Merwe, J. P., Van Houtan, K. S., Vander Zanden, H. B., Wallace, B. P., Wedemeyer-Strombel, K. R., Work, T. M. and Godley, B. J. (2016). Are we working towards global research priorities for management and conservation of sea turtles? *Endangered Species Research,* 31, pp. 337-382

Reisser, J., Proietti, M., Kinas, P. and Sazima, I. (2008). Photographic identification of sea turtles: method description and validation, with an estimation of tag loss. *Endangered Species Research,* 5(1), pp. 73-82

Rincon-Diaz, M. P., Diez, C. E., van Dam, R. P. and Sabat, A. M. (2011). Effect of Food Availability on the Abundance of Juvenile Hawksbill Sea Turtles (*Eretmochelys imbricata*) in Inshore Aggregation Areas of the Culebra Archipelago, Puerto Rico. *Chelonian Conservation and Biology,* 10(2), pp. 213-221

Rohner, C. A., Richardson, A. J., Marshall, A. D., Weeks, S. J. and Pierce, S. J. (2011). How large is the world's largest fish? Measuring whale sharks *Rhincodon typus* with laser photogrammetry. *J Fish Biol,* 78(1), pp. 378-85

RStudio Team (2022). RStudio: Integrated Development Environment for R. RStudio, PBC. http://www.rstudio.com/.

Schleyer, M. H. and Porter, S. N. (2018) Drivers of soft and stony coral community distribution on the high-latitude coral reefs of South Africa, *Advances in marine biology*: Elsevier, pp. 1-55.

Schofield, G., Hobson, V. J., Lilley, M. K., Katselidis, K. A., Bishop, C. M., Brown, P. and Hays, G. C. (2010). Inter-annual variability in the home range of breeding turtles: implications for current and future conservation management. *Biological Conservation,* 143(3), pp. 722-730

Schofield, G., Katselidis, K. A., Dimopoulos, P. and Pantis, J. D. (2008). Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations. *Journal of Experimental Marine Biology and Ecology,* 360(2), pp. 103-108

Sink, K. J., Harris, L. R., Skowno, A. L., Livingstone, T., Franken, M., Porter, S., Atkinson, L. J., Bernard, A., Cawthra, H., Currie, J., Dayaram, A., de Wet, W., Dunga, L. V., Filander, Z., Green, A., Herbert, D., Karenyi, N., Palmer, R., Pfaff, M., Makwela, M., Mackay, F., van Niekerk, L., van Zyl, W., Bessinger, M., Holness, S., Kirkman, S. P., Lamberth, S. and Lück-Vogel, M. (2019) *Chapter 3: Marine Ecosystem Classification and Mapping. In: Sink, K. J., van der Bank, M. G., Majiedt, P. A., Harris, L. R., Atkinson, L.J., Kirkman, S.P., Karenyi, N. (eds). 2019. South African National Biodiversity Assessment 2018 Technical Report Volume 4: Marine Realm. South African National Biodiversity Institute, Pretoria. South Africa. http://hdl.handle.net/20.500.12143/6372*.

Stokes, H. J., Mortimer, J. A., Laloë, J. O., Hays, G. C. and Esteban, N. (2023). Synergistic use of UAV surveys, satellite tracking data, and mark-recapture to estimate abundance of elusive species. *Ecosphere,* 14(3)

Taquet, C., Taquet, M., Dempster, T., Soria, M., Ciccione, S., Roos, D. and Dagorn, L. (2006). Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. *Marine Ecology Progress Series,* 306, pp. 295-302

van de Geer, C. H., Bourjea, J., Broderick, A. C., Dalleau, M., Fernandes, R. S., Harris, L. R., Inteca, G. E., Kiponda, F. K., Louro, C. M. M., Mortimer, J. A., Msangameno, D., Mwasi, L. D., Nel, R., Okemwa, G. M., Olendo, M., Pereira, M. A. M., Rees, A. F., Silva, I., Singh, S., West, L., Williams, J. L. and Godley, B. J. (2022). Marine turtles of the African east coast: current knowledge and priorities for conservation and research. *Endangered Species Research,* 47, pp. 297-331

von Brandis, R. G. (2010) The Ecology of Foraging Hawksbill Turtles (*Eretmochelys imbricata*) at D'Arros Island and St. Joseph Atoll in the Seychelles, Western Indian Ocean. Doctoral thesis, Tshwane University of Technology

von Brandis, R. G., Mortimer, J. A., Van De Geer, C. and Lea, J. S. (2017). A long migratory record for a small post-pelagic hawksbill. *Mar. Turt. Newsl,* 152, pp. 13-15

Wibbels, T. (1999). Diagnosing the sex of sea turtles in foraging habitats. *Research and management techniques for the conservation of sea Turtles. IUCN/SSC Marine Turtle Specialist Group Publication,* (4), pp. 139-143

Wildermann, N. E., Gredzens, C., Avens, L., Barrios-Garrido, H. A., Bell, I., Blumenthal, J., Bolten, A. B., Braun McNeill, J., Casale, P., Di Domenico, M., Domit, C., Epperly, S. P., Godfrey, M. H., Godley, B. J., González-Carman, V., Hamann, M., Hart, K. M., Ishihara, T., Mansfield, K. L., Metz, T. L., Miller, J. D., Pilcher, N. J., Read, M. A., Sasso, C., Seminoff, J. A., Seney, E. E., Willard, A. S., Tomás, J., Vélez-Rubio, G. M., Ware, M., Williams, J. L., Wyneken, J. and Fuentes, M. (2018). Informing research priorities for immature sea turtles through expert elicitation. *Endangered Species Research,* 37, pp. 55-76

Williams, J. L., Pierce, S. J., Fuentes, M. M. and Hamann, M. (2015). Effectiveness of recreational divers for monitoring sea turtle populations. *Endangered Species Research,* 26(3), pp. 209-219

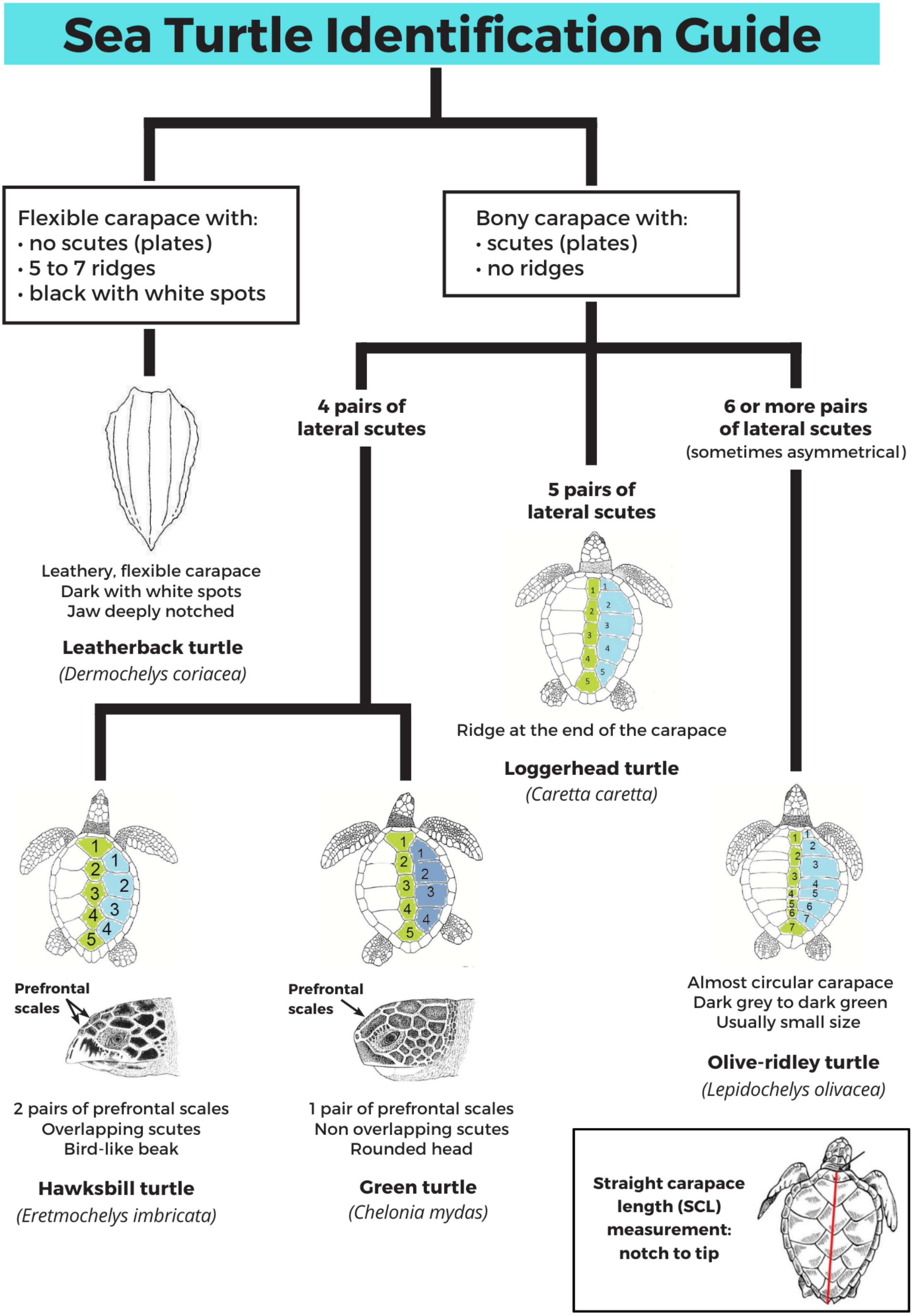
Williams, J. L., Pierce, S. J., Hamann, M. and Fuentes, M. M. (2019). Using expert opinion to identify and determine the relative impact of threats to sea turtles in Mozambique. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 29(11), pp. 1936-1948

Williams, J. L., Pierce, S. J., Rohner, C. A., Fuentes, M. M. and Hamann, M. (2017). Spatial distribution and residency of green and loggerhead sea turtles using coastal reef habitats in southern Mozambique. *Frontiers in Marine Science,* 3, pp. 288

Zanre, R. (2005). Report on Watamu Turtle Watch's sea turtle bycatch release programme, Watamu, Kenya. Local Ocean Conservation, Watamu, Kenya.

2.8 Appendix

Appendix 2.1 Identification guide for all five sea turtle species recorded in South African waters.



Sea Turtle Identification Guide

Flexible carapace with:
- no scutes (plates)
- 5 to 7 ridges
- black with white spots

Leathery, flexible carapace
Dark with white spots
Jaw deeply notched

Leatherback turtle
(Dermochelys coriacea)

Bony carapace with:
- scutes (plates)
- no ridges

4 pairs of lateral scutes

2 pairs of prefrontal scales
Overlapping scutes
Bird-like beak

Hawksbill turtle
(Eretmochelys imbricata)

1 pair of prefrontal scales
Non overlapping scutes
Rounded head

Green turtle
(Chelonia mydas)

5 pairs of lateral scutes

Ridge at the end of the carapace

Loggerhead turtle
(Caretta caretta)

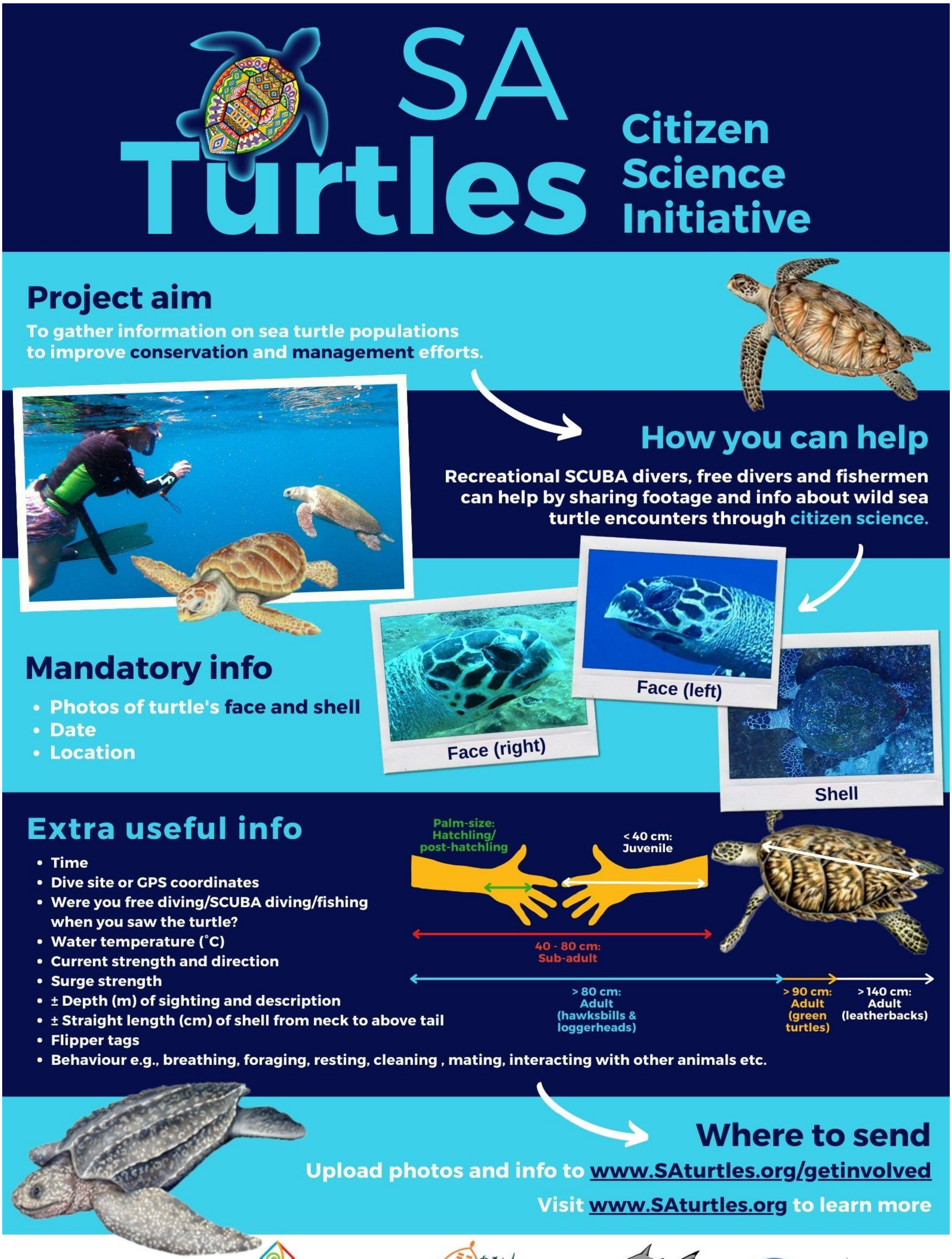
6 or more pairs of lateral scutes
(sometimes asymmetrical)

Almost circular carapace
Dark grey to dark green
Usually small size

Olive-ridley turtle
(Lepidochelys olivacea)

Straight carapace length (SCL) measurement: notch to tip

Appendix 2.2 Long-term in-water citizen science monitoring initiative poster for dive centres.



SA Turtles Citizen Science Initiative

Project aim

To gather information on sea turtle populations to improve **conservation** and **management** efforts.

How you can help

Recreational SCUBA divers, free divers and fishermen can help by sharing footage and info about wild sea turtle encounters through **citizen science.**

Mandatory info

- Photos of turtle's **face and shell**
- Date
- Location

Face (right)

Face (left)

Shell

Extra useful info

- Time
- Dive site or GPS coordinates
- Were you free diving/SCUBA diving/fishing when you saw the turtle?
- Water temperature (˚C)
- Current strength and direction
- Surge strength
- ± Depth (m) of sighting and description
- ± Straight length (cm) of shell from neck to above tail
- Flipper tags
- Behaviour e.g., breathing, foraging, resting, cleaning , mating, interacting with other animals etc.

Where to send

Upload photos and info to www.SAturtles.org/getinvolved

Visit www.SAturtles.org to learn more

Appendix 2.3 Example of an individual (a) adult-sized green turtle, (b) subadult hawksbill and (c) adult-sized loggerhead photo-ID resighting records over a two-year study period showing unique left and right facial profiles. White arrows indicate tick lines (lines projecting midway through a scute) on the first records of individuals (a) and (c).

Appendix 2.4 Relative abundance of sea turtles as mean number of turtles per hour (± SD) among study sites from timed research surveys over a two-year study period. Cm: green turtle; Ei: hawksbill; Cc: loggerhead. Symbols *, $^{\#}$, °, ~ indicate significant differences in SPUE among species per site.

	Total # sea turtles sighted					Mean turtles/hour (± SD)			
Study site	**Total effort (hrs)**	**Cm**	**Ei**	**Cc**	**Hard-shelled**	**Cm**	**Ei**	**Cc**	**Hard-shelled**
Green Turtle Gully	2.5	13	0	0	0	5.8 ± 3.90$^{\#°}$	0 ± 0*	0 ± 0	0 ± 0
Bhanga Nek Reef	3.3	8	1	0	0	2.7 ± 2.83	0.3 ± 0.50	0 ± 0	0 ± 0
Sodwana Bay	126.6	206	23	47	13	2.5 ± 4.89$^{\sim°}$	0.3 ± 1.30	0.5 ± 1.65*	0.2 ± 1.30
Adlam's Reef	3.2	10	0	1	1	2.3 ± 2.7	0 ± 0*	0.3 ± 0.76	0.4 ± 0.99
Raggie Reef	59.9	26	8	17	2	0.5 ± 1.24$^{*\#\sim}$	0.2 ± 0.50*	0.4 ± 1.13	0.03 ± 0.22
Total for five iSimangaliso sites	195.5	263	32	65	16	2.2 ± 4.47	0.2 ± 1.20	0.5 ± 1.54	0.1 ± 1.15
Aliwal Shoal	69.4	60	48	36	14	1.2 ± 1.98*	0.8 ± 1.35*	0.5 ± 1.16*	0.2 ± 0.67
Total for all sites	264.9	323	80	101	30	2.1 ± 4.21	0.3 ± 1.21	0.5 ± 1.49	0.1 ± 1.09

Appendix 2.5 Relative abundance of sea turtles as mean number of turtles per dive trip (± SD) among study sites from citizen science contributions over a two-year study period. Cm: green turtle; Ei: hawksbill; Cc: loggerhead; Dc: leatherback. Symbol * indicates significant differences in SPUE among species per site.

	Total # sea turtles sighted						Mean turtles/dive trip (± SD)				
Study site	**Total effort (dive trips)**	**Cm**	**Ei**	**Cc**	**Dc**	**Hard-shelled**	**Cm**	**Ei**	**Cc**	**Dc**	**Hard-shelled**
Sodwana Bay	34	33	12	14	1	0	1.0 ± 1.11*	0.4 ± 0.54*	0.4 ± 0.70	0.03 ± 0.17	0 ± 0
Aliwal Shoal	113	50	88	39	0	2	0.4 ± 0.89*	0.8 ± 0.85*	0.4 ± 0.58	0 ± 0	0.02 ± 0.13
Total	147	83	100	53	1	2	0.6 ± 0.97	0.7 ± 0.81	0.4 ± 0.61	0.03 ± 0.17	0.01 ± 0.12

Chapter 3: Spatiotemporal behaviour of sea turtles on reefs along the east coast of South Africa

3.1 Abstract

Observing sea turtle behaviour provides information essential to a comprehensive understanding of their basic ecology, ecological function, and response to environmental and population perturbations in specific habitats. This study conducts the first investigation into the spatiotemporal behaviour of sea turtles *in situ* on reefs along the east coast of South Africa. A total of 974 behavioural observations were recorded during 264.9 hours of timed research surveys, 147 dive trips by citizen scientists, and 271 opportunistic sightings. Green turtles (juvenile–adult-sized), immature hawksbills, and adult-sized loggerheads were observed foraging, resting, cleaning and engaging in intraspecific competition year-round in the iSimangaliso and Aliwal Shoal MPAs. Hawksbills foraged most frequently of all species at both sites (24% of all observed behaviours, n = 48), whilst green turtles and loggerheads foraged on <10% of all observed behaviours (n = 15 and 9 respectively). Observations revealed that these species follow conventional diets but also display diverse foraging strategies; hawksbills often consumed Rhodophyta and Ochrophyta, and one green turtle consumed poriferans. Green turtles used cleaning stations most frequently of all species (10% of all observed behaviours, n = 52), and engaged in competitive interactions with other green turtles over their use, indicating the value of this service to them. Loggerhead abundance peaked at the start of the annual nesting season (October) in iSimangaliso, where mating occurred, revealing that resident males mate with transient females. Leatherbacks were only present at the start the nesting season adjacent nesting beaches, where patrolling behaviour was observed, indicating their seasonal use of the area. Seven significant variables (day of the year, time of day, site, visibility, depth, wind speed and air temperature) explained 20.13% of variance in sea turtle sightings in a generalised linear model. All hard-shelled species displayed two diel peaks in activity; early-morning and late-afternoon, with the period of lowest sightings (08h00–10h00) coinciding with the highest levels human disturbance on local reefs. Larger flight initiation distances indicated that sea turtles on frequently dived reefs were more habituated to humans than those on less frequented reefs, but had a higher incidence of boat strike injuries (48% of all injuries). This study provides a window to the cryptic yet diverse in-water behaviours of both resident and transient species on the east coast of South Africa, contributing to the growing body of knowledge on their seasonal habitat use, ecological interactions and value of certain resources, sites and services in these neritic habitats.

3.2 Introduction

Direct observations of animal behaviour and interactions at the level of individuals have been increasingly recognised among scientists as key to unravel fundamental ecological dynamics. Such observations provide an understanding of how animals use, affect and interact with their environment and other animals in it, and thus how they contribute to ecosystem functioning (Houghton *et al.* 2003; Mills *et al.* 2005; Schofield *et al.* 2006). Direct observations are also essential to understand how animals respond to environmental perturbation over time and how environments respond to fluctuating animal populations over time, which is critical to effectively safeguard both animal populations and the broader ecosystems they inhabit (Piraino *et al.* 2002; van der Zee *et al.* 2019).

Within this context, the ecological contributions of sea turtles have emerged as a high research priority in recent years (e.g., Eckert *et al*. 1999; Hamann *et al*. 2010) as this knowledge is not only central to basic ecology but is crucial to underpin species-specific management strategies based on population abundances at which sea turtles can fulfill their ecological roles (Bjorndal and Bolten 2003). The success of conservation efforts on nesting beaches is evident in the exponential rebounds of sea turtle populations worldwide following historic overexploitation (e.g., Mortimer *et al.* 2011; Weber *et al.* 2014). However, the effects of sea turtle population recoveries on species composition and ecological dynamics in foraging habitats remain unclear, considering these habitats have undergone substantial transformations from the loss of ecologically important megafauna (including sea turtles) over time (Estes *et al.* 1989; Jackson 1997; McClenachan *et al.* 2006).

Studies have shown that green sea turtles spend all their waking hours (nine hours per day) foraging on small seagrass beds in the U.S. Virgin Islands (Caribbean Sea), grazing all available habitat rather than creating discrete grazing scars allowing for regrowth (Ogden *et al.* 1983; Williams 1988). Seagrass overgrazing episodes as a result of green turtle population recovery have increasingly been recorded in other parts of the Caribbean Sea (Christianen *et al.* 2014; Christianen *et al.* 2022) as well as Bermuda (Fourqurean *et al.* 2010; Fourqurean *et al.* 2019) and Lakshadweep Archipelago in the northwestern Indian Ocean (Gangal *et al.* 2021). These examples underscore the importance of ensuring that sea turtle conservation efforts effectively safeguard both adult breeding grounds and developmental foraging grounds on an ecosystem scale (van der Zee *et al.* 2019). Achieving this requires a comprehensive understanding of sea turtle behaviour and ecology on foraging grounds, best discerned at a resolution only attainable via direct observation (Mills *et al.* 2005).

Since direct in-water observation of sea turtle behaviour is hindered by the difficulty of locating animals and often harsh and unpredictable operating environment (Eckert *et al.* 1999; Mills *et al.* 2005), most studies have depended on inferences from expensive animal-borne data loggers and transmitters. For example, devices such as time-depth recorders, acoustic transmitters and satellite transmitters have made great advances in the understanding of sea turtle diving behaviour (e.g., Hays *et al.* 2000), home ranges (e.g., Matley *et al.* 2020), and migratory patterns (e.g., Harris *et al.* 2018) respectively. A fundamental limit to these techniques, however, besides their financial cost is that they cannot identify specific underwater activities as conclusively as direct in-water observations can (Houghton *et al.* 2000; Seminoff *et al.* 2006). In-water observations thus represent an important yet underutilised method in sea turtle research (Blumenthal *et al.* 2009).

In the last two decades, in-water observations on sea turtle foraging grounds have revealed important information on the ecological roles of sea turtles. For example, Leon and Bjorndal (2002) found foraging hawksbills to have indirect positive effects on corals through the consumption of their competitors (sponges) that in turn enhances overall coral reef benthic biodiversity. The extraction of cryptic sponges within coral reefs by hawksbills has also been shown to create foraging opportunities and microhabitats used as shelter for numerous fish species (von Brandis 2010). In-water observations have also been used to study courtship behaviour of loggerheads in Greece, where males seemed to patrol the coastline for receptive mates, and unreceptive females were observed using avoidance strategies to escape these males (Schofield *et al.* 2006). Female loggerheads were also documented to rest, occasionally forage and use cleaning stations during internesting periods (Schofield *et al.* 2006). In-water observations have also been coupled with temporal, environmental and oceanographic variables to investigate how these affect sea turtle abundance, distribution and behaviour, with variables such as habitat type, season, temperature and current strength being important drivers (Williams *et al.* 2017; Araujo *et al.* 2019).

The second Chapter of this thesis described the overall in-water relative abundance, demographics and distribution of sea turtles on reefs along the east coast of South Africa, but in-water behaviours have not yet been described, and further analyses are required to understand how these aspects may vary seasonally. Valuable information on foraging sea turtles in local habitats has been obtained via satellite tracking and stomach content and stable isotope analyses (Rambaran 2020). For example, satellite tracking has revealed fine-scale movements and habitat preferences of resident green and hawksbill turtles in Sodwana Bay, indicating they are adequately protected within the iSimangaliso MPA (Rambaran 2020). Stranded and bycaught (KZNSB) green turtles, hawksbills and loggerheads on the east coast have been shown to have conventional diets dominated by algae, sponges, and molluscs and crustaceans respectively (Hughes 1973; Rambaran 2020) and species within the same geographic region have been shown to forage within a similar trophic level (Rambaran 2020). Similarly, satellite tracking of nesting female loggerheads and leatherbacks over the annual nesting season (October to March) has revealed that loggerheads remain close inshore (<9 km) adjacent nesting beaches in internesting periods, whilst leatherbacks venture ~ 60 km offshore (e.g., Harris *et al.* 2015), which largely drove the iSimangaliso MPA's expansion in 2019.

In-water observations will be useful to validate data gathered by remote methodologies and are likely to answer further questions such as whether diet is a function of food preference or availability, if there is competition for food sources or other resources, if sea turtles interact with other animals, if there are seasonal changes in behaviour, and if courtship and mating behaviour occurs off nesting beaches (e.g., Houghton *et al.* 2003; Schofield *et al.* 2006; von Brandis 2010). This information is essential to gain a better understanding of sea turtle behaviour and basic ecological interactions in local neritic habitats (Schofield *et al.* 2006).

This study aims to investigate the spatiotemporal behaviour of sea turtles *in situ* on reefs along the east coast of South Africa. The objectives are to describe and compare seasonal behaviour (and related seasonal changes in relative abundance) in the iSimangaliso and Aliwal Shoal MPAs and to identify potential drivers affecting sea turtle sightings. Since sea turtles may be adversely affected by the presence of humans (e.g., Hayes *et al.* 2016) and boat traffic (Papafitsoros *et al.* 2020), we will also quantify human disturbance to sea turtles using flight initiation distances and visible injuries. The same dataset described in Chapter 2, coupled with environmental variables, behavioural observations, flight initiation distances and visible injuries collected through timed research surveys (supplemented by voluntourism), citizen scientists and opportunistic sightings is used. It is hypothesised that 1) there will be seasonal changes in the relative abundance of transient nesting species/individuals (loggerheads and leatherbacks) but not resident foraging species/individuals (green turtles, hawksbills and non-breeding loggerheads); 2) behaviour will be reflective of life history stage i.e., resident species/individuals will be observed foraging year-round (in both MPAs) but transient adults will be observed courting and mating in iSimangaliso at the start of the nesting season; 3) sea turtle sightings will be affected by a combination of temporal, environmental, and oceanographic variables; and 4) sea turtles on frequently dived reefs will be more prone to human disturbance and thus have smaller flight initiation distances and a higher prevalence of boat strike injuries than those on less frequented reefs.

3.3 Materials and methods

3.3.1 Study sites

As described in Chapter 2.

3.3.2 In-water data collection

Timed research surveys

Timed research surveys (Chapter 2) were undertaken and supplemented by Sharklife voluntourism surveys, citizen science contributions and opportunistic sightings. These timed research surveys were conducted on all study sites by one or two trained observers who searched for sea turtles at a relatively constant rate whilst freediving or SCUBA diving over a two-year period (September 2020 to August 2022). The date, location, start time and length (minutes) were recorded on each timed research survey irrespective of sea turtle sightings for effort calculations.

When a sea turtle was encountered, behaviour at first sighting, flight initiation distance, injuries and environmental variables were recorded. Behaviour was categorised as breathing, swimming, foraging, resting, cleaning, mating or interacting intraspecifically (adapted from Houghton *et al.* 2003; Schofield *et al.* 2006; Blumenthal *et al.* 2009, Fig. 3.1). Breathing involved inhaling air at the surface (Fig. 3.1a) and swimming involved travelling across the benthos, through the water column or near the surface (Fig. 3.1b). Patrolling behaviour, evidenced by deliberate, repeated approaches by sea turtles (Fig. 3.1c) in search of mates over breeding season , was included in the 'swimming' behaviour category as per Schofield *et al*. (2006). Foraging involved ingesting food or excavating food from the benthos (Fig. 3.1d) and resting involved lying motionless on the substrate (Fig. 3.1e). Cleaning involved sea turtles positioning themselves almost stationary at a 'cleaning station' for several minutes whilst small fish ate epibionts off their bodies (Fig. 3.1f). Active scratching and scraping the carapace or plastron (ventral shell) repetitively on rocks was noted as self-cleaning. Mating involved two sea turtles copulating where males clung onto females for several minutes by hooking their front flipper claws onto the female's carapace (Fig. 3.1g). Intraspecific interactions involved two sea turtles of the same species associating, usually in an antagonistic manner (Fig. 3.1h). Interspecific interactions with, for example, scavenging fish were considered secondary behavioural observations and were thus described alongside behaviour at first sighting such as foraging. Observations such as the type of food being foraged, and fishes involved in cleaning were also noted and identified to lowest possible taxonomic level based on local field guides.

Figure 3.1 Examples of sea turtle behaviour categories at first sighting. (a) Adult-sized male loggerhead breathing at the surface; (b) juvenile and adult-sized green turtles swimming above the benthos; (c) male leatherback patrolling for females, categorised as 'swimming' behaviour; (d) subadult hawksbill foraging off the reef; (e) adult-sized male loggerhead resting against the reef; (f) adult-sized female loggerhead at a cleaning station manned by a surgeonfish; (g) adult-sized male and female loggerheads mating; (h) intraspecific interaction between two subadult green turtles. Photographers: Andy Coetzee (a, g), Sharklife (b), Digger (c), Michael Tarr (d) and Samantha Kruger (f, h).

Behavioural responses of sea turtles to divers were quantified using methods adapted from Griffin *et al*. (2017). When a trained observer approached a sea turtle to collect photographs and data, flight initiation distance, the distance between diver and animal upon initiating a flight response (Griffin *et al.* 2017), was recorded in 4-metre increments. Observers were trained to approach sea turtles slowly from alongside whenever possible to minimise disturbance.

Injuries to sea turtles were also recorded and categorised as boat strike injuries, shark bites or other injuries (Fig. 3.2). As per Denkinger *et al*. (2013), injuries were considered to be caused by boat strikes when carapaces were shattered (e.g., Fig. 3.2a), when carapaces or flippers had straight cuts parallel to one another (e.g., Fig. 3.2b), or when fins or tails were amputated with a straight cut. As per Heithaus *et al*. (2005), injuries were considered to be shark-inflicted when large crescent-shaped chunks were missing from the carapace (e.g., Fig. 3.2c) or at least a third of a flipper was amputated and left with a mangled tip (e.g., Fig. 3.2d). Injuries were classified as 'other' injuries when they clearly caused damage to the sea turtle, but sources could not be identified, such as V-shaped notches out the edges of flippers or carapaces or other abnormalities (e.g., Fig. 3.2e). Human-induced injuries related to fishing (e.g., Fig. 3.2f), or entanglement in plastic were also categorised as 'other' injuries given their infrequent occurrence. Photographs and notes were taken to describe all injuries and it was noted if injuries were present at first sighting or acquired over the study period.

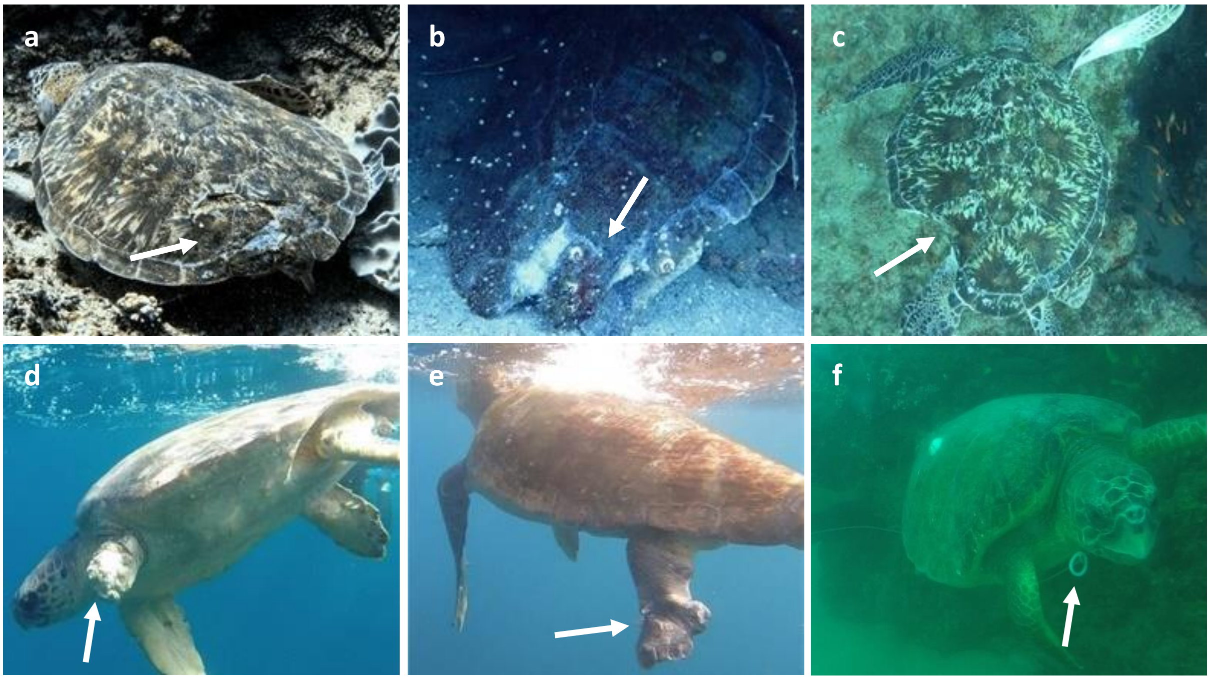


Figure 3.2 Examples of injuries to sea turtles. Boat strike injuries from (a) impact or (b) propeller cuts; shark bite injuries (c) removing sections of carapace or (d) amputating limbs; (e) other injuries that could not be explained with confidence; (f) ingestion of fishing hook also categorised as an 'other' injury. Photographers: Sharklife (a, c, f), Michelle Carpenter (d) and Andy Coetzee (e).

On each timed research survey, environmental data were recorded to understand variability in sea turtle sightings. Water temperature (°C) and depth (recorded in 10-metre intervals) were measured using a dive computer (Suunto D4i) and underwater visibility was categorised in 5-metre intervals. Current and surge strength were categorised as zero, weak, mild or strong depending on how fast the observer drifts with the current or is moved back-and forth by surge and the level of effort expended to remain stationary. Current direction was also recorded. Time from high tide (minutes) and tide range (metres) were recorded from the nearest tide chart readings. Wind speed (kilometres/hour), wind direction and air temperature (°C) were recorded from the nearest Windguru readings (https://www.windguru.cz/208317, https://www.windguru.cz/411478).

Citizen science and opportunistic sightings

Observations of sea turtle behaviour and injuries from citizen science contributions and opportunistic sightings (sightings from boats and sightings from RUV and BRUV footage) were also used to supplement data from timed research surveys. Environmental data were also gathered for each citizen science contribution and opportunistic sighting whenever possible. Sea turtle flight initiation distances in 4-metre increments were also obtained from footage contributed by citizen scientists whenever possible.

3.3.3 Statistical analyses

To determine if there were seasonal changes in relative abundance of transient nesting species and resident foraging species related to spatiotemporal behaviour, relative abundance was calculated per season (summer: December–February; autumn: March–May; winter: June–August; spring: September–November) from sites that were sampled consistently over the two-year study period (Sodwana Bay, Raggie Reef and Aliwal Shoal). SPUE was used as the index of relative abundance, in terms of 'turtles per hour' from timed research survey data and 'turtles per day' from citizen science data and opportunistic sightings. Non-parametric Kruskal-Wallis tests (H) were used to test for significant differences in SPUE of each species among seasons as the assumptions of One-Way ANOVAs were not met. Subsequently, Bonferroni-corrected Dunn's post-hoc tests were conducted to identify specific pairs of seasons with significant differences in SPUE for each species. Daytime changes in relative abundance at each site were also investigated by pooling SPUE by time of day (morning or afternoon/evening). Non-parametric Chi-square tests (χ^2) were used to compare observed behaviour frequencies of each species across seasons (Schofield *et al.* 2006).

To understand variability in sea turtle sightings, a generalised linear model (GLM) was used to investigate the effect of environmental variables on the count response variable, sea turtle sightings, using a Poisson distribution and natural splines. All sea turtle species across all sites were pooled together for this analysis as the dataset was too small to construct GLMs per species (as per Williams *et al.* 2017). Fourteen environmental variables were investigated as possible predictors of sea turtle sightings (Table 3.1). The best-fitting model was chosen conservatively in a stepwise selection process using Akaike's Information Criterion (AIC) with a default penalty factor of $k = 2$ applied to each parameter. To refine the AIC-supported model, a dropterm chi-squared function was performed to identify non-significant or redundant predictor variables that could be dropped from the model without significantly affecting its goodness of fit. Only significant predictor variables ($p < 0.05$) were included in the final GLM. Nagelkerke's R^2 value was calculated to determine what percentage of the total variance in sea turtle sightings was explained by the final GLM.

Six of the fourteen predictor variables (current strength, current direction, surge strength, time from high tide, tide range and wind direction) had too many missing values to include in the final GLM without affecting the overall outcome but their relationships with the response variable were still considered valuable and worth exploring. Therefore, separate GLMs were run for each of these predictor variables, as well as any non-significant predictor variables that were excluded from the final GLM, to see each of their relationships with the response variable in isolation.

Term plots were used to visualise the relationships between each predictor variable and the response variable. The y-axes are relative scales where a y-value of zero represents the mean effect of the adjusted predictor variable on the response variable. Positive y-values indicate a positive effect on the response variable while negative y-values indicate a negative effect. Confidence limits tend to diverge near the extremes of the range for continuous predictor variables due to fewer observations. All statistical analyses were conducted using R version 4.2.1 (R Core Team 2022) and RStudio (RStudio Team 2022). Significance was accepted at $p < 0.05$.

Table 3.1 Environmental variables that were investigated as potential predictors of sea turtle sightings in the GLM.

Predictor variable	Data type	Levels
Day of the year	Numerical	1–366
Time of day (h)	Numerical	05–22
Site	Categorical	Aliwal Shoal or iSimangaliso
Horizontal underwater visibility (m)	Categorical	0–4, 5–9, 10–14, 15–19, 20–24, 25–29, 30–34
Water temperature (°C)	Numerical	19 – 31
Current strength	Categorical	Zero, Weak, Mild, Strong
Current direction	Categorical	N, NE, E, SE, S, SW, W, NW
Surge strength	Categorical	Zero, Weak, Mild, Strong
Time from high tide (mins)	Numerical	-393–409
Tide range (m)	Numerical	0.1–2.9
Depth (m)	Categorical	0–9, 10–19, 20–29
Wind speed (km/hr)	Numerical	2–0
Wind direction	Categorical	N, NE, E, SE, S, SW, W, NW
Air temperature (°C)	Numerical	11–35

3.4 Results

3.4.1 Seasonal relative abundance

A total of 947 sea turtle sightings from Sodwana Bay, Raggie Reef and Aliwal Shoal were analysed across eight seasons in the two-year study period. Dive effort was highest in Sodwana Bay (126.6 hours) followed by Aliwal Shoal (69.4 hours) and Raggie Reef (59.9 hours) and was highest around summer months (December-March) and lowest at the end of winter/early spring (July-October) due to limiting weather conditions (Fig. 2.12).

All SPUE results are presented as means ± SD unless otherwise stated. Timed research surveys showed that green turtle SPUE in iSimangaliso peaked in autumn (3.4 ± 6.11 turtles/hour, $n = 91$) and dropped in winter (1.0 ± 2.23 turtles/hour, $n = 29$; Fig. 3.3), and showed significant seasonal differences (Kruskal-Wallis test, $H = 8.29$, $df = 3$, $p < 0.05$). Dunn's post-hoc tests confirmed the only significant difference to be between autumn and winter ($p < 0.05$). On Aliwal Shoal, green turtle SPUE peaked in winter (2.1 ± 2.01 turtles/hour, $n = 25$) and dropped in summer (0.6 ± 0.96 turtles/hour, $n = 8$; Fig. 3.3), with significant seasonal differences ($H = 9.78$, $df = 3$, $p < 0.05$). Dunn's post-hoc tests confirmed the only significant difference to be between winter and summer ($p < 0.05$).

Hawksbill SPUE in iSimangaliso was consistently highest in autumn (0.4 ± 1.57 turtles/hour, n = 14) and winter (0.4 ± 1.69 turtles/hour, n = 10) and lowest in summer (0.04 ± 0.37 turtles/hour, n = 3; Fig. 3.3) with significant seasonal differences (H = 10.56, df = 3, $p < 0.05$). Dunn's post-hoc tests revealed that the only significant difference was between winter and summer ($p < 0.05$). Whereas hawksbill SPUE on Aliwal Shoal was highest in summer (1.1 ± 1.40 turtles/hour, n = 16) and lowest in spring (0.3 ± 0.81 turtles/hour, n = 4; Fig. 3.3) and did not show any significant seasonal differences (H = 4.51, df = 3, $p > 0.05$).

Loggerhead SPUE was highest in iSimangaliso in spring (1.4 ± 3.00 turtles/hour, n = 21), at the start of the annual nesting season, and lowest in winter (0.06 ± 0.30 turtles/hour, n = 3; Fig. 3.3), and showed significant seasonal differences (H = 21.34, df = 3, $p < 0.05$). Dunn's post-hoc tests showed that there were significant differences in loggerhead SPUE among all seasons except autumn and summer ($p < 0.05$). On Aliwal Shoal, loggerhead relative abundance peaked in autumn (0.9 ± 1.67 turtles/hour, n = 21) and dropped in winter (0.2 ± 0.48 turtles/hour, n = 2; Fig. 3.3) and showed no significant seasonal differences (H = 5.96, df = 3, $p > 0.05$).

Leatherbacks were only sighted opportunistically in surface waters by citizen scientists, never on reefs during timed research surveys, and were the only species that were not present across all seasons among study sites (Fig. 3.3). Leatherbacks were only seen in spring (0.09 ± 0.28 turtles/day, n = 3), at the start of the annual nesting season, and only in iSimangaliso near nesting beaches (Fig. 3.3), and thus showed significant seasonal differences (H = 10.25, df = 3, $p < 0.05$). Dunn's post-hoc tests confirmed significant differences in leatherback SPUE to be between spring and autumn as well as spring and summer ($p < 0.05$).

Citizen science contributions and opportunistic sightings generally showed similar trends to timed research surveys in green turtle, hawksbill and loggerhead seasonal SPUE on Aliwal Shoal, but in iSimangaliso, loggerheads had a similar relative abundance across all seasons and did not peak in spring as shown by timed research surveys (Fig. 3.3).

SPUE from citizen science contributions and opportunistic sightings showed no significant seasonal differences for all hard-shelled species in iSimangaliso (Kruskal-Wallis test, green turtles: H = 1.78, df = 3, $p > 0.05$; hawksbills: 2.94, df = 3, $p > 0.05$; loggerheads: 1.42, df = 3, $p > 0.05$). On Aliwal Shoal, SPUE from citizen science contributions and opportunistic sightings showed no significant seasonal differences for green turtles (H = 4.89, df = 3, $p > 0.05$) and hawksbills (H = 2.98, df = 3, $p > 0.05$), but loggerhead SPUE differed significantly among seasons (H = 10.72, df = 3, $p < 0.05$). Dunn's post-hoc tests showed that the only significant difference in loggerhead SPUE on Aliwal Shoal was between autumn and summer ($p < 0.05$).

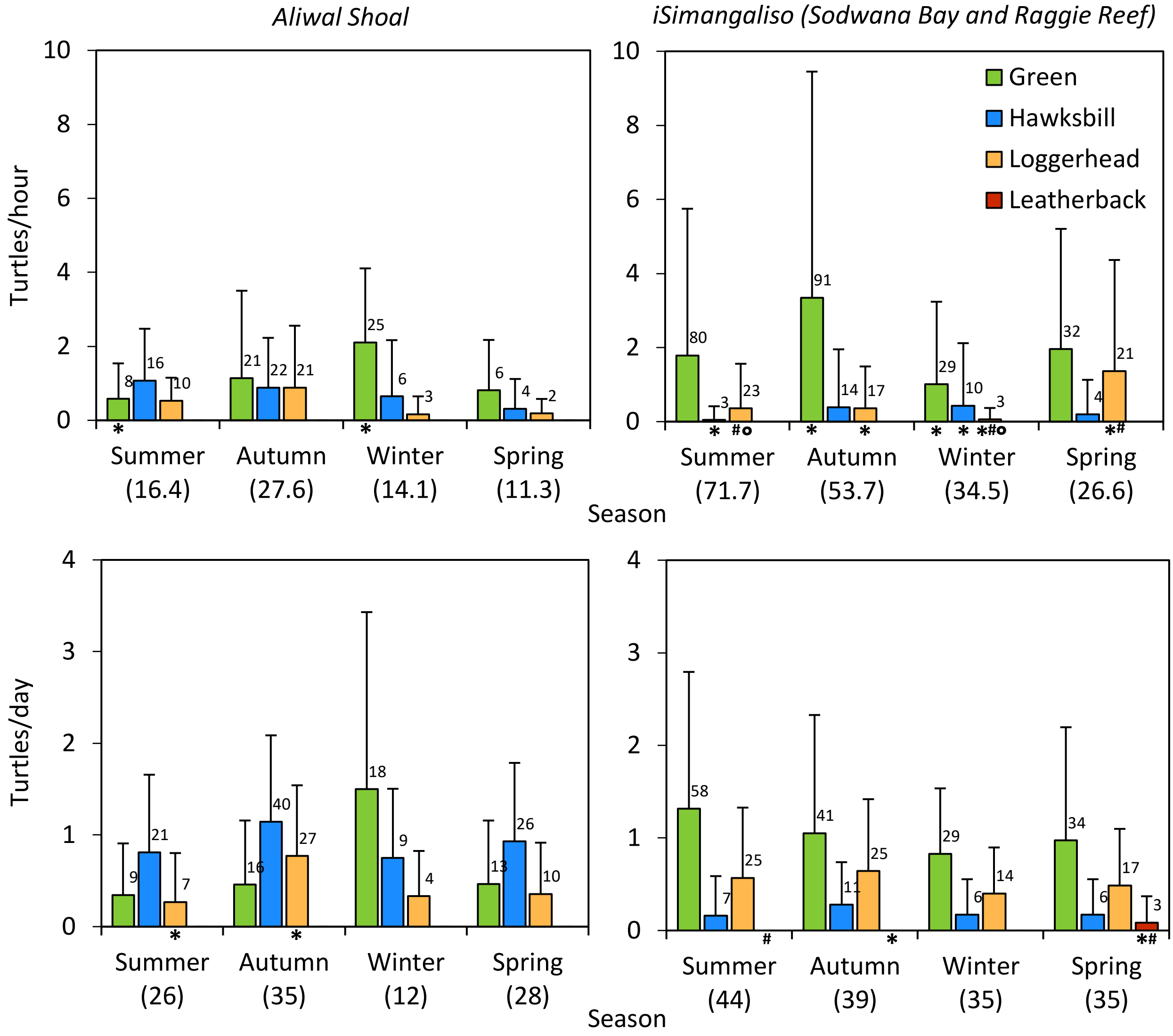


Figure 3.3 Seasonal relative abundance of sea turtles among study sites as mean number of turtles per hour (from timed research surveys) and mean number of turtles per day (from citizen science contributions and opportunistic sightings) over a two-year study period. Bars represent standard deviation. The total number of sightings is indicated above each column and dive effort (number of hours or days) is indicated below each season. Summer: Dec-Feb; Autumn: Mar-May; Winter: Jun-Aug; Spring: Sep-Nov. Symbols *, $^{\#}$, °, ~ indicate significant differences in SPUE among seasons per species per site.

Despite dive effort being biased to mornings at both iSimangaliso and Aliwal Shoal (n = 251.9 and 140.8 hours respectively) rather than afternoons/evenings (n = 29.5 and 45.1 hours respectively), SPUE was generally higher for all species at both major sites in the afternoons/evenings (Fig. 3.4). The only exceptions were in iSimangaliso, where hawksbill SPUE was the same in both mornings and afternoons and loggerheads were not present in afternoons (Fig. 3.4). Green Turtle Gully was the only site sampled at night (21h00–23h00) for logistical reasons, otherwise the last dives in iSimangaliso took place before 15h00.

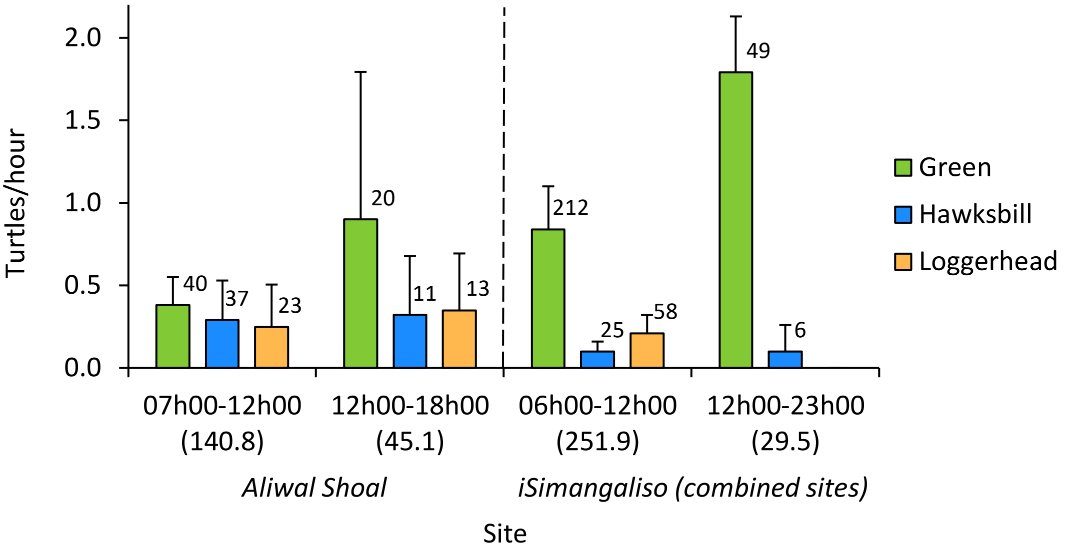


Figure 3.4 Relative abundance of sea turtles as mean turtles per hour in the mornings and afternoons/evenings in iSimangaliso (all five study sites combined) and on Aliwal Shoal from timed research surveys over a two-year study period. Bars represent standard deviation. The total number of sightings is indicated above each column and dive effort (hours) is indicated below time periods.

3.4.2 In-water behaviour

Overview

A total of 974 observations of behaviour at first sighting were made of green turtles, hawksbills, loggerheads and leatherbacks in the iSimangaliso and Aliwal Shoal MPAs during 264.9 hours of timed research surveys, 147 dive trips by citizen scientists and 271 opportunistic sightings (Fig. 3.5). Sea turtles were observed breathing on the surface (15% of all observed behaviours), swimming (50%), foraging (7%), resting (16%), cleaning (8%), mating (<0.5%) and interacting intraspecifically (3%) (Fig. 3.5).

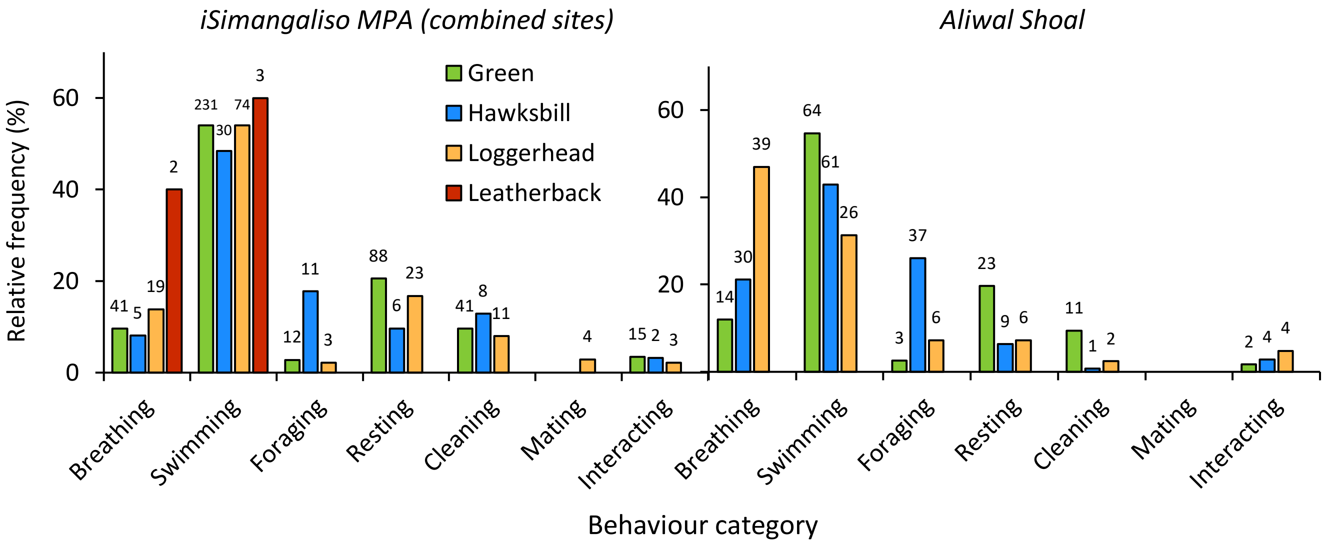


Figure 3.5. Relative frequency of observed behaviours at first sighting (n = 974) of sea turtles across all study sites from timed research surveys, citizen science contributions and opportunistic sightings over a two-year study period. Actual frequencies are above each bar.

Breathing

Breathing occurred on 11% and 24% of all behavioural observations at iSimangaliso and Aliwal Shoal respectively (Fig. 3.5). Breathing was observed at similar relative frequencies among hard-shelled species in iSimangaliso (green turtle: 10%, n = 41; hawksbill: 8%, n = 5; loggerhead: 14%, n = 19; Fig. 3.5). Whereas on Aliwal Shoal, the relative frequency of observed breathing behaviour was highest for loggerheads (47%, n = 39), followed by hawksbills (21%, n = 30) and green turtles (12%, n = 14) (Fig. 3.5). Leatherbacks were observed breathing on 40% (n = 2) of observed behaviours at first sighting (Fig. 3.5). As sea turtles surfaced, they forcefully exhaled air, inhaled, then scanned their surroundings below the water (Fig. 3.6a–c). This was repeated about three to six times before diving down immediately after the final inhalation (Fig. 3.6d) and the process took about ten seconds to a minute.

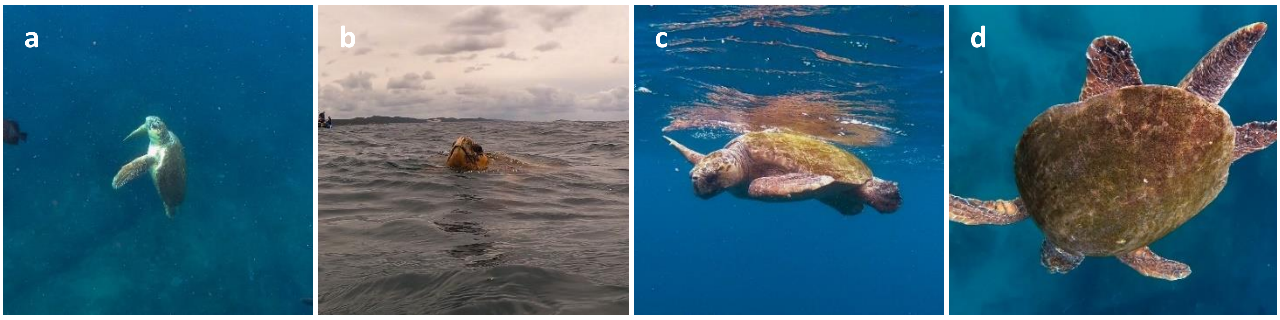


Figure 3.6 (a) An adult-sized male loggerhead approaching the surface, (b) extending head above the surface to exhale and take a breath, (c) scanning surroundings below the water's surface in between breaths, and (d) returning to the reef immediately after a final breath.

Swimming

Swimming was the most observed behaviour at first sighting, occurring on 53% and 44% of all behavioural observations at iSimangaliso and Aliwal Shoal respectively (Fig. 3.5). All four sea turtle species were observed swimming at similar relative frequencies in iSimangaliso (green turtle: 54%, n = 231; hawksbill: 48%, n = 30; loggerhead: 54%, n = 74; leatherback: 60%, n = 3; Fig. 3.5). On Aliwal Shoal, the relative frequency of observed swimming behaviour was highest for green turtles (55%, n = 64), followed by hawksbills (43%, n = 61) and loggerheads (31%, n = 26) (Fig. 3.5).

Patrolling behaviour by adult-sized sea turtles was noticeably different from regular swimming. Patrolling sea turtles made repeated, deliberate approaches coupled with slow and obvious movements such as turning their heads from side to side to visually inspect potential mates. Sea turtles were not observed patrolling around other turtles, only boats, kayaks and divers. Three unidentified adult-sized leatherbacks displayed patrolling behaviour in surface waters < 1 kilometre offshore Five Mile Reef, Island Rock and Cape Vidal in iSimangaliso (e.g., Fig. 3.7). One adult-sized male loggerhead was also observed patrolling for mates < 1 kilometre offshore Cape Vidal.

Figure 3.7 (a) An adult-sized female leatherback approaching a kayak on the surface off Cape Vidal, (b) patrolling alongside slowly and visually scanning for potential mates above and below the surface, and (c) repeatedly turning around underwater and drifting past alongside whilst visually inspecting before swimming away. Photographer: Paul Nixon.

Foraging

Foraging was observed on 4% and 13% of all behavioural observations at iSimangaliso and Aliwal Shoal respectively (Fig. 3.5). The relative frequency of observed foraging behaviour was highest for hawksbills at both sites (iSimangaliso: 18%, n = 11; Aliwal Shoal: 26%, n = 37). Green turtles and loggerheads were observed foraging on < 10% of all observed behaviours at both sites (Fig. 3.5).

Green turtles (juvenile–adult-sized) on Aliwal Shoal were mainly seen foraging on Rhodophyta (red algae, Fig. 3.8a), whereas in iSimangaliso they were seen foraging on red algae, Chlorophyta (green algae) and Ochrophyta (brown algae). On two occasions, adult-sized green turtles on Aliwal Shoal were observed exhaling a bright red discharge out their nostrils (Fig. 3.8b), possibly indicating a high consumption of red algae (C. Figgener, pers. comm.). Juvenile and subadult hawksbills were mainly seen foraging on Porifera (sponges) and other unidentified benthic invertebrates (Fig. 3.8c) at all sites. These food sources were practically always cryptic and hawksbills often probed the reef with their beaks before excavating cryptic food in small crevices. Adult-sized loggerheads were mainly seen foraging on unidentified benthic invertebrates at both sites, either on the benthos or on large clumps that had been removed from the benthos (Fig. 3.8d) possibly by active extraction or strong surge. All sea turtles foraging on reefs seemed to target a particular species but ingested whatever was near their chosen food source, ingesting a variety of different species and sand in the process.

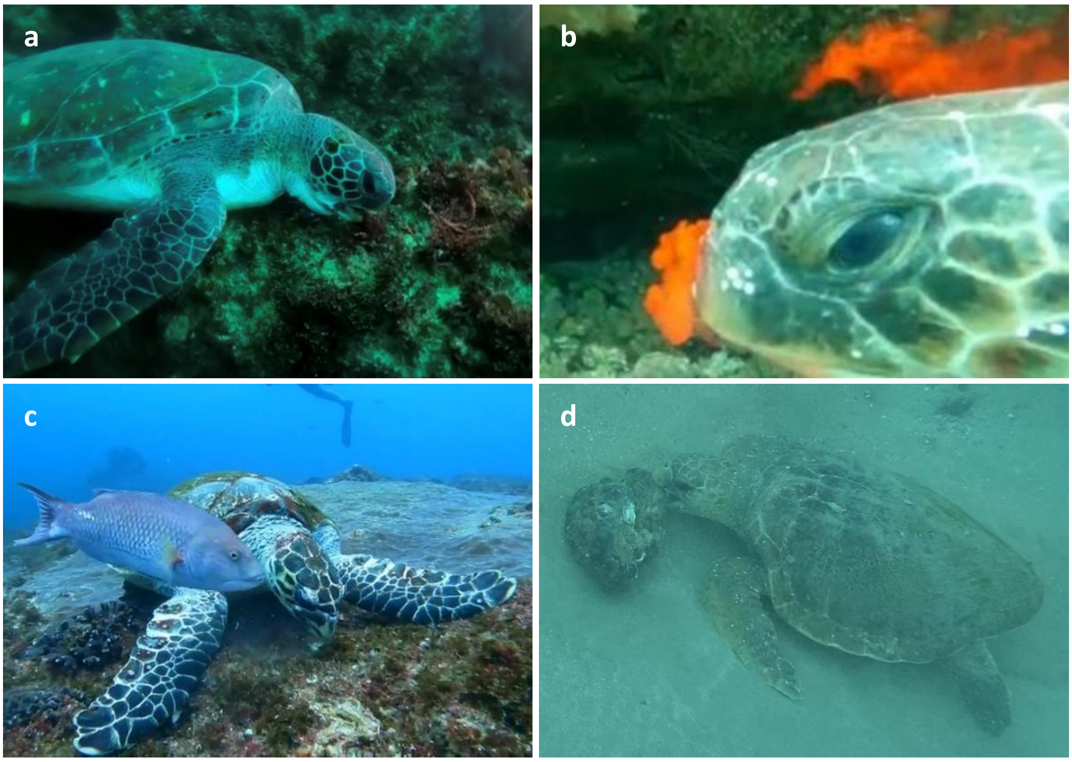


Figure 3.8 Main food sources observed being eaten by sea turtles. (a) A juvenile green turtle eating Rhodophyta on Aliwal Shoal; (b) an adult green turtle on Aliwal Shoal exhaling a bright red discharge from nostrils possibly indicating a high consumption of Rhodophyta; (c) a subadult hawksbill eating cryptic poriferans on Aliwal Shoal; (d) an adult female loggerhead eating a clump of benthic invertebrates broken off from a reef in Sodwana Bay. Photographers: Summer Newton (a), Walter Bernadis (b), Emma Tomkins (c) and Samantha Kruger.

Green turtles (juvenile–adult-sized) and adult-sized loggerheads also opportunistically fed on various siphonophores in the water-column when strong north-easterly winds brought large amounts to surface waters over reefs. Two identified species in this taxon were *Forskalia edwardsi*, eaten by an adult-sized green turtle (Fig. 3.9a) and *Agalma sp.*, eaten by loggerheads (Fig. 3.9b). This type of opportunistic foraging by hawksbills was rare as only one individual, a subadult, foraged on hydrozoans on two occasions (one pictured below, identified as an aequoreid (ribbed jelly), Fig. 3.9c). Hawksbills on Aliwal Shoal were also observed foraging on brown algae and red algae in between foraging on sponges, with one species of brown algae identified as *Lobophora variegata* (Fig. 3.9d). On one rare occasion, a juvenile green turtle on Two Mile Reef in Sodwana Bay was seen foraging vigorously on an unidentified sponge species (Fig. 3.9e).

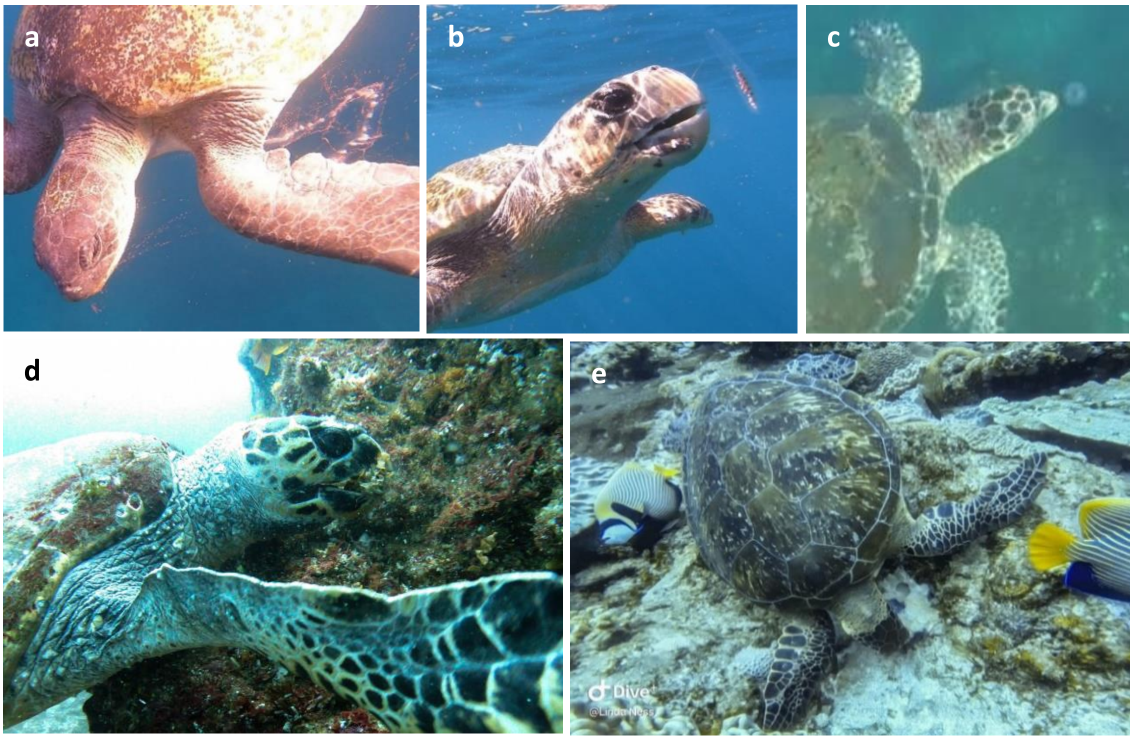


Figure 3.9 Less common food sources observed being eaten by sea turtles. (a) An adult-sized green turtle eating *Forskalia edwardsi* in the water column; (b) an adult-sized female loggerhead foraging on *Agalma sp.*; (c) a subadult hawksbill eating an aequoreid; (d) a subadult hawksbill foraging on *Lobophora variegata on Aliwal Shoal*; and (e) a juvenile green turtle eating Porifera in Sodwana Bay. Photographers: Andy Coetzee (a, c), Casey de Lange (b) and Linda Ness (e).

Scavenging fishes often took advantage of foraging hawksbills and loggerheads who exposed cryptic benthic invertebrates. The most common scavenger was the saddleback hogfish (*Bodianus bilunulatus*) (Fig. 3.7c) at both sites which was often observed following hawksbills even when they weren’t yet foraging. The Diana's hogfish (*Bodianus diana*), crescent-tail wrasse (*Thalassoma lunare*) and gold-bar wrasse (*Thalassoma hebraicum*) were also observed scavenging on benthic invertebrates exposed by foraging hawksbills and loggerheads. Emperor angelfish were also seen scavenging on the interior tissue of the sponge exposed by the juvenile green turtle (Fig. 3.9e).

Resting

Resting was observed on 19% and 11% of all behavioural observations at iSimangaliso and Aliwal Shoal respectively (Fig. 3.5). The relative frequency of observed resting behaviour was highest for green turtles at both sites (iSimangaliso: 21%, n = 88; Aliwal Shoal: 20%, n = 23), followed by loggerheads (iSimangaliso: 17%, n = 23; Aliwal Shoal: 7%, n = 6) and hawksbills (iSimangaliso: 10%, n = 6; Aliwal Shoal: 9%, n = 6) (Fig. 3.5).

Sea turtles typically rested in small crevices on reefs, under ledges and overhangs, or up against sand-reef interfaces. These areas were frequented by different sea turtles throughout the day, but the same individuals were observed repeatedly using the same resting area throughout the two-year study period (e.g., Fig. 3.10). Surface-basking was never observed.

One of the surveyed sites, Green Turtle Gully (Fig. 2.2a, b), was frequented as a shallow water night-time refuge by many resting juvenile and subadult green turtles. The shallow pools allowed sea turtles to rest and conserve energy in the safety of restricted access from large predators.

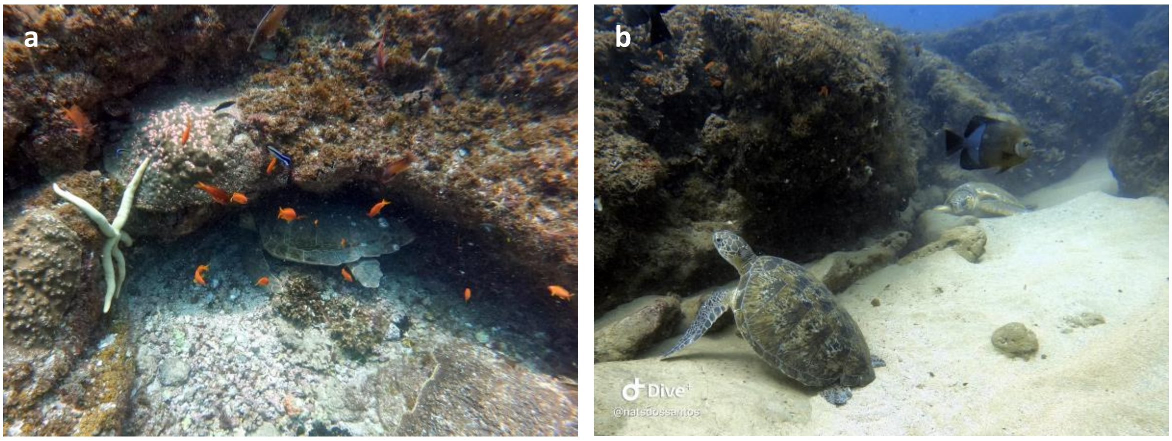


Figure 3.10 (a) An adult-sized male loggerhead resting beneath a frequented overhang on Aliwal Shoal with tail tucked in. (b) Sea turtles frequently made use of the sand-reef interface on the inshore side of Quarter Mile Reef in Sodwana Bay as a resting area. Green turtles and loggerheads were often observed resting here simultaneously as pictured above, along with various species of whiprays.

Cleaning

Cleaning was observed on 9% and 4% of all behavioural observations at iSimangaliso and Aliwal Shoal respectively (Fig. 3.5). Cleaning was observed at similar relative frequencies among species in iSimangaliso (green turtle: 10%, n = 41; hawksbill: 13%, n = 8; loggerhead: 8%, n = 11; Fig. 3.5). On Aliwal Shoal, the relative frequency of observed cleaning behaviour was highest for green turtles (9%, n = 11) and very low for loggerheads (2%, n = 2) and hawksbills (1%, n = 1) (Fig. 3.5).

Sea turtles regularly positioned themselves purposefully at cleaning stations where they would generally hover just above the benthos and often appear to be resting whilst fish ate epibionts off their bodies (Fig. 3.11a), or they would swim slow repeated circles within a metre or two of the cleaning station with cleaning fish in tow (Fig. 3.11b).

The RUV on Raggie Reef is placed strategically in front of a cleaning station frequented by ragged-tooth sharks (*Carcharias taurus*) but RUV footage often shows green turtles, hawksbills and loggerheads frequenting this cleaning station, occasionally at the same time as sharks and large potato basses (*Epinephelus tukula*) (Fig. 3.11c and d).

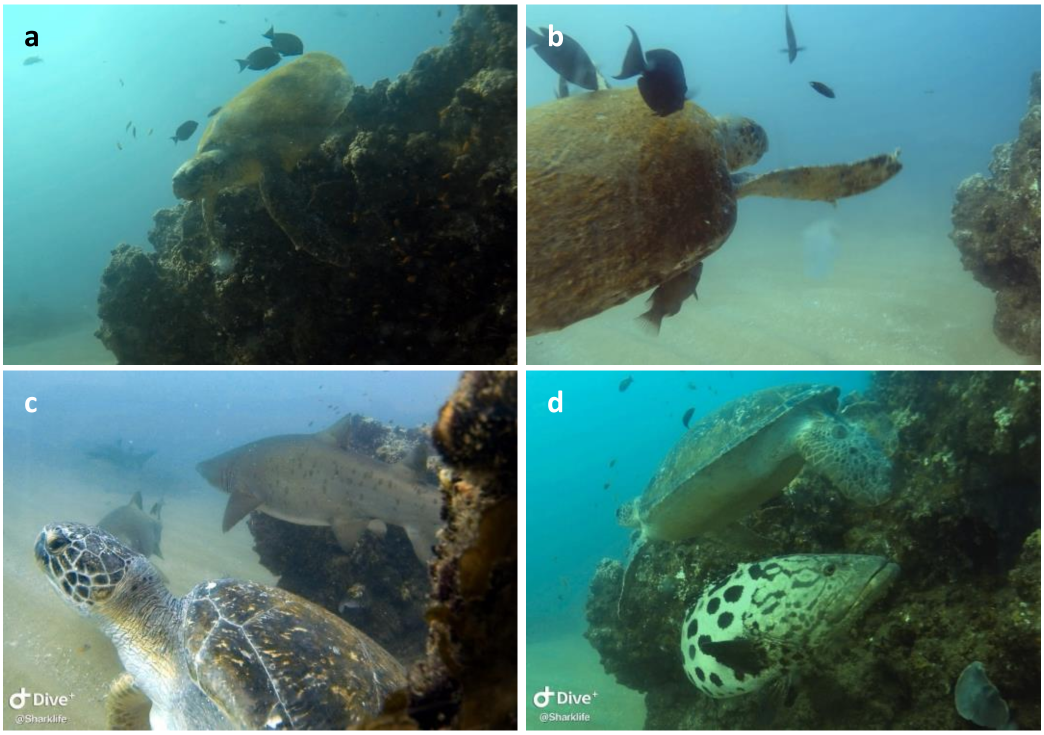


Figure 3.11 (a) A female loggerhead turtle visiting the cleaning station on Raggie Reef manned by Acanthurids, and (b) swimming slow repeated circles near the cleaning station with cleaning fish in tow. (c) An adult-sized female green turtle sharing the same cleaning station with *Carcharias taurus* and (d) *Epinephelus tukula*. Photos captured by Sharklife's RUV.

Fish that were commonly observed cleaning sea turtles were the bluestreak cleaner wrasse (*Labroides dimidiatus*), bicolour cleaner wrasse (*Labroides bicolour*), crescent-tail wrasse (*Thalassoma lunare*) and various surgeonfishes (Acanthuridae) and damselfishes (Pomacentridae).

Outside of cleaning stations, hawksbills and loggerheads on Aliwal Shoal were occasionally cleaned by juvenile natal knifejaws (*Oplegnathus robinsoni*). Sea turtles often did not appear to initiate this interaction but tolerated it. One hawksbill facilitated cleaning by turning its body to clean different parts, even surfacing to breathe in between cleaning with the fish in tow, and approaching the fish when it swam away to initiate cleaning again (Fig. 3.12).

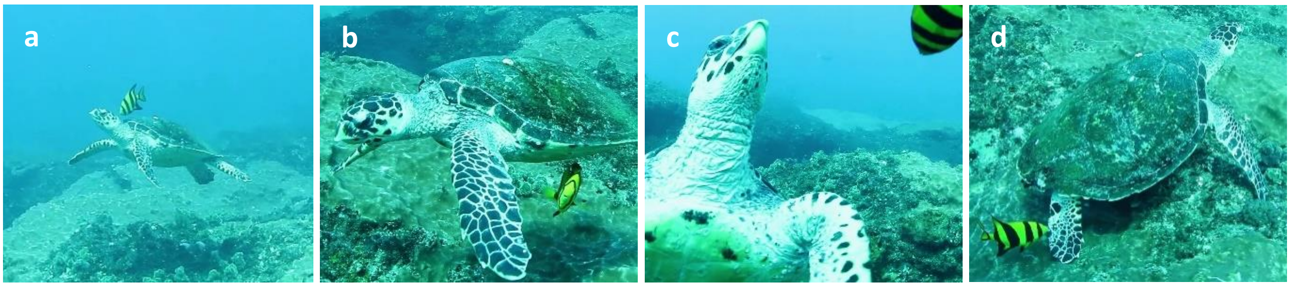


Figure 3.12 (a) A subadult hawksbill facilitating cleaning by *Oplegnathus robinsoni*. (b) The fish swims towards the diver filming the interaction, leaving the turtle. (c) The turtle approaches the fish a few metres away to initiate cleaning again and (d) the pair continue the interspecific interaction. Photographer: Charles Kruger.

At both sites, sea turtles were also observed positioned under ledges using their front flippers to vigorously scratch their carapaces on the reef above, or their plastrons on the reef below, in a form of self-cleaning. (Fig. 3.13). The same part of the reef was used to self-clean on numerous occasions, to the extent where the benthos wore smooth.

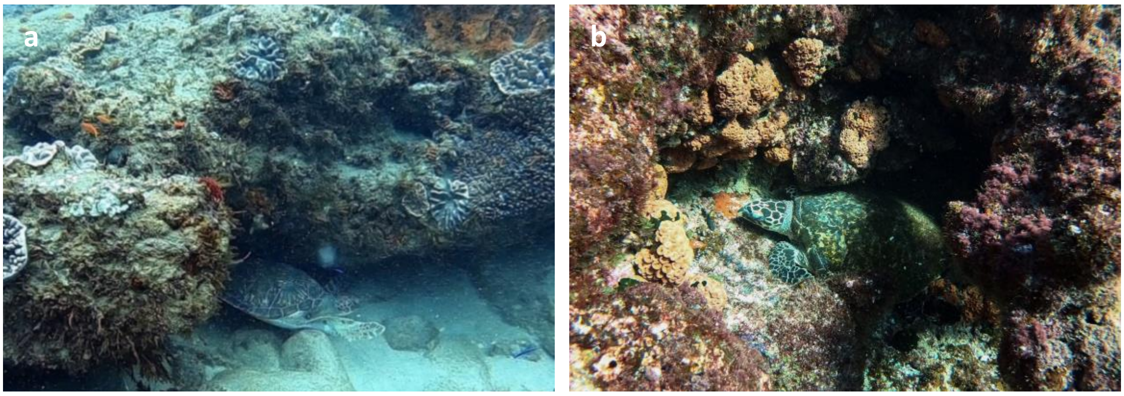


Figure 3.13 Self-cleaning behaviour displayed by an immature (a) green turtle and (b) hawksbill at frequented scratching posts on Quarter Mile Reef (Sodwana Bay) and Aliwal Shoal respectively. Photographer: Samantha Kruger (a).

Mating

Mating only occurred on <1% of all behavioural observations and it was the only behaviour observed solely by loggerheads (3% of observed behaviours, n = 4) in iSimangaliso (Fig. 3.5). Two pairs of adult-sized loggerheads were observed mating in surface waters over Red Sands and Raggie Reef within one kilometre of the shoreline (Fig. 3.14). Both pairs were already copulating on discovery and were observed for up to five minutes. Males clung onto female carapaces using their front flipper claws and females would power and steer the pair through the water column. When pairs were just below the surface, males took breaths and females kept their heads underwater, scanning the surroundings. Both pairs swam away slowly, likely due to human disturbance, but continued copulating the entire time.

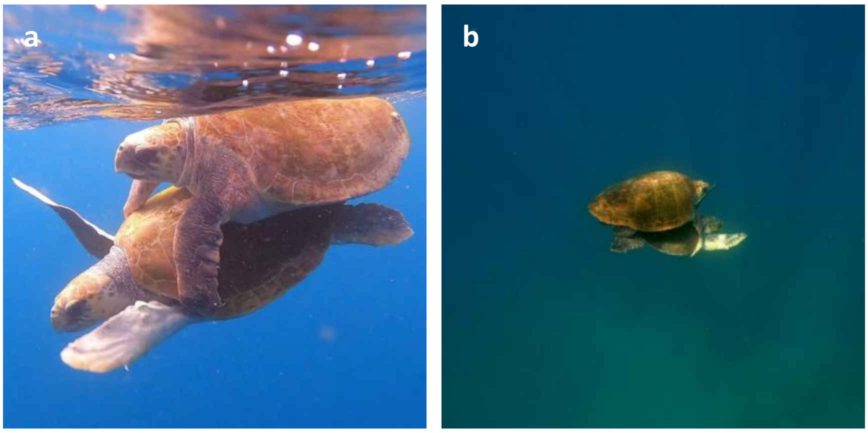


Figure 3.14 (a) The first pair of mating loggerheads observed in surface waters over Red Sands showing the female power and steer the pair through the water column. (b) The second mating pair observed near Raggie Reef swimming away slowly whilst still copulating. Photographer: Andy Coetzee.

Both mating females were identified as new individuals (i.e., not known residents), one mating male couldn't be identified to individual level, and the other mating male was identified as a known individual with regular resightings (n = 6) on Raggie Reef (pictured in Fig. 3.14a and 3.15). The minimum residence period of this individual was 621 days, which was the longest for all loggerheads in this study (Table 2.5; Chapter 2). This individual mated off Red Sands, ~ 20 kilometres north of Raggie Reef, despite never being resighted away from Raggie Reef on other occasions. He still copulated successfully despite only having half a front left flipper remaining since he still had the large claw that allowed him to cling onto the female's carapace (Fig. 3.15).

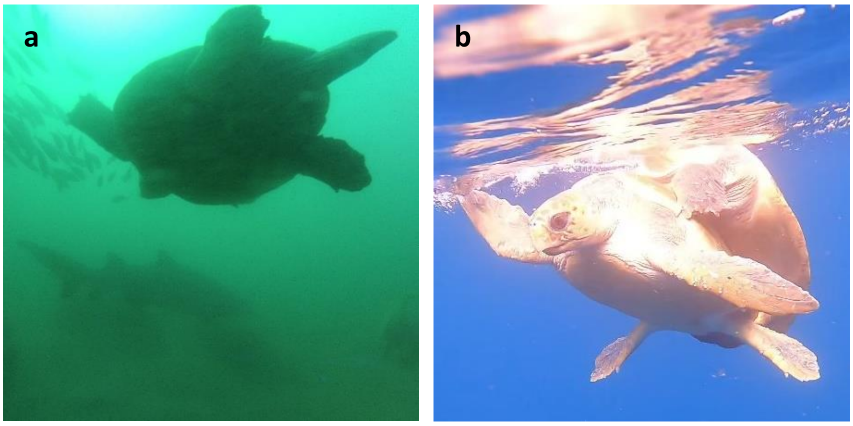


Figure 3.15 (a) The male loggerhead resighted regularly on Raggie Reef showing his partially missing front left flipper. (b) The same male loggerhead from Raggie Reef identified as one of the mating individuals over Red Sands successfully copulating with a partially missing front left flipper. Photographers: Sharklife RUV (a) and Andy Coetzee (b).

Intraspecific interactions

Intraspecific interactions occurred on 3% of all behavioural observations at both sites, and sea turtles were observed interacting intraspecifically at similar relative frequencies, <5% of all observed behaviours among hard-shelled species (Fig. 3.5).

Intraspecific interactions were always between two individuals of the same size class and appeared to be antagonistic. Individuals generally began by passively head-tail circling one another until one individual made attempts to ram or bite the other's soft flesh (such as the neck, tail or flippers), resulting in the other pivoting its carapace towards the aggressive turtle in defense (Fig. 3.16a). It was always the same individual initiating aggressive biting or ramming behaviour. Passive head-tail circling with no escalation to aggressive contact was also observed (Fig. 3.16b). These interactions generally lasted a few minutes and ended in both individuals retreating passively. One interaction appeared to be initiated by competition over food (siphonophores in the water-column, Fig. 3.16c).

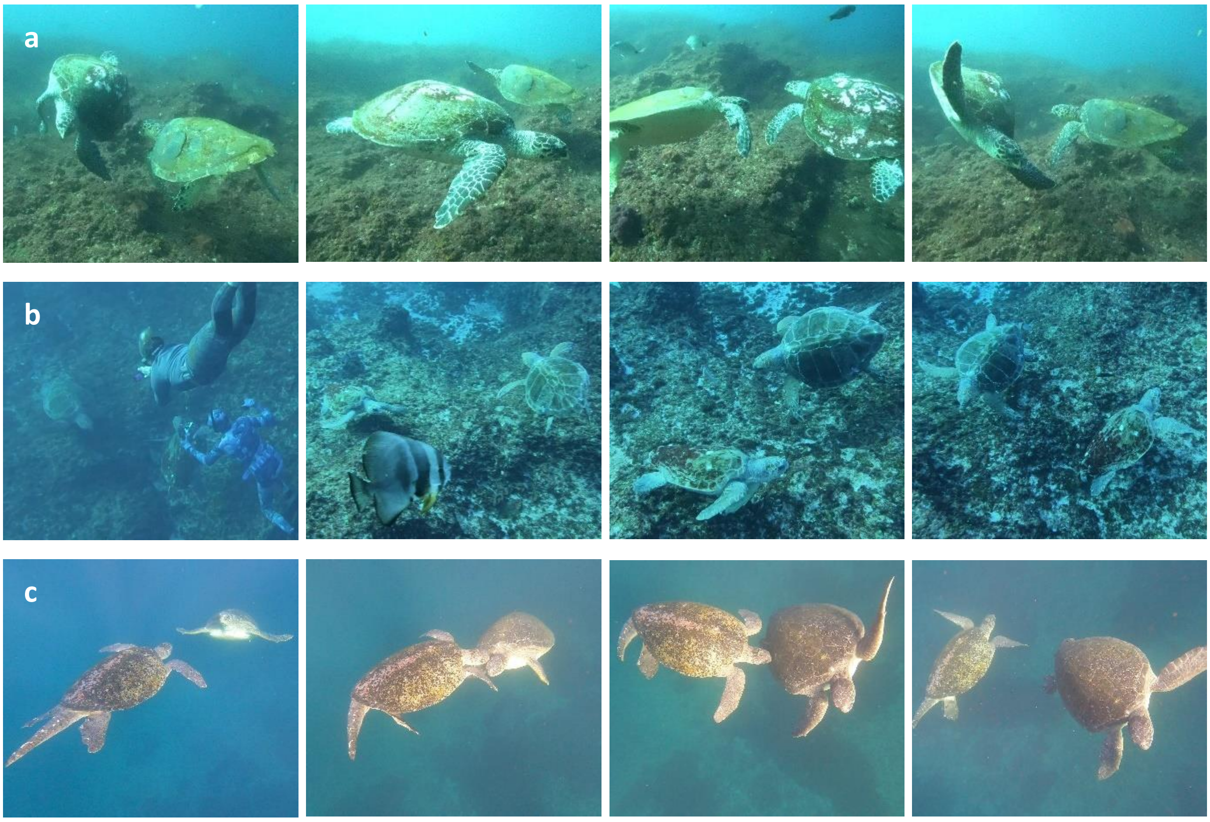


Figure 3.16 Examples of intraspecific interactions between sea turtles. (a) Two subadult hawksbills repeatedly head-tail circling one another above the benthos, with only one individual aggressively ramming and biting and the other pivoting in defense; (b) an adult-sized male and female loggerhead repeatedly head-tail circling each other above the benthos with no escalation to aggressive contact, and undisturbed by freedivers; (c) an adult-sized male and female green turtle approaching each other in the water column in between foraging on siphonophores, with the male ramming the female's neck and carapace causing her to pivot in defense and retreat passively. Photographers: Andy Coetzee (a, c) and Dino Giovannoni (b).

Two green turtles were often seen sharing a cleaning station and resting area on Quarter Mile Reef in Sodwana Bay without any aggressive behaviour towards one another (Fig. 3.17), but on two occasions, green turtles launched surprise assaults on other green turtles at the same cleaning station and resting area by attempting to bite their flippers, causing them to flee immediately.

Figure 3.17 An adult-sized female (left) and male (right) green turtle taking turns to use a cleaning station (left, indicated by sea goldies *Pseudanthias squamipinnis*) on Quarter Mile Reef in Sodwana Bay. Photographer: Andy Coetzee.

Spatiotemporal behaviour

At the most consistently sampled sites (Sodwana Bay and Raggie Reef in iSimangaliso as well as Aliwal Shoal), green turtles, hawksbills and loggerheads were generally observed breathing, swimming, foraging, resting, cleaning and interacting intraspecifically across all seasons (Fig. 3.18).

Leatherbacks were only seen breathing and swimming (generally patrolling for mates) in spring, at the start of the annual nesting season, in iSimangaliso near nesting beaches (Fig. 3.18). Loggerheads were also only seen mating and patrolling for mates in spring in iSimangaliso (Fig. 3.18). The one adult-sized male loggerhead observed mating near Red Sands in spring, who was the only mating individual identified as a known individual with previous resightings, was observed swimming on Raggie Reef across all seasons year-round.

There were significant seasonal differences in observed behaviours of green turtles ($\chi^2 = 46.91$, df = 15, $p< 0.05$), hawksbills ($\chi^2 = 37.07$, df = 15, $p < 0.05$) and loggerheads ($\chi^2 = 33.36$, df = 18, $p < 0.05$) in iSimangaliso. On Aliwal Shoal, green turtle behaviour showed significant seasonal differences ($\chi^2 = 31.39$, df = 15, $p < 0.05$) but hawksbill ($\chi^2 = 10.87$, df = 15, $p > 0.05$) and loggerhead behaviour did not ($\chi^2 = 14.06$, df = 15, $p > 0.05$).

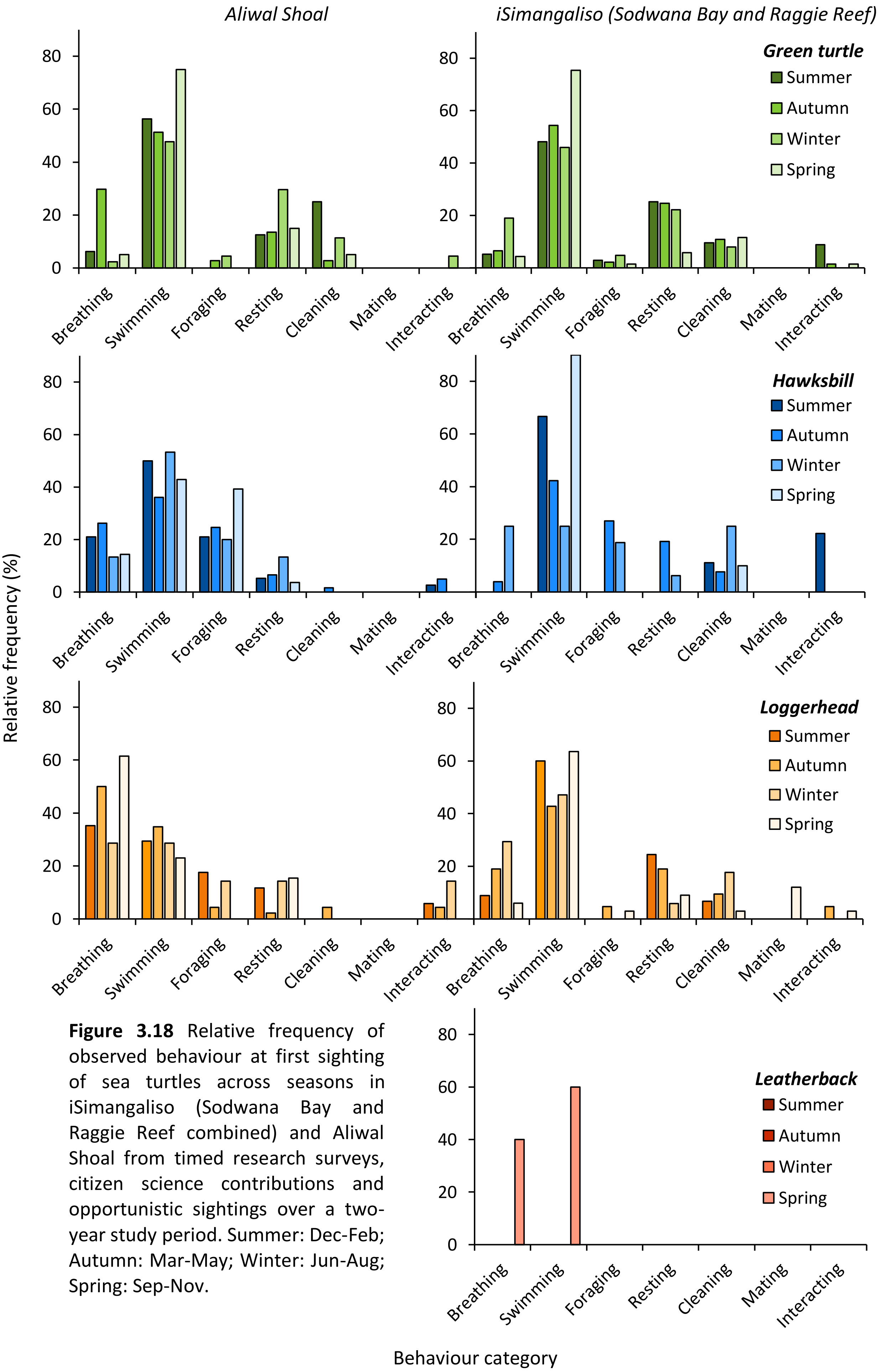


Figure 3.18 Relative frequency of observed behaviour at first sighting of sea turtles across seasons in iSimangaliso (Sodwana Bay and Raggie Reef combined) and Aliwal Shoal from timed research surveys, citizen science contributions and opportunistic sightings over a two-year study period. Summer: Dec-Feb; Autumn: Mar-May; Winter: Jun-Aug; Spring: Sep-Nov.

3.4.3 Variability in sea turtle sightings

The final GLM only explained 20.13% (Nagelkerke's R^2 value) of the total variance in sea turtle sightings. The seven predictor variables that were significant and thus included in the final GLM were day of the year, time of day, site, underwater visibility, depth, wind speed and air temperature ($p < 0.05$). Table 3.2 summarises the final GLM output.

Table 3.2 Summary of the final GLM investigating variability in sea turtle sightings on the east coast of South Africa.

Predictor variable	**Coefficient**	**Standard error**	**p-value**
Intercept	0.897	0.272	0.00098 *
Day of the year	-0.002	0.000	2.60e-08 *
Time of day (h)	0.033	0.012	0.00758 *
Site (iSimangaliso)	-0.316	0.072	1.11e-05 *
Visibility (5–9 m)	0.157	0.146	0.27985
Visibility (10–14 m)	0.040	0.146	0.78384
Visibility (15–19 m)	-0.251	0.156	0.10892
Visibility (20–24 m)	-0.165	0.180	0.35890
Visibility (25–29 m)	-0.056	0.258	0.82746
Visibility 30–34 m)	-0.400	0.282	0.15639
Depth (10–19 m)	-0.359	0.066	5.69e-08 *
Depth (20–29 m)	-1.818	0.264	5.96e-12 *
Wind speed (km/hr)	0.008	0.004	0.04184 *
Air temperature (°C)	-0.029	0.011	0.00653 *

* denotes significance tested at $p < 0.05$

Graphical output of the final GLM revealed that sea turtle sightings peaked around day 100 of the year (mid-autumn), and then gradually dropped from days 110 to 250 (mid-autumn to early spring) (Fig. 3.19a). Sea turtle sightings decreased from 05h00 to 08h00 in the morning with the lowest number of sightings between 08h00 and 10h00 and then a gradual increase throughout the rest of day (Fig. 3.19b), confirming results above which showed a higher abundance of sea turtles in the afternoons/evenings despite dive effort being biased to mornings (Fig. 3.4). There were relatively more sea turtle sightings on Aliwal Shoal than in iSimangaliso (Fig. 3.19c). There were more sightings in 5–9 metre visibility, shallow depths less than ten metres, wind speeds between 15 and 25 km/h and air temperatures between 15–20 °C (Fig. 3.19d–g). There was a negative linear relationship between the number of sightings and wind speeds over 25 km/h (Fig. 3.19f).

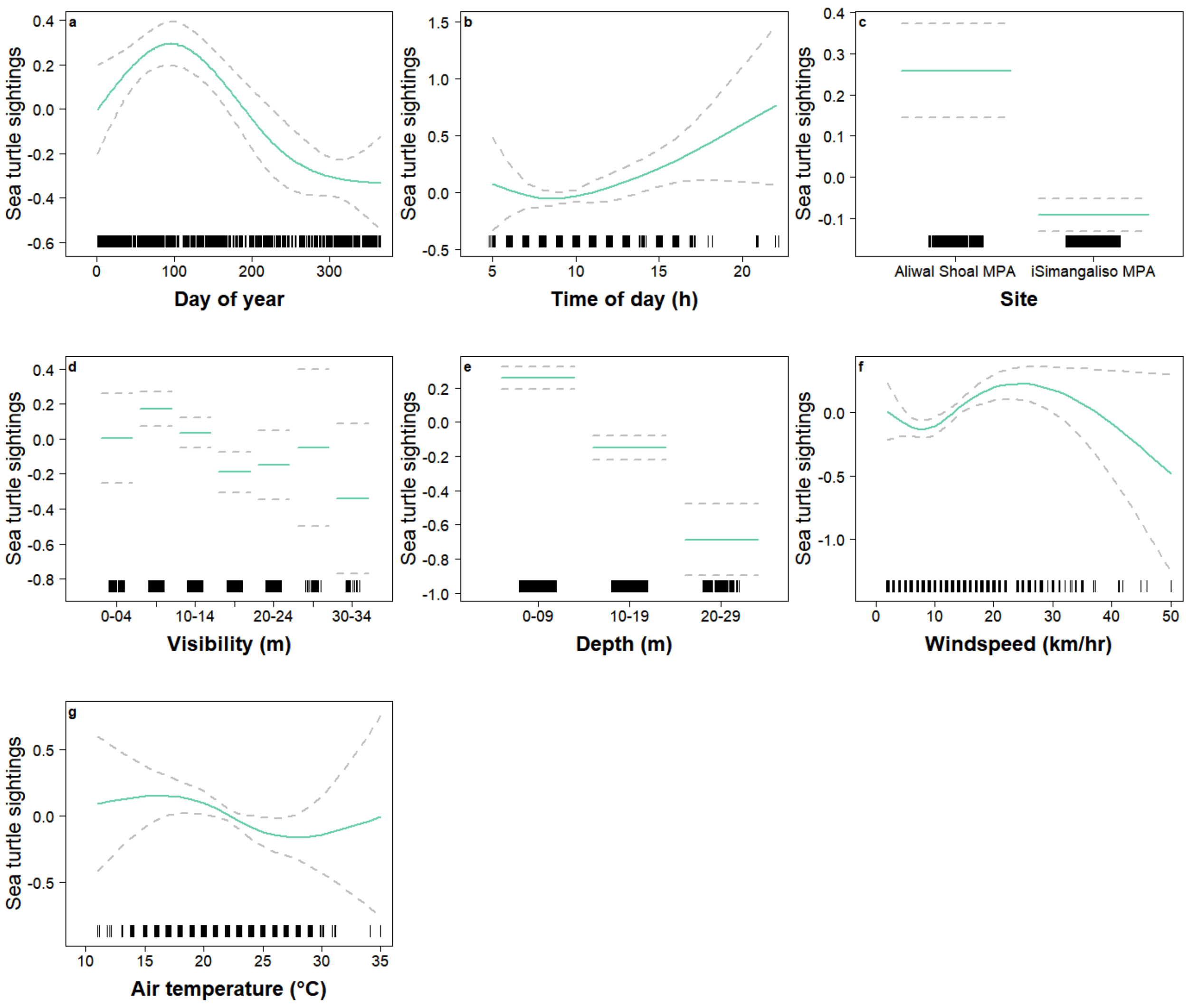


Figure 3.19 Generalised linear model outputs showing the relationships between sea turtle sightings and all significant predictor variables. Rug plots along x-axes show the density of data points for each predictor variable. Broken lines indicate 95% confidence intervals.

Water temperature was excluded from the final GLM as it was not a significant predictor of sea turtle sightings ($p > 0.05$), but graphical output of a separate GLM studying this relationship in isolation showed that there was a peak in sightings between water temperatures of 24–26 °C (Fig. 3.20a). Graphical output of other separate GLMs studying relationships between sea turtle sightings and predictor variables with too many missing data to include in the final GLM are shown in Figure 3.20. There were more sea turtle sightings in weak and mild currents, north currents moving towards the south, and in weak surge (Fig. 3.20b–d). The number of sightings dropped just before high tide and gradually increased on the ebb tide, peaking on low tide (Fig. 3.20e), and a strong peak in sightings occurred between tidal ranges of 1–1.5 metres in between neap and spring tides (Fig. 3.20f). Most sightings occurred in north-easterly and south-westerly winds (Fig. 3.20g).

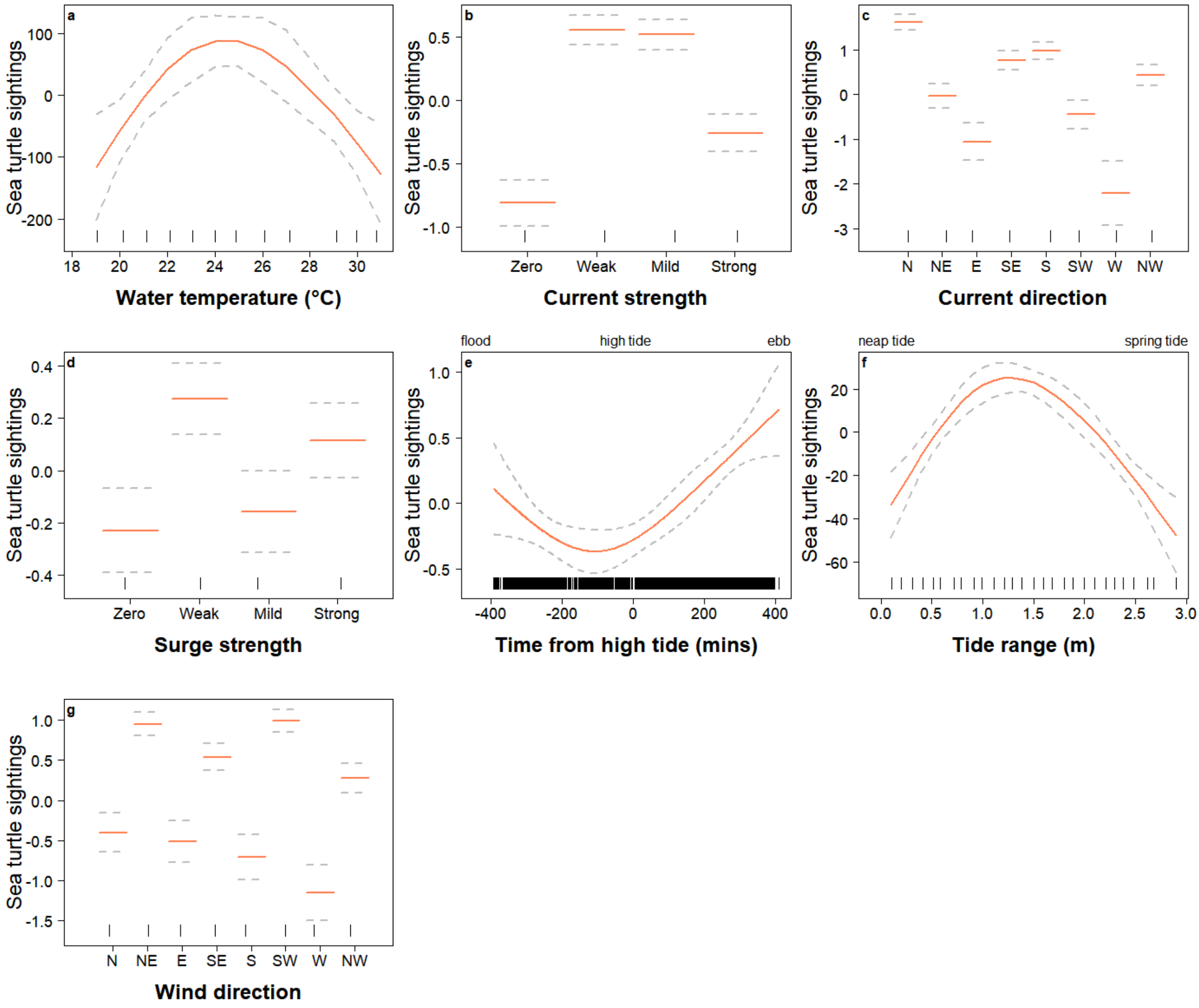


Figure 3.20 The relationship between sea turtle sightings and all predictor variables that were either non-significant or had too many missing data to be included in GLMs without affecting the overall outcome. Rug plots along x-axes show the density of data points for each predictor variable. Broken lines indicate 95% confidence intervals.

3.4.4 Human disturbance to sea turtles

Flight initiation distances

Flight initiation distance was recorded for a total of 546 sea turtle encounters, of which 69% (n = 376) occurred on timed research surveys and 31% (n = 170) were obtained from footage contributed by citizen scientists. Across all sites, 45% of sea turtles approached by divers (n = 248) did not flee, 40% (n = 217) initiated flight responses at distances of < 4 m, 13% (n = 73) initiated flight responses between 5–9 m, and 2% (n = 9) initiated flight responses between 10–14 m.

The highest frequency of sea turtles that did not flee from divers was found on the two most frequently dived sites, Sodwana Bay (green turtles: 48%, n = 91; hawksbills: 45%, n = 14; loggerheads: 55%, n = 18; Fig. 3.21) and Aliwal Shoal (green turtles: 34%, n = 39; hawksbills: 58%, n = 61; loggerheads: 54%, n = 28; Fig. 3.21). There was also a relatively high frequency of sea turtles that initiated flight responses at distances of < 4 m at Sodwana Bay (green turtles: 39%, n = 74; hawksbills: 48%, n = 15; loggerheads: 27%, n = 9; Fig. 3.21) and Aliwal Shoal (green turtles: 47%, n = 41; hawksbills: 31%, n = 33; loggerheads: 35%, n = 18; Fig. 3.21).

Bhanga Nek Reef, a much less frequently dived site, had the highest frequency of 10–14 m flight initiation distances (green turtles: 70%, n = 7; Fig. 3.21). On Adlam's Reef (not frequently dived), all green turtles (n = 6) approached by divers initiated flight responses between 5–9 m (Fig. 3.21). Flight initiation distances of < 4 m were most frequent on Raggie Reef (green turtles: 69%, n = 11; hawksbills: 80%, n = 4; loggerheads: 100%, n = 9; Fig. 3.21). Sea turtles in Green Turtle Gully were not approached underwater thus human disturbance was not quantified.

Signs of disturbance of sea turtles to a diver's approach included the abandonment of foraging, resting and cleaning activities as well as increased swimming speeds and pivoting behaviour of free-swimming turtles. On frequently dived sites, observations of short-term disturbance to sea turtles by recreational divers were noted on numerous occasions. If resting sea turtles were disturbed and moved away from their resting areas, they surfaced to breathe and swam nearby before returning to the same resting area once divers left within five to ten minutes. In contrast, sea turtles on less frequently dived sites, when disturbed, often left the immediate area and were resighted on the same dive less frequently. A slow approach alongside sea turtles allowed for close observations of natural behaviour for extensive time periods. In cases where free-swimming sea turtles were approached from above rather than alongside for paired-laser photogrammetry measurements, a diver positioned ~ 2–4 m above and slightly behind the sea turtle allowed for photos to be captured without causing signs of disturbance.

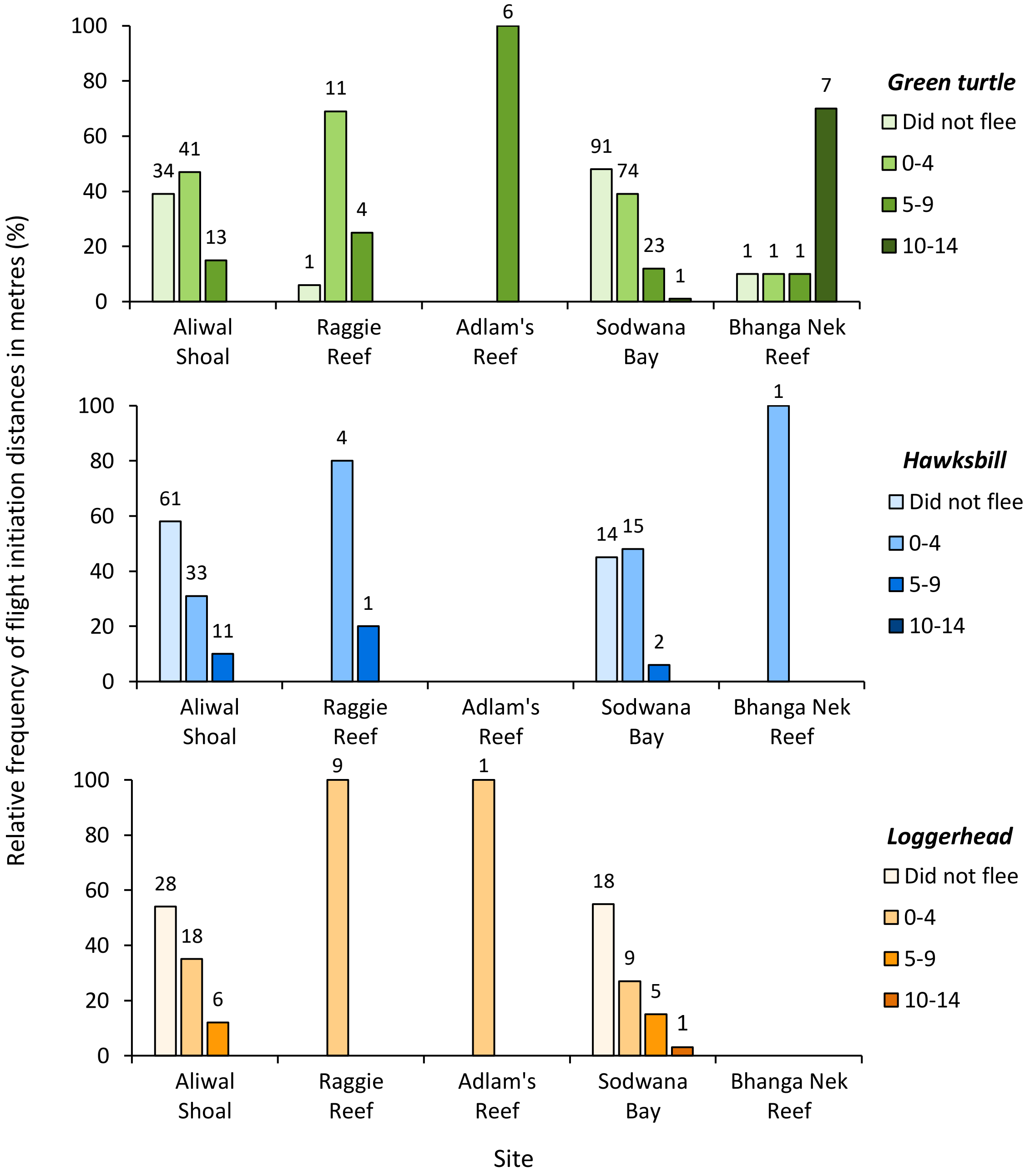


Figure 3.21 Relative frequency of flight initiation distances (m) by sea turtles approached by divers (researchers and citizen scientists) across study sites over the two-year study period. Actual frequencies are above each bar.

Injuries

Out of 1057 sea turtle sightings on the east coast, 57% (n = 605) were recorded with no injuries, 17% (n = 178) were recorded with injuries and it was unknown whether 26% (n = 274) had injuries or not (Fig. 3.22). Out of the sea turtles sighted with injuries, 47% (n = 84) were caused by boat strikes, 24% (n = 42) were caused by shark bites, and 29% (n = 52) had other injuries caused by possible entanglement in debris, ingestion of fishing hooks or unknown causes (Fig. 3.22).

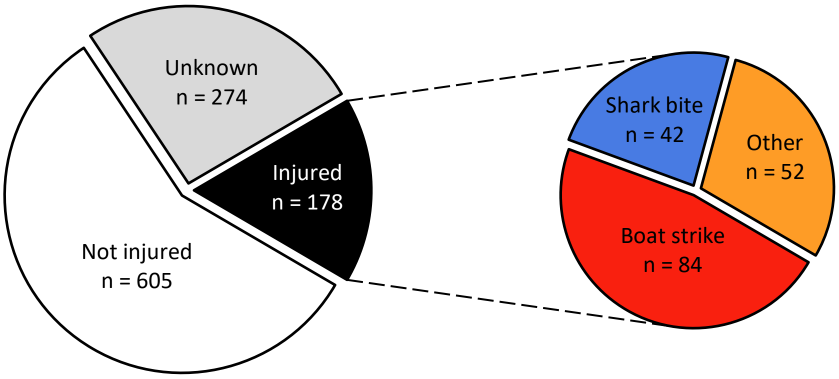


Figure 3.22 Prevalence of injury in all sea turtles sighted on the east coast of South Africa (n = 1057) and main causes of injured turtles (n = 178) from timed research surveys, citizen science contributions and opportunistic sightings over a two-year study period.

Boat strike injuries were only observed on individuals at study sites where high levels of recreational diving take place, namely Sodwana Bay (green turtles: 15%, n = 7; hawksbills: 9%, n = 1; loggerheads: 6%, n = 1) and Aliwal Shoal (green turtles: 11%, n = 3; loggerheads: 10%, n = 3) (Fig. 3.23). None of the individuals in Green Turtle Gully were injured whereas all other sites had individuals with 'other' injuries (Fig. 3.23). Sodwana Bay, Raggie Reef and Aliwal Shoal all had individuals with shark bite injuries with the most occurring on Aliwal Shoal (green turtles: 7%, n = 2; hawksbills: 3%, n = 1; loggerheads: 17%, n = 5) (Fig. 3.23).

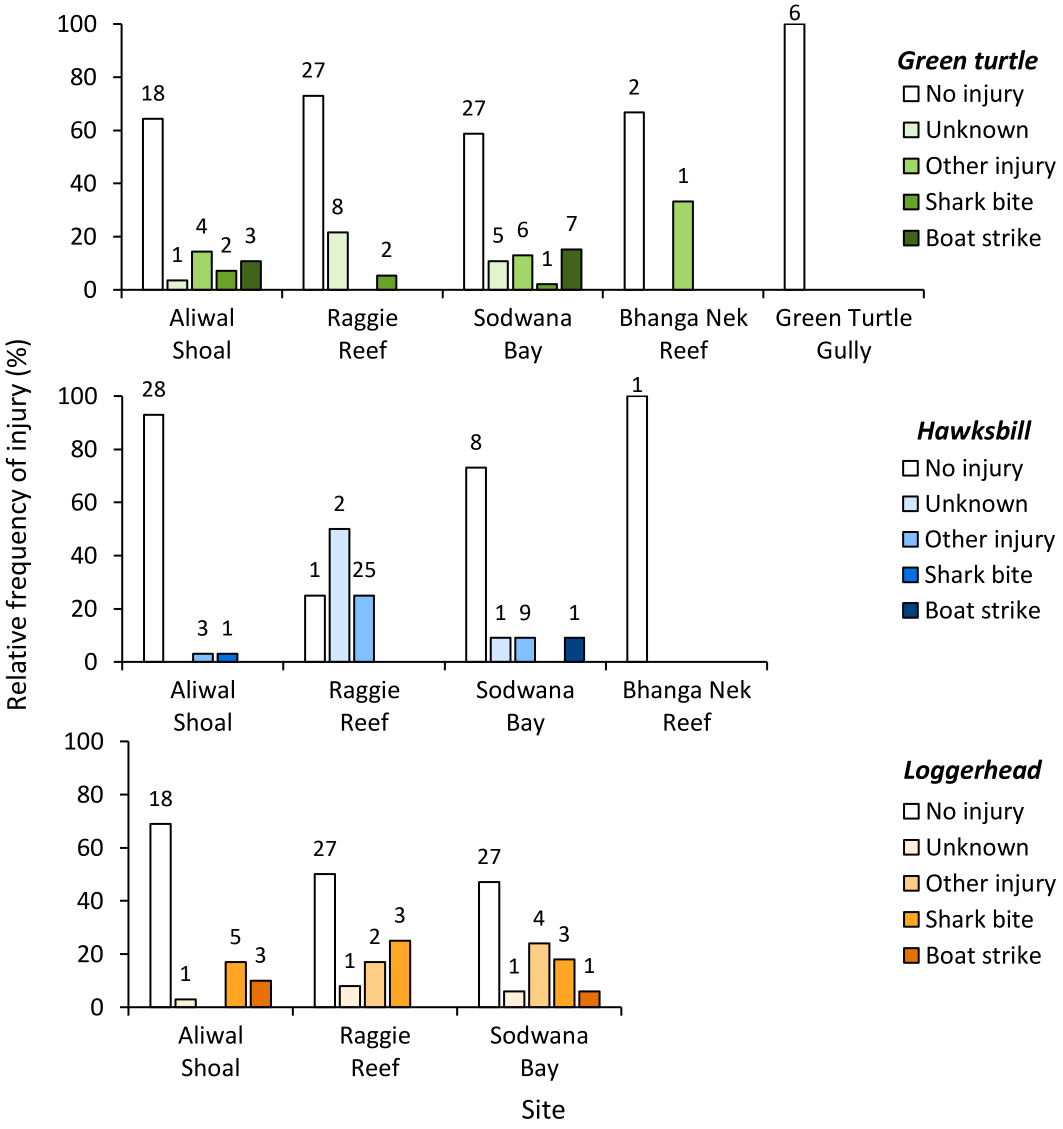


Figure 3.23 Relative frequency of injuries to all identified individual turtles among study sites (n = 224) over a two-year study period. Actual frequencies are above each bar.

Of the 15 individuals with boat strike injuries, 12 individuals already had their injuries at first sighting and three individuals only acquired their boat strike injuries during the study period. Of these three individuals, two were resighted numerous times over a year after being injured (Fig. 3.24a, b) and one was never seen again, likely because its injury was fatal (Fig. 3.24c). One of the individuals that already had a boat strike injury at first sighting acquired a second boat strike injury in the study period (Fig. 3.24d). Whilst conducting timed research surveys on Aliwal Shoal on recreational dive boats, there were two occasions where skippers struck a hard-shelled turtle with the boat on the way to the reef, and we heard of four more incidents via word of mouth (two on Aliwal Shoal and two in Sodwana Bay). All observed boat strike injuries were on the mid to lower half of the carapace.

Figure 3.24 Photos of the (a) juvenile green turtle and (b) adult-sized male green turtle in Sodwana Bay who were first sighted with no injuries (1st row) and acquired boat strike injuries during the study period (2nd row) which healed over time (subsequent rows). (c) Subadult green turtle on Aliwal Shoal before (1st row) and after (2nd row) acquiring a boat strike injury, who was never seen again. (d) Adult-sized male green turtle on Aliwal Shoal who was first seen with most of his tail cut off (likely by a propeller, 1st row) and then seen again with a second boat strike injury (2nd row). Photographers: Alexandra Torborg, Andy Coetzee, Kent Taylor, Miriam Staiger, Samantha Kruger and Sharklife.

All individuals with shark bite injuries had these injuries at first sighting and none were acquired during the study period. Tiger shark (*Galeocerdo cuvier*) predation on loggerheads on Aliwal Shoal occurred on three occasions that we know of in the study period, with two attacks being fatal and the other intercepted by humans.

3.5 Discussion

This study aimed to investigate the spatiotemporal behaviour of sea turtles *in situ* on reefs within the iSimangaliso and Aliwal Shoal MPAs on the east coast of South Africa. It is hypothesised that 1) there will be seasonal changes in the relative abundance of transient nesting species/individuals (loggerheads and leatherbacks) but not resident foraging species/individuals (green turtles, hawksbills and non-breeding loggerheads); 2) behaviour will be reflective of life history stage i.e., resident species/individuals will be observed foraging year-round (in both MPAs) but transient adults will be observed courting and mating in iSimangaliso at the start of the nesting season; 3) sea turtle sightings will be affected by a combination of temporal, environmental, and oceanographic variables; and 4) sea turtles on frequently dived reefs will be more prone to human disturbance and thus have smaller flight initiation distances and a higher prevalence of boat strike injuries than those on less frequented reefs.

Seasonal relative abundance

Results supported the first hypothesis; there were seasonal changes in the relative abundance of transient nesting species but not resident foraging species. The peak in loggerhead SPUE in spring, off nesting beaches (1.4 ± 3.00 turtles/hour, n = 21) was likely due to the arrival of transient breeding individuals at the start of the annual nesting season (October to March) (Hughes 1973). Even though adult-sized loggerheads are resident in iSimangaliso year-round, the two adult-sized female loggerheads seen mating in spring off nesting beaches were both identified as new individuals, suggesting they were transient individuals on breeding migrations. Leatherbacks, being primarily oceanic and only returning to coastal waters to reproduce (Hughes 1996; Harris *et al.* 2015), were only present off nesting beaches at the start of the nesting season. These findings were also consistent with increased catches of loggerheads and leatherbacks in the KZNSB shark nets near northern beaches around the nesting season from 1981–1992 (Brazier *et al.* 2012) and 2010–2021 (KZNSB unpubl. data).

Whilst there were some seasonal differences in SPUE of resident species, these were not as pronounced as those of transient species. Green turtle SPUE peaked in autumn and dropped in winter in iSimangaliso which was generally consistent with seasonal shark net catches near northern beaches (Brazier *et al.* 2012; KZNSB unpubl. data). However, green turtle SPUE on Aliwal Shoal peaked in winter (2.1 ± 2.01 turtles/hour, n = 25) and dropped in summer (0.6 ± 0.96 turtles/hour, n = 8); inconsistent with seasonal shark net catches in central southern KZN, which showed the highest green turtle catches (particularly juveniles) in summer/autumn (Brazier *et al.* 2012). Perhaps high levels of recreational diving on Aliwal Shoal in summer/autumn displace green turtles closer inshore towards the shark nets, especially juveniles who are generally more timid than adults (pers. obs.). Green turtles have also been shown to be displaced to less favourable foraging habitats by the arrival of predators, namely tiger sharks (Heithaus *et al.* 2008). A seasonal peak in large tiger sharks on Aliwal Shoal occurs from December to April (Dicken *et al.* 2016), and green turtles have been found in stomach contents of large tiger sharks caught in shark nets close to Aliwal Shoal (Dicken *et al.* 2017). Therefore, green turtles may also be displaced inshore by the annual arrival of large tiger sharks on Aliwal Shoal each summer.

Hawksbill SPUE was relatively similar year-round across sites, with a slight drop in winter/spring which was consistent with KZN shark net catches from 2010–2021 (KZNSB unpubl. data). The overall pattern of lower SPUE of green turtles, hawksbills and loggerheads at the end of winter/early spring may possibly be a result of lower survey effort due to poor weather conditions. However, catches of all four sea turtle species in KZN shark nets also dropped at this time of year from 1981–1992 (Brazier *et al.* 2012) and 2010–2021 (KZNSB unpubl. data) despite the KZNSB checking nets daily even in poor weather conditions. A slightly lower occurrence in these cooler months may thus be attributed to some individuals shifting northward to warmer waters, as seasonal aerial surveys coupled with sea surface temperature analyses have shown that sea turtles shift their home ranges to stay within preferred seasonally variable temperature ranges (Coles and Musick 2000), and long-term satellite tracking data has also identified seasonal trends in habitat selection (González Carman *et al.* 2012; Shimada *et al.* 2016).

In-water behaviour

The first part of the second hypothesis, which predicted that behaviour will be reflective of life history stage i.e., resident species/individuals will be observed foraging year-round (in both MPAs), was supported in this study. Direct in-water foraging observations showed that food consumed by green turtles, hawksbills and loggerheads was consistent with stomach contents found by Rambaran (2020) and Hughes (1973) in the same area. Food consumed opportunistically such as siphonophores were also found in trace amounts in stomach contents identified by Rambaran (2020). Sponges were not documented in stomach contents of green turtles by Rambaran (2020), and only trace amounts of red algae were present in hawksbill stomach contents. Only one other known study has documented sponges in the stomach contents of green turtles (Seminoff *et al.* 2002). This rare activity may perhaps be a strategy to meet nutritional requirements not satisfied by a herbivorous diet (Bjorndal 1985). Several studies have reported trace amounts of algae in hawksbill stomach contents and have attributed this to incidental ingestion of the benthos surrounding targeted prey items (e.g., Carr and Stancyk 1975; León and Bjorndal 2002; von Brandis *et al.* 2014; Rambaran 2020). However, in the current study, hawksbills were observed deliberately feeding on algae in-between feeding on sponges, which has only been observed in one other known study (Baumbach *et al.* 2022) at Roatán Island, Honduras. Only two known studies have documented algae as the predominant diet item in hawksbill stomach contents (Green 1996; Bell 2013).

Whilst sponges are widely recognized as the preferred food source of hawksbills (e.g., León and Bjorndal 2002), it has been suggested that the occasional consumption of algae by hawksbills is done purposefully to facilitate digestion, since hawksbills are not morphologically adapted to facilitate the passage of large quantities of sponge spicules (Meylan 1988; Baumbach *et al.* 2022). It is also plausible that if the availability of sponges were diminished, hawksbills might consume more algae. The relative abundance of food sources was not quantified in this study, however, the observation that sponges targeted by hawksbills on local reefs were practically always cryptic and required hawksbills to employ a probing approach to locate them by scent, as confirmed by von Brandis (2010), then extract them from beneath the epibenthic layer, suggests a possible limited availability on studied reefs. This may also be supported by the relative frequencies of observed behaviours among hard-shelled sea turtles; hawksbills were observed foraging the most and resting the least of all hard-shelled species, suggesting that they may have more difficulty finding food as shown by Rincon-Diaz *et al*. (2011). This may, however, also be attributed to the nutritional value of food sources and volumes required to meet energy demands (Bjorndal 1985; Baumbach *et al.* 2022). For example, leatherbacks are known to consume substantially large amounts of gelatinous zooplankton and forage for extensive time periods, even when in a jellyfish bloom, because the food is of such poor quality (Duron 1978; Lutcavage and Lutz 1986).

These results highlight that the diet choice of green and hawksbill turtles on the east coast of South Africa may be a function of both preference and local abundance, as suggested by Leon and Bjorndal (2002), and also highlight just how diverse the foraging strategies of some sea turtle species are, which we are yet to fully understand. Understanding long-term trends in specific behaviours such as foraging techniques and interactions with other animals, which are best discerned at the resolution of direct observation (Mills *et al.* 2005) may provide important information on the status of foraging grounds and resident sea turtle populations. Marine ecosystems are highly variable and intraspecific competition may provide insight into what is important to sea turtles and perhaps a limited, high-quality resource (Fretwell 1972; Sutherland 1985; Schofield *et al.* 2007). In this study, for example, opportunistic foraging by green turtles on intermittent influxes of siphonophores caused an adult-sized male green turtle to attack an adult-sized female green turtle travelling in close proximity, indicating the value of this occasional resource, as well as the dominance of the slightly larger male over the female in this particular instance (Fig. 3.16c). Further, the lack of interspecific competition as well as intraspecific competition between individuals of different size classes observed in this study suggests that resource partitioning between species as well as between size classes of the same species is effective to avoid competition (Polis 1984; Lamont and Iverson 2018), but further sampling may reveal its occurrence.

It has also been suggested that certain sites may be preferentially sought after and actively defended by sea turtles (Booth and Peters 1972; Fretwell 1972; Sutherland 1985; Lee and Hays 2004; Schofield *et al.* 2007; Matley *et al.* 2021). For instance, research has demonstrated that seabed resting sites may represent a valuable resource over which individuals compete, whilst surface-basking and swimming activities in the water-column are less constrained by competition (Fretwell 1972; Sutherland 1985). Likewise at some breeding grounds, female turtles have been observed to seek refuge from energetically demanding encounters with reproductively active patrolling males by choosing to inhabit nearshore waters (Booth and Peters 1972; Lee and Hays 2004; Schofield *et al.* 2007). Female-female aggressive competition has been observed in such cases, possibly over space, as females resting near one another may attract unwanted male attention (Schofield *et al.* 2007).

The surprise assaults of resting sea turtles on other intruding sea turtles observed in this study may thus indicate the significance of specific resting areas for sea turtles. The consistent use of these areas by the same individuals further underscores their value. Research has demonstrated that complex reef structures offering refuge and assisted resting sites hold considerable value for sea turtles, to the extent that these sites may be preferred over others with superior food sources in terms of quality and availability (Rincon-Diaz *et al.* 2011). It is plausible that sea turtles seeking refuge from predators like sharks (and perhaps human disturbance) in certain resting areas would prefer to avoid the presence of other sea turtles, which could draw unwelcome attention to them. Furthermore, the occasional observation of green turtles competing for the use of cleaning stations in this study also underscores the value of these cleaning services to them, which are believed to aid in the removal of damaged tissue and epibionts that could lead to infections or hamper hydrodynamic efficiency if left unchecked (Zamzow 1998; Stamper *et al.* 2005). Their particular value to green turtles is further emphasised by the relative frequencies of observed cleaning behaviour in this study, which were highest for green turtles at all sites and comparatively very low for loggerheads and lastly hawksbills. These findings mirrored global patterns in taxonomic richness and diversity of sea turtle epibionts, which are highest for loggerheads, followed by hawksbills and then green turtles (Robinson and Pfaller 2022). Since all intraspecific interactions only occurred on <5% of all observed behaviours among hard-shelled species in this study, it may be suggested that local neritic habitats provide adequate primary food sources, resting sites and cleaning station services to avoid extensive competition among resident sea turtles.

These interactions are essential to gain a better understanding of how individuals use habitats and function within broader ecosystems. The manner in which individual sea turtles within different species compete for resources or sites in foraging habitats allows researchers to objectively quantify their significance, and also provides detailed information about the quality of species-specific foraging habitats (Schofield *et al.* 2007; Matley *et al.* 2021).

Results also supported the subsequent part of the second hypothesis that transient adults will be observed courting and mating in iSimangaliso at the start of the nesting season. These observations provide the first conclusive evidence that loggerhead courtship and mating behaviour takes place in neritic waters of iSimangaliso at the start of the nesting season. This behaviour also occurs in prominent loggerhead breeding grounds worldwide, such as Greece (Schofield *et al.* 2006) and Florida (Frick *et al.* 2000).

Whilst leatherbacks were not observed mating, they were observed displaying patrolling behaviour within one kilometre of the shoreline at the start of the nesting season. It has been suggested that leatherbacks do not mate in the vicinity of nesting beaches (Pritchard 1982). However, given the small SWIO population size (< 100 nesting females annually, Nel *et al.* 2013a), concentrating courting and mating activity in the relatively small area adjacent nesting beaches at the start of the nesting season, rather than offshore, would substantially reduce the challenge of finding mates and increase the likelihood of successful reproduction (Schofield *et al.* 2010b; Mazaris *et al.* 2017). This approach aligns with the concept of the Allee effect, which suggests a positive response between components of individual fitness and the number or density of conspecifics (Stephens *et al.* 1999). James *et al*. (2005) presented further support for leatherback courtship and mating behaviour near nesting beaches off eastern Canada, where satellite-tracked males remained in closer proximity to inshore areas adjacent to nesting beaches compared to breeding females, who moved offshore during internesting periods, similar to local findings of Harris *et al*. (2015).

One adult male loggerhead observed mating over Red Sands was a known resident with year-round resightings and a minimum residence period of 621 days (the longest recorded for all loggerheads in this study). This is the first evidence suggesting that resident adult male loggerheads in iSimangaliso mate in these waters. There is a large knowledge gap on adult male sea turtles, particularly those breeding, as they do not come ashore to nest. However, satellite tracking studies on breeding Kemp's ridley turtles (*Lepidochelys kempii*) (Shaver *et al.* 2005), hawksbills (Van Dam *et al.* 2008), loggerheads (Schofield *et al.* 2010a, 2013), and green turtles (Beal *et al.* 2022) have suggested that males may remain closer to breeding grounds than their female counterparts, with some males residing in the vicinity of nesting beaches year-round. For example, Schofield *et al*. (2013) satellite tracked 75 adult loggerheads (n = 38 male and 37 female) from the breeding area of Zakynthos Island, Greece, and found that 25% of males remained < 100 km of the breeding area whereas all females (except one) migrated to disparate foraging grounds > 200 km away. Males have also been shown to have a shorter breeding periodicity than females whereby they breed annually, at least twice as frequently as females (Hays *et al.* 2010). Therefore, foraging closer to breeding grounds may minimise energy expenditure of long-distance migrations and maximise mating opportunities (Schofield *et al.* 2013).

There is no evidence of resident adult female loggerheads mating in these waters. Harris *et al*. (2018) showed that all satellite tracked nesting female loggerheads were transient to iSimangaliso as they all embarked on post-nesting migrations to coastal waters of Mozambique (n = 17), Madagascar (n = 2), and the Cape of Good Hope (n = 1). It is likely that we did not observe any transient flipper-tagged adult female loggerheads on surveyed reefs in the study period (only one in Sodwana Bay before study commenced as shown in Chapter 2) because satellite tracks have shown that they spend most of their internesting period on Saxon's reef complex north of Bhanga Nek and Mabibi reef complexes north of Sodwana Bay (Harris *et al.* 2015), which were not surveyed in this study due to logistical constraints.

Variability in sea turtle sightings

The GLM supported the third hypothesis; sea turtle sightings were affected by a combination of temporal, environmental, and oceanographic variables. Diel trends in sea turtle sightings were fairly consistent with acoustic tracking and surface sighting data showing two distinct activity peaks per day (Kemmerer *et al.* 1983; Mendonça 1983; Ogden *et al.* 1983), albeit at slightly different timing. Juvenile green turtles in shallow seagrass foraging habitats in Florida showed a similar diel activity pattern to this study with an early-morning peak (06h00) followed by an inactive period (08h00–10h00) and a mid-afternoon peak (14h00–16h00) (Mendonça 1983). Juvenile green turtles in another shallow seagrass foraging habitat in the U.S. Virgin Islands showed fairly similar activity peaks at mid- to late-morning (10h00–11h00) and mid-afternoon (15h00–16h00) with inactive periods in the early morning and at midday (Ogden *et al.* 1983). Similar patterns were also shown by loggerheads in the Canaveral Channel, Florida (Kemmerer *et al.* 1983). At Mayotte Island, mixed green turtle foraging aggregations are shown to be active on seagrass meadows all day (06h00–18h00) with only a slight drop in acoustic receiver detections at midday (Taquet *et al.* 2006). Mixed green turtle foraging aggregations in Bahia, Brazil, only had one diel peak in the late afternoon (16h00–18h00) because of tide-imposed restrictions to foraging areas in the mornings (Jardim *et al.* 2016). Mendonca (1983) provided evidence that activity peaks coincided with slightly cooler temperatures and resting periods coincided with the warmest time of day, which may explain the similar diel pattern observed in this study and many other studies with two diel activity peaks (besides those more affected by tides than temperature).

However, the drop in sea turtle sightings from 08h00–10h00 in this study also coincided with a period of increased human activity on local reefs. This suggests that sea turtles may take refuge or move out the study area when there are high levels of boat traffic and human disturbance on reefs. Recreational dive boat traffic and human disturbance on local reefs is heaviest from 08h00–10h00 with a notably reduced presence in the afternoons/evenings (pers. obs.). Schofield *et al.* (2021) provided evidence that loggerheads detect differences in human activity levels at fine spatial and temporal scales and respond by adjusting their distribution accordingly, by comparing loggerhead sightings in nearshore habitats adjacent breeding grounds in Greece under heavy tourism pressure and under coronavirus-driven absence of tourism. Casale *et al.* (2019) also suggested that the low occurrence of loggerheads around the main island of Lampedusa in the Pelagie Archipelago, Mediterranean Sea, was due to displacement by heavy boat traffic and human presence on reefs, since there were high occurrences of loggerheads in areas with less human disturbance.

Sea turtles are known to frequent shallow depths in neritic foraging habitats more so than greater depths worldwide, as shallower depths are suggested to provide better foraging opportunities, more optimal (warmer) water temperatures, and potentially more protection from predators (e.g., Van Dam and Diez 1996; Jean *et al.* 2010). This supports the significantly higher number of sea turtle sightings at depths < 10 m in this study, despite sampling being biased towards these depths.

Physical processes such as wind and current are well-known drivers of zooplankton (including jellyfish) concentration in specific areas of reefs (e.g., Carleton *et al.* 2001). Strong northeasterly winds commonly bring increased concentrations of zooplankton over inshore reefs along the KZN coastline (pers. obs.), which were shown to provide foraging opportunities for green turtles, hawksbills and loggerheads. Thus, increased sea turtle sightings in northeasterly winds as shown by the GLM may be related to increased food availability.

Underwater visibility may not necessarily drive turtle presence or absence but better visibility does make it easier for observers to detect turtles. Both Williams *et al*. (2017) and Araujo *et al*. (2019) found that higher underwater visibility positively correlated with more sea turtle sightings on reefs. The GLM did not show this correlation, indicating that underwater visibility was not a limiting factor to sea turtle detection by observers.

The GLM indicated that water temperature was not a significant driver of sea turtle sightings on reefs in this study. Whilst temperature may influence diel activity patterns, it seems unlikely to serve as a compelling driver for substantial migrations of individuals in and out of the study area. Surface-basking, where sea turtles rest up to one metre beneath or at the sea surface, is a commonly observed behaviour in cooler temperate waters such as the Mediterranean (Schofield *et al.* 2006) as it is believed to assist with thermoregulation (Spotila and Standora 1985). The absence of surface-basking behaviour in local neritic habitats suggests favourable temperatures year-round. Similarly, Shimada (2016) showed that there was no apparent shift in the satellite tracks of green turtles or loggerheads resembling an escape from cooler temperatures at subtropical and tropical foraging habitats along the Queensland coast of Australia from 1991 to 2015. Matley *et al*. (2020) also showed that whilst water temperature affected dive duration and movement rate of juvenile hawksbills in the U.S. Virgin Islands, 16 of 17 acoustic-tagged individuals were detected on >95% of days over a three-year period, indicating that temperature did not drive individual movement in and out the study area.

Whilst the effects of certain temporal, environmental and oceanographic variables on sea turtle sightings were evident, the final GLM only explained 20.13% of the total variance in sea turtle sightings. Williams *et al*. (2017) also had only 8% of the total variance in sea turtle presence in southern Mozambique explained in a GLM with predictor variables year, day of the year, time of day, habitat type and underwater visibility. It is thus suspected that a combination of several temporal, environmental and oceanographic variables as well as other factors such as predator activity, human disturbance, and availability of food and shelter (some of which were discussed above) drive fine-scale sea turtle abundance and distribution (Williams *et al.* 2017).

Flight initiation distances

The results supported the first part of the fourth hypothesis, that sea turtles on frequently dived reefs will be more prone to human disturbance and thus have smaller flight initiation distances than those on less frequented reefs. Mancini and Elsadek (2015) also found that sea turtles on heavily dived reefs were more habituated to humans as they were much easier to approach closely than those on less frequently dived reefs. Despite this habituation, sea turtles on frequently dived reefs may have still exhibited temporal differences in sightings throughout the day (as discussed above), where the period of highest human disturbance coincided with the period of lowest sea turtle sightings on reefs. By contrast, a study on shallow seagrass beds subjected to high levels of ecotourism in Puerto Rico showed that 90% of immature green turtles initiated flights at ≤3 m, indicating they are not habituated to the presence of divers (Griffin *et al.* 2017). However, Griffin *et al*. (2017) applied a standardised stimulus meant to mimic a snorkelling tourist approaching a sea turtle from above.

The flight initiation distance results of this study suggest divers had a relatively low impact on natural sea turtle behaviour using a slow alongside approach, as also shown by von Brandis (2010). It is thus recommended that recreational divers are guided on using this approach to minimise disturbance to sea turtles (Meadows 2004; Landry and Taggart 2009; Griffin *et al.* 2017) and increase the quality of citizen science data (Williams *et al.* 2015). Recreational divers should also be taught to recognise signs of disturbance of sea turtles such as the abandonment of activities, increased swimming speed and pivoting behaviour (Papafitsoros 2014), which will allow them to notice when sea turtles are uncomfortable in their presence to cease approaching before sea turtles initiate flight responses (Griffin *et al.* 2017).

Injuries

Results also supported the subsequent part of the fourth hypothesis that sea turtles on frequently dived reefs will be more prone to human disturbance and thus have a higher prevalence of boat strike injuries than those on less frequented reefs. Similarly, Denkinger *et al*. (2013) also found a higher incidence of boat strike injuries in areas with heavy boat traffic in the Galapagos Marine Reserve. Papafitsoros (2020) also found that 30% of resident loggerheads in Laganas Bay at Zakynthos Island, Greece, had propeller and boat strike injuries leading to trauma and mortality. The use of compulsory propeller guards by dive boats to decrease injury risk to marine animals has been recommended by numerous studies (e.g., Papafitsoros *et al.* 2020; Schoeman *et al.* 2020). However, studies have shown that propellor guards do not reduce the risk of lethal injury when boats travel at planing speeds (Work *et al.* 2010; Denkinger *et al.* 2013). Since most boat strike injuries appeared to be caused by impact of boat hulls on carapaces rather than propeller cuts, decreased speed limits of dive boats may be more effective than caging propellers in reducing injury risk to sea turtles, as indicated by Hazel *et al*. (2007) who showed that increased vessel speed increases the risk of sea turtle collision. Thus, reduced speeds will give skippers a better chance of seeing turtles on the surface and avoiding collision (Hazel *et al*. 2007).

Citizen science

The importance of citizen science as a method to supplement timed research surveys was demonstrated again from results of this study where citizen scientists reported year-round sea turtle sightings that contributed to seasonal SPUE analyses. Most importantly, the extra effort expended by citizen scientists allowed for footage of rarely observed behaviours such as mating by loggerheads and patrolling for mates by leatherbacks in neritic waters to be captured. Hanna *et al*. (2021) also demonstrated the value of citizen science as the sole method to revealing novel insights on the behaviour of a small aggregation of green turtles in Southern California. With increased effort from citizen scientists as local initiatives grow, we may have a better chance of documenting cryptic behaviours in future, particularly from fishermen who frequent coastal waters where many of these observations took place.

Study limitations and future research improvements

Whilst the results of this study provide novel insights into the seasonal habitat use and behaviours of sea turtles in local neritic habitats, recording the amount of time each animal spent on a particular activity (especially foraging), rather than the relative frequency of behaviours at first sighting, may have provided more useful data for interpretations. The time each animal spent on each behaviour was not recorded in this study because we used the same timed research surveys to collect sighting data and photo-IDs for other analyses presented in this thesis (e.g., SPUE), which would have been biased if we did not search for sea turtles at a relatively constant rate (i.e., if we spent a substantial amount of our 'search effort' observing one individual's activities). However, this study demonstrated the potential of using direct in-water observations to collect detailed behavioural data related to the foraging ecology and habitat use of sea turtles, making it a foundational first step for further detailed investigations on sea turtle habitat use and behavioural ecology. It is suggested that such further studies should focus solely on behavioural observations whereby researchers attempt to remain with an individual for as long as possible to record specific details such as the type and quantity of food consumed and the time spent doing so (e.g., von Brandis 2010; Baumbach *et al.* 2022), or use minimally invasive techniques such as RUVs or turtle-mounted video time-depth recorders (VTDRs) (e.g., Seminoff *et al.* 2006).

It is acknowledged that there may be bias in the detectability of certain behaviours over others, and that behaviours that are done for longer may be more represented in the data than rarer or less frequent behaviours. For example, swimming (moving) sea turtles may have been easier to see than resting sea turtles, and resting behaviour may be more represented than foraging behaviour due to the time spent doing each. It would thus be valuable to test for bias in behavioural observations and develop techniques to quantify these biases in future.

The GLM also provided valuable insights into factors affecting sea turtle sightings in this study, however, patchy environmental data limited the construction of species-specific GLMs. Environmental data was recorded consistently for each timed research survey, but volunteer tourists and citizen scientists did not report it as frequently given the extra effort it takes. If we make it mandatory for citizen scientists to provide detailed information on environmental conditions (e.g., water temperature, underwater visibility, surge and current strength and direction), we risk not receiving citizen science data altogether. It is thus recommended that future studies disentangle the drivers of fine-scale species-specific sea turtle abundance and distribution using models combining several high-resolution variables obtained via remote technology (e.g., acoustic tags or satellite tags) coupled with temperature and depth recorders, as well as other factors such as predator activity, human disturbance, and availability of food and shelter (e.g., Williams *et al.* 2017; Matley *et al.* 2020).

3.6 Conclusion

This is the first study to date to investigate the spatiotemporal behaviour of sea turtles *in situ* on reefs along the east coast of South Africa. The results confirm that green turtles (juvenile–adult-sized), immature hawksbills, and non-breeding adult-sized loggerheads forage year-round in the iSimangaliso and Aliwal Shoal MPAs and follow conventional diets described for each species in regional and global literature, but also display diverse foraging strategies. The results also confirm that transient nesting adult female loggerheads use iSimangaliso's neritic waters as a courtship and mating area at the start of the annual nesting season. The first evidence suggesting that resident adult-sized male loggerheads mate in iSimangaliso's neritic waters, and that adult-sized leatherbacks search for mates here too, is provided. These findings contribute to the growing body of knowledge on the cryptic yet diverse in-water behaviours, ecological roles and seasonal habitat use of both resident and transient sea turtle species along the east coast of South Africa. Observations of intraspecific competition over certain food sources, resting areas and cleaning stations also provide novel insight into their value to sea turtles in local neritic habitats. The findings also demonstrate the significant potential of direct in-water observations for further detailed investigations to gain a better understanding of the specific ecological roles of sea turtles.

A set of seven temporal, environmental, and oceanographic variables (day of the year, time of day, site, underwater visibility, depth, wind speed and air temperature) had significant effects on sea turtle sightings, but only explained 20.13% of their variance. This indicates that a combination of several variables as well as other factors such as predator activity, human disturbance, and availability of food and shelter likely affect sea turtle sightings.

The results also indicated that high levels of human disturbance on frequently dived reefs may affect sea turtles through temporal displacement in sightings, despite these turtles being more habituated to divers than those on less frequented reefs. There was also a higher prevalence of boat strike injuries on frequently dived reefs. These findings suggest that there is trade-off between humans and sea turtles; whilst sea turtles may be more habituated to divers when there is a higher human presence on reefs, it may come at the cost of more frequent disturbance and injuries to sea turtles. These findings could be used to guide recreational divers on ways to minimise human disturbance and risk of injury to sea turtles, and to increase the quality of citizen science data.

3.7 References

Araujo, G., Legaspi, C. G., Ferber, S., Murray, R., Burdett, K., Grundy, S., Labaja, J., Snow, S., Yaptinchay, A. and Ponzo, A. (2019). In-water methods reveal population dynamics of a green turtle *Chelonia mydas* foraging aggregation in the Philippines. *Endangered Species Research,* 40, pp. 207-218

Baumbach, D. S., Zhang, R., Hayes, C. T., Wright, M. K. and Dunbar, S. G. (2022). Strategic foraging: Understanding hawksbill (*Eretmochelys imbricata*) prey item energy values and distribution within a marine protected area. *Marine Ecology,* 43(2)

Beal, M., Catry, P., Regalla, A., Barbosa, C., Pires, A. J., Mestre, J., Senhoury, C., Sidina, E. and Patrício, A. R. (2022). Satellite tracking reveals sex-specific migration distance in green turtles (*Chelonia mydas*). *Biology Letters,* 18(9), pp. 20220325

Bell, I. (2013). Algivory in hawksbill turtles: *Eretmochelys imbricata* food selection within a foraging area on the Northern Great Barrier Reef. *Marine Ecology,* 34(1), pp. 43-55

Bjorndal, K. A. (1985). Nutritional ecology of sea turtles. *Copeia*, pp. 736-751

Blumenthal, J., Austin, T., Bell, C., Bothwell, J., Broderick, A., Ebanks-Petrie, G., Gibb, J., Luke, K., Olynik, J. and Orr, M. (2009). Ecology of hawksbill turtles, *Eretmochelys imbricata*, on a western Caribbean foraging ground. *Chelonian Conservation and Biology,* 8(1), pp. 1-10

Booth, J. and Peters, J. A. (1972). Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. *Animal Behaviour,* 20(4), pp. 808-812

Brazier, W., Nel, R., Cliff, G. and Dudley, S. (2012). Impact of protective shark nets on sea turtles in KwaZulu-Natal, South Africa, 1981–2008. *African Journal of Marine Science,* 34(2), pp. 249-257

Carleton, J., Brinkman, R. and Doherty, P. (2001). Zooplankton community structure and water flow in the lee of Helix Reef (Great Barrier Reef, Australia). *Marine Biology,* 139, pp. 705-717

Carr, A. and Stancyk, S. (1975). Observations on the ecology and survival outlook of the hawksbill turtle. *Biological Conservation,* 8(3), pp. 161-172

Casale, P., Ciccocioppo, A., Vagnoli, G., Rigoli, A., Freggi, D., Tolve, L. and Luschi, P. (2019). Citizen science helps assessing spatio-temporal distribution of sea turtles in foraging areas. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 30(1), pp. 123-130

Christianen, M. J., Herman, P. M., Bouma, T. J., Lamers, L. P., van Katwijk, M. M., van der Heide, T., Mumby, P. J., Silliman, B. R., Engelhard, S. L., van de Kerk, M., Kiswara, W. and van de Koppel, J. (2014). Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. *Proc Biol Sci,* 281(1777), pp. 20132890

Christianen, M. J. A., Smulders, F. O. H., Vonk, J. A., Becking, L. E., Bouma, T. J., Engel, S. M., James, R. K., Nava, M. I., de Smit, J. C., van der Zee, J. P., Palsboll, P. J. and Bakker, E. S. (2022). Seagrass ecosystem multifunctionality under the rise of a flagship marine megaherbivore. *Glob Chang Biol,* 29(1), pp. 215-230

Coles, W. and Musick, J. A. (2000). Satellite sea surface temperature analysis and correlation with sea turtle distribution off North Carolina. *Copeia,* 2000(2), pp. 551-554

Denkinger, J., Parra, M., Muñoz, J. P., Carrasco, C., Murillo, J. C., Espinosa, E., Rubianes, F. and Koch, V. (2013). Are boat strikes a threat to sea turtles in the Galapagos Marine Reserve? *Ocean & Coastal Management,* 80, pp. 29-35

Dicken, M. L., Cliff, G. and Winker, H. (2016). Sharks caught in the KwaZulu-Natal bather protection programme, South Africa. 13. The tiger shark *Galeocerdo cuvier*. *African Journal of Marine Science,* 38(3), pp. 285-301

Dicken, M. L., Hussey, N. E., Christiansen, H. M., Smale, M. J., Nkabi, N., Cliff, G. and Wintner, S. P. (2017). Diet and trophic ecology of the tiger shark (*Galeocerdo cuvier*) from South African waters. *PLoS One,* 12(6), pp. e0177897

Duron, M. (1978) *Contribution à l'étude de la biologie de Dermochelys coriacea (Linné) dans les Pertuis Charentais.* Université de Bordeaux.

Eckert, K., Bjorndal, K., Abreu-Grobois, F. and Donnelly, M. (1999). Priorities for research in foraging habitats. *Research and management techniques for the conservation of sea turtles,* 4, pp. 12-18

Estes, J. A., Duggins, D. O. and Rathbun, G. B. (1989). The ecology of extinctions in kelp forest communities. *Conservation Biology,* 3(3), pp. 252-264

Fourqurean, J. W., Manuel, S., Coates, K. A., Kenworthy, W. J. and Smith, S. R. (2010). Effects of excluding sea turtle herbivores from a seagrass bed: Overgrazing may have led to loss of seagrass meadows in Bermuda. *Marine Ecology Progress Series,* 419, pp. 223-232

Fourqurean, J. W., Manuel, S. A., Coates, K. A., Massey, S. C. and Kenworthy, W. J. (2019). Decadal Monitoring in Bermuda Shows a Widespread Loss of Seagrasses Attributable to Overgrazing by the Green Sea Turtle *Chelonia mydas*. *Estuaries and Coasts,* 42(6), pp. 1524-1540

Fretwell, S. D. (1972) *Populations in a Seasonal Environment.* Princeton, New Jersey: Princeton University Press.

Frick, M. G., Slay, C. K., Quinn, C. A., Windham-Reid, A., Duley, P. A., Ryder, C. M. and Morse, L. J. (2000). Aerial observations of courtship behavior in loggerhead sea turtles (*Caretta caretta*) from southeastern Georgia and northeastern Florida. *Journal of Herpetology,* 34(1), pp. 153-158

Gangal, M., Gafoor, A.-B., D'Souza, E., Kelkar, N., Karkarey, R., Marbà, N., Arthur, R. and Alcoverro, T. (2021). Sequential overgrazing by green turtles causes archipelago-wide functional extinctions of seagrass meadows. *Biological Conservation,* 260

González Carman, V., Falabella, V., Maxwell, S., Albareda, D., Campagna, C. and Mianzan, H. (2012). Revisiting the ontogenetic shift paradigm: The case of juvenile green turtles in the SW Atlantic. *Journal of Experimental Marine Biology and Ecology,* 429, pp. 64-72

Green, D. Sea turtles of north Yemen (Yemen Arab Republic). *proceedings of the fifteenth annual symposium on sea turtle biology and conservation, Hilton Head, NOAA, NMFS-SEFSC-387*, 116-118.

Griffin, L. P., Brownscombe, J. W., Gagne, T. O., Wilson, A. D., Cooke, S. J. and Danylchuk, A. J. (2017). Individual-level behavioral responses of immature green turtles to snorkeler disturbance. *Oecologia,* 183(3), pp. 909-917

Hanna, M. E., Chandler, E. M., Semmens, B. X., Eguchi, T., Lemons, G. E. and Seminoff, J. A. (2021). Citizen-sourced sightings and underwater photography reveal novel insights about green sea turtle distribution and ecology in southern California. *Frontiers in Marine Science,* 8, pp. 671061

Harris, L. R., Nel, R., Oosthuizen, H., Meÿer, M., Kotze, D., Anders, D., McCue, S. and Bachoo, S. (2018). Managing conflicts between economic activities and threatened migratory marine species toward creating a multiobjective blue economy. *Conservation Biology,* 32(2), pp. 411-423

Harris, L. R., Nel, R., Oosthuizen, H., Meyer, M., Kotze, D., Anders, D., McCue, S. and Bachoo, S. (2015). Paper-efficient multi-species conservation and management are not always field-effective: The status and future of Western Indian Ocean leatherbacks. *Biological Conservation,* 191, pp. 383-390

Hayes, C. T., Baumbach, D. S., Juma, D. and Dunbar, S. G. (2016). Impacts of recreational diving on hawksbill sea turtle (*Eretmochelys imbricata*) behaviour in a marine protected area. *Journal of Sustainable Tourism,* 25(1), pp. 79-95

Hays, G. C., Adams, C. R., Broderick, A. C., Godley, B. J., Lucas, D. J., Metcalfe, J. D. and Prior, A. A. (2000). The diving behaviour of green turtles at Ascension Island. *Anim Behav,* 59(3), pp. 577-586

Hays, G. C., Fossette, S., Katselidis, K. A., Schofield, G. and Gravenor, M. B. (2010). Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. *Conservation Biology,* 24(6), pp. 1636-1643

Hazel, J., Lawler, I. R., Marsh, H. and Robson, S. (2007). Vessel speed increases collision risk for the green turtle *Chelonia mydas*. *Endangered Species Research,* 3(2), pp. 105-113

Heithaus, M. R., Frid, A., Wirsing, A. J., Bejder, L. and Dill, L. M. (2005). Biology of sea turtles under risk from tiger sharks at a foraging ground. *Marine Ecology Progress Series,* 288, pp. 285-294

Heithaus, M. R., Wirsing, A. J., Thomson, J. A. and Burkholder, D. A. (2008). A review of lethal and non-lethal effects of predators on adult marine turtles. *Journal of Experimental Marine Biology and Ecology,* 356(1-2), pp. 43-51

Houghton, J. D., Woolmer, A. and Hays, G. C. (2000). Sea turtle diving and foraging behaviour around the Greek Island of Kefalonia. *Journal of the Marine Biological Association of the United Kingdom,* 80(4), pp. 761-762

Houghton, J. D. R., Callow, M. J. and Hays, G. C. (2003). Habitat utilization by juvenile hawksbill turtles (*Eretmochelys imbricata*, Linnaeus, 1766) around a shallow water coral reef. *Journal of Natural History,* 37(10), pp. 1269-1280

Hughes, G. (1996). Nesting of the Leatherback Turtle (*Dermochelys coriacea*) in Tongaland, KwaZulu-Natal, South Africa, 1963-1995. *Chelonian Conservation and Biology,* 2(2), pp. 153-158

Hughes, G. R. (1973) The sea turtles of South East Africa.

Jackson, J. B. (1997). Reefs since columbus. *Coral Reefs,* 16, pp. S23-S32

James, M. C., Eckert, S. A. and Myers, R. A. (2005). Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). *Marine Biology,* 147, pp. 845-853

Jardim, A., Lopez-Mendilaharsu, M. and Barros, F. (2016). Demography and foraging ecology of *Chelonia mydas* on tropical shallow reefs in Bahia, Brazil. *Journal of the Marine Biological Association of the United Kingdom,* 96(6), pp. 1295-1304

Jean, C., Ciccione, S., Talma, E., Ballorain, K. and Bourjea, J. (2010). Photo-identification method for green and hawksbill turtles-First results from Reunion. *Indian ocean turtle NewsLeTTER,* 11, pp. 8-13

Kemmerer, A. J., Timko, R. E. and Burkett, S. B. (1983). Movement and surfacing behavior patterns of loggerhead sea turtles in and near Canaveral Channel, Florida:(September and October 1981).

Lamont, M. M. and Iverson, A. R. (2018). Shared habitat use by juveniles of three sea turtle species. *Marine Ecology Progress Series,* 606, pp. 187-200

Landry, M. S. and Taggart, C. T. (2009). “Turtle watching” conservation guidelines: green turtle (*Chelonia mydas*) tourism in nearshore coastal environments. *Biodiversity and Conservation,* 19(1), pp. 305-312

Lee, P. L. and Hays, G. C. (2004). Polyandry in a marine turtle: females make the best of a bad job. *Proceedings of the National Academy of Sciences,* 101(17), pp. 6530-6535

León, Y. M. and Bjorndal, K. A. (2002). Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. *Marine Ecology Progress Series,* 245, pp. 249-258

Lutcavage, M. and Lutz, P. L. (1986). Metabolic rate and food energy requirements of the leatherback sea turtle, *Dermochelys coriacea*. *Copeia,* 1986(3), pp. 796-798

Mancini, A., Elsadek, I. and Madon, B. (2015). When simple is better: Comparing two sampling methods to estimate green turtles abundance at coastal feeding grounds. *Journal of Experimental Marine Biology and Ecology,* 465, pp. 113-120

Matley, J., Jossart, J., Johansen, L. and Jobsis, P. (2020). Environmental drivers of diving behavior and space-use of juvenile endangered Caribbean hawksbill sea turtles identified using acoustic telemetry. *Marine Ecology Progress Series,* 652, pp. 157-171

Matley, J. K., Johansen, L. K., Klinard, N. V., Eanes, S. T. and Jobsis, P. D. (2021). Habitat selection and 3D space use partitioning of resident juvenile hawksbill sea turtles in a small Caribbean bay. *Marine Biology,* 168(8)

Mazaris, A. D., Schofield, G., Gkazinou, C., Almpanidou, V. and Hays, G. C. (2017). Global sea turtle conservation successes. *Science advances,* 3(9), pp. e1600730

McClenachan, L., Jackson, J. B. and Newman, M. J. (2006). Conservation implications of historic sea turtle nesting beach loss. *Frontiers in Ecology and the Environment,* 4(6), pp. 290-296

Meadows, D. (2004). Behavior of green sea turtles in the presence and absence of recreational snorkelers. *Marine Turtle Newsletter,* 103(1), pp. 4

Mendonça, M. T. (1983). Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. *Copeia*, pp. 1013-1023

Meylan, A. (1988). Spongivory in hawksbill turtles: a diet of glass. *Science,* 239(4838), pp. 393-395

Mills, D. J., Verdouw, G. and Frusher, S. D. (2005). Remote multi-camera system for in situ observations of behaviour and predator/prey interactions of marine benthic macrofauna.

Mortimer, J. A., Von Brandis, R. G., Liljevik, A., Chapman, R. and Collie, J. (2011). Fall and rise of nesting green turtles (*Chelonia mydas*) at Aldabra Atoll, Seychelles: positive response to four decades of protection (1968–2008). *Chelonian Conservation and Biology,* 10(2), pp. 165-176

Nel, R., Punt, A. E. and Hughes, G. R. (2013a). Are coastal protected areas always effective in achieving population recovery for nesting sea turtles? *PLoS One,* 8(5), pp. e63525

Ogden, J. C., Robinson, L., Whitlock, K., Daganhardt, H. and Cebula, R. (1983). Diel foraging patterns in juvenile green turtles (*Chelonia mydas* L.) in St. Croix United States Virgin Islands. *Journal of Experimental Marine Biology and Ecology,* 66(3), pp. 199-205

Papafitsoros, K. (2014). In-water behaviour of the loggerhead sea turtle (*Caretta caretta*) under the presence of humans (*Homo sapiens*) in a major Mediterranean nesting site. *Encounters,* 24(26), pp. 28

Papafitsoros, K., Panagopoulou, A. and Schofield, G. (2020). Social media reveals consistently disproportionate tourism pressure on a threatened marine vertebrate. *Animal Conservation,* 24(4), pp. 568-579

Piraino, S., Fanelli, G. and Boero, F. (2002). Variability of species' roles in marine communities: change of paradigms for conservation priorities. *Marine Biology,* 140, pp. 1067-1074

Polis, G. A. (1984). Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *The American Naturalist,* 123(4), pp. 541-564

Pritchard, P. C. (1982). Nesting of the leatherback turtle, *Dermochelys coriacea* in Pacific Mexico, with a new estimate of the world population status. *Copeia*, pp. 741-747

R Core Team (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Rambaran, R. (2020) Defining the potential ecological roles of three sea turtle species (*Caretta caretta*, *Chelonia mydas* and *Eretmochelys imbricata*) along the Eastern seaboard of South Africa. Masters thesis, Nelson Mandela Metropolitan University

Rincon-Diaz, M. P., Diez, C. E., van Dam, R. P. and Sabat, A. M. (2011). Effect of Food Availability on the Abundance of Juvenile Hawksbill Sea Turtles (*Eretmochelys imbricata*) in Inshore Aggregation Areas of the Culebra Archipelago, Puerto Rico. *Chelonian Conservation and Biology,* 10(2), pp. 213-221

Robinson, N. J. and Pfaller, J. B. (2022). Sea Turtle Epibiosis: Global Patterns and Knowledge Gaps. *Frontiers in Ecology and Evolution,* 10

RStudio Team (2022). RStudio: Integrated Development Environment for R. RStudio, PBC. http://www.rstudio.com/.

Schoeman, R. P., Patterson-Abrolat, C. and Plön, S. (2020). A Global Review of Vessel Collisions With Marine Animals. *Frontiers in Marine Science,* 7

Schofield, G., Dickson, L. C. D., Westover, L., Dujon, A. M. and Katselidis, K. A. (2021). COVID-19 disruption reveals mass-tourism pressure on nearshore sea turtle distributions and access to optimal breeding habitat. *Evol Appl,* 14(10), pp. 2516-2526

Schofield, G., Dimadi, A., Fossette, S., Katselidis, K. A., Koutsoubas, D., Lilley, M. K., Luckman, A., Pantis, J. D., Karagouni, A. D. and Hays, G. C. (2013). Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. *Diversity and Distributions,* 19(7), pp. 834-844

Schofield, G., Hobson, V. J., Lilley, M. K., Katselidis, K. A., Bishop, C. M., Brown, P. and Hays, G. C. (2010a). Inter-annual variability in the home range of breeding turtles: implications for current and future conservation management. *Biological Conservation,* 143(3), pp. 722-730

Schofield, G., Hobson, V. J., Lilley, M. K. S., Katselidis, K. A., Bishop, C. M., Brown, P. and Hays, G. C. (2010b). Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management. *Biological Conservation,* 143(3), pp. 722-730

Schofield, G., Katselidis, K. A., Dimopoulos, P., Pantis, J. D. and Hays, G. C. (2006). Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. *Endangered Species Research,* 2, pp. 71-79

Schofield, G., Katselidis, K. A., Pantis, J. D., Dimopoulos, P. and Hays, G. C. (2007). Female–female aggression: structure of interaction and outcome in loggerhead sea turtles. *Marine Ecology Progress Series,* 336, pp. 267-274

Seminoff, J. A., Jones, T. T. and Marshall, G. J. (2006). Underwater behaviour of green turtles monitored with video-time-depth recorders: what's missing from dive profiles? *Marine Ecology Progress Series,* 322, pp. 269-280

Seminoff, J. A., Resendiz, A. and Nichols, W. J. (2002). Diet of East Pacific green turtles (*Chelonia mydas*) in the central Gulf of California, Mexico. *Journal of Herpetology,* 36(3), pp. 447-453

Shaver, D. J., Schroeder, B. A., Byles, R. A., Burchfield, P. M., Peña, J., Márquez, R. and Martinez, H. J. (2005). Movements and Home Ranges of Adult Male Kemp's Ridley Sea Turtles (*Lepidochelys kempii*) in the Gulf of Mexico Investigated by Satellite Telemetry. *Chelonian Conservation and Biology,* 4(4), pp. 817-827

Shimada, T., Jones, R., Limpus, C., Groom, R. and Hamann, M. (2016). Long-term and seasonal patterns of sea turtle home ranges in warm coastal foraging habitats: implications for conservation. *Marine Ecology Progress Series,* 562, pp. 163-179

Spotila, J. R. and Standora, E. A. (1985). Environmental constraints on the thermal energetics of sea turtles. *Copeia*, pp. 694-702

Stamper, M. A., Harms, C., Epperly, S. P., Braun-McNeill, J., Avens, L. and Stoskopf, M. K. (2005). Relationship between barnacle epibiotic load and hematologic parameters in loggerhead sea turtles (*Caretta caretta*), a comparison between migratory and residential animals in Pamlico Sound, North Carolina. *Journal of Zoo and Wildlife Medicine,* 36(4), pp. 635-641

Stephens, P. A., Sutherland, W. J. and Freckleton, R. P. (1999). What is the Allee effect? *Oikos*, pp. 185-190

Sutherland, W. J. (1985). Distribution of unequal competitors. *Behavioural ecology: ecological consequences of adaptive behaviour,*

Taquet, C., Taquet, M., Dempster, T., Soria, M., Ciccione, S., Roos, D. and Dagorn, L. (2006). Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. *Marine Ecology Progress Series,* 306, pp. 295-302

Van Dam, R. and Diez, C. (1996). Diving behavior of immature hawksbills (*Eretmochelys imbricata*) in a Caribbean cliff-wall habitat. *Marine Biology,* 127, pp. 171-178

Van Dam, R. P., Diez, C. E., Balazs, G. H., Colón, L. A. C., McMillan, W. O. and Schroeder, B. (2008). Sex-specific migration patterns of hawksbill turtles breeding at Mona Island, Puerto Rico. *Endangered Species Research,* 4(1-2), pp. 85-94

van der Zee, J. P., Christianen, M. J. A., Nava, M., Velez-Zuazo, X., Hao, W., Berube, M., van Lavieren, H., Hiwat, M., Berzins, R., Chevalier, J., Chevallier, D., Lankester, M. C., Bjorndal, K. A., Bolten, A. B., Becking, L. E. and Palsboll, P. J. (2019). Population recovery changes population composition at a major southern Caribbean juvenile developmental habitat for the green turtle, *Chelonia mydas*. *Sci Rep,* 9(1), pp. 14392

von Brandis, R. G. (2010) The Ecology of Foraging Hawksbill Turtles (*Eretmochelys imbricata*) at D'Arros Island and St. Joseph Atoll in the Seychelles, Western Indian Ocean. Doctoral thesis, Tshwane University of Technology

von Brandis, R. G., Mortimer, J., Reilly, B., Van Soest, R. and Branch, G. (2014). Taxonomic composition of the diet of hawksbill turtles (*Eretmochelys imbricata*) in the Republic of Seychelles. *Western Indian Ocean Journal of Marine Science,* 13(1), pp. 81-91

Weber, S. B., Weber, N., Ellick, J., Avery, A., Frauenstein, R., Godley, B. J., Sim, J., Williams, N. and Broderick, A. C. (2014). Recovery of the South Atlantic's largest green turtle nesting population. *Biodiversity and Conservation,* 23(12), pp. 3005-3018

Williams, J. L., Pierce, S. J., Fuentes, M. M. and Hamann, M. (2015). Effectiveness of recreational divers for monitoring sea turtle populations. *Endangered Species Research,* 26(3), pp. 209-219

Williams, J. L., Pierce, S. J., Rohner, C. A., Fuentes, M. M. and Hamann, M. (2017). Spatial distribution and residency of green and loggerhead sea turtles using coastal reef habitats in southern Mozambique. *Frontiers in Marine Science,* 3, pp. 288

Williams, S. (1988). *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. *Marine Biology,* 98(3), pp. 447-455

Work, P. A., Sapp, A. L., Scott, D. W. and Dodd, M. G. (2010). Influence of small vessel operation and propulsion system on loggerhead sea turtle injuries. *Journal of Experimental Marine Biology and Ecology,* 393(1-2), pp. 168-175

Zamzow, J. P. Cleaning symbioses between Hawaiian reef fishes and green sea turtles, *Chelonia mydas*. *18th International Sea Turtle Symposium*, 235.

Chapter 4: Conclusion and Recommendations

4.1 Background

Global marine ecosystems have been severely transformed by the overexploitation of long-lived, ecologically important marine megafauna like sea turtles (Jackson 1997), because their removal has severely compromised marine ecosystem structure, functioning and resilience (Estes *et al.* 1989; Pauly *et al.* 1998). Efforts to conserve sea turtles are challenged by their complex life cycles, broad geographic ranges, shifting baselines and a global lack of knowledge on their lives at sea given the challenges of in-water studies relative to nesting beach studies (Jackson 1997; Bjorndal and Bolten 2003; McClenachan *et al.* 2006). The growing recognition of the need for in-water studies among scientists (Bjorndal and Bolten 2000) has led to great advances in in-water methods over the last two decades. These make it an opportune time to conduct in-water studies, particularly where extensive nesting beach research and conservation efforts have provided significant insights and success in population recovery, whilst knowledge remains severely limited for non-nesting species.

The overall aim of this study was to conduct the first in-water assessment of relative abundance, demographics, distribution, and behaviour of sea turtles on reefs along the east coast of South Africa. Several objectives were described and compared among species in the iSimangaliso and Aliwal Shoal MPAs using a variety of techniques and stakeholder groups (research dives, voluntourism and citizen scientists).

4.2 Insights from the hypotheses

Relative abundance

It was proposed that the relative abundance of sea turtles on reefs will be proportional to the nesting female abundance in the SWIO (Cm > Ei > Cc > Dc > Lo) given that locally stranded and bycaught juvenile green turtles originate from Îles Éparses and Ascension Island, and juvenile hawksbills originate from Seychelles (Hickman 2017). Whilst this hypothesis was largely supported, SPUE results in Chapter 2 (section 2.4.1) indicated that loggerheads were more prevalent than hawksbills in iSimangaliso, likely due to its proximity to this rookery. These results suggest that reefs along the east coast of South Africa host sea turtle aggregations with some of the highest SPUE results recorded for the region (e.g., Fulanda *et al.* 2007; von Brandis 2010; Williams *et al.* 2017). These findings highlight how local variations in habitat and rookery size and distance from foraging grounds influence their species composition and abundance, but may particularly highlight the successful long-term conservation afforded to sea turtles in South African waters which face significantly fewer threats of bycatch and illegal trade than those in other SWIO countries (Zanre 2005; Bourjea *et al.* 2008; Williams *et al.* 2019).

Size classes

Size classes of non-nesting species (green turtles and hawksbills) were expected to be dominated by juveniles, and size classes of nesting species (loggerheads and leatherbacks) were expected to be dominated by adults, similar to other SWIO foraging grounds (e.g., Fulanda *et al.* 2007; Ballorain *et al.* 2010; von Brandis 2010; Williams *et al.* 2017; Stokes *et al.* 2023). This hypothesis was supported (Chapter 2, section 2.4.2), confirming that local neritic habitats are a regionally important developmental area for immature green turtles from SWIO Island rookeries (e.g., Îles Éparses) and Ascension Island, as well as immature hawksbills from Seychelles Islands (Hickman 2017). Furthermore, these habitats also host adult-sized green turtles (thus mixed green turtle aggregations) likely also from regional rookeries (Bourjea *et al.* 2007b), and subadult and adult-sized loggerheads from the North West Atlantic Ocean, Mediterranean and South African rookeries (Hickman 2017).

Sex ratios

The hypothesis that adult sex ratios will be balanced (1 male: 1 female) for all species was not supported. Even though they were not significantly different from 1:1, adult sex ratios were slightly female-biased (Chapter 2, section 2.4.2) and consistent with other regions (Hays *et al.* 2014). Findings were also consistent with female-biased hatchling sex ratios of source populations based on sand temperatures (e.g., Ascension Island, Godley *et al.* 2002).

Residency

Juvenile sea turtles were expected to have longer residence periods than adults given that adults may depart for seasonal breeding migrations elsewhere. This was supported for green and hawksbill turtles, and evidence suggested that adult-sized female green turtles (who likely nest at SWIO rookeries; Bourjea *et al.* 2007b) may depart for seasonal breeding migrations but display strong site fidelity to local reefs, and that adult-sized female hawksbills may use these coastal waters as a migratory pathway (Chapter 2, section 2.4.3). No juvenile loggerheads or leatherbacks were present but adult-sized loggerheads displayed high levels of residency and strong site fidelity (Chapter 2, section 2.4.3). These findings further emphasize the regional importance of neritic habitats on the South African east coast.

Spatiotemporal relative abundance and behaviour

It was hypothesised that there will be seasonal changes in the relative abundance of transient nesting species/individuals (loggerheads and leatherbacks) but not resident foraging species/individuals (green turtles, hawksbills and non-breeding loggerheads), and that behaviour will be reflective of life history stage i.e., resident species/individuals will be observed foraging year-round (in both MPAs) but transient adults will be observed courting and mating in iSimangaliso at the start of the nesting season. The findings (Chapter 3, section 3.4.1 and 3.4.2) highlight the use of local neritic habitats as both year-round foraging grounds for green turtles (juvenile to adult-sized), immature hawksbills, and subadult and adult-sized loggerheads stocked by regional and global rookeries (Hickman 2017) as well as seasonal courtship and mating grounds for transient adult loggerheads and leatherbacks on breeding migrations.

Variability in sea turtle sightings

It was proposed that sea turtle sightings will be affected by a combination of temporal, environmental, and oceanographic variables. This hypothesis was supported, as shown in Chapter 3 (section 3.4.3), however, the factors driving fine-scale sea turtle abundance and distribution remain complex and multifaceted and require further research to unravel.

Human disturbance

The hypothesis that sea turtles on frequently dived reefs will be more prone to human disturbance and thus have smaller flight initiation distances and a higher prevalence of boat strike injuries than those on less frequented reefs was supported, as shown in Chapter 3 (section 3.4.4). These findings are relevant for future monitoring efforts to guide recreational divers on ways to minimise human disturbance and injury risk to sea turtles and thus increase the quality of citizen science data.

4.3 Citizen science

This study demonstrated the potential of citizen science to gather valuable data useful for specific investigations on sea turtle distribution and behaviour. Requests for public data submission made via talks at dive centres and aquaria (± 390 attendees to date) and word of mouth in coastal communities received a positive response (n = 391 sea turtle sightings by 62 members of the public), resulting in a modest yet useful citizen science initiative (Appendix 2.2). During this study, a dedicated website centred around sea turtles in southern Africa (www.SAturtles.org)[1] was established which will now also serve as a platform for citizen science data submission into a growing database of sea turtle sightings (currently n = 1635 records) and individuals (currently n = 250). If driven and maintained, the still growing citizen science initiative may be essential to vastly and rapidly improve the current state of sea turtle knowledge in South Africa and to monitor future trends on foraging grounds. It may also contribute to a greater appreciation of sea turtles and the marine ecosystems they inhabit by members of the public. It is recommended to use the website and related social media platforms, along with public presentations and word of mouth, to 1) actively encourage the public to participate as citizen scientists, 2) express gratitude for their involvement, and 3) share interesting findings stemming from their contributions. These steps were essential to engage local groups of avid recreational divers and fishermen who regularly provided high-quality sea turtle sighting reports throughout the two-year study period. They were equally indispensable to the growth of one of the greatest citizen science initiatives in the country, the Oceanographic Research Institute's Cooperative Fish Tagging Project (Potts *et al.* 2021), which continues to be highly successful today.

4.4 Concluding remarks

This study revealed novel insights into sea turtles on the east coast of South Africa, contributing to a more comprehensive understanding of their cryptic in-water lives that may have significant implications for management and conservation plans[2] that work towards effectively safeguarding these ecologically important, conservation-dependent species. The findings and in-water database serve as the baseline assessment for future work and the foundation for a new long-term in-water monitoring programme using research surveys supplemented by ongoing voluntourism and citizen science contributions, marking the start of South Africa's shift to a more even distribution of research effort on nesting beaches and foraging grounds. The relevance of this work may resonate beyond South African waters to any scientists whose research and conservation efforts involve

---

[1] This website was created to share the findings of decades of successful sea turtle research and conservation efforts led by Dr. George Hughes (Ezemvelo KZN Wildlife, formerly Natal Parks Board) and Prof. Ronel Nel (Nelson Mandela University). It also serves as an educational resource for the public, offering information on sea turtles and opportunities for personal engagement (via aquaria visits, nesting beach tours, or recreational diving).

[2] These data are already included in the National Coastal Biodiversity Plan (L. Harris, in prep.) which informs the biodiversity sector's input to the national marine spatial planning process (Harris *et al*. 2023).

rookeries which stock these local neritic habitats (green turtles: Îles Éparses and Ascension Island; hawksbills: Seychelles Islands; loggerheads: North West Atlantic Ocean, Mediterranean and South Africa; Hickman 2017). This study highlights the importance of research at both nesting beaches and foraging habitats for a comprehensive understanding of sea turtles throughout their life cycle.

4.5 Recommendations for further research

It is recommended to build on findings from genetic analyses (mitochondrial DNA) of previous work at regional neritic foraging grounds (e.g., Bourjea *et al.* 2007b; Hickman 2017) to determine the natal origin of sea turtles (Bowen and Karl 2007). This will provide significant insights into juvenile dispersal and migration from rookeries and thus contribute to a better understanding of regional connectivity of sea turtle populations.

It is also recommended to continue expanding the recently established photo-ID database with new individuals and resightings of existing individuals coupled with morphometric data along the entire South African coastline and neighbouring countries. This expansion will not only allow for more robust in-water estimates of sea turtle abundance and density to be made but will also open a myriad of avenues for further detailed investigations. For example, investigation into species-specific growth rates and foraging ecology could provide insight into drivers of varying growth rates among foraging grounds, and perhaps explain different remigration intervals of the same species in different breeding populations. This should be coupled with data obtained from some individuals fitted with satellite or acoustic tags to understand size- and species-specific movement patterns, home ranges and possible migrations (e.g., Matley *et al.* 2020). Long-term data collection should also be used to construct statistical models to determine population dynamics (e.g., immigration, emigration, re-immigration, mortality) of sea turtles in local neritic habitats (e.g., Williams *et al.* 2017).

Given that direct observations of foraging and intraspecific competition among sea turtles in this study provided insight into their diverse foraging strategies and value of certain resources, sites and services, it is recommended to use this method to gain further detailed insight into the species-specific ecological roles of sea turtles in local neritic habitats. This has been addressed as a high research priority globally (Eckert *et al.* 1999; Bjorndal and Bolten 2003; Hamann *et al.* 2010). Direct observations should be used to quantify the amount of food consumed per species (per size class) daily, availability of food sources, effects of species-specific foraging on benthic biomass and species composition, and competition (e.g., von Brandis 2010). This information could be used to quantify the ecological roles of sea turtles in maintaining biodiversity (controlling prey populations) and influencing habitat structure in local neritic habitats, which is necessary to understand how they impact ecosystem function and to determine if they are keystone species in local marine ecosystems (e.g., Bjorndal and Jackson 2002; von Brandis 2010). This information is essential to set realistic and effective conservation targets based on population abundances at which sea turtles can fulfill their ecological roles (Bjorndal and Bolten 2003).

4.6 References

Ballorain, K., Ciccione, S., Bourjea, J., Grizel, H., Enstipp, M. and Georges, J.-Y. (2010). Habitat use of a multispecific seagrass meadow by green turtles *Chelonia mydas* at Mayotte Island. *Marine Biology,* 157(12), pp. 2581-2590

Bjorndal, K. A. and Bolten, A. B. (2000). Proceedings of a Workshop on Assessing Abundance and Trends for In-Water Sea Turtle Populations, held at the Archie Carr Center for Sea Turtle Research University of Florida, Gainesville, Florida, 24-26 March 2000.

Bjorndal, K. A. and Bolten, A. B. (2003). From ghosts to key species: restoring sea turtle populations to fulfill their ecological roles. *Marine Turtle Newsletter,* 100(100), pp. 16-21

Bjorndal, K. A. and Jackson, J. (2002). 10 roles of sea turtles in marine ecosystems: reconstructing the past. *The biology of sea turtles,* 2, pp. 259

Bourjea, J., Lapegue, S., Gagnevin, L., Broderick, D., Mortimer, J. A., Ciccione, S., Roos, D., Taquet, C. and Grizel, H. (2007b). Phylogeography of the green turtle, *Chelonia mydas*, in the South West Indian Ocean. *Mol Ecol,* 16(1), pp. 175-86

Bourjea, J., Nel, R., Jiddawi, N., Koonjul, M. and Bianchi, G. (2008). Sea turtle bycatch in the West Indian Ocean: review, recommendations and research priorities. *Western Indian Ocean Journal of Marine Science,* 7(2), pp. 137-150

Bowen, B. W. and Karl, S. (2007). Population genetics and phylogeography of sea turtles. *Molecular ecology,* 16(23), pp. 4886-4907

Eckert, K., Bjorndal, K., Abreu-Grobois, F. and Donnelly, M. (1999). Priorities for research in foraging habitats. *Research and management techniques for the conservation of sea turtles,* 4, pp. 12-18

Estes, J. A., Duggins, D. O. and Rathbun, G. B. (1989). The ecology of extinctions in kelp forest communities. *Conservation Biology,* 3(3), pp. 252-264

Fulanda, B., Ohtomi, J., Mueni, E., Nzuki, S., Muasa, J., Muthama, C. and Hossain, Y. (2007). A preliminary assessment of the green sea turtle *Chelonia mydas* population and its foraging grounds in Kilifi Creek, Kenya. *South Pacific Studies,* 28, pp. 31-41

Godley, B., Broderick, A., Glen, F. and Hays, G. (2002). Temperature-dependent sex determination of Ascension Island green turtles. *Marine Ecology Progress Series,* 226, pp. 115-124

Hamann, M., Godfrey, M. H., Seminoff, J. A., Arthur, K., Barata, P. C. R., Bjorndal, K. A., Bolten, A. B., Broderick, A. C., Campbell, L. M., Carreras, C., Casale, P., Chaloupka, M., Chan, S. K. F., Coyne, M. S., Crowder, L. B., Diez, C. E., Dutton, P. H., Epperly, S. P., FitzSimmons, N. N., Formia, A., Girondot, M., Hays, G. C., Cheng, I. S., Kaska, Y., Lewison, R., Mortimer, J. A., Nichols, W. J., Reina, R. D., Shanker, K., Spotila, J. R., Tomás, J., Wallace, B. P., Work, T. M., Zbinden, J. and Godley, B. J. (2010). Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endangered Species Research,* 11(3), pp. 245-269

Harris, L. R., Van Niekerk, L., Holness, S. D., Sink, K. J., Skowno, A. L., Dayaram, A., Van Deventer, H., Job, N., Lamberth, S. J., Adams, J. B., Raw, J. L., Riddin, T., MacKay, F. and Perschke, M. J. (2023). Spatial biodiversity planning in the coastal zone: guidelines for cross-realm planning and integration, and a CBA Map for the seashore and estuaries. Technical Report for the MeerWissen Project, CoastWise. Nelson Mandela University, Gqeberha.

Hays, G. C., Mazaris, A. D. and Schofield, G. (2014). Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science,* 1, pp. 43

Hickman, S. (2017) The genetic diversity and home populations of immature loggerhead (*Caretta caretta*), green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles frequenting South African waters. Honours thesis, Nelson Mandela University

Jackson, J. B. (1997). Reefs since columbus. *Coral Reefs,* 16, pp. S23-S32

Matley, J., Jossart, J., Johansen, L. and Jobsis, P. (2020). Environmental drivers of diving behavior and space-use of juvenile endangered Caribbean hawksbill sea turtles identified using acoustic telemetry. *Marine Ecology Progress Series,* 652, pp. 157-171

McClenachan, L., Jackson, J. B. and Newman, M. J. (2006). Conservation implications of historic sea turtle nesting beach loss. *Frontiers in Ecology and the Environment,* 4(6), pp. 290-296

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres Jr, F. (1998). Fishing down marine food webs. *Science,* 279(5352), pp. 860-863

Potts, W., Mann-Lang, J., Mann, B., Griffiths, C., Attwood, C., de Blocq, A., Elwen, S., Nel, R., Sink, K. and Thornycroft, R. (2021). South African marine citizen science–benefits, challenges and future directions. *African Journal of Marine Science,* 43(3), pp. 353-366

Stokes, H. J., Mortimer, J. A., Laloë, J. O., Hays, G. C. and Esteban, N. (2023). Synergistic use of UAV surveys, satellite tracking data, and mark-recapture to estimate abundance of elusive species. *Ecosphere,* 14(3)

von Brandis, R. G. (2010) The Ecology of Foraging Hawksbill Turtles (*Eretmochelys imbricata*) at D'Arros Island and St. Joseph Atoll in the Seychelles, Western Indian Ocean. Doctoral thesis, Tshwane University of Technology

Williams, J. L., Pierce, S. J., Hamann, M. and Fuentes, M. M. (2019). Using expert opinion to identify and determine the relative impact of threats to sea turtles in Mozambique. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 29(11), pp. 1936-1948

Williams, J. L., Pierce, S. J., Rohner, C. A., Fuentes, M. M. and Hamann, M. (2017). Spatial distribution and residency of green and loggerhead sea turtles using coastal reef habitats in southern Mozambique. *Frontiers in Marine Science,* 3, pp. 288

Zanre, R. (2005). Report on Watamu Turtle Watch's sea turtle bycatch release programme, Watamu, Kenya. Local Ocean Conservation, Watamu, Kenya.