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Recreational Diving and Hawksbill Sea Turtles (Eretmochelys imbricata) in a Marine Protected Area

Christian Hayes

LOMA LINDA UNIVERSITY
School of Medicine
in conjunction with the
Faculty of Graduate Studies

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Recreational Diving and Hawksbill Sea Turtles (*Eretmochelys imbricata*) in a Marine Protected Area

by

Christian Hayes

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A Thesis submitted in partial satisfaction of
the requirements for the degree
Master of Science in Biology

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Each person whose signature appears below certifies that this thesis in his/her opinion is adequate, in scope and quality, as a thesis for the degree Master of Science.

_____, Chairperson

Stephen G. Dunbar, Associate Professor of Biology

_____

William K. Hayes, Professor of Biology

_____

Ernest Schwab, Associate Professor of Allied Health Studies, School of Allied Health Professions

_____

Kenneth R. Wright, Professor of Anatomy

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DEDICATION

I dedicate this work to my parents, Paul and Tamara Hayes, who have supported me and sacrificed so much to help me pursue both my education and God's calling on my life.

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ABBREVIATIONS

CCL	Curved Carapace Length
I^3S	Interactive Individual Identification System
MPA	Marine Protected Area
RMP	Roatán Marine Park
SSF	Small Scale Fisheries
TDR	Time Depth Recorder

ABSTRACT OF THE THESIS

Recreational Diving and Hawksbill Sea Turtles (*Eretmochelys imbricata*) in a Marine Protected Area

by

Christian Hayes

Master of Science, Graduate Program in Biology
Loma Linda University, September 2015
Dr. Stephen G. Dunbar, Chairperson

Recreational diving is a form of ecotourism that is traditionally viewed as an ecologically sustainable activity prompting increased awareness for the marine environment. Recent studies, however, indicate that recreational diving may cause unintended behavioral changes in marine macrofauna. Few studies, however, have specifically investigated the effects of recreational diving on sea turtles. I conducted in-water observations and turtle sightings surveys from June 9 to August 21, 2014, in Roatán, Honduras, to determine if differences in dive site use and diver behavior alter the behavior of critically endangered hawksbill sea turtles (*Eretmochelys imbricata*) in a marine protected area (MPA). I found that hawksbill sightings distributions within the RMP did not vary with recreational diving pressure during an 82-day study period suggesting that turtle abundance within the RMP is independent of diving pressure. We found that turtles decreased the amount of time they spent eating, investigating, and breathing when approached by divers (1-4). Additionally, sightings studies indicated that divers in the RMP require additional training to accurately identify sea turtles species and record sightings data. Based on my findings, I made several recommendations to the Roatán Marine Park including the implementation of long-term sea turtle sightings and

photo-identification surveys in the RMP, and suggested additional studies for other MPAs and researchers. Specifically I recommended that additional studies be conducted to compare recreational diver impacts on hawksbill sea turtle behavior within and outside MPAs, and measure seasonal variation in turtle sightings, dive site use, and foraging habitat in MPAs. As recreational diving continues to increase worldwide, it is imperative that management officials and researchers understand the impacts of recreational diving on sea turtle behavior, physiology, and population dynamics, in order to protect these important marine macrofauna. The current study provides the first data on the impacts of recreational diving on sea turtles. The results of this study will enable local management officials to implement effective regulations for diver and sea turtle interactions. Additional research building from the current study, should be conducted both in Honduras and globally, to further elucidate the impacts of recreational diving on different sea turtle species.

CHAPTER ONE

INTRODUCTION

Goal, Objectives and Specific Aims

Goal

The goal of my research was to understand how intentional human interactions with wild animals in their natural ecosystems impact animal behavior.

Objectives

Given the critically endangered status of the hawksbill sea turtle (*Eretmochelys imbricata*) (Meylan and Donnelly 1999) and the increasing numbers of divers interacting with sea turtles each year, understanding the effects of diving on turtle behavior is essential for conservation work to be effective. In light of this increasing need, I undertook a research project to quantify the effects of human diving on juvenile hawksbill behavior within the Roatán Marine Park (RMP), Honduras. I combined in-water observations with turtle sightings reports to delineate potential impacts of SCUBA diving on hawksbill behavior within the RMP. The results of my research have helped create a working baseline for analyzing the effects of human diving on hawksbill behavior worldwide.

First Objective

My first objective was to quantify turtle sightings rates and dive site use for multiple sites in the RMP and determine if dive site use impacts hawksbill sighting rate.

Specific Aim 1

My first specific aim was to determine if hawksbill sightings rates are affected by anthropogenic stress from recreational diving. Since increased diving corresponds to more divers searching for turtles each dive, I hypothesized that:

- H_1, hawksbill sightings rates would be higher for sites that experience heavy diving pressure and lower for sites with lower diving pressure.

Second Objective

My second objective was to measure sea turtle behavior during interactions with recreational divers and quantify the effects of diver approach and dive site use on hawksbill behavior.

Specific Aim 2

My second specific aim was to determine if turtles in heavily used dive sites exhibited different behaviors than turtles in dive sites that are less heavily used. Since foraging requires turtles to spend less time scanning for potential predators and more time scanning for food, I hypothesized that:

- H_2, turtles would spend less time investigating and eating, and more time swimming in heavily used dive sites than they would in dive sites that are less heavily used.

Specific Aim 3

My third specific aim was to determine if diver approach affects the amount of time hawksbills spend in each behavior and the number of behavior bouts turtles engage in. Since I expected turtles within the RMP to be accustomed to divers and interested in diver activity (Hayes, personal observation), I hypothesized that:

- H_3, turtles would spend less time investigating, eating, and breathing, and more time swimming when divers (1-4) approached turtles than when divers were at baseline position.

Since I expected turtles to switch between behaviors more rapidly when divers approached (as per Meadows 2004), I hypothesized that:

- H_4, turtles would engage in more investigating, eating, and swimming bouts when divers (1-4) approached turtles than when divers were at baseline position.

Significance Statement

My study has expanded our limited knowledge of hawksbill ecology, tested hypotheses regarding the effects of SCUBA diving and dive site use on hawksbill behavior, and increased local and global awareness of the impacts of humans on sea turtles. As part of ongoing work by the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR Inc., http://www.turtleprotector.org), my study will enable RMP managers, conservation agencies, and government officials to design more effective management strategies for areas accessible to SCUBA diving, and implement better protocols for turtle-diver interactions in marine protected areas (MPAs).

State of Hawksbill Sea Turtles

The hawksbill sea turtle (*Eretmochelys imbricata*) is a circumtropically distributed, migratory, marine species in severe decline throughout the world's oceans (McClenachan et al. 2006). Hawksbills were first listed as critically endangered in 1996 following several decades of decline due to widespread hunting (Mortimer and Donnelly 2008), and global populations have continued to decline substantially from incidental catch, habitat loss, water pollution, egg poaching, and the illegal tortoiseshell trade (McClenachan et al. 2006, for alternative perspective see Campbell 2012).

Caribbean hawksbill populations have declined 80–95% since pre-exploitation, with some regional population estimates of nesting females at 30,000 individuals, < 1% of estimated historic levels (Campbell and Didier 2008). Total population estimates, however, are difficult to make and are often imprecise due to a lack of access to males, juveniles, and non-reproductive females. Thus the most common method for estimating hawksbill population numbers is to compile the number of females that nest annually at nesting beaches (Meylan and Donnelly 1999). Meylan (1999a) conducted a comprehensive review of the status of hawksbills in the Caribbean and estimated that approximately 5,000 adult females nest annually in 35 geopolitical units of the Caribbean. At the regional level, she found that most countries in the Caribbean host female nesting populations of fewer than 100 individuals (Meylan 1999a). Population trends for hawksbills in the Caribbean are predominately negative, with populations in 22 of 26 geopolitical areas reported as declining or depleted (Meylan 1999a). Of the four stable populations in the Caribbean, only a few areas in two countries show positive

trends (Mona Island, Puerto Rico; Campeche, Yucatán, and Quintana Roo, Mexico) because of improved management and monitoring techniques (Meylan 1999a)

Hawksbill Ecology

If we seek to effectively conserve hawksbill populations in the Caribbean, it is of critical importance that we first understand hawksbill life history and ecology. Hawksbills, as migratory macrofauna with complex life cycles, inhabit variable and often geographically distant marine ecosystems (Bolten 2003). Each ecosystem presents various threats to hawksbills, which can only be addressed via conservation techniques specifically targeted at hawksbills in particular stages of their life history. Thus, to effectively apply conservation principles to a specific population of Caribbean hawksbills, we must first develop a working understanding of hawksbill life history, foraging ecology, migratory patterns, and role in reef ecosystems.

Life History

Hawksbills, like other sea turtle species, are long lived and utilize a variety of habitats during various life stages (Bolten 2003). The first stage of the hawksbill life cycle begins in the nest. Approximately 2 months after a female lays her clutch, the hatchlings will emerge from the nest, crawl to the water, and swim out to sea to reach the comparative safety of the neritic zone (water depth < 200 m) (Musick et al. 1997). Unlike loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), and green (*Chelonia mydas*) hatchlings which enter into a 24–48 hour swimming frenzy stage after hatching (Wyneken and Salmon 1992), hawksbill hatchlings do not exhibit a prolonged period of frenzied activity (Chung et al. 2009a, b).

Little is known about the early stages of the hawksbill life cycle after hatching, yet limited data from Carr (1987), Parker (1995), and Musick et al. (1997) suggest that hatchlings in the neritic zone pass through a transitional growth stage and then venture out into the oceanic zone (water depth > 200 m). Additional molecular work from Blumenthal et al. (2009a) indicates that juveniles from some rookeries become dispersed by ocean currents during the oceanic phase of their life cycle, and end up in different foraging habitats when they return to the neritic zone. After an unknown period of growth in the oceanic zone, in which they grow up to 20–35 cm curved carapace length (CCL) (Meylan 1988), hawksbills return to the neritic zone and establish local foraging home ranges in tropical latitudes where they subsist until reaching sexual maturity (Bjorndal et al. 1997, Musick et al. 1997, van Dam and Diez 1998b, Berube et al. 2012). The amount of time hawksbills spend in the oceanic zone is currently unknown, yet based on somatic growth models of juvenile loggerheads, the oceanic period is estimated at less than 6.5 years (Bjorndal et al. 2000, Bolten 2003).

During the juvenile stage, hawksbills will subsist in one or more foraging ranges until they reach sexual maturity at approximately 20–40 years (Boulon 1994, Mortimer 1998). Limpus (1992) studied juvenile hawksbills in the Great Barrier Reef, and found that juveniles > 35 cm (CCL) maintained high fidelity to foraging areas, with some individuals being associated with the same site for over a decade. Studies of juveniles in Puerto Rico (van Dam and Diez 1998b) and Japan (Okuyama et al. 2005) indicate that hawksbill home range size varies significantly in different populations (Puerto Rico, 0.07–0.14 km^2; Japan 1 km^2). Berube et al. (2012) studied the home range of juvenile hawksbills in Roatán, Honduras and found that turtles (n = 6) tended to occupy an area of

less than 1 km^2. Based on their results, Berube et al. (2012) concluded that small home range sizes in Honduras may be the result of high-quality prey items and habitat.

Boulon (1989) studied juvenile hawksbills in the United States Virgin Islands, and found that some individuals, rather than associating with a singular foraging site, migrated to multiple disparate foraging grounds throughout their juvenile years. Additional studies from Bjorndal et al. (1985), and Marcovaldi and Filippini (1991) documented long-distance juvenile migrations from Great Inagua, Bahamas to the Turks and Caicos Islands, and from Brazil to Dakar, Senegal, respectively. Why juveniles undertake long developmental migrations remains unknown and warrants additional study.

After reaching sexual maturity, adult female hawksbills will migrate back to their original nesting beaches, breed with males offshore, and lay their eggs. Studies of hawksbill laying frequency in the Caribbean indicates that female laying frequency and clutch size varies with location and population. Work in the Seychelles by Diamond (1976) found that, on average, adult hawksbills (n = 30) laid four clutches during a season, with an average clutch size of 182 eggs. Recent studies from the West Indies (Richardson et al. 1999, Kamel and Delcroix 2009) found similar results, with the average female laying 3–5 clutches in a season with an average clutch size of 155–159 eggs. Only limited data exits for hawksbill nests in Honduras, but work from Damazo (2014) on the island of Utila found that females (n = 5) laid 1.4 clutches a season with 126–164 eggs in a clutch. After laying, females will return to the water and swim to specific foraging areas (Plotkin 2002).

Hawksbills, similar to other sea turtle species, have complex life cycles with multiple developmental stages and migratory periods. If hawksbill conservation efforts are to be effective, environmental agencies and governments must design management plans that take into account the different stages of the hawksbill life cycle.

Foraging Ecology

Typical foraging ecosystems for both juvenile and adult hawksbills include shallow coral reefs (< 20 m), hard bottom surfaces, seagrass flats, cliff wall habitats, (Musick et al. 1997, Dunbar et al. 2008). Limpus (1992), Grant et al. (1997), and van Dam and Diez (1998a, b) studied sea turtles in Australia, American Samoa, and Puerto Rico, respectively, and found that adults and juveniles utilize the same foraging grounds (for an alternative view see Meylan 2011), but it is unknown if juveniles and adults subsist on the same prey items in these foraging environments.

Traditionally, hawksbills are considered selective feeders that subsist primarily on sponges and only minimally on other benthic organisms, such as octocorals, zoanthids, anemones, and algae (Meylan 1988, Anderes and Uchida 1994, Bjorndal et al. 1997, Dunbar et al. 2008, Berube et al. 2012). Recent studies, however, indicate that feeding strategies for hawksbills can vary substantially in different regions, potentially as a means of countering environmental change and loss of primary prey (Gaos et al. 2012a, Bell 2013, Baumbach et al. 2014). Bell (2013) examined the prey selection of hawksbills in the Northern Great Barrier Reef and found that algae, rather than sponge, made up the majority (72.7%) of the buccal and lavage samples (n = 538). From these results, Bell (2013) concluded that hawksbills that employ algivory as a foraging strategy may be better able to withstand regional changes in sponge and coral abundance due to climate

change than other hawksbills populations. Similarly, Baumbach et al. (2014) found that 40% of juvenile hawksbills (n = 35) in the Roatán Marine Park, Honduras subsisted heavily on several algae species prevalent throughout the region. Baumbach et al. (2014) suggested that hawksbills may be shifting feeding strategies in the region to account for an overgrowth of algal foraging items. Gaos et al. (2012a) studied hawksbill habitat use in the Eastern Pacific and found that adult hawksbills foraged primarily in mangrove estuaries, a radically novel habitat for hawksbills. Gaos et al. (2012a) concluded that unique environmental pressures in the Eastern Pacific (Saba et al. 2008) may alter sea turtle life history and foraging strategies.

It is well established that hawksbills are selective feeders that consume specific species of sponges, corals, and algae. Still, the relationship between hawksbill foraging strategies and prey abundance is poorly understood. Whereas some researchers have concluded that hawksbill diet choice depends on the combination of prey selectivity and regional abundance (Leon and Bjorndal 2002, Berube et al. 2012), others have found that hawksbills exhibit strong positive selectivity for particular food items, even when spatial availability for those food items is low (Rincon-Diaz et al. 2011b, Baumbach et al. 2014).

Our understanding of hawksbill foraging ecology is limited and mandates that additional studies be conducted to determine how hawksbills respond to foraging pressures, habitat changes, and anthropogenic threats.

Migration

As adults, hawksbills undertake seasonal migrations traveling hundreds or thousands of kilometers among various foraging habitats and their nesting beaches (Miller et al. 1998, Meylan 1999b, Plotkin 2002). Bjorndal et al. (1985) tagged adult

female hawksbills (n = 6) in Tortuguero, Costa Rica and found that turtles migrated to several beaches in Nicaragua (200–385 km), Panama (380 km), and Honduras (541–850 km). Similarly, Damazo (2014) tagged adult females (n = 2) in Utila, Honduras, and tracked their migrations to the Drowned Cayes, Belize, and the Yucatan Peninsula, Mexico. Additional work from Márquez and del Carmen Farías (2000) in the Yucatan Peninsula, Mexico, Miller et al. (1998) in Northeast Australia, and Hillis-Star (1994) in the US Virgin Islands indicate that female hawksbills will also undertake trans-oceanic migrations (1622–2425 km) to reach local foraging grounds.

Over the last 20 years scientists have studied the navigational abilities of turtles and have discovered several potential navigational mechanisms, including the use of bathymetry (Morreale et al. 1994), currents (Morreale et al. 1996), biological compasses (Luschi et al. 1998), windborne information (Luschi et al. 2001), waterborne chemicals (Papi et al. 2000), and magnetic field detection (Lohmann et al. 2001). The exact mechanisms of hawksbill migration, however, are poorly understood.

Little is known about hawksbill reproductive migrations from local foraging grounds to natal beaches, due to the difficulty of tagging females in foraging environments, yet limited tagging data for females (Parmenter 1983) and satellite telemetry for males (van Dam et al. 2008) indicates that hawksbills will migrate hundreds or thousands of miles every 2–3 years from foraging grounds to nesting beaches where they mate offshore. After an approximately 30 day gestation period the females will begin nesting onshore (Owens 1980). During internesting periods (12–15 days between clutches), females remain nearshore (Starbird et al. 1999) and, after laying their final clutch, they migrate to foraging areas where they remain in residency until the next

reproductive period (Broderick et al. 2007). After mating, males will remain near breeding areas for an unknown period of time (6 days to 11 months for 8 hawksbills in Mona Island) and then migrate to their foraging grounds which can be geographically close (< 200 km) or distant (> 200 km) (van Dam et al. 2008).

Based on the post-nesting movement classification system by Godley et al. (2008), Caribbean hawksbills exhibit an A1 migratory pattern, characterized by departure from nesting sites, active swimming through both oceanic and neritic zones, and residency in specific foraging zones. Cuevas et al. (2008) conducted satellite tagging studies in the Yucatan Peninsula, Mexico, and found that turtles nesting on the same beach will migrate to separate foraging grounds following laying. Flipper tagging studies from Bjorndal et al. (1985) in Costa Rica, Horrocks et al. (2001) in Barbados, and Parker et al. (2009) in Hawaii found that female post-nesting migrations occur over both short (25–200 km) and long-range scales (200+ km) for different turtles nesting at the same beach. Hawkes et al. (2012) tracked female hawksbills (n = 10) after nesting in the Dominican Republic and found a similar dichotomy in migration patterns, with some individuals (n = 2) remaining in Dominican Republic waters, and others (n = 5) migrating to foraging grounds in Honduras and Nicaragua. Little is known about hawksbill post-nesting migration patterns in Honduras, but preliminary satellite tagging work from Damazo and Dunbar (2013) found that adult females in Utila, Honduras, will migrate to both close (181 km) and distant foraging grounds (403 km). The reasons why some individuals choose to migrate longer distances than others remains unknown (Plotkin 2002).

Role in Reef Ecosystems

Due to their selective diet and high mobility, hawksbills provide several key environmental services for coral reef ecosystems. Primary ecological roles include preventing coral overrun from sponges and algae, facilitating fish foraging, and transporting nutrients across and within ecosystems.

Hill (1998) studied the controlling effect of various spongivores on coral reef cover dynamics and found that excluding key spongivores (i.e. hawksbills and angelfish) caused a significant decrease in total coral cover and increase in the sponge *Chondrilla nucula*. He concluded that spongivores were critical components in maintaining species diversity on Caribbean reefs and preventing *C. nucula* from overgrowing important coral species (Hill 1998). Leon and Bjorndal (2002) examined the prey selection of hawksbills in the Dominican Republic and found a similar controlling effect on *C. nucula* and the corallimorpharian, *Ricordea florida*. More recent work from Pawlik et al. (2013) examined the bottom-up and top-down factors impacting sponge community composition, and found that sponge communities were primarily dependent on the predatory effects of spongivores, including hawksbills. From their results, Pawlik et al. (2013) concluded that the removal of sponge predators from coral ecosystems can negatively impact sponge communities by encouraging the growth of faster-growing species that compete with threatened reef-building corals. Additionally, because hawksbills forage in both shallow and deep water (80–120 m) (Blumenthal et al. 2009c), they may act as critical sponge predators for a wide variety of benthic habitats.

In addition to promoting biodiversity by grazing on sponge species, hawksbills also facilitate sponge foraging for multiple fish species. Hawksbills in the Cayman Islands will directly facilitate angelfish (Pomacanthidae) foraging by biting off the hard

outer layer of sponges and allowing the fish to feed on the softer interior of the sponge (Blumenthal et al. 2009b). Hayes (personal observation) observed similar interactions between hawksbills and angelfish in Roatán, Honduras.

Finally, hawksbills act as important nutrient transport systems, moving nutrients from local foraging grounds, to waters off nesting beaches, and into beach ecosystems (Michael 2013). Bouchard and Bjorndal (2000) quantified the amount of energy and nutrients released into a beach environment from nesting loggerheads. Each nest in their experiment produced 688 g of organic matter, 18,724 kJ of energy, 151 g of lipids, 72 g of nitrogen, and 6.5 g of phosphorous (Bouchard and Bjorndal 2000). Of these total values only 27% of the energy, 34% of the lipids, 29% of the nitrogen, and 39% of the phosphorus returned to the marine environment as hatchlings (Bouchard and Bjorndal 2000). The nutrients and energy that remain in the soil after the hatchlings have departed (i.e. dead hatchlings and undeveloped embryos) serve as important inputs for terrestrial ecosystem growth and may help maintain stable beach conditions for future nesting (Bouchard and Bjorndal 2000)

Human Impacts on Hawksbills

For hawksbill conservation efforts to be effective, scientists must understand the various human threats that adversely impact hawksbill survival. A full description of human activities impacting hawksbill sea turtles is beyond the scope of this study. Rather, I here provide a general review of the major threats facing hawksbills and the potential conservation measures necessary to address each of these threats. I divide hawksbill threats into two primary categories—indirect and direct—based on the wildlife impact classification system from Sorice et al. (2003).

Indirect Threats

Hawksbills are threatened indirectly by a number of threats including, habitat alteration at nesting beaches and foraging habitats, and oil and plastic pollution. I have defined indirect threats (as per Sorice et al. 2003) as impacts resulting from disturbance of species' habitat. Indirect threats may, or may not lead to direct sea turtle mortality.

Habitat Alteration and Loss

I have divided the threat of habitat alteration and loss into two primary sections, nesting beaches and foraging habitat, based on the habitat each threat affects.

Nesting Beaches

One of the most vulnerable periods of the hawksbill life cycle is when turtles return to their natal beach to reproduce. In addition to encountering potential predators and poaching by humans, hawksbills are threatened by substantial habitat alteration of their nesting beaches. Beach habitat alteration occurs in many forms and at various levels, mandating specific conservation techniques to maintain this critical habitat. I will briefly outline each of the major threats to hawksbill nesting beaches and some of the potential conservation solutions.

Beach armoring and nourishment are two forms of active human alteration that can destroy nesting beach habitat. Whereas beach armoring is the installation of various hardened structures, including sea walls, rock revetments, and sand bags to protect dune property, beach nourishment is the intentional dumping or pumping of sand onto an eroded beach in order to maintain "pristine beach" conditions (Lutcavage et al. 1997).

Armoring can alter the natural flow of water to a beach and over time can lead to the disappearance of beaches and the loss of nesting territory (Bouchard et al. 1998). Bouchard et al. (1998) studied the effects of stabilizer pilings utilizing the STABLER™ Disc System on nesting loggerhead sea turtles and found that the presence of the pilings reduced sea turtle nesting activity by 41%. They concluded that proximity of the structures near the mean high water line, may have made it difficult for some turtles to nest (Bouchard et al. 1998)

Similar to beach armoring, beach nourishment replaces original native sand with non-native sand that may differ in multiple properties, including moisture content, reflection, and conduction. Each of these properties directly effects nest architecture and incubation temperature, and may alter hatching survivorship and sex ratio (Milton et al. 1997). When poorly implemented, beach nourishment may cause detrimental effects to turtle nesting habitat. However, when nourishment is conducted according to adaptive management techniques, it can be used to restore sea turtle habitat in highly eroded areas (Montague 1993, 2008). Brock et al. (2009) studied the effect of beach nourishment on loggerhead and green sea turtles in Florida, USA and found that altering beach profiles can cause a 52.2% decrease in the reproductive output (hatchlings km^{-1} yr^{-1}) of loggerheads and 0.8% reduction in the reproductive output of greens. As the nourished area equilibrated to a natural state, the reproductive output for loggerheads recovered substantially (44%) two years post-nourishment, whereas the reproductive output for greens did not (Brock et al. 2009). Similarly, Rumbold et al. (2001) compared the frequency of nesting over three seasons for two natural beaches and one nourished beach, and found, after a single season, that nesting on the nourished beach declined by 4.4 to

5.4 nests km^{-1} day^{-1} compared to the two natural beaches. Additionally, the number of false crawls (turtle crawling onto beach and then returning to the water without laying) increased from 5.0 to 5.6 false crawls km^{-1} day^{-1} during the first season. During subsequent seasons, nesting and false crawl frequencies returned to normal levels (Rumbold et al. 2001)

Another threat negatively impacting hawksbill nesting beaches is artificial lighting. Artificial lighting on beaches disrupts the normal sea-finding behavior of both hatchlings and adults (Witherington 1992, Peters and Verhoeven 1994, Tuxbury and Salmon 2005, Sella et al. 2006). Hatchlings emerging on beaches with high light pollution will move toward artificial lights rather than the sea, and will fall victim to predation, death by car, exhaustion, and dehydration (McFarlane 1963, Philibosian 1976). McFarlane (1963) studied the effect of artificial road lighting on loggerhead hatchlings in Florida and found that for a single nest of 115 hatchlings, 90 individuals were killed on a highway 30.5 m away. Philibosian (1976) reported a similar incident in the US Virgin Islands, where 63 turtles crossed over multiple roads to reach the bright lights of a baseball field. Of the 63 turtles, 24 turtles were run over by cars (Philibosian 1976). Similarly, adult females may become disoriented from artificial lighting during nesting, wander aimlessly, and fail to nest (Ferreira and Martins 2013). Studies by Pendoley (1999) on green turtle hatchlings in Western Australia also indicated that flares from oil production facilities may disorient hatchlings on nights with low external light sources (new moon).

The effects of light pollution on turtles can be partially reduced by using lower wavelength lights and filtered lighting, yet even these techniques may have a slight

detrimental effect on sea turtle navigation (Witherington and Bjorndal 1991b, a, Sella et al. 2006). Witherington and Bjorndal (1991a) found that low-pressure sodium vapor lights emitting only yellow light, effect loggerhead hatchling dispersion and orientation less than other low-pressure and high pressure lights. In a later study, Witherington and Bjorndal (1991b) found that both loggerhead and green sea turtles were attracted to near-ultraviolet (360 nm), violet (400 nm), and blue green (500 nm) light, and preferred a light source with constant intensity and color (1.26×10^{15} photons s^{-1} m^{-2} at 520 nm) over a light source with fluctuating intensity. Additional work from Sella et al. (2006) examining the effect of filtered streetlights on loggerhead hatchlings in Florida, USA, also found that hatchlings were attracted to lights with both low and high wavelengths. When combined, the results from Witherington and Bjorndal (1991a, b) and Sella et al. (2006) indicate that low wavelength (360 nm) light may negatively impact sea turtle hatchlings and should be taken into account when designing conservations plans for turtle nesting beaches.

Conservation programs to eliminate, reduce, and redirect artificial lights on nesting turtle beaches have been effectively applied in many developed countries, including the U.S., Costa Rica, Greece, and Australia (Brei et al. 2014). Many Caribbean countries, however, do not have such programs, and widespread light pollution at sea turtle nesting beaches continues to be a common problem throughout the Caribbean (Brei et al. 2014).

Beach cleaning and driving are two additional forms of active habitat alteration that negatively impact hawksbill sea turtles. Business owners in the Caribbean will often employ locals to rake beaches to maintain cleanliness (personal observation), but raking

can also expose and destroy buried nests and leave large ruts in the sand that are difficult for hatchlings to surmount after hatching (Lutcavage et al. 1997). Similarly, driving on beaches can crush developing eggs and emerging hatchlings as well as leave large ruts that can hinder hatchling sea-finding behavior (Hosier et al. 1981, Salmon et al. 1992).

Human presence on beaches during hawksbill nesting and post-nesting periods can also negatively impact sea turtle survival. Similar to cars and rakes, tourists walking a beach at night may inadvertently destroy buried eggs or kill newly emerged hatchlings. Humans can also increase light pollution through the use of flashlights and cameras and potentially hinder turtles during nesting events (Jacobson and Lopez 1994). Reproductive females that are disturbed during nesting may abort nesting attempts entirely and return to the ocean (Jacobson and Lopez 1994). In an effort to reduce the negative effects of unrestricted turtle watching, many countries have established turtle watch centers that establish proper guidelines and venues for turtle watching. Turtle watch centers, if organized correctly, can serve as critical for sea turtle environmental education and protection throughout the Caribbean and the world (Johnson 1996).

An additional threat to sea turtle nesting beaches is the predation of eggs and hatchlings by local animals drawn to human rubbish left on the beach. Recent studies indicate that nest predation from animals found in close association with humans, including dogs, raccoons, swine, feral hogs, coyotes, coatis, and mongooses can result in 100% mortality of sea turtle nests (Leighton et al. 2008, Engeman et al. 2014). Some municipalities throughout the Caribbean actively combat the spread of local pests and clean up beach rubbish, but many cities and towns throughout the region still suffer from

significant littering problems and large numbers of feral dogs (Lutcavage et al. 1997, Ruiz-Izaguirre et al. 2014).

Foraging Habitat

Caribbean hawksbills are impacted by humans, not only at nesting beaches, but also in coral reef foraging grounds. Coral reefs are often located in close proximity to towns and cities and are used extensively by tourists and locals for recreation, travel, and work. Because coral reefs are heavily used, boat traffic in many coral reefs is substantial and, if not properly regulated, can lead to high incidences of boat strikes on turtles. Data on boat strikes in the Caribbean are limited, but historical records from Australia (Hazel and Gyuris 2006) and Hawaii (Chaloupka et al. 2008) indicate that boat strikes can pose a significant threat to local sea turtle populations. Hazel and Gyuris (2006) studied boat strikes on sea turtles in Queensland, Australia and found that boat strike mortality rate for sea turtles between 1992–2002, was 14.13% (n = 4777). Additional studies from Chaloupka et al. (2008) in Hawaii indicate that boat strikes from 1982–2003 caused an estimated 2.5% mortality of sea turtles (n = 3861). A short-term study by Blumenthal et al. (2009b) of hawksbills (n = 41) in the Cayman Islands found that the majority of boat strikes occur around areas of significant commerce and tourism.

Another potential threat to hawksbill foraging grounds is dredging. Large ports and municipalities in the USA and Caribbean will conduct dredge and fill operations to keep waterways navigable for boat traffic. Dredging, however, may inadvertently cause substantial damage to coral reef ecosystems that are vital foraging grounds for hawksbill sea turtles (Bak 1978, Rogers 1983). Recent studies of hopper dredging in Florida and

Georgia indicated that dredging without knowledge of local sea turtle foraging areas can lead to direct mortality of sea turtles (Slay and Richardson 1988, Dickerson et al. 1991).

Pollution

In addition to altering and destroying hawksbill sea turtle habitat, humans indirectly threaten hawksbills through the widespread dispersal of pollution throughout the marine environment. Several forms of pollution, including oil, plastic, and derelict fishing gear, pose significant health risks to hawksbill sea turtles.

Oil Pollution

The detrimental effects of oil pollution on sea turtles is a growing global problem that has been recorded throughout the Red Sea (Frazier and Salas 1984), the Atlantic (Witham 1978), the Mediterranean (Gramentz 1988), the Gulf of Iraq (Hutchinson and Simmonds 1992), the Gulf of Mexico (Hall et al. 1983), and the Caribbean Sea (Yender and Mearns 2003). Butler et al. (1973) studied the Sargasso Sea in the Atlantic and estimated that the sea could entrap 70,000 metric tons of tar. Between 1992 and 2001 seventy-three oil spills occurred worldwide that had the potential to impact sea turtles (Yender and Mearns 2003). The total volume spilled from the seventy-three spills was 3.3 million gallons, of which 2.5 million was from vessels and 737,400 gallons were from stationary sources (Yender and Mearns 2003). Of the seventy-three spills, 16 spills occurred in the Caribbean, 13 of which were in Puerto Rico (Yender and Mearns 2003).

The effect of oil pollution on sea turtles is not well understood, but clinical studies of loggerheads indicate that exposure to oil causes a wide variety of health problems in

sea turtles (Lutcavage et al. 1995). When surfacing in an oil slick to breathe, sea turtles are exposed to harmful physical contact with the oil and inhale petroleum vapor into their lungs (Van Vleet and Pauly 1987). Lutcavage et al. (1995) found that prolonged exposure to the oil from multiple resurfacings can lead to debilitating carcinogenesis, decreased aerobic capacity, reduced foraging time, failure of salt glands, and reduced sensory capabilities. Additional work from Milton et al. (2003) indicates that turtles will eat other animals contaminated by oil or ingest tar balls, which can lead to injury of various body systems, including, gut blockage leading to starvation, buoyancy problems, organ dysfunction, hormone imbalance, and reduced growth. While little work has been done to examine the effect of oil on sea turtle eggs, laboratory trials from Fritts and McGehee (1981) indicated that exposure to fresh oil at the beginning of incubation can cause embryos to develop scute deformities. Fritts and McGehee (1981) also found that fresh oil poured on eggs near the end of the incubation resulted in a significant decrease in hatchling survival.

Plastic Pollution

Plastic pollution is another major threat to hawksbills. Because plastic is a highly durable and buoyant material, it can easily be dispersed across long distances and persist for centuries (Derraik 2002, Gregory 2009). In the oceans, plastic materials will accumulate in oceanographic convergences and eddies, and then spiral outward until eventually being deposited on beaches (Moore et al. 2001). Law et al. (2010) calculated the plastic concentration for 6136 surface plankton net tows in the North Atlantic Subtropical Gyre from 1986 to 2008, and found that more than 60% of the tows

contained buoyant plastic pieces. Globally, Law et al. (2010) found that the highest concentration of plastic pieces was found in subtropical latitudes where large surface currents converge.

Plastic pollution often accumulates in costal zones from industrial, urban, and agricultural inputs, and can pose a major threat to sea turtles (Magnuson et al. 1990). Regional estimates of the effect of plastic pollution on hawksbills in the Caribbean is unknown, but reports of plastic ingestion and debris entanglement are numerous and geographically disparate, suggesting that plastic pollution is widespread throughout the Caribbean (Balazs 1984). Analyses of sea turtle digestive tract contents indicate that sea turtles will ingest a wide variety of items including string, rope line, cardboard, Styrofoam™, plastic bags, glass, aluminum, paper, charcoal, cellophane, and latex balloons (Plotkin and Amos 1990, Burke et al. 1993, Bjorndal et al. 1994). Larger items can obstruct the esophagus, amputate limbs, or perforate the bowel causing severe injury or mortality (Mascarenhas et al. 2004), and smaller items can build up in the stomach, altering gut function and releasing harmful toxins into the body (Bjorndal et al. 1994).

Although the effects of plastic and refuse ingestion on sea turtle physiology are still poorly understood, studies of green sea turtles ingesting latex material found that, following ingestion, some individuals became positively buoyant (Lutz and Alfaro-Schulman 1991). Because sea turtles dive to find prey and avoid predation, positive buoyancy reduces foraging efficiency and increases the risk of predation and boat strike (Lutz and Alfaro-Schulman 1991). Recent studies examining the effect of pollution on green and hawksbill nesting beaches found that increased pollution density reduced

hatchling crawling rates, increased exposure time to predators, and wasted stored energy (Triessnig et al. 2012, Sung et al. 2014).

Derelict Fishing Gear

Similar to both oil and plastic pollution, derelict fishing gear also poses a threat to hawksbill populations. Dumped materials originate primarily from commercial fishing vessels and offshore drilling platforms, but they also come from inland material that enters the ocean via rivers. Sea turtles can become entangled in derelict fishing gear making them susceptible to predation and drowning (Lutcavage et al. 1997). Trailing debris can also amputate sea turtle limbs, leading to wound infection and death (Lutcavage et al. 1997). Monofilament line from commercial rope, trawl-, and gill-nets is the most commonly encountered fishing gear that threatens sea turtles, and according to some estimates, accounts for the majority (68%) of all entanglements worldwide (O'Hara and Iudicello 1987, Magnuson et al. 1990). Other items, including anchor lines, sheets, straps, burlap bags, plastic bags, 6-pack yokes, aluminum chairs, and steel cables may also cause turtle entanglement (Balazs 1984, O'Hara and Iudicello 1987, Laist 1997).

Balazs (1984) conducted a comprehensive overview on the effects of marine debris on sea turtle species and concluded that Styrofoam™, synthetic lines, and other plastics make up 31.2% of all marine debris and pose a significant threat to sea turtle species. Similarly, Laist (1997) catalogued a comprehensive list of debris ingestion and entanglement records to measure the impact of marine debris on marine life. Laist (1997) concluded, based on stranding records for the U.S. Atlantic and Gulf of Mexico, that entangling debris was found on 0.8% (142 of 16, 327) of loggerheads, 6.6% (123 of

1,874) of greens, 6.8% (66 of 970) of leatherbacks, and 14% (36 of 258) of hawksbill sea turtles.

Direct Threats

I define direct threats (as per Sorice et al. 2003) as any primary disturbance from direct interactions with humans. I have classified direct threats into three primary categories: poaching, fishing bycatch, and human-turtle interactions.

Poaching

One of the major threats facing Caribbean hawksbill populations is poaching. Hawksbills have been greatly sought after from antiquity for the beautiful scales covering their shell. Tortoiseshell is imported into Asian countries where it is crafted into a wide assortment of jewelry and sold as tourist curios and gifts (Lutcavage et al. 1997). In the early 20th century, tortoiseshell was imported into the markets of Europe, the United States of America, and Asia, and local hawksbill populations began to decline rapidly (Seale 1917, Mortimer and Donnelly 2008). By the 1900's Japan became the world's largest importer of tortoiseshell (Canin 1991), importing over 1.3 million adults and 575,000 stuffed juveniles between 1950–1992 (Milliken and Tokunaga 1987).

Recognizing the rapid decline of hawksbill populations, hawksbills were put on the CITES list in 1975, and by 1977 all international trade of hawksbills became prohibited (Mortimer and Donnelly 2008). In 1992, Japan officially banned all sea turtle imports (Donnelly 1991), but the industry still continues to operate with stockpiled material (Mortimer and Donnelly 2008). Despite their endangered IUCN status, several

Central America and Caribbean countries and territories, including Saint Maarten, Saint Kitts and Nevis, Antigua and Barbados, Dominica, Saint Lucia, Barbados, Saint Vincent and the Grenadines, Grenada, Trinidad and Tobago, Aruba, Venezuela, Columbia, Panama, Costa Rica, Nicaragua, Honduras, Guatemala, Belize, the British Virgin Islands, the Dominican Republic, Haiti, and Jamaica continue to poach hawksbills for their shells (Fleming 2001, Bräutigam and Eckert 2006). Two of these countries, the Bahamas and Jamaica, are reported to have large stockpiles of tortoiseshell (Fleming 2001).

In addition to being exploited for their shells, hawksbills are also impacted by local meat trades and egg poaching. Sea turtle meat is considered a delicacy in many Caribbean and Latin American countries, and eggs are purported to have aphrodisiac qualities (Lutcavage et al. 1997). Because hawksbills can nest 3–5 times in a season (Witzell 1983) and during nesting may encounter humans, they are highly susceptible to exploitation and unlikely to survive an entire nesting period in areas of high poaching (Mortimer and Bresson 1999). When subsistence hunting is tightly regulated by annual quotas, it may have little negative impact on turtle populations (Ross and Carr 1993, Campbell 1998, Campbell et al. 2007). Reliable hunting quotas, however, are difficult to enforce and many hawksbill populations throughout the Caribbean have been extirpated by unsustainable levels of sea turtle poaching (Lutcavage et al. 1997).

Fishing Bycatch

In addition to facing intense persecution from direct sea turtle poaching, hawksbill populations are also threatened by incidental catch from commercial and small scale fisheries. Wallace et al. (2011) evaluated specific threats to sea turtle survival in different

regional management units (see Wallace et al. 2010a for definition) and determined that bycatch was the highest threat for sea turtles globally. According to a comprehensive study of sea turtle bycatch from gillnet, longline, and trawl commercial fisheries worldwide, approximately 85,000 turtles were reported as bycatch from 1990–2008 (Wallace et al. 2010b). This value, however, is likely two orders of magnitude too small, because few fishing fleets report yearly fishing effort and bycatch rates (Wallace et al. 2010b). Mortality of turtles by bycatch is primarily caused by drowning, strangulation, and severe acidosis (Henwood and Stuntz 1987). Mortality rates vary substantially with different gear types used and fishery practices, but in general, sea turtle mortality is higher for net and trawl gear than for other gear types (Lewison et al. 2013). Within the USA, incidental catch from commercial shrimp trawls accounts for more sea turtle deaths than all other human-caused mortality sources combined (Magnuson et al. 1990). Finkbeiner et al. (2011) studied sea turtle bycatch and mortality in USA waters and estimated that 71,000 deaths occurred annually between 1990 and 2007. However, bycatch estimates in USA waters have dropped by 60% and mortality estimates have dropped by 94% with the implementation of bycatch mitigation measures, including turtle excluder devices (TEDs) and seasonal restrictions on gear types (Finkbeiner et al. 2011). Fisheries in several other countries, including Indonesia (Oravetz and Grant 1986), Australia (Brewer et al. 2006), and Venezuela (Alio et al. 2010) have also implemented bycatch mitigation measures, with varying levels of success.

In addition to being trapped in trawl nets, many turtles are killed by drowning or strangulation in a variety of other commercial nets (purse seine nets and gill nets) and fishing gear (lobster and crab pots, pelagic longline) (Magnuson et al. 1990). Within the

Caribbean, gill nets are particularly lethal with over 6,000 turtles killed between the years of 1980 and 2008 (Wallace et al. 2010b).

Much like commercial fisheries bycatch, small scale fisheries (SSF) bycatch also poses a significant threat to sea turtles (Lewison and Crowder 2007, Soykan et al. 2008, Wallace et al. 2010a). SSFs are an important part of the global economy, particularly in developing countries, that provide food and employment for approximately 1 billion people (Béné 2006). Typically SSFs are defined by a low degree of capital investment, small vessel size, limited mechanization, and the decentralization of resources and effort (Lewison et al. 2013). The majority of bycatch research has targeted commercial fisheries, but recent studies in Trinidad and Tobago (Lum 2006), Brazil (Gallo et al. 2006), Baja California, Mexico (Peckham et al. 2007), Peru (Alfaro-Shigueto et al. 2010), and the Mediterranean (Casale 2011) indicate that SSFs can have high and potentially unsustainable levels of bycatch. Regional estimates of SSF bycatch indicate that the threat from SSF bycatch may be similar in magnitude to that of commercial fisheries bycatch (Lewison and Crowder 2007). Peckham et al. (2007), for example, studied SSF bycatch mortality of loggerheads in Baja California and found an annual bycatch of approximately 1000 individuals. This value, they calculated, was comparable to the bycatch rate of the entire Pacific commercial longline fleet (Peckham et al. 2007).

Studies of SSF turtle bycatch in the Caribbean are limited, yet preliminary studies from Aucoin and Leon (2007) estimated that within the Jaragua National Park, an average of 0.75 hawksbills were caught daily with gill nets. Other nets, such as trammel and lobster nets, have the potential to have even higher rates of turtle bycatch (Aucoin and Leon 2007). Studies of turtle bycatch in Honduras are limited, but surveys from

Dunbar et al. (2013) in Cuero Y Salado, Honduras indicated that artisanal fisheries employing trammel, shrimp, and seine nets may constitute a threat to sea turtles in the area. Additional studies need to be conducted throughout the Caribbean to determine what level of threat SSF bycatch poses to sea turtle species.

Impacts of Human Interaction

Human impacts on Caribbean hawksbills from poaching and fishing bycatch are significant threats to hawksbills that must be addressed with scientifically based management policies if conservation efforts are to be effective. These threats, however, are not the only human activities threatening sea turtles. In addition to these threats, recent research has demonstrated that even simple interactions between humans and sea turtles may have long-lasting effects on sea turtle behavior and ecology.

Ecotourism

Within the last 64 years, a new form of non-consumptive human-nature interaction, known as ecotourism, has rapidly developed to become a multibillion dollar industry and a critical funding source for conservation (Filion et al. 1994, Aylward et al. 1996, Davenport and Davenport 2006). Although often touted as an exemplary form of sustainable development in the developing world (Tisdell and Wilson 2002, Butcher 2006), ecotourism may also cause degradation and alteration of fragile ecosystems and sensitive fauna (Krüger 2005). If the potential social, economic, and environmental impacts of ecotourism are not considered and actively managed, ecotourism industries may inadvertently destroy the natural resources they depend on (Moore and Carter 1993).

Simple activities, such as wildlife viewing and hiking, may result in unanticipated negative impacts to animal health and behavior, including reduced foraging time (Yasué 2005), lower survival rates (Müllner et al. 2004), and diminished breeding success (Ellenberg et al. 2006). Yasué (2005) found that as tourism increased on beaches in British Columbia, Canada, semipalmated plovers' (*Charadrius semipalmatus*) swallowing rates decreased. Müllner et al. (2004) found that temporal overlap of the tourism high season with the hoatzin (*Opisthocomus hoatzin*) fledging period in the Cuyabeno Reserve, Ecuador, caused increased chick stress and mortality in tourist-exposed sites. Similarly, Ellenberg et al. (2006) found that Humboldt penguin (*Spheniscus humboldti*) breeding successes in the Damas, Choros, and Chañaral islands, Chile, was significantly reduced at sites frequently visited by tourists. Ellenberg et al. (2006) also found that a person passing within 150 m of an incubating penguin provoked a significant heart rate response in the penguin. After human disturbance, penguins required up to half an hour to reduce heart rate levels to normal; a response associated with high energy costs (Ellenberg et al. 2006).

In North America, the detrimental effects of improperly managed ecotourism on bird and mammal species have been well documented (Boyle and Samson 1985), yet similar studies for sensitive ecosystems (i.e. coral reefs, wetlands, estuaries) in Central and South America are rare (Boo 1990, Moreno 2005). If ecotourism is to function effectively as a key driver of conservation in these areas, it must be ecologically sustainable. Additional research examining the effects of ecotourism on wildlife should be conducted in areas of high tourism and biodiversity hotspots, such as the Caribbean, for conservation and ecotourism to be effective.

Diver Impacts on Marine Ecosystems

With increases in international tourism and improved safety equipment, diving ecotourism has grown substantially in the last 64 years, with over 1 million new recreational divers trained each year (Davenport and Davenport 2006). Divers particularly favor coral reefs and marine protected areas (MPAs) because of their beauty and biodiversity, which leads to expansion of ecotourism in these sensitive habitats, with subsequent increases in environmental degradation and potential diver-turtle interactions (Rouphael and Inglis 2002).

Since its inception, recreational diving has been viewed as an ecologically sustainable activity promoting increased awareness of marine environments (Tilmant 1987). Recent studies, however, indicate that recreational diving can cause increased coral mortality and spatiotemporal variability within coral ecosystems (Tratalos and Austin 2001, Rouphael and Inglis 2002, Zakai and Chadwick-Furman 2002). For example, Tratalos and Austin (2001) found that diver number and distance from mooring buoys in the Cayman Islands were highly correlated with declines of the reef building coral, *Montastrea annularis*, and increases in dead coral coverage. Additional studies from Zakai and Chadwick-Furman (2002) in the northern Red Sea indicated that over-use of dive sites (> 30,000 dives per year) can lead to unsustainable levels of coral damage, independent of site topography. Conversely, Rouphael and Inglis (2002) found that coral degradation in the Great Barrier Reef Marine Park, Australia was associated with variability in diver behavior, and not primarily with dive site overuse.

Worachananant et al. (2008), Luna et al. (2009), and Chung et al. (2013) studied the behavior of divers in Thailand, Spain, and Hong Kong, respectively, and found that

inexperienced divers swimming in high impact areas caused more damage to coral reef ecosystems than experienced divers. Similarly, Barker and Roberts (2004) studied diver behavior in St. Lucia, Lesser Antilles, and found that specific factors, including the use of cameras and the time of day, significantly increased diver contact with the reef and may have led to increased reef degradation. As coral reef ecosystems continue to decline globally from overfishing (Jessen et al. 2013, Pawlik et al. 2013), habitat degradation (Davenport and Davenport 2006), and global climate change (Reaser et al. 2000), increased knowledge of the potential impacts of human diving on reef ecosystems is critical for conservation efforts to be effective.

Constantine (2001) studied swim-with-dolphin tourism in the Bay of Islands, New Zealand, and found that large numbers of human swimmers (31 swimmers approaching one individual per year) can cause bottlenose dolphins (*Tursiops truncatus*) to become sensitized to humans and lead to reduced dolphin foraging, resting, nursing, and socializing behavior. Relatedly, Constantine et al. (2004) found that an increase in the number of dolphin-watching boats (from 49 to 60) following dolphins caused a decrease in the amount of time dolphins spend resting, which could lead to higher stress levels and a reduction in energy reserves. A loss in energy reserves could lead to subsequent reductions in foraging, resting, nursing, and socializing behavior (Constantine et al. 2004).

Similarly, Quiros (2007) studied the impacts of recreational swimmers on whale sharks (*Rhincodon typus*) during feeding in an MPA in Donsol, Philippines, and found that small groups of recreational swimmers could alter whale shark swimming patterns through path obstruction and proximity. She also found that specific diver activities,

including direct touch, close approach, and flash photography, significantly increased the magnitude of the disturbance, concluding that alterations in whale shark behavior may reduce survivability by diverting metabolic energy away from feeding and toward avoidance behaviors (Quiros 2007).

Human Interactions with Sea Turtles

Although much is known about the detrimental effects of divers on coral ecosystems, and while we are beginning to understand diver interactions with dolphins and whale sharks, few studies have examined the effects of recreational diving on behavior in any species of sea turtle. Meadows (2004) used focal-animal activity budget observations to study the impacts of recreational snorkelers on Hawaiian green turtle behavior, and found that a small number of snorkelers (n = 10) making regular approaches (4 per hour) toward turtles caused a 30% increase in total bouts of swimming, eating, and cleaning behavior. While Meadows (2004) found that the proportion of time each turtle spent in each behavior did not vary significantly in the presence or absence of divers, the total number of behavioral bouts overall increased significantly in the presence of divers. Meadows (2004) concluded that the change in behavior frequency was likely a consequence of turtles rapidly switching between behaviors to avoid snorkelers attempting to view, chase, touch, or ride them. If an increase in turtle energy expenditure accompanies a change in behavior frequency, it follows that human-turtle interactions may be energetically expensive for turtles and lead to reductions in growth rate and fecundity (Meadows 2004). Clearly the notion that non-consumptive ecotourism

poses no threat to sea turtle conservation may be underestimating human impacts that could potentially negatively impact turtles in the long run (Jacobson and Lopez 1994).

Although enlightening, Meadows (2004) focused solely on the group effect of snorkelers on turtle behavior and did not account for individual effects of snorkelers on turtles. Snorkeler interactions with turtles also tend to be short (< 5 min; Meadows, 2004) and may not accurately represent the effects of SCUBA diver interactions, which have the potential to be longer and more impactful. Hawaiian green turtles exhibit unique behaviors due to their close proximity to humans (Balazs 1996), making the results of Meadows' (2004) study difficult to extrapolate to other turtle species and populations.

Similar to Meadows (2004), Kostas (2015) found that female loggerhead sea turtles (*Caretta caretta*) in Zakynthos, Greece are impacted by human snorkelers and may seek an optimal balance between conserving energy and avoiding snorkelers. This is similar to the results of Slater (2014), who found that the presence of snorkelers in Akumal Bay, Mexico significantly reduced green sea turtle feeding behavior. Both Kostas (2015) and Slater (2014), however did not measure the impact of scuba diving on sea turtle behavior.

Recreational Diving and Hawksbills

Substantial work has been done in recent years examining hawksbill behavior, ecology, diving, habitat preference, and migration (van Dam and Diez 1997, Dunbar et al. 2008, Hawkes et al. 2012), yet little work has focused on hawksbills interactions with recreational divers. Despite the lack of data on diver-hawksbill interactions, no studies have been reported in the literature that examine the effects of human diving on hawksbill

behavior or ecology. Additional studies which quantify the effects of human diving on sea turtle behavior, particularly in areas heavily affected by diving, are of critical importance, and will allow conservation agencies to incorporate more effective regulations for sea turtle preservation.

Studying Sea Turtle and Human Interactions

In the following section I briefly outline some of the known research methods used to study sea turtle and human interactions in the field. I have divided the section into two primary categories—direct methods and indirect methods—based on the type of methods being employed.

Direct Methods

I define direct methods as techniques which involve physical observation or mechanical measurements of sea turtles and their behavior. Direct methods are split into two primary categories: time depth recorders and in-water observations.

Time Depth Recorders

In order to properly understand hawksbill responses to human activity, it is necessary to obtain a working knowledge of hawksbill diving behavior as it relates to local habitat and prey items through time and space. Often, weather conditions and time limitations make it difficult to visually track sea turtles, making time depth recorders (TDRs) a useful method for remotely collecting dive depth and time profiles. TDRs are small digital data loggers attached via zip ties and fast setting epoxy to a turtle's post-

marginal scutes (Hochscheid 2014) or directly to its head (for reproductively active individuals; Hays et al. 2000). Often TDRs are coupled with Passive Integrated Transponders (PITs) or radio transmitters for easy retrieval (van Dam and Diez 1997).

van Dam and Diez (1997), Blumenthal et al. (2009c), and Witt et al. (2010) used TDRs to study hawksbill diving patterns around Mona Island (Puerto Rico), Little Cayman (Cayman Islands), and Anegada Island (Virgin Islands) respectively, and found that hawksbills exhibited consistent periods of diurnal diving and nocturnal resting. During the day, turtles tended to make multiple, short dives to various depths, interpreted as foraging behavior, whereas at night they tended to make fewer, longer dives to constant depths, presumably to rest (van Dam and Diez 1997). Both van Dam and Diez (1997) and Blumenthal et al. (2009c) noted that larger turtles tended to make longer and deeper dives than smaller turtles, suggesting that physiological factors may constrain turtle diving behavior. Conversely, Witt et al. (2010) in the Virgin Islands found that dive metrics did not scale with turtle body size, and concluded that diving metrics may be constrained by bathymetric and foraging constraints of shallow reef habitats.

Additional work by Gaos et al. (2012b) found that hawksbills in the Eastern Pacific almost exclusively prefer shallow water diving (< 10 m) to deep water diving (> 10 m), and only occasionally dive below 20 meters. Gaos et al. (2012b) also found that hawksbill diving behavior was similar across diel periods, suggesting that hawksbills may be as active at night as during the day. Gaos et al. (2012b) concluded that Eastern Pacific Hawksbills may engage in shallow water diving preferentially as a mechanism for optimizing foraging success in inshore estuary habitats. A cursory survey of TDR studies shows that hawksbill diving characteristics are far from being completely described or

understood, and additional research is needed to adequately characterize turtle diving behavior.

TDR techniques, although useful in delineating diurnal diving patterns, are insufficient to describe the full range of turtle behaviors in a given habitat (Seminoff et al. 2006). Conflicting dive profiles, multiple behaviors in a single dive, and variations in habitat usage can lead to incorrect interpretations of turtle diving behavior (Houghton et al. 2003, Francke et al. 2013). Additionally, turtle behavior may vary over time in a manner not detectable by TDRs, necessitating supplemental methods of behavior measurements.

In-water Observations

Recognizing the inherent limitations of TDRs, scientists have used direct in-water observations as a supplemental method of behavior analysis (Houghton et al. 2003, Schofield et al. 2006, Dunbar et al. 2008, Blumenthal et al. 2009b, Stimmelmayr et al. 2010, von Brandis et al. 2010). Using in-water observations, scientists can quantify actions, such as food preference, swimming behavior, and foraging, to provide reliable insights into turtle behavior and physiology that are difficult to infer from remote sensing alone (von Brandis et al. 2010).

In-water observations from Dunbar et al. (2008) and von Brandis et al. (2010) indicate that hawksbills spend the majority of the daytime swimming (76–81%) and comparatively little time resting, investigating, eating, cleaning, or surfacing (19–21%). Blumenthal et al. (2009b) recorded similar behaviors in Little Cayman and noted that many turtles rested under ledges during the night, possibly to increase dive duration and

minimize energy expenditure. Given the logistical difficulty of following turtles at night, nocturnal activity has not been readily assessed from in-water observations, making analysis of nocturnal behaviors tentative at best and difficult to correlate with nocturnal TDR profiles (van Dam and Diez 1996).

Unlike Dunbar et al. (2008) or von Brandis et al. (2010), Blumenthal et al. (2009c) conducted TDR studies in conjunction with in-water observations to test for correlations between diving and behavior. They found that nocturnal dive depth was significantly correlated with turtle size, as was maximum diurnal dive depth and deepest daily dive depth (Blumenthal et al. 2009c). In a recent study of juvenile green turtles off Oahu, Hawaii, Francke et al. (2013) combined TDR and in-water observations to survey turtle behavior in a coastal neritic habitat. He found that TDRs were sufficient to describe generic shallow water diving behavior, but additional in-water observations were required for a full characterization of turtle behaviors in deeper waters. Results of these studies suggest that the integration of TDR measurements with in-water observations is a highly effective, yet underutilized method of turtle behavioral analyses (Houghton et al. 2000, Schofield et al. 2013).

Indirect Methods

In addition to using direct methods such as TDRs and in-water observations, scientists also utilize indirect methods to study sea turtles. Specifically, I define indirect methods as those techniques which do not require active handling of turtles or continual observation. Indirect methods include habitat assessments and turtle sightings surveys.

Habitat Assessments

In-water observations and TDR studies are useful techniques for delineating turtle movements associated with human activity, yet they lack the spatial context necessary to accurately describe complex species-specific behaviors without additional foraging habitat data. Restrictions in underwater visibility, variable sea conditions, limited depth quantification, and differences in turtle habitat preferences are variables affecting sea turtle behavior that are difficult to assess using traditional TDR and in-water observation techniques (Schofield et al. 2006). Consequently, analyzing TDR and observational data without incorporating spatial information may require the researcher to make overarching assumptions and arbitrary interpretations not supported by the data (Francke et al. 2013).

In order to accurately quantify juvenile hawksbill behavior, one must first develop a working understanding of hawksbill foraging habitat. Most research to date, however, has focused primarily on home range and diet preference analysis rather than on resource availability and its effect on turtle behavior (Rincon-Diaz et al. 2011b). Additionally, due to problems with site accessibility and difficulty in data retrieval for juveniles, most researchers have focused on nesting turtle habitat rather than juvenile foraging grounds, making additional study of these critical habitats increasingly important (Cuevas et al. 2007, Hamann et al. 2010). Hawksbill foraging ecology and behavior, in particular, is poorly understood, with few investigators studying critical links between habitat and behaviors of juvenile turtles (Scales et al. 2011).

Cuevas et al. (2007) used video transects, spot-checks, and GIS to characterize benthic habitats and hawksbill distributions in foraging areas off the Yucatan Peninsula, Mexico. Unlike many studies which give only a general description of bottom habitat,

Cuevas et al. (2007) conducted in-depth habitat surveys paired with in-water observations to analyze hawksbill habitat preference. Their results indicated that hawksbills in the area preferred hard bottom sites covered with octocorals and sponges, particularly species of the genera *Chondrilla* and *Spheciospongia* (Cuevas et al. 2007).

In a series of studies off the Culebra Archipelago, Puerto Rico, Rincon-Diaz et al. (2011a, b) conducted benthic surveys and gastric lavages to quantify prey availability and juvenile hawksbill diet preference. From their analyses they concluded, in agreement with Leon and Bjorndal (2002), that juvenile hawksbill diet preference is based both on individual prey selectivity and the spatial abundance of prey species. Thus hawksbills have strong foraging preferences for certain prey items (e.g. the rare corallimorph, *Ricordea florida*) independent of environmental availability, but also forage for other species (e.g. the algae, *Lobophora variegate*) based on their local abundance. Based on these results, Rincon-Diaz et al. (2011b) concluded, in agreement with Blumenthal et al. (2009a), that juvenile hawksbills exhibit high plasticity in foraging preferences and thus require a wide diversity of foraging habitats during their developmental years.

In summary, hawksbill foraging preference may vary in different populations and environments, leading to different behaviors and dive patterns that are not readily detectable from in-water observations or TDR profiles. When coupled with TDR studies and in-water observations, habitat surveys can provide vital information on habitat-specific behaviors and foraging preferences that are difficult to determine from TDR or in-water observation studies alone.

Dive Sightings

In conjunction with the above techniques, scientists can also use dive sightings from recreational divers to study human and sea turtle interactions. Houmeau (2007) worked with divers in French Guadeloupe to successfully quantify impacts of food abundance on hawksbills turtles. Similarly, Bell et al. (2009) utilized recreational divers in the Cayman Islands to assess sea turtle abundance and spatiotemporal patterns within and outside MPAs over a 26-month period (Bell et al. 2009). During the study, divers were instructed to fill out turtle sightings sheets which included data on species, number, and size of turtles sighted at particular dive sites. These results were then compared to capture data from the Cayman Islands Department of Environment to assess the quality and accuracy of the data collected (Bell et al. 2009). Based on their findings, Bell et al. (2009) concluded that data collected from divers was comparable to other studies, and that no obvious relationship existed between MPAs and turtle sightings abundance within the Cayman Islands.

Similar to Houmeau (2007) and Bell et al. (2009), Williams et al. (2015) utilized recreational divers to monitor sea turtle populations in Inhambane Province, southern Mozambique. Williams et al. (2015) collected sightings surveys from 2008 to 2011 which they coupled with dedicated research survey to test the effectiveness of diver monitoring. From their results, Williams et al. (2015) concluded that utilizing recreational divers to monitor sea turtle populations was a useful method for collecting sea turtle population data that should be combined with photo-identification surveys to reduce species identification error.

Similar to the Cayman Islands and Mozambique, many countries throughout the Caribbean have substantial diving tourism in MPAs, but the potential effects of diving in those areas have not yet been assessed. Utilizing recreational divers to aid in sea turtle research in these areas may be an effective means of measuring the effect of human presence on sea turtle populations and behavior (Foster-Smith and Evans 2003, Bell et al. 2009).

Conclusions

Hawksbill sea turtles are a circumtropically distributed species in severe decline throughout the Caribbean. Hawksbills are significantly threatened by a wide variety of human impacts, including poaching, fishing, habitat alteration, pollution, and human-sea turtle interactions. As selective spongivores, hawksbills serve a key role as foragers in coral reef ecosystems by maintaining species diversity and preventing coral overrun by sponges and algae. The effects of recreational diving on hawksbills in these coral reef environments, however, is unknown and additional research using established methods, including time depth recorders, in-water observations, habitat assessments, and turtle sightings will allow conservation agencies to create effective regulations for hawksbill preservation.

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CHAPTER TWO

IMPACTS OF RECREATIONAL DIVING ON HAWKSBILL SEA TURTLE (*ERETMOCHELYS IMBRICATA*) BEHAVIOR IN A MARINE PROTECTED AREA

Christian T. Hayes[a,b,*], Dustin S. Baumbach[a,b], David Juma[c], and Stephen G. Dunbar[a,b,d]

Affiliations

[1]Marine Research Group, Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92350, USA

[2]Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR). Colton, CA 92324, USA

[3]Research Consulting Group, Loma Linda University, Loma Linda, CA 92350, USA

[4]Protective Turtle Ecology Center for Training, Outreach, and Research, Inc., Honduras (ProTECTOR - H), Tegucigalpa, Honduras

***Corresponding Author**

Christian Hayes
cthayes@llu.edu

Abstract

The hawksbill sea turtle (*Eretmochelys imbricata*) is a critically endangered species encountered by recreational divers within and outside of marine protected areas (MPAs) around the globe. Few studies, however, have examined the impacts of recreational diving on hawksbill behaviors. We collected turtle sightings surveys and dive logs from 14 dive operations, and conducted in-water observations of 61 juvenile hawksbill turtles in Roatán, Honduras, to determine if differences in dive site use and diver behaviors affected sea turtle behaviors in the Roatán Marine Park (RMP). Sightings distributions did not vary with diving pressure during an 82-day study period. Although swimming was the most commonly observed behavior followed by eating, we found the amount of time turtles spent eating, investigating, and breathing decreased when approached by divers (1-4). Our results suggest diver habituation may negatively impact sea turtle behaviors, however it is unknown if recreational diving has a cumulative effect on turtles over time. We found that divers within the RMP require additional training to accurately identify turtle species and properly record sightings data. We recommend that as recreational diving continues to increase, additional studies be conducted in MPAs to determine if current regulations provide adequate protection for endangered turtle species.

Keywords: marine ecotourism; behavioral studies; scuba diving; tourism impacts; in-water observations; coral reefs

Introduction

Within the last 64 years, a new form of non-consumptive interaction with the natural world, known as ecotourism, has rapidly developed to become a multibillion-dollar industry and a critical funding source for conservation (Filion et al. 1994, Aylward et al. 1996, Davenport and Davenport 2006). Although often touted as an exemplary form of sustainable development in the developing world (Aylward et al. 1996, Tisdell and Wilson 2002, Butcher 2006), ecotourism may also cause degradation and alteration of fragile ecosystems and sensitive fauna (Boo 1990, Müllner et al. 2004, Krüger 2005). If the potential social, economic, and environmental impacts of ecotourism are not considered and actively managed, ecotourism industries may inadvertently destroy the natural resources they depend on (Moore and Carter 1993, Doiron and Weissenberger 2014).

Simple activities, such as wildlife viewing and hiking, may result in unanticipated negative impacts on animal health and behavior, including reduced foraging time (Yasué 2005), lower survival rates (Müllner et al. 2004), and diminished breeding success (Ellenberg et al. 2006). Yasué (2005) found that as tourism increased on beaches in British Columbia, Canada, semipalmated plovers' (*Charadrius semipalmatus*) swallowing rates decreased. Müllner et al. (2004) found that temporal overlap of the tourism high season with the hoatzin (*Opisthocomus hoatzin*) fledging period in the Cuyabeno Reserve, Ecuador, caused increased chick stress and mortality in tourist-exposed sites. Similarly, Ellenberg et al. (2006) found that Humboldt penguin (*Spheniscus humboldti*) breeding successes in the Damas, Choros, and Chañaral islands, Chile, was significantly reduced at sites frequently visited by tourists.

In North America, the detrimental effects of improperly managed ecotourism on bird and mammal species have been well documented (Boyle and Samson 1985), yet similar studies for sensitive ecosystems (i.e. coral reefs, wetlands, estuaries) in Central and South America are rare (Boo 1990, Moreno 2005). Additional research examining the effects of ecotourism on wildlife should be conducted in areas where biodiversity hotspots intersect with high tourism, such as the Caribbean, for both conservation and ecotourism to be effective and sustainable.

Recreational diving is a form of ecotourism traditionally viewed as an ecologically sustainable activity promoting increased awareness of marine environments (Tilmant 1987). However, if recreational diving is to function effectively as a key driver of conservation, it must be ecologically sustainable. As international tourism has increased and safety equipment has improved, diving tourism has grown substantially in the last 64 years, with over 1 million new recreational divers trained each year (Davenport and Davenport 2006).

Recent studies indicate that diving can cause increased coral mortality and spatiotemporal variability within marine protected areas (MPAs). For example, Tratalos and Austin (2001) found that diver number and distance from mooring buoys in the Cayman Islands were highly correlated with declines of the reef building coral, *Montastrea annularis*, and increases in dead coral coverage. Additional studies from Zakai and Chadwick-Furman (2002) in the northern Red Sea indicated that over-use of dive sites (> 30,000 dives per year) can lead to unsustainable levels of coral damage, independent of site topography. Conversely, Rouphael and Inglis (2002) found that coral

degradation in the Great Barrier Reef Marine Park, Australia was associated with variability in diver behavior, and not primarily with dive site overuse.

In addition to causing environmental degradation, recreational swimming and diving can cause unintended behavioral changes in marine macrofauna. Constantine (2001) studied swim-with-dolphin tourism in the Bay of Islands, New Zealand, and found that large numbers of human swimmers (31 swimmers approaching one individual per year) can cause bottlenose dolphins (*Tursiops truncatus*) to become sensitized to humans and lead to reduced dolphin foraging, resting, nursing, and socializing behavior. Relatedly, Constantine et al. (2004) found that an increase in the number of dolphin-watching boats (from 49 to 60) following dolphins caused a decrease in the amount of time dolphins spend resting, which could lead to higher stress levels and a reduction in energy reserves.

Similarly, Quiros (2007) studied the impacts of recreational swimmers on whale sharks (*Rhincodon typus*) during feeding in an MPA in Donsol, Philippines, and found that small groups of recreational swimmers could alter whale shark swimming patterns through path obstruction and proximity. She also found that specific diver activities, including direct touch, close approach, and flash photography, significantly increased the magnitude of the disturbance, concluding that alterations in whale shark behavior may reduce survivability by diverting metabolic energy away from feeding and toward avoidance behaviors (Quiros 2007).

Few studies, however, have examined the effects of recreational diving on behavior in any species of sea turtle. Meadows (2004) used focal-animal activity budget observations to study the impacts of recreational snorkelers on green turtle (*Chelonia*

mydas) behavior, and found that as few as 10 snorkelers making regular approaches (4 per hour) toward turtles caused a 30% increase in total bouts of swimming, eating, and cleaning behaviors. Snorkeler interactions, however, tend to be short (< 5 min; Meadows, 2004) and may not accurately represent the effects of SCUBA diver interactions, which have the potential to be longer and more impactful. Hawaiian green turtles exhibit unique behaviors due to their close proximity to humans (Balazs 1996), making the results of Meadows' (2004) study difficult to extrapolate to other turtle species and populations. Similarly, Kostas (2015) studied the impact of snorkeler interactions on loggerhead sea turtle (*Caretta caretta*) disturbance behavior in Zakynthos, Greece, and concluded that adult females may seek an optimal balance between conserving energy and avoiding snorkelers. This is similar to results of Slater (2014), who found that the presence of snorkelers in Akumal Bay, Mexico significantly reduced green sea turtle feeding behavior. Both Kostas (2015) and Slater (2014), however did not measure the impact of SCUBA diving on sea turtle behavior.

Multiple studies worldwide have utilized SCUBA diving to measure sea turtle behaviors (Houghton et al. 2003, Schofield et al. 2006, Dunbar et al. 2008, Blumenthal et al. 2009a, Stimmelmayr et al. 2010, von Brandis et al. 2010). However, few of these studies have taken into account the potential impacts of SCUBA diving itself, on sea turtles. If in-water observational studies are to accurately quantify sea turtle behavior, they must take into account the potential effects of SCUBA divers.

Several recent studies have emphasized the need for additional research on the potential impacts of divers on sea turtle behavior. Schofield et al. (2006) conducted in-water observations of male and female loggerheads (*Carreta carreta*) in Zakynthos, Greece,

and concluded that existing in-water turtle watching protocols should be refined to limit tourist activities to areas where turtle behaviors are minimally impacted. Schofield et al. (2006), however, did not specifically measure the effect of human in-water activities on sea turtles. Similarly, Dunbar et al. (2008), conducted in-water observations of recently released juvenile hawksbills in Roatán, Honduras, and noted that observer proximity may have affected observed turtle behavior. Dunbar et al. (2008), however, did not quantify the potential impacts of recreational diving on sea turtle behavior. These studies emphasize the need for additional research on the potential effects of recreational diving on sea turtle behavior.

The hawksbill sea turtle (*Eretmochelys imbricata*) is a circumtropically distributed, critically endangered species (Meylan 1999, McClenachan et al. 2006, Mortimer and Donnelly 2008). However, no studies to date have reported the effect of human diving on hawksbill behavior or ecology. Additional studies quantifying the effects of recreational diving on hawksbill turtle behaviors are of critical importance, and will allow conservation agencies to design and implement more effective regulations for sea turtle interactions in areas heavily impacted by diving.

In the current study, our aim was to determine if differences in dive site use and diver behaviors affected hawksbill sea turtle behaviors in a MPA. Since foraging behavior requires turtles to spend less time scanning for potential predators and more time scanning for food, we hypothesized that turtles would spend less time investigating and eating, and more time swimming in heavily used dive sites than they would in dive sites that are less heavily used. Similarly, since we expected turtles within a MPA to be accustomed to divers, we hypothesized that turtles would spend less time investigating

and eating, and more time swimming when divers approached turtles than when divers were at baseline position. As hawksbill populations continue to be threatened worldwide from poaching (Mortimer and Donnelly 2008), bycatch (Lewison et al. 2013), pollution (Yender and Mearns 2003), and climate change (Poloczanska et al. 2009), increased knowledge of the potential impacts of human diving on hawksbills is critical for conservation, if efforts in MPAs are to be effective.

Methods

Study Area

Roatán is a 77 km island located approximately 52 km off the north coast of Honduras (16°20′24″N, 86°19′48″W). The Bay Islands, of which Roatán is the largest island, form part of the Mesoamerican Barrier Reef complex, and were once one of the seven major historical hawksbill nesting areas in the Caribbean, (Long 1774, Meylan 1999, McClenachan et al. 2006) To date, local hawksbill populations in the area are poorly understood (Dunbar and Berube 2008). The Roatán Marine Park (RMP) is a community-based MPA covering a network of coastal coral reefs and mangrove estuaries extending approximately 13 km from the towns of West Bay, West End, and Sandy Bay, and around the western tip of Roatán (Fig. 1).

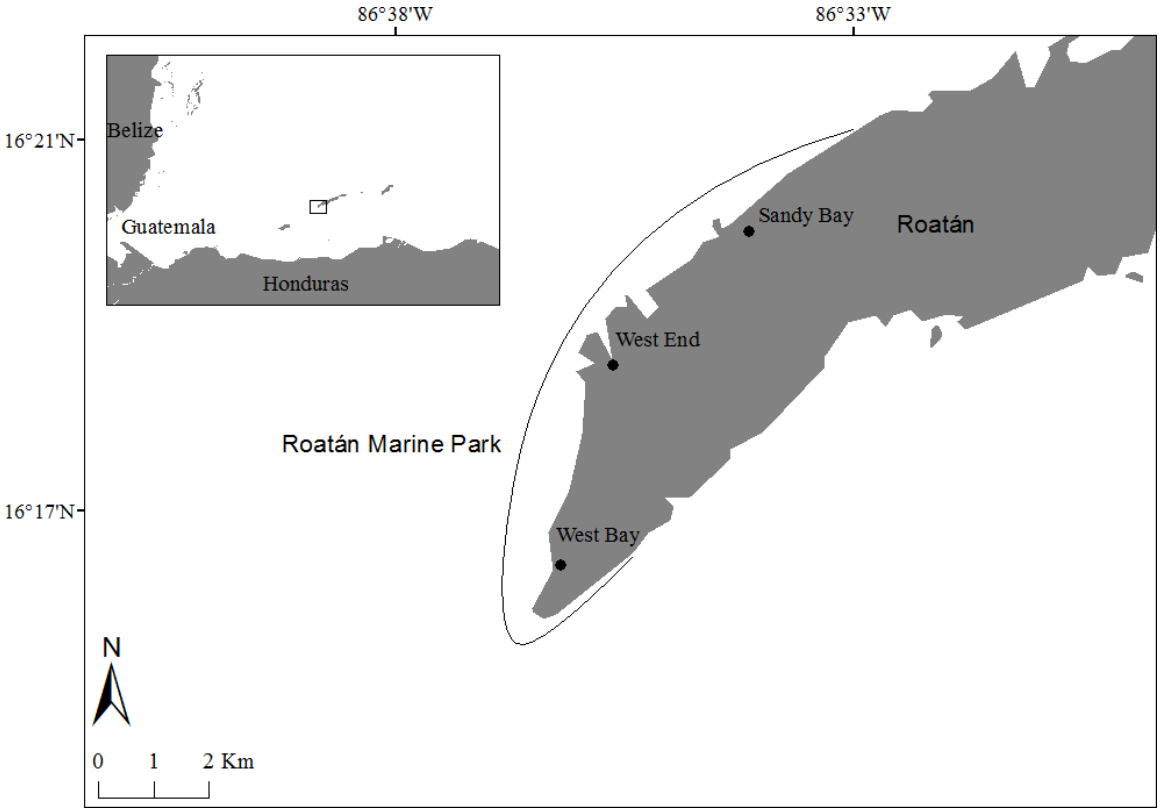

Figure 1. Map of Roatán and the Roatán Marine Park, Bay Islands, Honduras. Black line indicates the approximate area of the Roatán Marine Park. Inset shows regional location of Roatán.

Within the RMP, the reef crest lies approximately 92 meters off shore and slopes gradually for 2.2 km before dropping off steeply (> 130 m) at the reef wall (Gonzalez 2013). Bathymetry is varied, composed primarily of hard corals from the families Faviidae, Milleporidae, and Pocilloporidae; soft corals from the families Gorgoniidae and Plexauridae; sponges of Chondrillidae, Geodiidae, and Petrosiidae; turtle grass (*Thalassia testudinum*); and sandy substrate (Dunbar et al. 2008, Berube et al. 2012). Diving tourism within the RMP has increased substantially within the last 15 years and is concentrated in the towns of West End and West Bay (Doiron and Weissenberger 2014).

Sightings and Dive Logs

From June 9 to August 29, 2014 we distributed weekly survey forms to dive operators in the West End. On each data sheet, divers recorded the site, date, name of the diver logging the information, depth of sighting (meters), species, life stage of the turtle (adult or juvenile), and number of individuals sighted. All values that divers gave in imperial units were converted to metric. Participants were given identification sheets (in both English and Spanish) to aid in species identification and promote awareness. When species were unable to be identified, they were assigned to the "unknown" group for analysis. We collected data sheets 1–2 times per week as able, combined this data with turtle sightings from our own dives, and input the information into a Microsoft Excel (2003) file for analysis. Over the duration of the study period, we also collected daily dive logs from dive operations within the West End to calculate monthly dive site use. On each dive log sheet, divers recorded date, site visited, time of day (if available), and number of divers. To avoid pseudoreplication we only analyzed the point-of-entry dive site for drift dives.

In-water Observations

We conducted continuous focal and video in-water observations of hawksbills using modified methods from Dunbar et al. (2008) and von Brandis et al. (2010) during dive trips between 09:00 and 16:00 hrs. We followed each individual as long as possible and recorded observed behaviors using an underwater camera (Olympus Stylus Tough-8000 12 MP with Ikelite underwater camera housing) and video camera (GoPro Hero 3+ Black Edition with underwater housing; GoPro Inc., San Mateo CA). We recorded water depth (m) using a standard wrist-worn dive computer (Leonardo; Cressi Inc., Genova,

Italy), and start and stop time (to the nearest second) for all observed activities using a water resistant watch (Expedition T4005; Timex Group USA Inc., Middlebury, Connecticut). We recorded notes of observations underwater using underwater paper. All behaviors were characterized into six solitary and two social behavior categories. The six solitary behavior categories included swimming (active movement along the bottom, through the water column, or near the surface), resting (coming to a stationary position on the sea floor), surfacing (to breathe), investigating (active searching for food material indicated by a pause in swimming and active examination of nearby material), eating (the intentional ingestion of a substance), and scratching (on coral or object) (as per Dunbar, et al. 2008). The two social behavior categories included reacting (physical response to diver presence) and intraspecific interacting (reacting to presence of other turtles). In addition to measuring time, we also recorded the total number of occasions a turtle engaged in each behavior and defined this value as the number of bouts for a given activity. When visibility permitted, we counted the number of times a turtle lifted its head out of the water as a proxy for total number of breaths taken at the surface (as per Von Brandis et al. 2010).

As a control for diver interaction, we began all observations (when possible) by recording turtle behaviors for approximately 5 min with divers keeping at a constant distance of approximately 3–5 m from turtles (Meadows, 2004). We defined this position as the baseline position for divers. To test if diver approach affected a change in the amount of time turtles engaged in specific behaviors, we instructed different sized groups of 1–4 divers to slowly approach and observe each turtle. We defined diver approach as the intentional movement of divers from baseline position to within 1–2 m of sea turtles.

To remove user bias for choosing particular group sizes, we varied the test group size randomly on each dive. During diver-turtle interactions we recorded all relevant diver parameters, including the number of divers watching a turtle at the beginning and end of an interaction, the number of touches on a turtle by a diver, and the closest estimated distance a diver approached a turtle. We conducted repeated in-water observations for turtles (as able) to test for turtle habituation to diver presence.

To test for repeat observations of the same turtle, we collected left, right, and dorsal facial photographs of all observed turtles and analyzed them with the Interactive Individual Identification System (I^3S): Pattern (Version 4.0.1; den Hartog and Reijns 2014) using methods as per Dunbar et al. (2014) and Baeza et al. (2015).

Statistical Analysis

We consolidated turtle sightings and dive log data into an 82-day database for June 9–August 29, and used linear regression to test for a relationship between number of sightings and sighting survey effort. To test for relationships between recreational diving pressure and sighting rate, we ran a Spearman's correlation (r_s) for hawksbill sighting rate (number of hawksbill sightings/number of dives) and the number of divers per logged visit. Using ArcGIS for Desktop (Version 10.2; ESRI 2013), we mapped fixed kernel density (1 km) estimates of hawksbill sighting rate against the total number of divers logged at each site for 46 dive sites in the RMP.

For analyses of turtle behavior, we only analyzed behaviors from the first interaction with a given turtle to avoid pseudoreplication. To maximize sample size and test for the overall effect of diver presence on turtle behavior, we pooled all diver group size categories (1–4) together and calculated the total mean time for each turtle behavior.

To test for association of turtle behaviors with dive site use, we ran Spearman's correlations comparing the total number of divers per visit to the total amount of time turtles engaged in each behavior. Similarly, to test for an association between the duration of surface intervals and the number of breaths turtles took at the surface, we ran a Spearman's correlation comparing total breathing time to total number of breaths. We also ran Spearman's correlations to test for associations between the mean time turtles engaged in each activity and the mean number of behavior bouts for each observed behavior. Separate Spearman's correlations were run for each observed behavior before and during diver approach.

We ran paired T-tests and nonparametric Wilcoxon signed ranks tests comparing the total number of bouts and time for each behavior that turtles engaged in before and after divers approached. We also ran repeated measures ANCOVAs, adjusting for total baseline and diver approach time covariates, comparing the total time turtles engaged in each behavior before and after divers approached turtles. When necessary, we normalized the data using square root transformations and back transformed the adjusted means, as specified in the results. Means are reported with ± 1.0 standard error and sample range, and medians are reported with interquartile range (IQR). Effect size for repeated measures ANCOVAs are reported as β estimates. We used IBM SPSS Statistics (Version 13; IBM Corporation 1989–2004) and SAS (Proc Mixed, Version 9.4; SAS Institute Inc. 2013) for all statistical analyses. Alpha level was set at 0.05 for all analyses.

Results

Sightings and Dive Logs

We collected turtle sightings information from 14 dive operations in the West End. Dive operations recorded 701 dives at 46 sites between June 9 and August 29, 2014. Ten survey entries did not specify either the dive site or date, and were excluded from analysis. On the majority of occasions (n = 445), one turtle was seen, and 26 dives recorded no turtle sightings (Table 1). A total of 666 hawksbills, 420 greens (*Chelonia mydas*), four loggerhead (*Caretta caretta*), and 22 unknown turtles were reported during the study. Of the hawksbills reported, 393 (59%) were reported as adults and 273 (41%) as juveniles. Of the greens reported, 282 were reported as adults and 138 as juveniles.

Table 1. Turtle sightings frequencies in the Roatán Marine Park.

Occasions	Turtles	Occasions	Turtles
26	0	7	6
445	1	3	7
133	2	2	8
48	3	1	9
23	4	1	10
11	5	1	12

We compiled 648 dive logs involving 3092 divers between June 9 and August 29. Mean number of divers per dive was 5.0 ± 0.3 SE and mean hawksbill sightings rate per dive was 1.0 ± 0.1 SE. Spearman's correlations indicated there was no relationship between hawksbill sighting rate and the number of divers per visit (n = 46, r_s = 0.07, p = 0.67), the total number of divers (n = 46, r_s = -0.12, p = 0.44), or the total number of dives at each site (n = 46, r_s = -0.110, p = 0.47). Spatial distribution of sightings and

divers indicated that divers tended to make more sightings between West End and West Bay and fewer between West End and Sandy Bay (Fig. 2).

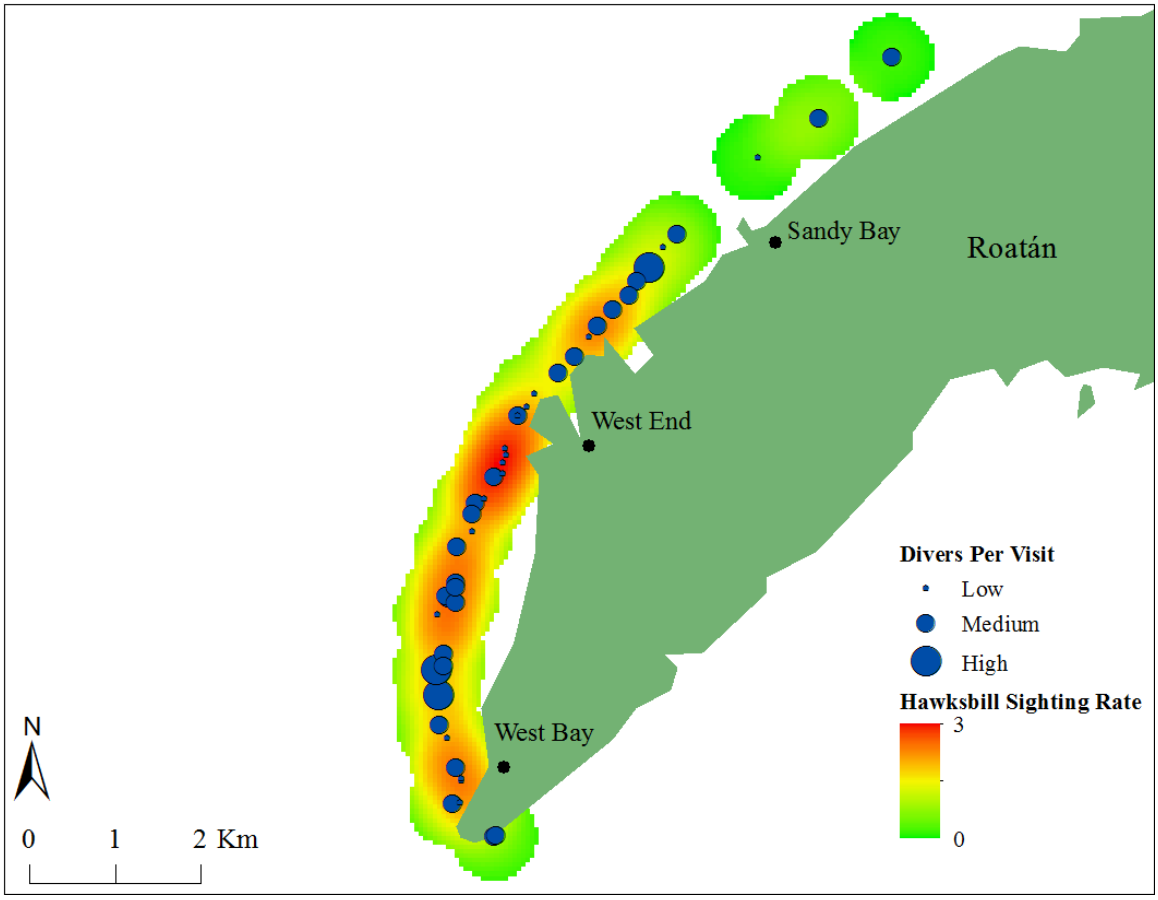

Figure 2. Hawksbill sightings rate and diver density for 46 dive sites in the Roatán Marine Park. Size of dots indicates mean number of divers per visit from two dive operations to each site over an 82 day period. Color gradation indicates fixed kernel density (1 km) estimate of hawksbill sightings rates from 14 dive operations. Hawksbill sighting rates are associated with dive site coordinates.

Sightings survey effort was unevenly distributed over the 3 months, with peak intensity occurring in July. This distribution significantly correlated with total turtle sightings (Fig 3; $n = 46$, $r_s = 1.00$, $p < 0.01$).

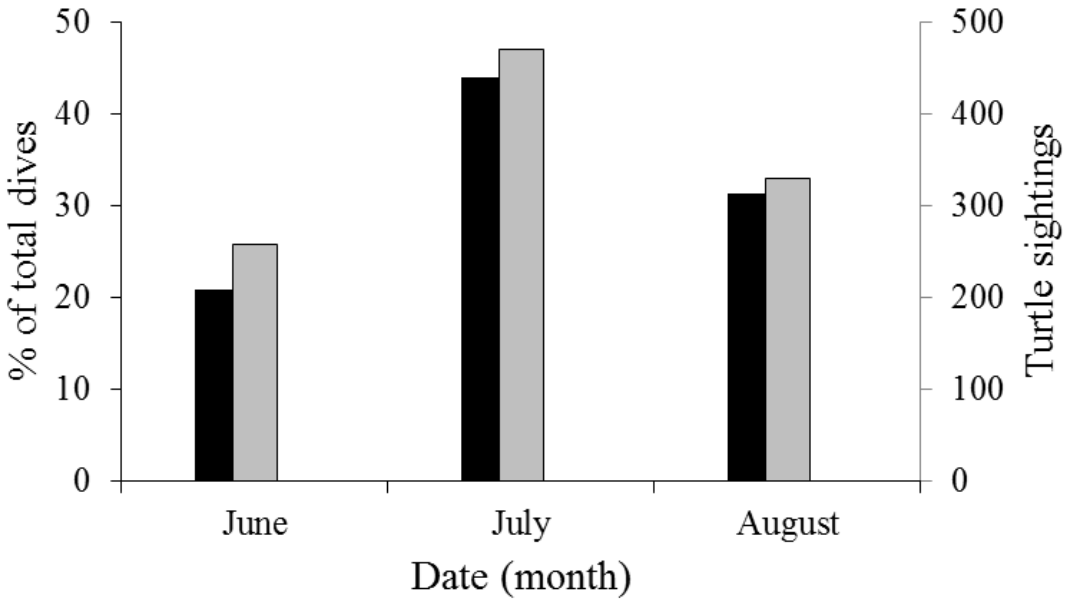

Figure 3. Monthly survey effort and turtle sightings. Black bars (left vertical axis) are the percentage of total dives from sightings survey occurring in each month. Grey bars (right vertical axis) are the total turtle sightings for each month. Scale: 500 max.

In-water Observations

From 12 June to 2 September, 2014, we conducted 6092.0 min of in-water surveys at 23 sites in the Roatán Marine Park. We devoted 1027.3 min (16.9% of total survey time) conducting in-water observations of 61 juvenile hawksbills. The average number of hawksbills observed per dive was 0.7 ± 0.1. We obtained repeated observations of 11 turtles, with nine individuals observed twice and two individuals observed three times. Total initial observation time was 823.9 min. and total time for repeated observation (not including initial observation time) was 203.4 min. All re-observed turtles were found within five sites of their initial observation location (Fig. 4).

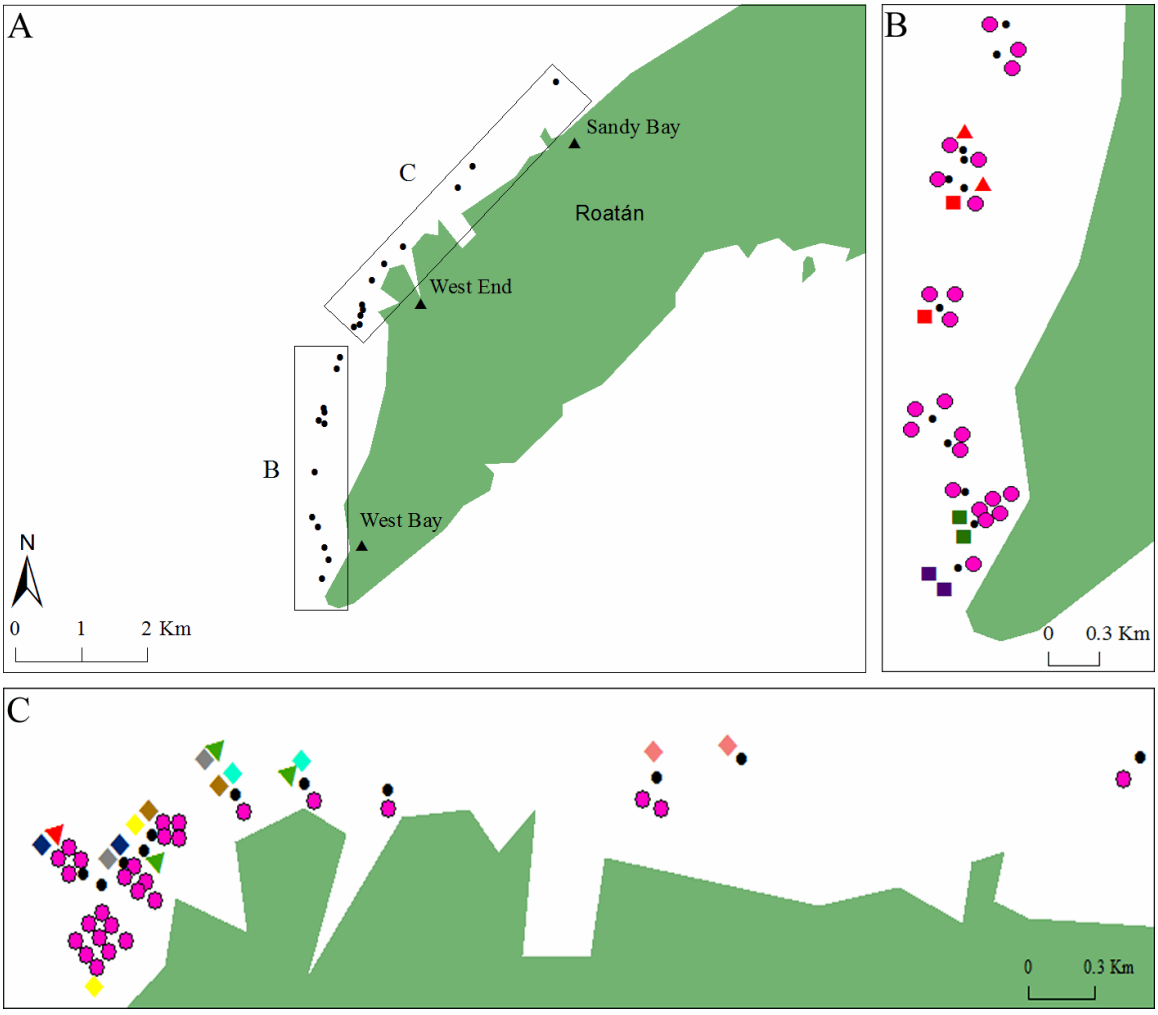

Figure 4. (A) In-water observation locations from 61 hawksbills in the Roatán Marine Park between (B) West Bay to West End (n = 30) and (C) West End to Sandy Bay (n = 31). Black dots: dive sites (n = 23). Pink circles: single observations of individuals (n = 50). Colored squares: Individuals observed twice (n = 18). Colored triangles: Individuals observed three times (n = 6). All observations are associated with the geographic coordinates of the closest dive site.

Mean turtle observation depth (*n* = 61) was 14.3 ± 1.0 m (range 4.6–39.6 m). Mean observation time per turtle was 13.3 ± 7.5 min (1.2–36.0 min). During 823.9 min of observations, swimming was the most commonly observed behavior. Mean turtle swimming time was 7.8 ± 0.7 min (0.0–25.5), and represented 57.9% of all observation time (Table 2). Turtles spent a mean of 0.5 ± 0.1 min breathing (0–3.6 min) and took a mean of 3.3 ± 0.1 breaths (*n* = 203, 0–12) at the surface. Mean number of divers (*n* =

183) observing turtles was 3.0 ± 0.2 (1–8). Although 21 turtles (34.4%) exhibited an obvious reaction (indicated by a rapid change in turtle swimming direction or activity) when approached by divers, 40 (65.6%) did not. On three occasions, we observed intraspecific interactions between hawksbills. Twice, two hawksbills approached each other, circled for several seconds and then swam away, and once, two individuals pressed their left ventral postocular and tympanic scales flat against each other, circled around each other for 26.0 seconds, and then swam in different directions.

Table 2. Behavior categories, mean time (min) displaying behavior, time range of each activity, and proportion of total observation time of each activity for 61 hawksbills in the Roatán Marine Park. Total observation time: 823.9 min.

Behavior	Mean time of each activity ± S.E.	Range (min)	Proportion of observation time
Swimming	7.8 ± 0.7	0.0 – 25.5	57.9
Eating	2.2 ± 0.5	0.0 – 15.9	16.5
Investigating	2.2 ± 0.4	0.0 – 12.8	16.3
Breathing	0.5 ± 0.1	0.0 – 3.6	4
Reacting	0.5 ± 0.2	0.0 – 7.0	3.4
Interacting	0.2 ± 0.1	0.0 – 5.8	1.4
Resting	0.1 ± 0.1	0.0 – 3.0	0.4
Scratching	0.1 ± 0.1	0.0 – 0.5	0.1

Spearman's correlations indicated that the time turtles (n = 61) spent in each of the three most common behavior categories was independent of the numbers of divers per site ($r_s < 0.25$, $p > 0.05$), and that total number of breaths was highly correlated with total breathing time ($r_s = 0.92$, $p < 0.0001$). Spearman's correlations also indicated that the mean proportion of time turtles (n = 61) engaged in eating, investigating and breathing

behaviors correlated with the total number of turtle behavioral bouts for each behavior (r_s > 0.80, p < 0.0001).

Diver approach did not impact the median number of bouts that hawksbills (n = 42) engaged in swimming, eating, investigating, and breathing behavior (Wilcoxon Signed Rank: S < 41; p > 0.05). Similarly, Paired T-tests and Wilcoxon Signed Rank tests indicated that diver approach did not alter the median time that turtles (n = 45) engaged in swimming, eating, and investigating behavior (swimming: $t_{(DF)} = 0.97_{(44)}$, p = 0.34; eating: S = -55.5, p = 0.21; investigating: S = -4, p = 0.94). Conversely, turtle (n = 45) median breathing time was significantly less during diver approach (Median = 0.00, IQR = [0.00, 0.00]) than when divers were at baseline position (Median = 0.00, IQR = [0.00, 30.00]) (Wilcoxon Signed Rank: S = -38.5, p = 0.01).

To normalize time variables, we square root transformed the mean time turtles spent eating and investigating and back transformed the adjusted means. Repeated measures ANCOVAs, adjusted for total baseline time and diver approach time, indicated that diver approach did not impact the mean time turtles (n = 53) spent swimming (Fig. 5A; $F_{(1, 43)} = 0.33$, p = 0.57, β estimate = -15.00). Conversely, the mean time turtles (n = 53) spent eating and investigating was significantly lower during diver approach than when divers were at baseline position (Fig. 5B; eating: $F_{(1, 43)} = 4.31$, p = 0.044, β estimate = -1.79; investigating: $F_{(1, 43)} = 5.12$, p = 0.029, β estimate = -2.48).

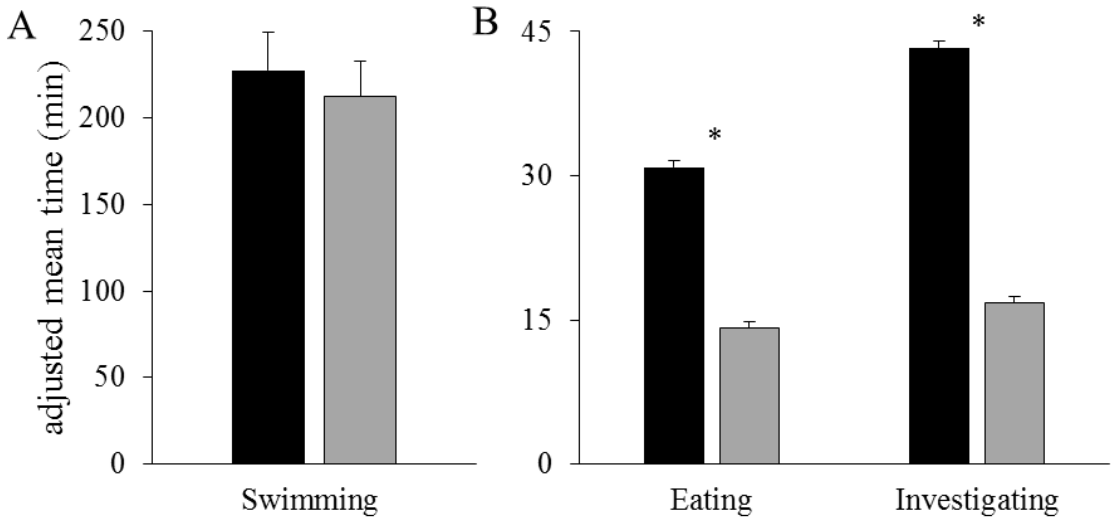

Figure 5. Adjusted mean time (min) + 1 SE that turtles (n = 53) engaged in (A) swimming behavior, and (B) eating and investigating behavior when divers were at baseline position (black bar) and during diver approach (grey bar). Time values are adjusted by the total time when divers were at baseline position (285.5 min) and the total time during diver approach (538.4 min). Asterisk (*) indicates $p < 0.05$.

Discussion

Sightings and Dive Logs

Our study is among the first to quantify the impacts of recreational diving on sea turtle sightings rates. Turtle sightings distributions throughout the RMP did not vary with the total number of divers per visit at each site over the 82-day period, suggesting that hawksbill abundance in the RMP is independent of diving pressure. Similarly, Bell et al. (2009) studied recreational diving in the Cayman Islands and found that the most heavily dived area in the Cayman Islands, Bloody Bay Marine Park in Little Cayman, had hawksbill sightings comparable to less frequently dived areas. We also found that turtle eating, swimming, and breathing behavior, did not differ with dive site use, suggesting that turtle behavior is independent of diving pressure within the RMP. These results are supported by Slater (2014) who found that green turtle (*Chelonia mydas*) foraging

behavior was not correlated with tourist abundance. However, because our sightings and dive log survey results are limited to a single time period (June–August, 2014), our results may represent seasonal trends in turtle sightings and diving pressure.

In-water Observations

The behavior of juvenile hawksbills in local foraging grounds has been previously described at Mona Island, Puerto Rico (van Dam and Diez 1996, 1997a, b), at D'Arros Island, Republic of Seychelles (von Brandis et al. 2010), at St. Kitts, Lesser Antilles (Stimmelmayr et al. 2010), and in Roatán, Honduras (Dunbar et al. 2008). However, the current study is the first to measure effects of recreational diving on hawksbill behavior. Similar to Dunbar et al. (2008), we found that swimming was the most commonly observed behavior in hawksbills (57.9% of total observation time). However, unlike Dunbar et al. (2008), we found that eating was the second most commonly observed behavior (16.5%). Whereas Dunbar et al. (2008) conducted observations in an area outside the RMP, where sea turtle protection is not enforced, our study was conducted within the RMP, where daily patrols regulate sea turtle poaching and harassment.

Studies of state-dependent risk-taking in green turtles by Heithaus et al. (2007) in Shark Bay, Western Australia, indicated that turtles preferentially foraged closer to bank edges in safer, yet lower foraging quality micro-habitats, when tiger shark (*Galeocerdo cuvier*) populations are high, and move farther from bank edges into areas with better foraging quality when shark population levels are reduced. If foraging behavior in hawksbills is similar to predation-dependent foraging behavior in green sea turtles, it is possible that turtles within the RMP spend a larger proportion of time eating than turtles outside the RMP due to reduced predation and harassment risk within the RMP.

However, it is important to note that, we observed the behaviors of turtles that had never been captured, whereas Dunbar et al. (2008) observed the behaviors of recently released hawksbills that may have exhibited atypical behavior. Consequently, care must be taken when comparing results from the two studies.

In support of our original hypothesis and the findings of Slater (2014) we found that hawksbills within the RMP spent less time eating, investigating and breathing during diver approach. However, contrary to Meadows (2004) and our original hypothesis, we found that human approach had no significant effect on hawksbill behavior bouts. In his study, Meadows (2004) concluded that the frequency change in the number of behavior bouts was likely a consequence of turtles switching rapidly between behaviors to avoid snorkeler attempts to chase, touch, or ride them. Unlike Meadows (2004), however, we did not observe any attempts by recreational divers to chase, touch, or ride turtles. Thus, we suggest that turtles in our study were affected differently by human approach because divers followed strictly enforced policies prohibiting the harassment of sea turtles. Instead, we hypothesize that hawksbills within the RMP are habituated to diver presence and interested in diver activity, leading them to engage in less investigating, eating, and breathing behavior when divers are present.

These results as well as multiple other examples suggest that diver habituation, may negatively impact marine macrofauna behavior. On multiple occasions we observed groupers (Epinephelinae) alter their normal foraging behaviors and follow spear-hunting divers, in order to take advantage of speared fish as an accessible food resource. Similarly, we were informed by multiple dive operations, that divers will feed groupers at certain dive sites, causing large numbers of groupers to periodically abandon regular

foraging behaviors and form large aggregations at those sites (Hayes, personal observation). Moreover, Titus et al. (2015) found that cleaning behavior of reef fish on a heavily dived reed in Utila, Honduras was suppressed > 50% when divers were nearby, and concluded that diver presence could reduce the fitness and lifespan of coral reef fish communities. These studies suggest that habituation of marine fauna to recreational divers can cause unintended behavioral changes over time.

It remains unknown, however, if recreational diving may have a cumulative effect on turtles over time. If long-term changes in behavior are energetically expensive for turtles, divers may negatively impact sea turtle growth and fecundity, as suggested by Meadows (2004), and may cause changes to short- and long-term fitness levels (Amo et al. 2006). For example, Amo et al. (2006) found that common wall lizards (*Podarcis muralis*) inhabiting areas of higher tourism in the Guadarrama mountains, Spain, had a higher infestation of ticks and poorer body condition at the end of the breeding season compared with lizards inhabiting areas of lower tourism. Counterintuitively, lizards in high tourism areas did not alter approach and flight-initiation distance behaviors in response to potential human threat (Amo et al. 2006). Similarly, Ellenberg et al. (2006) found that Humboldt penguin heart rates significantly increased during human approaches, and recover to baseline hear rate required up to half an hour. Ellenberg et al. (2006) concluded that the long recovery phase following human approach was likely associated with significant energetic costs to penguins. Implications of these studies suggest that a similar phenomenon may be taking place in MPAs, and that divers may negatively impact sea turtle physiology without causing sea turtles to visibly alter their behavior patterns.

In addition to having potential physiological effects, diver interactions with sea turtles could have long-term population effects. Long-term studies (13.5 years) by Bejder et al. (2006b) of *T. truncatus* in Shark Bay, Australia, indicated that increases in dolphin-watching tourism led to a significant decline in local dolphin populations over time. In a similar study, Bejder et al. (2006a) found that dolphins in regions of low dolphin-watching vessel traffic exhibited longer lasting behavioral changes than dolphins in regions of high vessel traffic. Bejder et al. (2006a) concluded that individual dolphins sensitive to dolphin-watching tourism departed the study area, whereas dolphins less sensitive to tourism remained in Shark Bay. It follows that individual hawksbills within the RMP may be differentially susceptible to recreational diving tourism. As recreational diving tourism continues to increase in the RMP (Doiron and Weissenberger 2014), hawksbills that are more susceptible to recreational tourism may move into foraging areas outside the RMP, where diving pressure is lower, while poaching pressure is much higher. This alternation in foraging behavior may result in increased numbers of hawksbills being captured and killed.

Our study used multiple methods to delineate the impacts of recreational diving on hawksbill sea turtles. However several caveats must be noted. Following the observations of Bell et al. (2009) and Williams et al. (2015), positive sighting bias may have been a problem. Divemasters tended to record dive sightings only when a turtle was observed during a dive, and did not fill in forms when no turtles were sighted. Additionally, we had little control over preventing divers from recording multiple sightings of the same individual on the same dive, which may have positively skewed turtle sightings. Moreover, because hawksbills in Roatán exhibit high fidelity to local

foraging areas (Berube et al. 2012), we could not determine whether turtle sightings comprised unique records of multiple individuals or repeated sightings of single individuals.

Species identification accuracy could not be confirmed for individual sightings, and although participating divers were given ID sheets and instructed on species identification, incorrect identifications may still have occurred. Widespread misidentification of sea turtle species is a common problem in sea turtle sightings surveys. Hickerson (2000) found that divers in the Gulf of Mexico will disagree on correct species identification of an individual turtle observed by multiple divers on the same dive. Similarly, Houmeau (2007) found that divers in French Guadeloupe commonly misidentified sea turtle species. Studies from Bell et al. (2009) in the Cayman Islands noted that divers, when identifying species, may fail to take into account differences in weather conditions, which may impact sighting ease and identification. Similarly, Williams et al. (2015) found that divers at Tofu Beach, Mozambique tended to misidentify green turtles, particularly juveniles, as hawksbills.

One potential mechanism to reduce replication error and species misidentification in volunteer-based surveys, is to utilize sea turtle photo identification methods. Both Hickerson (2000) and Williams et al. (2015) recommend the use of photographic surveys, and multiple studies indicate that photo identification systems are an effective method to identify sea turtle species and individuals (Reisser et al. 2008, Schofield et al. 2008, Jean et al. 2010, Dunbar et al. 2014, Baeza et al. 2015). Dunbar et al. (2014) used I^3S Spot to re-identify hawksbills that had lost their flipper tags, illustrating the viability of using photo-identification software for long-term identification. Similarly, Baeza et al. (2015)

used I^3S Pattern to successfully re-identify nine hawksbills observed on multiple occasions. Based on the current and previous studies, we concluded that photographic identification software systems (e.g. I^3S Spot and I^3S Pattern, den Hartog and Reijns 2014) offer a useful method to re-identify specific individuals, reduce replication error, and allow for long-term studies of individual turtles.

In addition to potentially misidentifying species and repeat individuals, divers may also have misidentified turtle life stages. Divers were not specifically trained to estimate sea turtle carapace length underwater or determine life stages, and may have failed to take into account the magnification effect of water, potentially positively skewing sea turtle size estimates. Additionally, divers did not record how far away turtles were from observers during sightings or quantify water quality variability, which may introduce inaccuracy in size estimation and species identification (Bell et al. 2009). Williams et al. (2015) compared local sightings logs to dedicated sea turtle sightings surveys intended for scientific use, and found that divers made biologically implausible overestimates of sea turtle carapace length in 11.7% of survey records (n = 22). These studies combined with the results of our current study suggest that divers in the RMP require additional training in sea turtle identification and data recording methods prior to beginning future turtle sightings surveys.

Care must be taken when interpreting dive logs, as differences in sample sizes and recording frequencies can skew comparisons of dive logs and turtle sightings. There is a negative bias in our dive log survey data, because we were only able to collect monthly dive logs from two dive operations within the West End. However, during the study, dive operations within the West End tended to frequent the same sites each month (Hayes,

personal observation), suggesting that dive logs from a small number of dive operations may accurately estimate relative diving pressure at different sites.

During the current study, we observed the impacts of small groups (1-4) of volunteer divers that may not have exhibited the same behaviors as larger dive groups from local dive operations. Unlike large dive groups, which tend to proceed slowly and explore within 1–2 dive sites of the original buoy, our group swam rapidly, specifically focused on finding turtles, and covered more ground (1-4 dive sites). Moreover, unlike many commercial dive groups, which consist of both experienced and inexperienced divers, most of our volunteers had several months of diving experience. Multiple studies of diver impacts on marine ecosystems suggest that inexperienced divers have greater impacts on coral reef ecosystems than experienced divers (Thapa et al. 2006, Worachananant et al. 2008, Chung et al. 2013). Worachananant et al. (2008) found a negative correlation between the number of dive logs and the number of diver contacts with coral in Thailand. Likewise, Thapa et al. (2006) found a correlation between diver experience level and environmentally responsible behaviors of divers in southwest Florida. If the behavior of inexperienced divers (i.e. contact with coral, harassment of local biota, mixing of seafloor sediment) is detrimental to coral reef health, it follows that inexperienced diver behavior may also negatively impact the behavior and health of animals, including sea turtles, that live in coral reef ecosystems. However, to date, few studies have examined whether inexperienced divers negatively impact marine macrofauna.

Conclusions

Our results suggest that small groups of intermediate to experienced divers (1-4 divers) in MPAs can significantly reduce the amount of time hawksbills spend foraging and breathing. Conversely, we found that current levels of recreational diving within the RMP do not significantly impact hawksbill abundance.

Based on these findings we make the following recommendations. First, additional in-water observation studies should be conducted both inside and outside MPAs to determine if policies and management enforcement within MPAs protect sea turtles from the potential impacts of recreational diving. Specifically, foraging and flight response behaviors of turtles within and outside MPAs should be compared to quantify the effect of recreational diving policy on sea turtle behaviors. When conducting these studies, researchers should take into account differences in diver group size and experience level. Second, in-water observations should be conducted in conjunction with TDR studies (similar to Blumenthal et al. 2009 and Francke et al. 2013) to form a comprehensive overview of recreational diving impacts on sea turtle behaviors within MPAs. Third, additional long-term sightings and dive log surveys should be conducted in MPAs, particularly in areas heavily impacted by diving. These surveys should be combined with habitat assessments of local sea turtle foraging grounds to evaluate if recreational diving pressure indirectly impacts sea turtle population levels through the degradation of foraging habitats.

Finally, long-term sea turtle photo-identification surveys using software systems, such as I^3S Spot and I^3S Pattern (den Hartog and Reijns 2014), should be implemented in MPAs to facilitate accurate species identification and long-term studies of individuals turtles. If implemented over an entire MPA, long-term photo-identification surveys would

enable management officials to estimate sea turtle population sizes, monitor changes in sea turtle populations over multiple years, and re-identify resident and migrating individuals. Results of these studies would allow management officials to design improved regulations for managing recreational diving interactions with sea turtles, both within and outside MPAs.

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CHAPTER THREE

CONCLUSIONS AND FUTURE WORK

Study

The purpose of this study was to quantify the effects of recreational diving on hawksbill sea turtle behaviors in Roatán, Honduras. I successfully conducted in-water observations of 61 juvenile hawksbills in the Roatán Marine Park (RMP) to test the effects of diver presence on turtle behavior and collected sea turtle sightings surveys from 14 dive operations in the RMP to determine if dive site use impacted sea turtle behaviors.

I was successful in achieving my first objective of conducting sightings surveys within the RMP and determining if dive site use impacted hawksbill sighting rate. My original hypothesis, that hawksbill sighting rates would be higher for sites experiencing heavy diving pressure and lower for sites with lower diving pressure, was incorrect. Instead, I found that turtle sightings distributions within the RMP from June 9 to August 31 did not vary with the number of divers visiting each site. I concluded that hawksbill abundance within the RMP during the duration of study was not significantly impacted by diver density at dive sites. This finding is supported by work from Bell et al. (2009) in the Cayman Island who found that the most heavily dived area in the Cayman Islands, Bloody Bay Marine Park in Little Cayman, had hawksbill populations comparable to less frequently dived areas. It is important to note, however, that in my study, I was unable to procure dive sightings from dive operations in West Bay or Sandy Bay and was only able to collect dive logs from two dive operations in the West End. Consequently, it is possible that a larger dive log sample size from multiple dive operations could yield different results. Additionally, conducting sightings and dive log surveys over multiple seasons, rather than a single season, could yield different results.

My second objective to measure sea turtle behavior during interactions with recreational divers and quantify the effects of diver approach and dive site use was completed successfully. I carried out 72 in-water observations of 61 hawksbills within the RMP and tested the impact of diver approach and dive site use on sea turtle behavior. My original hypothesis that turtles would spend less time investigating and eating in heavily used dive sites than they would in dive sites that are less heavily used, were both incorrect. Similarly I found that, contrary to my original hypothesis, turtles did not spend more time swimming in heavily used dive sites than in dive sites that are less heavily used. These results suggest that behaviors of hawksbills within the RMP are independent of diving pressure at specific sites. However, it is possible that turtle sightings and dive log surveys from additional dive operations collected over a longer period of time could yield different results.

In addition to testing the effect of dive site use on sea turtle behaviors, I also successfully tested the effects of diver approach on sea turtle behaviors. In support of my original hypothesis, I found that the amount of time hawksbills spent investigating, eating, and breathing was significantly reduced during diver approach. Contrary to my original hypothesis, I found that human approach had no significant effect on hawksbill behavior bouts. In his study, Meadows (2004) concluded that the observed frequency change in the number of behavioral bouts was likely a consequence of turtles switching rapidly between behaviors to avoid snorkeler attempts to chase, touch, or ride them. Unlike Meadows (2004), however, I did not observe any attempts by recreational divers to chase, touch, or ride turtles. Thus, I suggest that turtles in the current study were affected differently by human approach because divers followed strictly enforced policies

prohibiting the harassment of sea turtles. I hypothesize that hawksbills within the RMP are habituated to diver presence and interested in diver activity, leading them to engage in less investigating, eating, and breathing behavior when divers are present. The results of my study suggest that habituation of marine fauna to recreational divers can cause unintended behavioral changes over time. Additionally, I concluded that the results of my study are specific to the interactions of small groups of experienced divers with sea turtles and may not accurately depict the interactions of larger dive groups with more inexperienced divers.

Management Recommendations

Recommendations for the Roatán Marine Park

Recreational diving within the RMP has increased substantially in the last 15 years and continues to increase annually (Doiron and Weissenberger 2014). Current rules governing recreational diver interactions in Roatán, Honduras are not well developed and poorly enforced (Doiron and Weissenberger 2014) suggesting that new, scientifically-based regulations should be implemented to properly monitor recreational diver interactions with sea turtles. Based on the results of the current study, I provide the following recommendations for the RMP.

1. Long Term Dive Log Reports from Dive Operations in the RMP

The RMP should implement regulations requiring that dive operations within Sandy Bay, West End, and West Bay keep daily dive logs and report those logs to the RMP on a regular basis, and for these logs to be made available to investigators undertaking research within the RMP. In the current study, I found that many dive

operations did not record daily dive logs or were unwillingly to allow us to access their dive logs. Better exchange of data and transparency among dive operations, the RMP, and researchers working with the RMP would allow more powerful analyses to be conducted and more effective regulations to be implemented. Requiring dive operations within the RMP to report daily dive logs on a regular basis, would allow RMP officials to measure diving pressure at different dive sites throughout the RMP over time, and create regulations that are specific to particular areas heavily affected by recreational diving.

2. Long Term Sea Turtle Sightings Survey in the RMP

I also recommend that the RMP begin a long term volunteer dive sightings program with dive operations in Sandy Bay, West End, and West Bay. A long term turtle sightings program in the RMP would enable RMP officials to measure changes in relative sea turtle populations over time and, when combined with long term dive log surveys, would allow regulations to be implemented that specifically target the impacts of recreational diving on sea turtles within the RMP.

However, in order for long term sea turtles sightings surveys to be effective, divemasters within the RMP will require training in proper sea turtle identification and data recording techniques. In the current study I found, similar to Bell et al. (2009) and Williams et al. (2015), that divemasters within the RMP tended to record dive sightings only when a turtle was observed during a dive, and forgot to fill in reporting forms when no turtle was sighted. Ensuring that divemasters report occasions on which zero turtles are sighted would allow RMP officials to compare rates of turtle sightings at different sites over time, and determine if turtle populations in specific areas are increasing or

decreasing. I also found that widespread misidentification of turtle life stage was a common problem for divemasters in the RMP. Similar to the findings of Williams et al. (2015), divers in the current study tended to overestimate life stage of sea turtles, and misidentify juveniles as adults. I also found that dive operations tended to record sightings sporadically and often only when specifically asked by researchers or RMP officials. To increase the accuracy and efficiency of dive sightings surveys, I recommend that a single divemaster per dive excursion update sightings records immediately following each dive and turn in a weekly dive sightings report to the RMP office. We also recommend that the RMP work in conjunction with ProTECTOR Inc. to conduct active training workshops for divers on proper sea turtle identification and data recording.

3. Long Term Photo Identification Survey of Sea Turtles in the RMP

I recommend that RMP officials participate with ProTECTOR Inc. in a long term turtle photo-identification survey in the RMP to identify and track the movements of individual sea turtles within the RMP. If implemented over a long period, photo-identification surveys would allow project managers to estimate total population numbers of local green and hawksbill populations, monitor changes in populations over time, and re-identify individuals migrating to and from nesting beaches and foraging areas. This information will allow RMP mangers to create and enforce effective policies to manage observed changes in sea turtle populations within the RMP.

4. Habitat Assessment, Diet Analysis, Heavy Metal, and Home Range Studies

I recommend that the RMP work with ProTECTOR Inc. and local communities to

conduct additional studies of hawksbill sea turtles within the RMP in order to develop a working knowledge of local sea turtle population and habitat health in relation to human activity and environmental variability. Specifically, I recommend that long-term habitat assessments, diet analysis, and home range studies be conducted within the RMP to determine if changes in dive site use and human behavior negatively impact sea turtle foraging habitat and lead to changes in sea turtle foraging patterns over time. I likewise recommend that additional pollution, blood, and heavy metal studies be carried out on hawksbills in the RMP to test for potential physiological effects on sea turtles species from human pollution. To test for effects of sea turtle handling by researchers on sea turtle behavior and health, RMP managers should implement the above studies on several individual turtles identified using a photographic identification system, and measure differences in sea turtle behavior and health over time.

Recommendation for Marine Protected Areas

I recommend that management officials in marine protected areas (MPAs) around the world implement research projects using in-water observations and turtles sighting surveys to quantify the impact of recreational diving on different species of sea turtles. Management officials in areas with high levels of regular diving tourism, such as marine protected areas in the Northern Red Sea (Zakai and Chadwick-Furman 2002), Bonaire (Hawkins et al. 1999), and Grand Cayman (Tratalos and Austin 2001), should be particularly concerned with the potential negative impacts of large groups of recreational divers on sea turtle behavior, and design management regulations to mitigate these impacts.

Suggestions for Future Work

The current study is the first to quantify the impacts of recreational diving on sea turtles. As recreational diving continues to expand globally (Davenport and Davenport 2006), additional studies on the effects of recreational diving on hawksbill behavior and ecology are of critical importance. Expanding on the work from the current study, future studies should employ in-water observation and sightings survey techniques along with other techniques, including time depth recorders (TDRs), habitat assessments, and photographic identification software, to quantify the impact of recreational diving on sea turtle behavior, physiology, and ecology.

1. Comparison of Recreational Diver Impacts on Hawksbill Sea Turtle Behaviors Inside and Outside of Marine Protected Areas

Additional in-water observation studies should be conducted both inside and outside MPAs to determine if policies and management enforcement within MPAs protect sea turtles from potential impacts of recreational diving. Specifically, foraging and flight response behaviors for turtles within and outside MPAs should be compared to quantify the effect of recreational diving policy on diver and sea turtle behaviors. In addition, it would be advantageous to conduct TDR studies in conjunction with in-water observations (similar to Blumenthal et al. 2009) to form a more comprehensive overview of recreational diving impacts on sea turtle behaviors within MPAs. Results of these studies would allow management officials to design better regulations for managing recreational diving interactions with sea turtles, both within and outside MPAs.

2. Seasonal Variation in Turtle Sightings, Dive Site Use, and Foraging Habitat for a Marine Protected Areas

To better understand the overall impact of dive site use and diving pressure on sea turtle populations in MPAs, additional long term sightings and dive log surveys should be conducted in MPAs, particularly in areas heavily impacted by diving. These surveys should be combined with habitat assessments of local sea turtle foraging grounds to evaluate if recreational diving pressure indirectly impacts sea turtle population levels through the degradation of their foraging habitats. Long-term sea turtle sightings surveys, dive log surveys, and habitat assessments would allow management officials to monitor sea turtle populations and recreational diving pressure in MPAs, and implement effective management policies for minimizing potential impacts of recreational diving on sea turtle populations in MPAs.

3. Determining Sea Turtle Population Size in Marine Protected Areas Using Facial Scale Digitization and Automated Search Programs

Long-term sea turtle photo-identification surveys using software systems, such as I^3S Spot and I^3S Pattern (den Hartog and Reijns 2014), should be implemented in MPAs to allow for accurate species identification and long-term studies of individuals turtles (Dunbar et al. 2014). Additionally, if implemented over an entire MPA, long-term photo-identification surveys would enable management officials to estimate sea turtle population sizes, monitor changes in sea turtle populations over multiple years, and re-identify resident and migrating individuals.

Conclusions

As recreational diving continues to increase worldwide, it is imperative that management officials and researchers understand the impacts of recreational diving on sea turtle behavior, physiology, and population dynamics, in order to protect these important marine macrofauna. The current study provides the first data on the impacts of recreational diving on hawksbill sea turtles, and will enable local management officials to implement effective regulations for diver and sea turtle interactions. Additional research building from the current study, should be conducted both in Honduras and globally, to further elucidate the impacts of recreational diving on different sea turtle species.

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