5-2020

The Sandy Bay West End Marine Reserve: Hawksbill Inhabitance and Reserve Suitability

Marsha Wright

Recommended Citation

Wright, Marsha, "The Sandy Bay West End Marine Reserve: Hawksbill Inhabitance and Reserve Suitability" (2020). *Loma Linda University Electronic Theses, Dissertations & Projects*. 1834.
https://scholarsrepository.llu.edu/etd/1834

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

The Sandy Bay West End Marine Reserve: Hawksbill Inhabitance and Reserve Suitability

By

Marsha Wright

A Dissertation submitted in partial satisfaction of
the requirements for the degree
Doctor of Philosophy in Biology

May 2020

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

____, Chairperson

Stephen G. Dunbar, Professor, Department Earth and Biological Sciences

____

Ronald L. Carter, Provost, Loma Linda University

____

Noemi Duran, Director, Inter-European Division Branch, Geoscience Research Institute

____

William K. Hayes, Professor, Department of Earth and Biological Sciences

____

Suzanne Phillips, Chair, Department of Earth and Biological Sciences

____

Kenneth Wright, Professor, Department of Pathology and Human Anatomy

ACKNOWLEDGEMENTS

The completion of this research and my time here at Loma Linda have been made possible by the support of many. I would first like to extend my gratitude to my advisor and committee chair, Dr. Stephen G. Dunbar, for his continued support throughout this process. I wish to thank each member of my dissertation committee, Doctors Ronald Carter, Noemi Duran, William Hayes, Suzanne Phillips, and Kenneth Wright for keeping me on track and providing valuable feedback along the way. I wish to thank my lab members Chelsey, Dustin, Emily, Magalie, Nellie, Robert, Sean, and Tyler for their support in the lab, in the field, and even in the office. I would like to recognize Elieze Strydom for her constant support, ensuring my time as a student went smoothly. I extend my gratitude to the Department of Earth and Biological Sciences and ProTECTOR, Inc. for funding this work.

To each ProTECTOR, Inc. Intern and Volunteer, without whom my time in Roatán would have been fruitless. I am indebted to Gary and Mary Miller and the Roatán Dive Center for the use of their facilities and I would like to pay my special regards to Mary Miller and Theris Dixon for their personal support, providing comfort and ensuring my safety during my time in Honduras.

I wish to express my gratitude to my family: my father, Wycliffe; my mother, Marie; my sisters, Toni-Ann and Alison; and my brother-in-law, Joseph. Thank you for supporting the pursuit of my dreams, no matter what they were. To Hansel and Pauline Fletcher, I extend my deepest gratitude for treating me as a child of their own. I wish to thank each of my friends for their unceasing support: a special thanks to Elysia Cohen for the days and nights you spent with me in the “dungeon”; Avonelle Henry, for always

being a sounding board during the good and bad times; Taylor Edwards, for your words of love and encouragement, even from a distance, and Yoshae Fletcher, for your constant companionship from the beginning to the end.

I give the uppermost thanks to God, my heavenly father. Without Him, none of this would have been possible.

CONTENT

Chapter

FIGURES

Figure Page

Chapter 2

Chapter 3

Chapter 4

TABLES

Table Page

Chapter 2

Chapter 3

Chapter 4

ABBREVIATIONS

ABI	Applied Biosystem
ANOVA	Analysis of Variance
ArcGIS	Aeronautical Reconnaissance Coverage Geographic Information System
ASCII	American Standard Code for Information Interchange
AUC	Area Under the Receiver Operating Curve
CCL	Curved Carapace Length
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CPCe	Coral Point Count with Excel Extensions
CS	Coral with Sand
dNTPs	Deoxyribonucleotide Triphosphate
ddNTPs	Dideoxyribonucleotide Triphosphate
DNs	Digital Numbers
F_{ST}	Fixation Index
ISODATA	Iterative Self Organizing Data
IUCN	International Union for Conservation of Nature
MaxEnt	Maximum Entropy Modeling
MCMC	Markov Chain Monte-Carlo
MSA	Mixed Stock Analysis
MPA	Marine Protected Area

mtDNA	Mitochondria DNA
NMMA	National Marine Manufacturers Association
NIR	Near-infrared
NOAA	National Ocean and Atmospheric Administration
OSCAR	Ocean Surface Current Analyses Real-time
PC	Principal Component
PCR	Polymerase Chain Reaction
PHP	Probability of Hawksbill Presence
ProTECTOR, Inc.	Protective Turtle Ecology Center for Training, Outreach and Research, Inc.
RFLPs	Restriction Fragment Length Polymorphisms
RMSE	Root Mean Squared Error
S	Sand
SBWEMR	Sandy Bay West End Marine Reserve
SCL	Straight Carapace Length
SDM	Species Distribution Model
SNPs	Single Nucleotide Polymorphisms
SS	Seagrass with Sand
TOA	Top-of-atmosphere
WMO	World Meteorological Organization

ABSTRACT OF THE DISSERTATION

The Sandy Bay West End Marine Reserve: Hawksbill Inhabitance and Reserve Suitability

by

Marsha Wright
Doctor of Philosophy, Graduate Program in Biology
Loma Linda University, May 2020
Dr. Stephen G. Dunbar, Chairperson

The hawksbill (*Eretmochelys imbricata*) sea turtle has been classified as critically endangered. Reductions in populations call for protective strategies, one being the implementation of protected areas. However, as a highly migratory species, preservation and restoration is difficult, as protection is required in nesting, foraging, and breeding regions. To establish adequate protected areas to aid hawksbill survival, a clear understanding of movement patterns between protected and unprotected regions is required. A foraging aggregation of juvenile hawksbills resides off the coast of Roatán, Honduras within the Sandy Bay West End Marine Reserve. The reserve is a protected area, but also spans the coast of a popular tourist region. As tourism in the area continues to increase, the use of boats continues to rise. Alteration of marine organism behavior, injury and mortality are common results of increased boating pressure, but boating activities in the reserve is increasing without assessment or the implementation of additional regulations. I set out to estimate international connections between this protected aggregation and international nesting rookeries, to assess the suitability of the reserve as a recruitment zone, and to further assess the effect of boating pressure on hawksbill distribution and behavior. Using mitochondrial DNA haplotypes, I evaluated the genetic structure of this foraging aggregation and further estimated natal origins through mixed stock analysis. I assessed the suitability of the reserve using species distribution modeling in MaxEnt and used resource, disturbance, and benthic environmental values as predictor variables. Using a series of in-water behavioral observations, I assessed the effect of boat traffic on hawksbill distribution and behavior. Haplotype analysis suggested the presence of unique haplotypes not currently associated with known nesting rookeries. Mixed stock analyses suggest that juveniles in the reserve originated from rookeries in Colombia, Puerto Rico, and Costa Rica. MaxEnt outputs suggested that the reserve is moderately to highly suitable for hawksbill inhabitance, with resource environmental variables having the greatest influence on species distribution. Although hawksbills remain at risk of boat strikes, increased boating pressure did not significantly affect in-water behavior. Since the reserve is an important local foraging area for juvenile hawksbills, measures to maintain and increase suitability should be implemented.

CHAPTER ONE

INTRODUCTION

According to the International Union for Conservation of Nature (IUCN), over 28,000 animal species are currently threatened. Whether classified as vulnerable, endangered, critically endangered, or extinct, several factors related to human activities have led to species decline. In addition to commercial development, human intrusion and disturbance, pollution, habitat shifting, and harvesting are some anthropogenic factors that negatively influence species survival (IUCN 2020). Apart from collecting general information on endangered species, laboratory and observational studies have taken place on threatened species to understand developmental processes, life histories, movement patterns, and characteristics of their required habitats. Using the information garnered from these studies, conservation strategies can be implemented to preserve species and overall species diversity.

Although once abundant, six of the seven sea turtle species are now listed on the IUCN Red List of Threatened Species as either vulnerable, threatened, endangered, or critically endangered (IUCN 2020). The decline in sea turtle populations can, to some extent, be attributed to anthropogenic activities, such as exploitation of eggs (Aguirre et al. 2006, Mancini et al. 2011), incidental fisheries by-catch (Poiner et al. 1996, Witzell 1999, Gallo et al. 2006, Lewison et al. 2007), exposure to pathogens or pollutants (Aguirre et al. 2006, Gallo et al. 2006), and the destruction of nests and foraging areas due to coastal development and dredging (Jackson et al. 2001, Marcovaldi et al. 2007, Finkbeiner et al. 2011, Gaos et al. 2012, Guimarães et al. 2017). Among these species, the hawksbill (*Eretmochelys imbricata*) is currently classified as critically endangered, worldwide.

In addition to the typical threats experienced by all sea turtle species, the hawksbill has been specifically targeted for direct capture and trade. In the last decade, hawksbill populations have diminished by approximately 80% due to trade and other anthropogenic activities (Bräutigam et al. 2006, Bowen et al. 2007, Mortimer et al. 2008). Earliest records of commercial trade for hawksbill shells, frequently referred to as “bekko” in Asian countries, began in the 19th and early 20th centuries (Witzell 1983). Unsustainable harvests persisted for hundreds of years as several European, Asian, and Caribbean countries participated in the harvest and trade. Trade remained unregulated until 1977 when the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES) banned international trade between attesting countries. Prior to joining CITES in 1980, Japan was the largest importer of sea turtle products, importing a minimum of 2,250,000 sea turtles, of which 40 tons per year were hawksbills (Canin 1991). An active market in bekko existed in the Caribbean in countries such as Honduras, Nicaragua, Panama, and the Cayman Islands (Cruz et al. 1987, Milliken et al. 1987, Canin 1989) where thousands of hawksbill were captured each year. Current global estimates suggest that well over 4 million hawksbills have been killed and traded in the past 150 years (Miller et al. 2019).

To preserve threatened species and replenish their populations, protected areas have been established to conserve and maintain biological diversity, and natural and cultural resources (Phillips et al. 2002). However, since the hawksbill is highly migratory throughout ontogeny, preservation and restoration of this diminishing species can be difficult, as protection is required in nesting, internesting, foraging, and breeding regions. Applied nesting conservation measures have increased nesting events and hatchling production (Hays 2004, Dutton et al. 2005, Troëng et al. 2005, Mortimer et al. 2011). However, in the remaining stages of ontogeny, few protected areas have been established with the sole intent of protecting sea turtles and their essential habitats. Instead, sea turtles traverse and settle into previously established protected areas that were implemented with management goals unrelated to sea turtle species. (Dobbs et al. 2007, Gaos et al. 2012, Hart et al. 2012, Gorham et al. 2014). Yet, in some cases, researchers have utilized data collected through telemetry to lobby for the extension of protected areas to include sea turtle internesting areas and foraging home ranges (Schofield et al. 2013, Hays et al. 2014, Dawson et al. 2017, Fuentes et al. 2018). While direct-take and other destructive practices by the public are prohibited and enforced in these protected areas, recreational activities and their effects on presence and distribution of threatened species are often overlooked (Hilborn 2015, Hayes et al. 2017, Gabriella et al. 2019).

Boating is a popular, often unregulated activity in marine protected areas. As tourism in coastal regions continues to grow, recreational activities requiring the use of boats and marine vessels continue to increase (McCarthy 2004). Studies have shown that boating alters the presence and behavior of several marine species. Vessel presence at assorted densities has been shown to negatively impact feeding, socializing, and resting behaviors in numerous species including Mediterranean damselfish (*Chromis chromis*) (Bracciali et al. 2012), bottlenose dolphins (*Tursiops truncatus*) (Bas et al. 2015), manatees (*Trichechus manatus*) (Miksis-Olds et al. 2007), and killer whales (*Orcinus orca*) (Lusseau et al. 2009). In addition to behavioral alteration, unregulated boating has led to injury and death in several aquatic species, such as the Atlantic sturgeon (*Acipenser ocyrinchus ocyrinchus*) (Brown et al. 2010), dugongs (*Dugong dugon*) (Greenland et al. 2007), and Spectacled Caiman crocodiles (*Caiman crocodilus fuscus*). During their neritic near-shore stage, hawksbills inhabit shallow reefs. During this period, their close proximity to shore increases the overlap of their core use areas with boating activities. Several reports of sea turtle injuries, deaths, and strandings have resulted from boat collisions (Orós et al. 2005, Casale et al. 2010, Denkinger et al. 2013). Previous studies have assessed the ability of sea turtles to avoid incoming vessel traffic, their diving capabilities in response to passing traffic, and the implementation of management strategies to reduce encounters (Hazel 2009), but few have assessed the influence of boat traffic on in-water behaviors and overall sea turtle distribution in neritic zones (Tyson et al. 2017).

In addition to the absence of regulations for recreational activities in protected areas, there is a paucity of data on benthic environments and overall suitability of protected areas for hawksbill residence. Habitat modeling and species mapping have become essential tools in predicting species distributions and identifying suitable regions for inhabitance (Hooker et al. 2011). Regression methods have been used to interpret habitat suitability from species occurrence records, however, these methods require systematic collection of both presence and absence occurrence points (Elith et al. 2011). MaxEnt (Phillips et al. 2017), a machine learning method, has been implemented to identify complex interactions within ecological systems when presence-only occurrence records are the only records available (Phillips et al. 2008). Using this method, the suitability of a protected area can be assessed for the inhabitance of endangered species, such as the hawksbill sea turtle.

Although efforts have been made to implement protected areas to safeguard various sea turtle populations and aggregations, a clear understanding of regional and international migration patterns throughout ontogeny and the connections between populations and aggregations is still relatively scarce. In order to establish adequate marine protected areas to aid hawksbill survival, a clear understanding of migration patterns between protected and unprotected areas is required. Studies have shown that foraging populations are composed of multiple nesting stocks, creating various relationships among remote populations (Bass 1999). Molecular methods have been employed to confirm mixed stock composition and estimate sea turtle movement patterns between these regions. According to a review by Lee (2008), one of the most widely used markers in sea turtle research is the maternally inherited mitochondrial DNA (mtDNA) haplotype. Using haplotypes, distinct nesting populations have been defined throughout sea turtle ranges (Browne et al. 2010, Leroux et al. 2012, Hill et al. 2018). With these distinctions, several nesting populations in the Caribbean (Troeng et al. 2005, Blumenthal et al. 2009), the Atlantic (Monzón-Argüello et al. 2011, Proietti et al. 2014), and the Pacific (Gaos et al. 2017, Zuñiga-Marroquin et al. 2017, Gaos et al. 2018) have been linked to both proximal (Bowen et al. 2007) and distal (Cazabon-Mannette et al. 2016) feeding aggregations.

A forging aggregation of juvenile hawksbill sea turtles has been reported off the northwestern coast of Roatán, Honduras, within the boundaries of the Sandy Bay West End Marine Reserve (SBWEMR) (Dunbar et al. 2016, Dunbar et al. 2017). Although another region off the coast of Roatán, approximately 30 km from the SBWEMR, has been suggested to be an important juvenile recruiting ground (Dunbar et al. 2008), studies on juvenile hawksbills in the region of the SBWEMR are limited. To date, no previous studies have linked hawksbill turtles foraging in Honduras to international nesting beaches. The population structure and natal origins of hawksbills turtles found foraging in the SBWEMR remain unknown. In addition, as a popular costal region known for tourism, both visitor influx and boat traffic in the area are increasing without assessment or the implementation of additional regulations (Ministry of Tourism, unpublished data). With tourism rapidly growing in the area, the suitability of the SBWEMR for hawksbill residence and future recruitment should be assessed. Hawksbills are essential contributors to the tropical near-shore environment, since they are able to influence the composition and distribution of species in coral reef ecosystems (Bjorndal et al. 2003). Effective implementation of protective measures that ensure the stabilization and growth of hawksbill populations will also assure the biodiversity and equilibrium of reef ecosystems remains viable. Hawksbill sea turtles and the reefs they occupy are also vital to the tourism industry. Without these creatures, the allure of the SBWEMR may decrease, negatively impacting the adjacent communities that heavily rely on income from the tourism sector.

Research Goals, Objectives and Hypotheses

The overarching goal of this dissertation was to estimate international connections between this protected aggregation and international nesting rookeries, and assess the suitability of the Sandy Bay West End Marine Reserve as a recruitment zone for foraging juvenile hawksbills.

- I specifically aimed to evaluate the genetic structure of the foraging aggregation and estimate natal origins through mixed stock analysis (MSA), defining the connection of juveniles in the SBWEMR to nesting rookeries in the wider Caribbean. I aimed to suggest international migration routes and assess how factors, such as rookery size and distance, and ocean surface currents, influence rookery contributions.
    - I hypothesized that the SBWEMR foraging aggregation would be a mixed stock composed of individuals from various rookeries in the wider Caribbean, as indicated by a haplotype diversity greater than the baseline rookeries.
    - I hypothesized that our aggregation would be comprised of juveniles from distal rookeries, indicated by higher percent contributions from Barbados, Antigua, and Tobago.
- Secondly, using species distribution modeling I aimed to assess the habitat suitability of the SBWEMR, combining hawksbill occurrence data with environmental variables likely influencing hawksbill distribution in the reserve. With MaxEnt, I aimed to evaluate habitat suitability using presence-only hawksbill occurrence points and three environmental variables: boat traffic intensities, prey item distributions, and benthic characterizations. I aimed to evaluate which environmental variables had the greatest effect on hawksbill

distribution and which regions of the SBWEMR were most suitable for hawksbill use.

  - I hypothesized that regions of high prey item count and percent cover within the SBWEMR would be more suitable for hawksbill inhabitance than those of low prey item count and percent cover.
  - I hypothesized high suitability in regions of low boat traffic intensity and high prey item distribution.

- Lastly, I aimed to evaluate the effect of boat traffic on the presence, distribution, and behavior of juvenile hawksbills found foraging within the reserve.
  - I hypothesized that boat traffic intensity in the SBWEMR would differ depending on the location and time of day. Specifically, I hypothesized that boat traffic intensity would be greatest in West End and West Bay, and during the afternoon time period.
  - I hypothesized that hawksbill distribution would be influenced by boat traffic intensity, with hawksbill presence greatest in regions of lower boat traffic intensity.
  - I hypothesized that hawksbills would spend less time foraging, eating, and surfacing in regions of high boat traffic intensity, compared to regions of low boat traffic intensity.

References

Aguirre, A. A., S. C. Gardner, J. C. Marsh, S. G. Delgado, C. J. Limpus and W. J. Nichols (2006). Hazards associated with the consumption of sea turtle meat and eggs: a review for health care workers and the general public. *EcoHealth* **3**(3): 141-153.

Bas, A. A., A. A. Ozturk and B. Ozturk (2015). Selection of critical habitats for bottlenose dolphins (*Tursiops truncatus*) based on behavioral data, in relation to marine traffic in the Istanbul Strait, Turkey. *Marine Mammal Science* **31**(3): 979-997.

Bass, A. L. (1999). Genetic analysis to elucidate the natural history and behavior of hawksbill turtles (*Eretmochelys imbricata*) in the wider Caribbean: A review and re-analysis. *Chelonian Conservation and Biology* **3**(2): 195-199.

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

Bowen, B. W., W. S. Grant, Z. Hillis-Starr, D. J. Shaver, A. Bjorndal, A. B. Bolten and A. L. Bass (2007). Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. *Molecular Ecology* **16**(1): 49-60.

Bracciali, C., D. Campobello, C. Giacoma and G. Sara (2012). Effects of nautical traffic and noise on foraging patterns of Mediterranean damselfish (*Chromis chromis*). *Plos One* **7**(7): e40582.

Bräutigam, A. and K. L. Eckert (2006). Turning the tide: exploitation, trade and management of marine turtles in the Lesser Antilles, Central America, Colombia and Venezuela. Cambridge, Traffic International.

Brown, J. J. and G. W. Murphy (2010). Atlantic sturgeon vessel-strike mortalities in the Delaware Estuary. *Fisheries* **35**(2): 72-83.

Browne, D. C., J. A. Horrocks and F. A. Abreu-Grobois (2010). Population subdivision in hawksbill turtles nesting on Barbados, West Indies, determined from mitochondrial DNA control region sequences. *Conservation Genetics* **11**(4): 1541-1546.

Canin, J. (1989). International Trade in Sea Turtle Products. Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology, Jekyll Island, Georgia, NOAA Technical Memorandum NMFS-SEFC-232.

Canin, J. (1991). International trade aspects of the Japanese Hawksbill shell (‘Bekko’) industry. *Marine Turtle Newsletter* **54**: 17-21.

Casale, P., M. Affronte, G. Insacco, D. Freggi, C. Vallini, P. Pino d'Astore, R. Basso, G. Paolillo, G. Abbate and R. Argano (2010). Sea turtle strandings reveal high anthropogenic mortality in Italian waters. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**(6): 611-620.

Cazabon-Mannette, M., D. Browne, N. Austin, A. Hailey and J. Horrocks (2016). Genetic structure of the hawksbill turtle rookery and foraging aggregation in Tobago, West Indies. *Journal of Experimental Marine Biology and Ecology* **485**: 94-101.

Cruz, G. A. and M. Espinal (1987). National Report for Honduras. Western Atlantic Turtle Symposium II. Mayagüez, Puerto Rico**:** WATS2-047.

Dawson, T. M., A. Formia, P. D. Agamboué, G. M. Asseko, F. Boussamba, F. Cardiec, E. Chartrain, P. D. Doherty, J. M. Fay and B. J. Godley (2017). Informing marine protected area designation and management for nesting olive ridley sea turtles using satellite tracking. *Frontiers in Marine Science* **4**: 312.

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

Dobbs, K., L. Fernandes, S. Slegers, B. Jago, L. Thompson, J. Hall, J. Day, D. Cameron, J. Tanzer and F. MacDonald (2007). Incorporating marine turtle habitats into the marine protected area design for the Great Barrier Reef Marine Park, Queensland, Australia. *Pacific Conservation Biology* **13**(4): 293-302.

Dunbar, S. G., D. S. Baumbach, C. T. Hayes, M. K. Wright and L. Salinas (2017). Activities of the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR) in Honduras. Annual Report of the 2015 and 2016 Seasons.

Dunbar, S. G., C. T. Hayes and D. S. Baumbach (2016). Impacts of Recreational Diving on Hawksbill Sea Turtles (*Eretmochelys imbricata*) in the Sandy Bay West End Marine Reserve, Honduras. Annual Report of the 2014 Summer Research Season.

Dunbar, S. G., L. Salinas and L. Stevenson (2008). In-Water Observations of Recently Released Juvenile Hawksbills (*Eretmochelys imbricata*). *Marine Turtle Newsletter* **121**: 5-9.

Dutton, D. L., P. H. Dutton, M. Chaloupka and R. H. Boulon (2005). Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biological Conservation* **126**(2): 186-194.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee and C. J. Yates (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17**(1): 43-57.

Finkbeiner, E. M., B. P. Wallace, J. E. Moore, R. L. Lewison, L. B. Crowder and A. J. Read (2011). Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. *Biological Conservation* **144**(11): 2719-2727.

Fuentes, M. M., A. J. Gillis, S. A. Ceriani, T. L. Guttridge, M. P. V. Z. Bergmann, M. Smukall, S. H. Gruber and N. Wildermann (2018). Informing marine protected areas in Bimini, Bahamas by considering hotspots for green turtles (*Chelonia mydas*). *Biodiversity and Conservation* **28**(1): 1-15.

Gabriella, L. M. and S. Gianluca (2019). A false sense of protection: recreational uses and illegal behaviour in a Mediterranean Marine Protected Area and implications for management. *Integrated Environmental Assessment and Management*.

Gallo, B. M., S. Macedo, B. d. B. Giffoni, J. H. Becker and P. C. Barata (2006). Sea turtle conservation in Ubatuba, southeastern Brazil, a feeding area with incidental capture in coastal fisheries. *Chelonia Conservation and Biology* **5**(1): 93-101.

Gaos, A. R., R. L. Lewison, M. P. Jensen, M. J. Liles, A. Henriquez, S. Chavarria, C. M. Pacheco, M. Valle, D. Melero and V. Gadea (2017). Natal foraging philopatry in eastern Pacific hawksbill turtles. *Royal Society Open Science* **4**(8): 170153.

Gaos, A. R., R. L. Lewison, M. P. Jensen, M. J. Liles, A. Henriquez, S. Chavarria, C. M. Pacheco, M. Valle, D. Melero and V. Gadea (2018). Rookery contributions, movements and conservation needs of hawksbill turtles at foraging grounds in the eastern Pacific Ocean. *Marine Ecology Progress Series* **586**: 203-216.

Gaos, A. R., R. L. Lewison, B. P. Wallace, I. L. Yanez, M. J. Liles, W. J. Nichols, A. Baquero, C. R. Hasbun, M. Vasquez, J. Urteaga, et al. (2012). Spatial ecology of critically endangered hawksbill turtles *Eretmochelys imbricata*: implications for management and conservation. *Marine Ecology Progress Series* **450**: 181-U198.

Gorham, J. C., D. R. Clark, M. J. Bresette, D. A. Bagley, C. L. Keske, S. L. Traxler, B. E. Witherington, B. M. Shamblin and C. J. Nairn (2014). Characterization of a Subtropical Hawksbill Sea Turtle (*Eretmocheyles imbricata*) Assemblage Utilizing Shallow Water Natural and Artificial Habitats in the Florida Keys. *Plos One* **9**(12): 16.

Greenland, J. A. and C. J. Limpus (2007). Marine wildlife stranding and mortality database annual report 2006, II Cetacean and pinniped, Brisbane, Environmental Protection Agency. **18:** 2011.

Guimarães, S. M., D. C. Tavares and C. Monteiro-Neto (2017). Incidental capture of sea turtles by industrial bottom trawl fishery in the Tropical South-western Atlantic.

Journal of the Marine Biological Association of the United Kingdom **98**(6): 1525-1531.

Hart, K. M., A. R. Sartain, I. Fujisaki, H. L. Pratt, D. Morley and M. W. Feeley (2012). Home range, habitat use, and migrations of hawksbill turtles tracked from Dry Tortugas National Park, Florida, USA. *Marine Ecology Progress Series* **457**: 193 - 207.

Hayes, C. T., D. S. Baumbach, D. Juma and S. G. Dunbar (2017). Impacts of recreational diving on hawksbill sea turtle (*Eretmochelys imbricata*) behaviour in a marine protected area. *Journal of Sustainable Tourism* **25**(1): 79-95.

Hays, G. C. (2004). Good news for sea turtles. *Trends in Ecology & Evolution* **19**(7): 349-351.

Hays, G. C., J. A. Mortimer, D. Ierodiaconou and N. Esteban (2014). Use of Long-Distance Migration Patterns of an Endangered Species to Inform Conservation Planning for the World's Largest Marine Protected Area. *Conservation Biology* **28**(6): 1636-1644.

Hazel, J. (2009). Turtles and vessels: threat evaluation and behavioural studies of green turtles in near-shore foraging grounds, James Cook University.

Hilborn, R. (2015). Marine Protected Areas miss the boat. *Science* **350**(6266): 1326-1326.

Hill, J. E., C. M. King, K. R. Stewart, F. V. Paladino and P. H. Dutton (2018). Genetic Differentiation of Hawksbill Turtle Rookeries on St. Croix, US Virgin Islands. *Chelonia Conservation and Biology* **17**(2): 303-308.

Hooker, S. K., A. Cañadas, K. D. Hyrenbach, C. Corrigan, J. J. Polovina and R. R. Reeves (2011). Making protected area networks effective for marine top predators. *Endangered Species Research* **13**(3): 203-218.

IUCN. "IUCN Red List of threatened species." Retrieved 2020, 2020, from www.iucnredlist.org.

Jackson, J. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson and J. A. Estes (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**(5530): 629-637.

Lee, P. L. M. (2008). Molecular ecology of marine turtles: New approaches and future directions. *Journal of Experimental Marine Biology and Ecology* **356**(1-2): 25-42.

Leroux, R. A., P. H. Dutton, F. Alberto Abreu-Grobois, C. J. Lagueux, C. L. Campbell, E. Delcroix, J. Chevalier, J. A. Horrocks, Z. Hillis-Starr, S. Troeng, et al. (2012). Re-examination of Population Structure and Phylogeography of Hawksbill Turtles in the Wider Caribbean Using Longer mtDNA Sequences. *Journal of Heredity* **103**(6): 806-820.

Lewison, R. L. and L. B. Crowder (2007). Putting longline bycatch of sea turtles into perspective. *Conservation Biology* **21**(1): 79-86.

Lusseau, D., D. E. Bain, R. Williams and J. C. Smith (2009). Vessel traffic disrupts the foraging behavior of southern resident killer whales Orcinus orca. *Endangered Species Research* **6**(3): 211-221.

Mancini, A., J. Senko, R. Borquez-Reyes, J. G. Póo, J. A. Seminoff and V. Koch (2011). To poach or not to poach an endangered species: elucidating the economic and social drivers behind illegal sea turtle hunting in Baja California Sur, Mexico. *Human Ecology* **39**(6): 743-756.

Marcovaldi, M. A., G. G. Lopez, L. S. Soares, A. J. Santos, C. Bellini and P. C. Barata (2007). Fifteen years of hawksbill sea turtle (*Eretmochelys imbricata*) nesting in Northern Brazil. *Chelonian Conservation and Biology* **6**(2): 223-228.

McCarthy, E. (2004). International Regulation of Underwater Sound: Establishing Rules and Standards to Address Ocean Noise Pollution. Boston, MA, Kluwer Academic Publishers.

Miksis-Olds, J. L., P. L. Donaghay, J. H. Miller, P. L. Tyack and J. A. Nystuen (2007). Noise level correlates with manatee use of foraging habitats. *The Journal of the Acoustical Society of America* **121**(5): 3011-3020.

Miller, E. A., L. McClenachan, Y. Uni, G. Phocas, M. E. Hagemann and K. Van Houtan (2019). The historical development of complex global trafficking networks for marine wildlife. *Science Advances* **5**(3): eaav5948.

Milliken, T. and H. Tokunaga (1987). The Japanese sea turtle trade, 1970-1986, Center for Environmental Education.

Monzón-Argüello, C., N. Loureiro, C. Delgado, A. Marco, J. Lopes, M. Gomes and A. Abreu-Grobois (2011). Príncipe island hawksbills: genetic isolation of an eastern Atlantic stock. *Journal of Experimental Marine Biology and Ecology* **407**(2): 345-354.

Mortimer, J. A. and M. Donnelly (2008). "Marine Turtle specialist group IUCN red list status assessment: Hawksbill turtle (*Eretmochelys imbricata*)."

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

Orós, J., A. Torrent, P. Calabuig and S. Déniz (2005). Diseases and causes of mortality among sea turtles stranded in the Canary Islands, Spain (1998–2001). *Dis Aquat Organ* **63**(1): 13-24.

Phillips, A. and W. C. Union (2002). Management guidelines for IUCN category V protected areas: Protected landscapes/seascapes, IUCN--the World Conservation Union.

Phillips, S. J. and M. Dudík (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**(2): 161-175.

Phillips, S. J., M. Dudík and R. E. Schapire (2017). Maxent software for modeling species niches and distributions (Version 3.4. 1). *Biodiversity Informatics*.

Poiner, I. and A. N. M. Harris (1996). Incidental capture, direct mortality and delayed mortality of sea turtles in Australia's Northern Prawn Fishery. *Marine Biology* **125**(4): 813-825.

Proietti, M. C., J. Reisser, L. F. Marins, C. Rodriguez-Zarate, M. A. Marcovaldi, D. S. Monteiro, C. Pattiaratchi and E. R. Secchi (2014). Genetic Structure and Natal Origins of Immature Hawksbill Turtles (Eretmochelys imbricata) in Brazilian Waters. *Plos One* **9**(2): 12.

Schofield, G., R. Scott, A. Dimadi, S. Fossette, K. A. Katselidis, D. Koutsoubas, M. K. S. Lilley, J. D. Pantis, A. D. Karagouni and G. C. Hays (2013). Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate. *Biological Conservation* **161**: 101-109.

Troeng, S., P. H. Dutton and D. Evans (2005). Migration of hawksbill turtles Eretmochelys imbricata from Tortuguero, Costa Rica. *Ecography* **28**(3): 394-402.

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

Tyson, R. B., W. E. Piniak, C. Domit, D. Mann, M. Hall, D. P. Nowacek and M. M. Fuentes (2017). Novel Bio-Logging Tool for Studying Fine-Scale Behaviors of Marine Turtles in Response to Sound. *Frontiers in Marine Science* **4**: 219.

Witzell, W. (1983). Synopsis of biological data on the hawksbill turtle, Eretmochelys imbricata (Linnaeus, 1766), Food & Agriculture Org.

Witzell, W. N. (1999). Distribution and relative abundance of sea turtles caught incidentally by the US pelagic longline fleet in the western North Atlantic Ocean, 1992-1995. *Fishery Bulletin* **97**(1): 200-211.

Zuñiga-Marroquin, T. and A. Espinosa de los Monteros (2017). Genetic characterization of the Critically Endangered hawksbill turtle (*Eretmochelys imbricata*) from the Mexican Pacific region. *Latin American Journal of Aquatic Research* **45**(3): 555-562.

CHAPTER TWO

UNCOVERING THE CONNECTION: ESTABLISHING GENETIC LINKAGES OF A JUVENILE HAWKSBILL FORAGING POPULATION USING HAPLOTYPE ANALYSIS

Marsha K. Wright[1,2,*]and Stephen G. Dunbar[1,2]

[1]Protective Turtle Ecology Center for Training, Outreach and Research, Inc.
(ProTECTOR, Inc.), Loma Linda, CA 92350, sdunbar@llu.edu
[2]Marine Research Group, Department of Earth and Biological Sciences, Loma Linda
University, Loma Linda, CA 92350
**Corresponding author: Marsha Wright mkwright@llu.edu*

Abstract

Hawksbill sea turtles are classified as a critically endangered species worldwide. They reside in tropical and subtropical regions of the world and their nesting populations and foraging aggregations can be found within the Indo-Pacific, Pacific, Caribbean, Atlantic, and Mediterranean regions. To estimate hawksbill movement patterns between nesting populations and foraging aggregations, molecular markers have been used to define relationships between the two. Specifically, mitochondrial DNA (mtDNA) markers have been utilized to estimate the contributions of source rookeries to a single mixed stock foraging aggregation through mixed stock analysis (MSA). The Sandy Bay West End Marine Reserve (SBWEMR) is a marine reserve off the coast of Roatán, Honduras. Presently, an uncharacterized aggregation of juvenile hawksbill turtles has been found foraging within the reserve. We used mtDNA haplotypes to analyze the population structure of this juvenile hawksbill foraging aggregation and estimated natal origins through MSA. MtDNA from 35 individual juvenile hawksbills indicated the presence of 14 haplotypes within the SBWEMR foraging aggregation. Bayesian mixed stock analysis with equal and weighted priors suggested greatest rookery contributions from Colombia (33 %), Costa Rica (17 %), and Puerto Rico (15 %). The trajectories of two prevalent ocean surface currents within the Caribbean helped strengthen these suggestions. Although Colombia, Costa Rica, and Puerto Rico were the highest estimated contributors of the entire baseline stock, the presence of several unique haplotypes within the SBWEMR foraging aggregation suggests the need for additional rookery data. The SBWEMR remains an important recruiting zone for juvenile hawksbills from both known and unknown rookeries of the wider Caribbean. Measures should be taken to ensure this valuable location remains viable for future juvenile recruitment.

Keywords: mtDNA, mixed stock analysis, foraging aggregation, Roatán, Honduras, *Eretmochelys imbricata*, Caribbean, population genetics, marine protected areas

Introduction

The hawksbill is a critically endangered sea turtle species that utilizes tropical and subtropical regions of the world. Various hawksbill populations can be found in the Indo-Pacific (Nishizawa et al. 2012), Pacific (Gaos et al. 2017), Caribbean (Bass et al. 1996, Bjorndal et al. 2003), Atlantic (Ferreira et al. 2018), and Mediterranean (Camiñas et al. 2004) oceans. Over the past several decades, hawksbill populations have diminished by approximately 80% due to anthropogenic activities that have decimated and destroyed regions important to hawksbill development and maturation (Meylan 1998, Meylan et al. 1999, Bowen et al. 2007, Mortimer et al. 2008). Similar to most sea turtle species, the hawksbill's "critically endangered" classification (IUCN 2020) can specifically be attributed to anthropogenic activities, such as exploitation of eggs (Wallace et al. 2011), exposure to pathogens or pollutants (Sarmiento-Ramírez et al. 2014), accidental by-catch (Jackson et al. 2001, Finkbeiner et al. 2011, Guimarães et al. 2017), coastal development, and dredging (Dickerson et al. 2007). In addition, the popularity of hawksbill shell as a commercial trade item has made this species a target for direct capture and trade (Witzell 1983, Meylan 1998, Harrison et al. 2017).

Hawksbill sea turtles are known to migrate throughout ontogeny, potentially spending their hatchling, post-hatchling, juvenile, and adult stages in separate regions. Adequate beaches are essential for adult females to nest and lay new clutches of hatchlings, while the pelagic and neritic zones of the ocean are also of great importance as hatchlings disperse through the open sea, develop into juveniles, and settle in near shore reefs to forage and continue development. As they reach maturity, adult sea turtles may transition to new foraging grounds before migrating to breeding grounds in the vicinity of their nesting region of choice (Meylan 1999, Spotila 2004, Reich et al. 2007). Since the hawksbill is a highly migratory species, preservation and restoration of declining populations may be difficult. Population loss due to the exploitation or damage of essential habitats in one region may negatively affect other distant, yet connected, populations and aggregations. Therefore, hawksbill preservation requires a clear understanding of regional movement patterns, the preservation of life during each stage, and the protection of habitats in which hawksbills spend each life stage. Understanding the connectivity between nesting, foraging, and breeding grounds is essential for accurate measures of sea turtle survivability and the implementation of management strategies.

Numerous methods have been employed to estimate movements of sea turtles and suggest connections between various populations. Massive capture-mark-recapture projects of tagged turtles have been used in the Caribbean to uniquely identify sea turtles and record their sightings and locations over time (Meylan 1999). However, tag loss is an important factor of concern in tagging projects (Limpus 1992). Since capture-mark-recapture methods of tagged turtles can be cumbersome and require years of opportunistic reoccurring captures to build connections among populations and aggregations (Blumenthal et al. 2009), acoustic (Carrion-Cortez et al. 2013), radio (Berube et al. 2012), and satellite telemetry (Godley et al. 2008) have also been employed as additional means to track turtle movements. However, using telemetry to analyze the movements of migratory animals can be difficult, expensive, and time consuming. To complement tagging projects, researchers have employed molecular markers to establish connections among sea turtle populations. The ability of molecular markers to identify and differentiate between populations has led researchers to use molecular markers in conservation research (Lee 2008).

Molecular markers have been used to estimate sea turtle movements and establish connections between nesting rookeries and foraging aggregations (Bass et al. 1996). Individual molecular markers and several combinations of molecular markers, such as microsatellites, single nucleotide polymorphisms (SNPs), restriction fragment length polymorphisms (RFLPs), and mitochondrial DNA (mtDNA) haplotypes have been used to asses genetic diversity (Bowen et al. 2007), estimate stock structure and population groupings (Karl et al. 1992), map evolutionary relationships (Naro-Maciel et al. 2008), evaluate bottleneck events (Natoli et al. 2017), and determine dispersal and recruitment patterns (Putman et al. 2014). Each of these molecular markers have various characteristics that enable them to reveal genetic variations between individuals and populations. However, according to Lee (2008), one of the most widely used molecular markers in sea turtle research is the mitochondrial DNA haplotype. Mitochondrial DNA (mtDNA) has become a popular marker due to its high variability and elevated mutation rate, and its strict clonal maternal inheritance (Galtier et al. 2009). Initial mtDNA studies used sequences of relatively short lengths averaging only about 300 – 500 bp in length

(Norman et al. 1994, Lahanas et al. 1998, Bowen et al. 2007, Blumenthal et al. 2009). Since longer sequences averaging about 800 bps in length are able to detect greater variation, many recent studies combine genetic analysis of shorter sequences with those of longer sequences, leading to enhanced differentiation among populations (Leroux et al. 2012). Using genetic markers, the contributions of source rookeries to a single mixed stock can be calculated through mixed stock analysis (Pella et al. 2001, Manel et al. 2005, Bolker et al. 2007).

Presently, an uncharacterized foraging aggregation of juvenile hawksbill sea turtles resides off the northwestern coast of Roatán, Honduras (Dunbar et al. 2016, Dunbar et al. 2017). The genetic compositions of numerous foraging aggregations in the Caribbean and around the world have been analyzed and connected with natal rookeries (Bass et al. 1996, Bowen et al. 1996, Bass 1999, Blumenthal et al. 2009, Leroux et al. 2012, Gorham et al. 2014, Cazabon-Mannette et al. 2016), yet the genetic structure of the foraging aggregation within the Sandy Bay West End Marine Reserve (SBWEMR) remains unknown. The goal of this study was to use mtDNA haplotype analysis to evaluate the genetic structure of the juvenile hawksbill aggregation foraging in the SBWEMR, and genetically characterize and estimate natal origins through mixed stock analysis (MSA). Using these data, our goal was to define the connection of juveniles in the SBWEMR to nesting rookeries in the wider Caribbean and assess how factors, such as rookery size and ocean surface currents, influence rookery contributions.

Methods

Study Site

Roatán is the largest and most populated of the three Bay Islands of Honduras, and is located about 55 km north of mainland Honduras (16˚21' 44'' N, 86˚25' 06'' W). Situated in the western Caribbean Sea as part of the Mesoamerican Barrier Reef system, Roatán is surrounded by barrier, fringing, patch, and sloping reefs that range in depths from 5 - 40 m. Roatán is approximately 60 km long and 8 km wide. Although several protected areas have been established off the coast of Honduras, the SBWEMR is located off the northwestern coast of Roatán. The reserve was established in 1988 to aid in reducing the impacts of deleterious human activities on inshore reef areas. Currently, the SBWEMR encompasses approximately 13 km of Roatán's coastline, stretching from the western tip of the island at West Bay along the northern shore to Sandy Bay (RMP 2015)(Figure 1).

In-water Surveys and Turtle Captures

Using SCUBA, in-water surveys were performed during dives in the morning (8:30 – 10:30) and afternoon (14:30 – 16:30) time periods. Dives were completed in a strip transect pattern at established dive sites within the SBWEMR, as described by Baumbach et al. (2019). When able, swimming or resting hawksbill turtles were gently captured by hand and brought to the surface.

Turtle Measurements and Identification

Captured turtles were transferred to the Roatán Dive Center for individual work-up and sample collection. Standard measurements (curved carapace length (CCL_{min}), curved carapace width (CCW) and weight were recorded for each turtle following methods by Dunbar et al. (2008) and Berube et al. (2012). For positive in-water identification, each turtle was tagged in the front right flipper using a unique Inconel style 681 metal tag (National Band and Tag Co.). Dorsal and lateral views of the head were photographed for each turtle and uploaded to the HotSpotter database for photo identification purposes (Dunbar et al. 2017).

Tissue Sample Collection and Storage

Once captured, measured, and tagged, blood samples were collected from each turtle. Using a 5 mL syringe and a 22-gauge needle inserted approximately 1 cm beneath the skin, approximately 3 - 4 mL of blood was collected from the dorsal cervical sinus (ProTECTOR 2015). While in the field, approximately 3 drops of whole blood were stored in 1.5 mL of cell lysis buffer and subsequently frozen. Once transferred to the laboratory, approximately 500 µL of each sample was relocated into new microcentrifuge tubes and placed in a -20 ˚C freezer. The remainder of each sample was stored in the refrigerator until ready for use.

Laboratory Analysis

DNA Extraction and Polymerase Chain Reaction (PCR)

DNA was extracted using the standard extraction protocol for reptilian blood as amended by Duran et al. (2015). A 10-µL portion of the extraction sample was used to check initial nucleic acid concentration and purity on a NanoDrop (Thermo Scientific NanoDrop 2000 spectrophotometer, Delaware, USA). Extraction products greater than 1µg in concentration were diluted 1, 2, or 3-fold prior to PCR. A segment of the mitochondrial control region (d-loop), approximately 900 bps in length, was amplified through PCR using LCM15382 forward primer and H950 reverse primer (see appendix for primer sequences) (Vargas et al. 2015, Gaos et al. 2016, Rees et al. 2017). PCR reaction mixtures (50µl) included 25 µL of PCR master mix, 1 µL of 100 µM forward primer, 1 µL of 100 µM reverse primer, 22 µL of nuclease-free water, and 1 µL of ~ 400 ng genomic DNA (Thermo Scientific Maxima Hot Start PCR Master Mix kit, Delaware, USA). Positive and negative controls were used to check for contamination and primer efficiency. PCR was performed using the following thermocycler conditions: 4 minutes at 95 °C, followed by 30 cycles of 30 seconds at 95 °C, 30 seconds at 52 °C, and 60 seconds at 72 °C, and a final extension step at 72 °C for 5 minutes. Amplified products were checked for quality and contamination by electrophoresis in a 1.2 % agarose gel (Vargas et al. 2015).

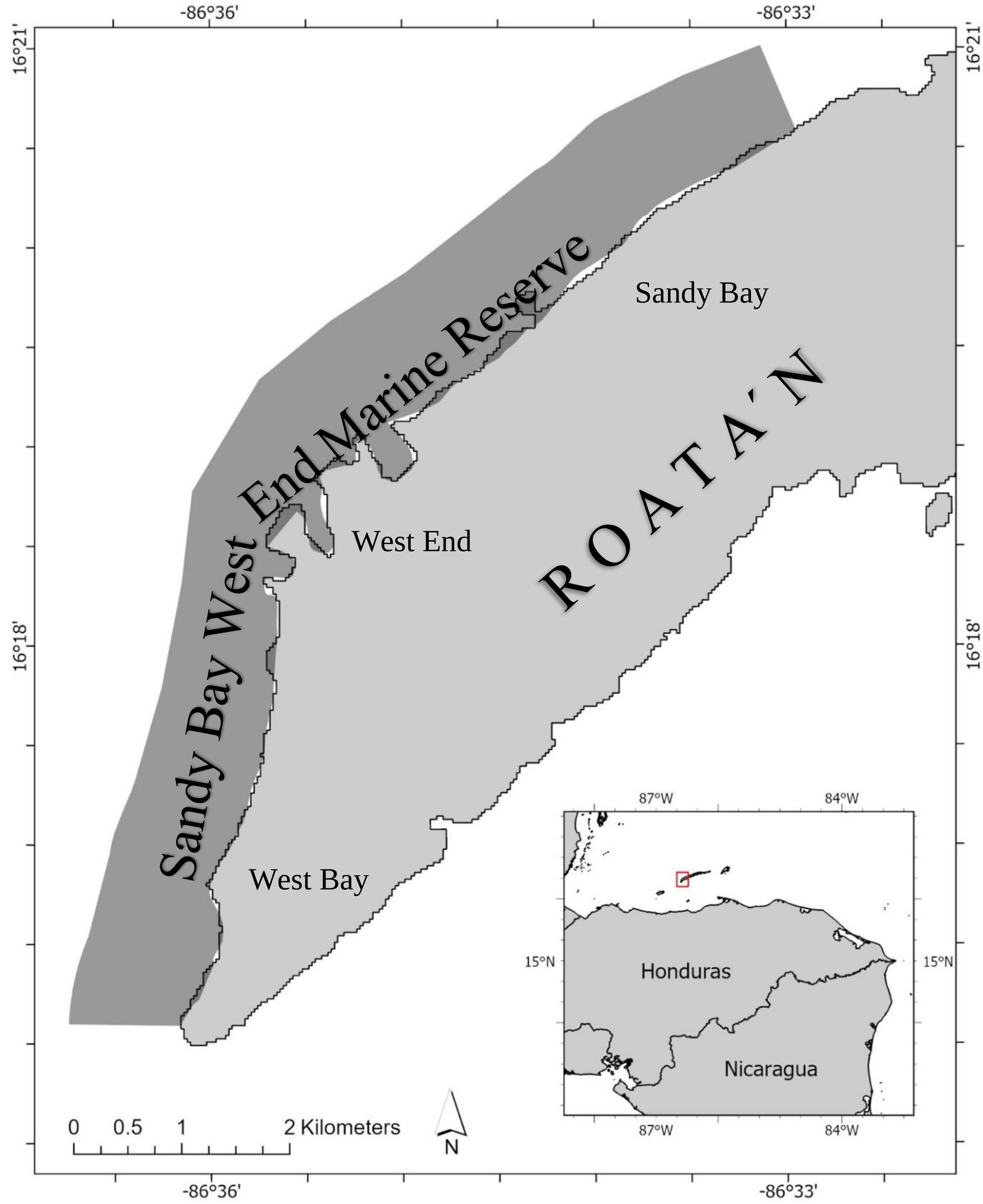

Figure 1. The Sandy Bay West End Marine Reserve (SBWEMR) - The SBWEMR encompasses approximately 13 km of Roatán's coastline, stretching from the western tip of the island at West Bay along the northern shore to Sandy Bay.

Sequencing and Characterization of Haplotypes

All purification and sequencing reactions were completed by Eton Bioscience, Inc (California, USA). Amplified PCR samples were purified and treated with ExoSAP-it (Eton Bioscience Inc., California, USA) according to the Eton Bioscience Inc. standard PCR purification protocol. Forward and reverse sequencing reactions were performed using LCM15382 and H950 as the forward and reverse primers, respectively. To ensure sequencing quality of the 3' end, we used an additional forward primer, EIIFP91, during sequencing reactions. PCR samples and primers were combined with BigDye Terminator (DNA Polymerase, dNTPs, ddNTPs) and run on a PCR Thermocycler. After sequencing, samples were purified using magnetic beads and ethanol washes. All procedures were performed on an ABI 3730xl DNA Sequencers. Sequences obtained using LCM15382 forward primer and EIIFP91 internal forward primers were combined and trimmed accordingly to form whole consensus sequences 736 bp in length. Using Geneious 11.0.2., we then aligned consensus sequences and named them according to haplotype matches made with published hawksbill haplotypes.

Data Analysis

Genetic Diversity and Rookery Contribution

Haplotype frequencies of 14 nesting rookeries were obtained from literature and personal communication for: Antigua (Levasseur et al. 2019), Barbados (Browne et al. 2010), Colombia (Trujillo-Arias et al. 2014), Costa Rica (Leroux et al. 2012), Cuba (Diaz-Fernandez et al. 1999), Dominican Republic, Guadeloupe, Mexico, Nicaragua (Leroux et al. 2012), Puerto Rico (Velez-Zuazo et al. 2008), Tobago (Cazabon-Mannette et al. 2016), and the US Virgin Islands (Leroux et al. 2012). Using Arlequin 3.5.2.2., we calculated genetic diversity of the SBWEMR foraging aggregation and each potential contributing rookery and reported haplotype diversity, nucleotide diversity, and F_{st} values. Rookery contributions were estimated using BAYES program. Markov Chain Monte Carlo (MCMC) analysis was conducted with equal weighted priors and weighted priors for rookery size and rookery distance. MCMC analyses were conducted using 14 chains, one for each baseline stock. In each analysis, MCMC runs for each chain were 50,000 steps in length and the starting value of stock proportions was 0.95 for the baseline sample corresponding with the chain analyzed, while the value of stock proportions for the remaining 14 baseline samples were 0.00385. Gelman and Rubin shrink factor was calculated for each analysis to assess convergence of the chains to the desired posterior density. Mixed-stock composition was estimated for each analysis from the mean of all fourteen chains after 25,000 burn-in steps. Dirichlet prior of stock proportions varied depending on the type of analysis; equal weighted priors, weighted priors for rookery size, or weighted priors for rookery distance (Table 1).

Buoy Dispersion – Drifter Analysis

To estimate the influence of surface ocean currents on hatchling dispersal, we identified surface currents leading to Honduras and the region of the SBWEMR. Data were acquired from drifter buoys placed by the National Oceanic and Atmospheric Administration (NOAA) as part of the Global Drifter Program (deployed drifter buoys continually record and transmit location data (accuracy 0.1 – 2.0 km) via satellite, which is then used to calculate ocean current direction and velocity) (NOAA, USA). A full database search (see appendix for link to database) was completed to identify drifter buoys within the Caribbean basin from 2012 – 2017. A fine-scale search identified buoys that drifted within the Mesoamerican Reef system and within 100 km of Honduras and the SBWEMR (Roatán) (See Appendix for buoy information). In addition, surface current patterns were assessed through time using the Ocean Surface Current Analyses Real-time (OSCAR) global surface current database. Surface current patterns within the Caribbean basin were evaluated for changes in surface current speed and direction from 2012 – 2017.

Results

Haplotype Composition and Genetic Diversity

We successfully extracted, amplified, and sequenced mtDNA from 35 individual juvenile hawksbills. Using 17 polymorphic sites, a total of 14 mtDNA control region haplotypes were identified within the SBWEMR foraging aggregation (see appendix for haplotype sequences). The following ten haplotype sequences identified within the SBWEMR foraging aggregation have been previously characterized and are associated with Atlantic/Caribbean rookeries: EiA01, EiA02, EiA09, EiA11, EiA20, EiA41, EiA43, EiA47, EiA63, EiA83. The four remaining haplotype sequences (EiA24, EiA42, EiA80, and EiA95) although present in the hawksbill haplotype database, have not yet been associated with specific rookeries (Table 2).

Table 1. Dirichlet Priors of Stock Proportions. Prior values used for mixed stock analysis for the equal weight model and models weighted for rookery size and distance. Values were scaled among rookeries, with larger and more distal rookeries receiving larger Dirichlet values.

Rookery	**Equal Priors**	**Weighted Priors - Size**	**Weighted Priors - Distance**
AJB	0.07143	0.02873	0.10543
BBL	0.07143	0.21228	0.11729
BBW	0.07143	0.02123	0.11729
CCV	0.07143	0.01274	0.06347
CRT	0.07143	0.00354	0.0384
CDL	0.07143	0.08732	0.03821
DRS	0.07143	0.00212	0.06923
GMG	0.07143	0.02137	0.10718
MXY	0.07143	0.36796	0.02707
NPC	0.07143	0.02901	0.02519
PMI	0.07143	0.10473	0.08568
TOB	0.07143	0.01585	0.11262
UBI	0.07143	0.02236	0.09293
USP	0.07143	0.07076	0.09293

Note: AJB = Antigua – Jumby Bay; BBL = Barbados – Leeward; BBW = Barbados – Windward; CCV = Colombia – Cabo de la Vela; CRT = Costa Rica – Tortugero; CDL = Cuba – Doce Leugas; DRS = Dominican Republic – Saona Island; GMG = Guadeloupe – Marine Galante; MXY = Mexico – Yucatan; NPC = Nicaragua – Pearl Cays; PMI = Puerto Rico – Mona Island; TOB = Tobago UBI = USVI – Buck Island; USP = USVI – Sandy Point.

Previously characterized haplotypes EiA01, EiA11, and EiA20 were the most abundant haplotypes found within the SBWEMR foraging population and accounted for 28 %, 25 %, and 8 % of the sampled population, respectively. The calculated haplotype (h) and nucleotide (π) diversities for the SBWEMR foraging aggregation were 0.862 (+/- 0.039 SD) and 0.008 (+/- 0.004 SD), respectively. Our study aggregation showed the greatest haplotype diversity when compared to the baseline stocks (Table 3). Ten haplotypes were present in both the SBWEMR foraging aggregation and the baseline stocks. An additional four haplotypes found within the SBWER foraging aggregation were not included in the contribution analyses since they were absent from the baseline stocks. Nucleotide diversity of the SBWEMR population (0.008 +/- 0.004 SD) was also greater than each of the rookeries in the baseline. Fixation index (F_{st}) comparison generated by an AMOVA test indicated significant variation in genetic composition between our aggregation and the baseline stocks (Fst = 0.549). F_{st} comparison between each baseline stock indicated significant genetic variation among all baseline rookeries included in the analyses (Table 4). Gelman and Rubin shrink factor for each chain was less than 1.2, indicating sufficient convergence.

Table 2. Haplotype frequencies of baseline stocks and the SBWEMR foraging aggregation. Fourteen different rookeries were used as the baseline for the analysis. Fourteen different haplotypes were found within the SBWEMR foraging aggregation. Of the fourteen haplotypes, four (bolded) were unique to the SBWEMR, not associated with published rookeries.

	N	EiA01	EiA02	EiA03	EiA09	EiA11	EiA12	EiA13	EiA18	EiA20	EiA21	EiA22	EiA23	EiA24	EiA28	EiA29	EiA30	EiA41	EiA42	EiA43	EiA47	EiA52	EiA63	EiA65	EiA80	EiA83	EiA84	EiA95	Reference
Jumby Bay, Antigua	250	155		89		3				2																1			Levasseur - unpublished
Barbados Leeward	54	54																											Browne et al. 2010
Barbados Windward	30	3			6	21																							Browne et al. 2010
Cabo de la Vela, Columbia	29	12		1	2	13																	1						Trujillo-Arias et al. 2014
Tortuguero, Costa Rica	60		11		3	33	5										1				6	1							LeRoux et al. 2012
Doce Leguas, Cuba	70	62				1		5								1	1												Diaz-Fernandez et al. 1999
Saona Island, Dominican Republic	33	3				22			2	6																			Carreras et al. 2013
Marie-Galante, Guadeloupe	72	2			69		1																						LeRoux et al. 2012
Yucatan, Mexico	20											2	16					1		1									LeRoux et al. 2012
Pearl Cays, Nicaragua	95		19			54														16				1			5		LeRoux et al. 2012
Mona Island, Puerto Rico	109	3			2	60			1	34	6									3									Velez-Zuazo et al. 2008
Tobago	39	24			2	9									3					1									Cazabon-Mannette et al. 2016
Buck Island, USVI	67	8		2	2	50				4			1																LeRoux et al. 2012
Sandy Point, St. Crois, USVI	41	33		1		7																							LeRoux et al. 2012
SBWEMR	35	10	1		2	9				3				**1**				1	**1**	1	2		1		**1**	2		**1**	Wright - unpublished
TOTAL:	1004	369	31	93	88	282	6	5	3	49	6	2	17	1	3	1	2	2	1	22	8	1	2	1	1	3	5	1	

Table 3. Haplotype and Nucleotide Diversities. Haplotype and nucleotide diversities of the SBWEMR foraging aggregation and each baseline rookery sampled in the wider caribbean, sample size (n), number of haplotypes (H), and haplotype (h) and nucleotide (π) diversities with respective SD.

Foraging Aggregation	n	H	h	SD+/-	π	SD+/-
SBWEMR	36	14	0.862	0.039	0.008	0.004

Rookery	n	H	h	SD+/-	π	SD+/-
Jumby Bay, Antigua	250	5	0.491	0.019	0.007	0.004
Barbados (Leeward)	54	1	0.000	0.000	0.000	0.000
Barbados (Windward)	30	3	0.476	0.091	0.003	0.002
Cabo de la Vela, Columbia	29	5	0.643	0.054	0.008	0.004
Tortuguero, Costa Rica	60	6	0.656	0.057	0.007	0.004
Doce Leguas, Cuba	70	5	0.213	0.064	0.003	0.002
Yucatan, Mexico	20	4	0.363	0.131	0.001	0.001
Pearl Cays, Nicaragua	95	4	0.552	0.044	0.005	0.003
Sandy Point, USVI	41	3	0.331	0.082	0.005	0.003
Buck Island, USVI	67	6	0.430	0.072	0.004	0.002
Galet, Guadeloupe	72	3	0.082	0.044	0.001	0.001
Tobago	39	5	0.574	0.074	0.007	0.004
Mona Island, Puerto Rico	109	7	0.600	0.035	0.003	0.002
Sanoa Island, Dominican Republic	33	4	0.527	0.089	0.003	0.002

Mixed Stock Analysis - Rookery Contributions

Bayesian estimates of rookery contributions with equal weighted priors and weighted priors for rookery size and distance indicated relatively low contributions from baseline rookeries. Bayesian mixed stock analysis with equal weighted priors estimated greatest contributions from Colombia – Cabo de la Vela (mean = 0.33, CI = 0 – 0.38) , Costa Rica - Tortugero (mean = 0.17, CI = 0 – 0.4), and Puerto Rico – Mona Island (mean = 0.15, CI = 0 – 0.4) (Figure 2A). Using weighted priors for rookery size, Bayesian mixed stock analysis suggested greatest contributions from Colombia – Cabo de la Vela (mean = 0.44, CI = 0 – 0.82), Puerto Rico – Mona Island (mean = 0.19, CI = 0 – 0.43), and Costa Rica - Tortugero (mean = 0.12, CI = 0 - 0.37) (Figure 2B). When we used weighted priors for rookery distance, Bayesian mixed stock analysis indicated greatest contributions from Colombia – Cabo de la Vela (mean = 0.26, CI = 0 – 0.68), Costa Rica - Tortugero (mean = 0.17, CI = 0 – 0.40), and Puerto Rico – Mona Island (mean = 0.16, CI = 0 – 0.41) (Figure 2C).

Buoy Dispersion – Drifter Analysis

A total of 70 drifters were located within the Caribbean between 2004 – 2017. Of these seventy, ten were associated within the Mesoamerican Reef basin, but only three were present in the Mesoamerican Reef basin within 100 km of Roatán, Honduras between 2012 – 2017 (see appendix for drifter data).   The first drifter buoy (WMO ID 43560) was found approximately 100 km west of Roatán and indicated a southern drift along the coast of Belize towards mainland Honduras. The current then shifted northeast sending the drifter buoy towards Roatán (Figure 3A & 3B). The second (WMO ID

42552) and third (WMO ID 42557) drifter buoys, indicated the same current pattern. Both buoys approached Roatán from the southeast and then shifted northeast towards Roatán (Figure 3C & 3D). Several other drifters were deployed directly into the Mesoamerican Reef system, but were removed after only approximately 30 days of drifting and were repositioned in other regions where they remained for several years. All buoys deployed in the Mesoamerican reef system remained relatively close to their initial deployment points for the entire duration of their individual drift periods. However, overall final movements of drifters indicated a slight northeastern drift within the Mesoamerican Reef basin (Figure 3). The paucity of drifting data collected from these buoys required us to undertake additional surface current assessments using OSCAR. OSCAR-simulated data suggested the presence of a westerly current sweeping south of Puerto Rico towards Central America (Figure 4A) and the presence of a circular current off the coast of Colombia, Panama, and Costa Rica (Figure 4B, C, D, & F). However, over time, the strength of this current dissipates, and the trajectory shifts north towards Honduras (Figure 4E).

Table 4. Fixation (Fst) index estimates. Values greater than 0.2 indicate population isolation and differentiation. All values were significant ($p < 0.005$). AJB = Antigua – Jumby Bay; BBL = Barbados – Leeward; BBW = Barbados – Windward; CCV = Colombia – Cabo de la Vela; CRT = Costa Rica – Tortugero; CDL = Cuba – Doce Leugas; DRS = Dominican Republic – Saona Island; GMG = Guadeloupe – Marine Galante; MXY = Mexico – Yucatan; NPC = Nicaragua – Pearl Cays; PMI = Puerto Rico – Mona Island; TOB = Tobago UBI = USVI – Buck Island; USP = USVI – Sandy Point.

	AJB	**BBL**	**BBW**	**CRT**	**MXY**	**NPC**	**USP**	**UBI**	**GMG**	**TOB**	**DRS**	**CCV**	**CDL**	**PMI**
AJB	0.0000	-	-	-	-	-	-	-	-	-	-	-	-	-
BBL	0.6500	0.0000	-	-	-	-	-	-	-	-	-	-	-	-
BBW	0.5137	0.8198	0.0000	-	-	-	-	-	-	-	-	-	-	-
CRT	0.4509	0.6611	0.4213	0.0000	-	-	-	-	-	-	-	-	-	-
MXY	0.4626	0.7547	0.4413	0.3507	0.0000	-	-	-	-	-	-	-	-	-
NPC	0.5421	0.8958	0.5734	0.4547	0.4829	0.0000	-	-	-	-	-	-	-	-
USP	0.4857	0.6718	0.4763	0.4020	0.4136	0.5089	0.0000	-	-	-	-	-	-	-
UBI	0.5565	0.8546	0.6041	0.4917	0.5287	0.6571	0.5344	0.0000	-	-	-	-	-	-
GMG	0.5303	0.7670	0.5524	0.4611	0.4858	0.5922	0.5038	0.6123	0.0000	-	-	-	-	-
TOB	0.4831	0.7492	0.4720	0.3825	0.3941	0.5124	0.4396	0.5498	0.5086	0.0000	-	-	-	-
DRS	0.4986	0.7887	0.4982	0.4015	0.4171	0.5431	0.4580	0.5780	0.5312	0.4490	0.0000	-	-	-
CCV	0.6403	0.9535	0.7872	0.6494	0.7280	0.8472	0.6614	0.8227	0.7491	0.7273	0.7608	0.0000	-	-
CDL	0.6005	0.8812	0.6937	0.5766	0.6311	0.7445	0.6019	0.7401	0.6804	0.6411	0.6696	0.8535	0.0000	-
PMI	0.4648	0.6339	0.4452	0.3759	0.3836	0.4762	0.4233	0.5025	0.4750	0.4104	0.4276	0.6250	0.5688	0.0000

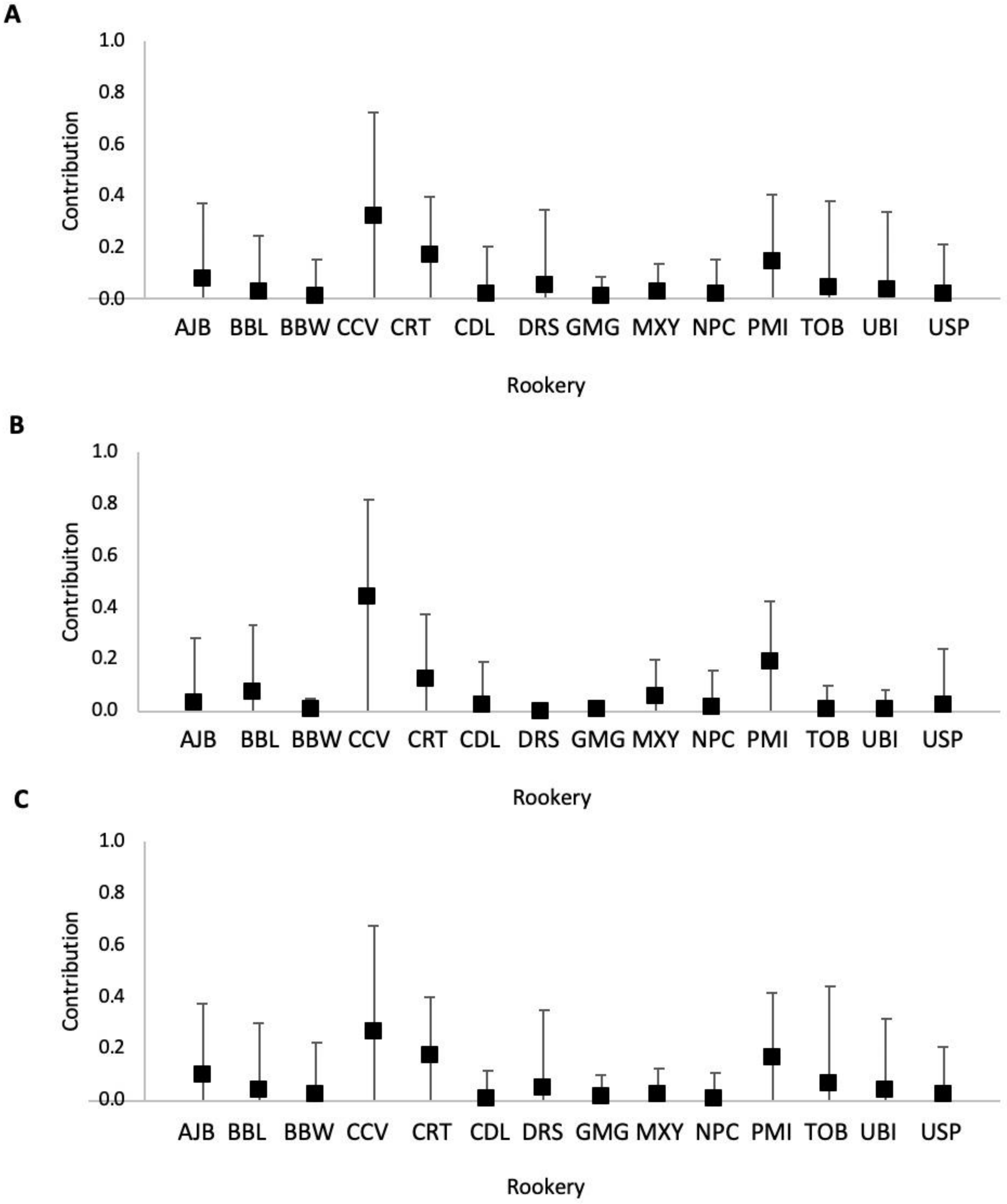

Figure 2. Rookery contributions (Equal Weight) (A), Rookery contributions (Weighted Size) (B), Rookery contributions (Weighted Distance) (C) – AJB = Antigua – Jumby Bay; BBL = Barbados – Leeward; BBW = Barbados – Windward; CCV = Colombia – Cabo de la Vela; CRT = Costa Rica – Tortugero; CDL = Cuba – Doce Leugas; DRS = Dominican Republic – Saona Island; GMG = Guadeloupe – Marine Galante; MXY = Mexico – Yucatan; NPC = Nicaragua – Pearl Cays; PMI = Puerto Rico – Mona Island; TOB = Tobago UBI = USVI – Buck Island; USP = USVI – Sandy Point.

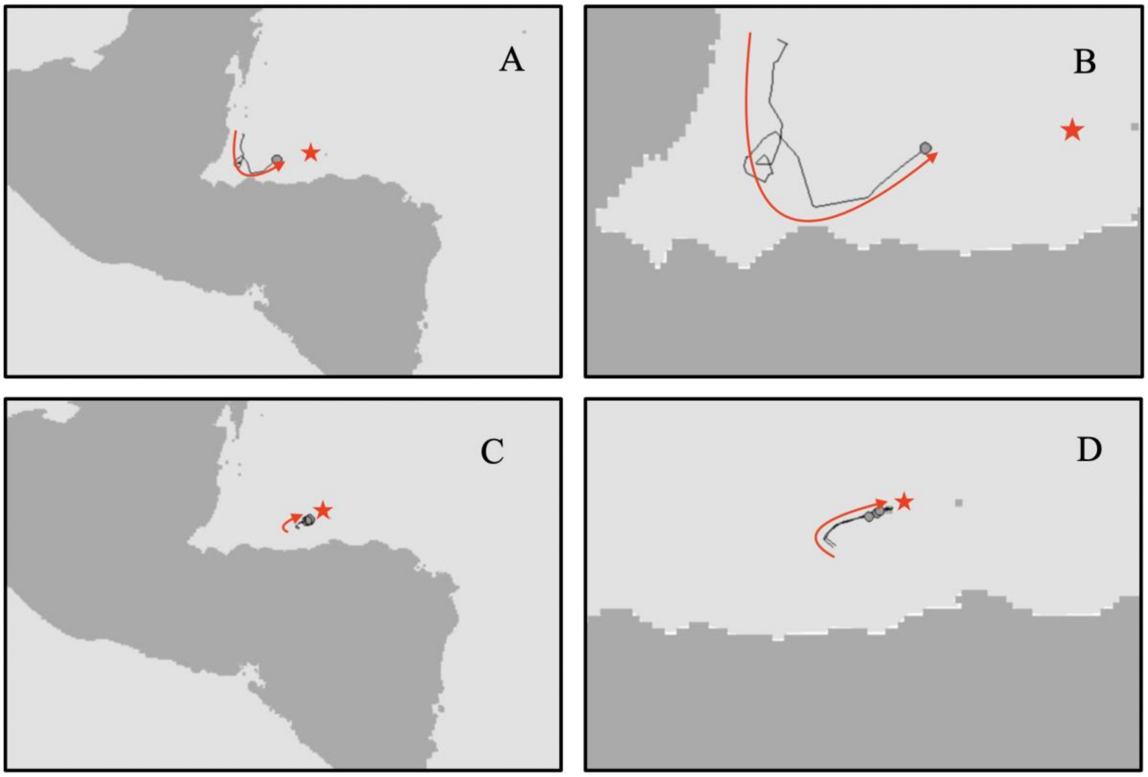

Figure 3. Drifter Buoy Trajectories – Drifter buoys, present between 2012 – 2017, indicated two trajectories located north of mainland Honduras. The direction of movement is indicated by arrows and the end of each buoy's trajectory is denoted with a filled circle. The first buoy (WMO ID 43560) drifted south along the coast of Belize towards mainland Honduras, then shifted northeast towards Roatán (A). A closer view of Figure 3a (B). The remaining two drifters (WMO ID 42252 and 42257) approached Roatán from the southeast and then shifted trajectories heading northeast (C). A closer view of figure 3b (D). Red stars indicate the general location of Roatán, Bay Island, Honduras.

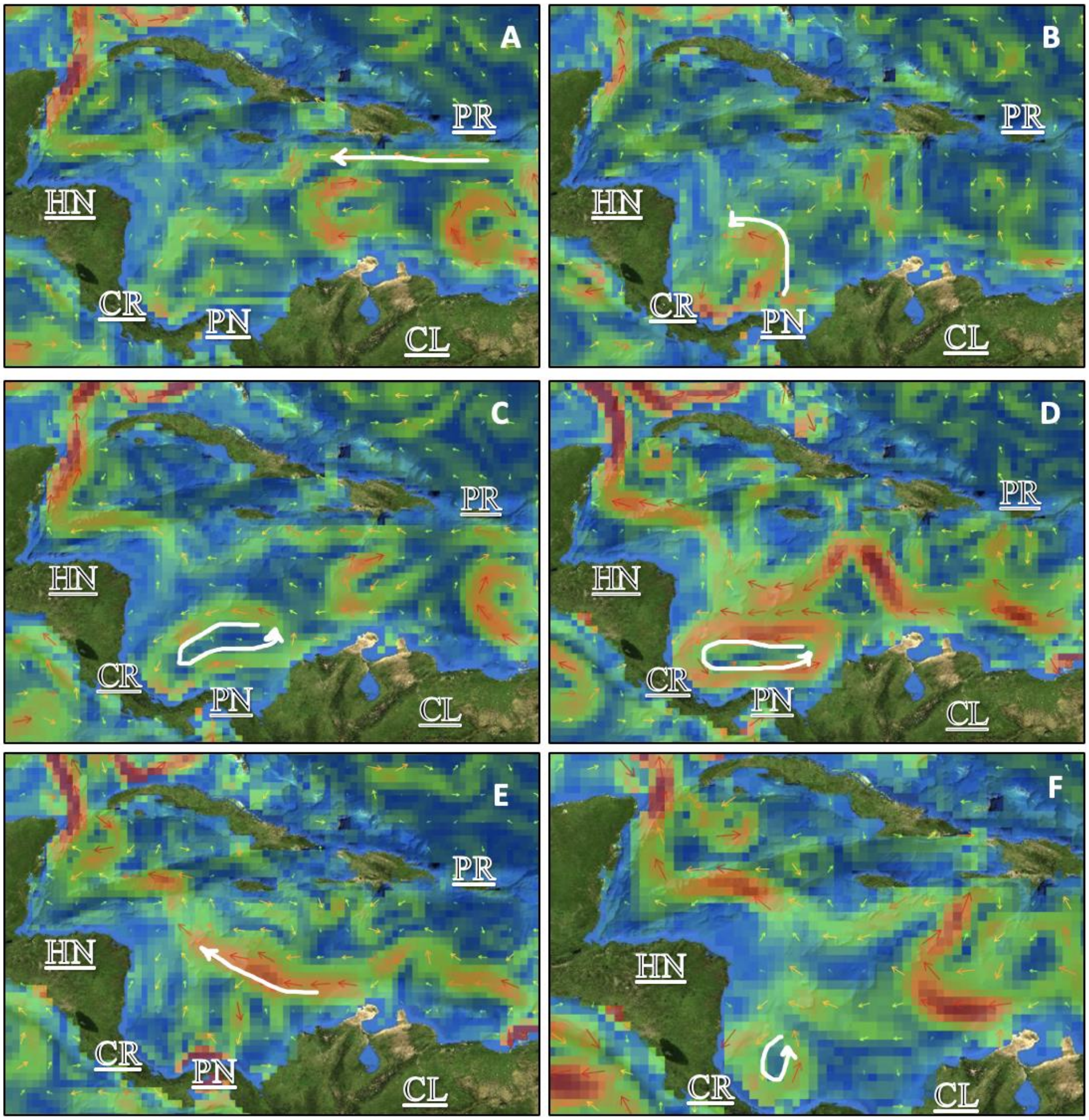

Figure 4. OSCAR Global Surface Currents – Arrow and current color depict strength of current in m/s, increasing from blue to red (blue – 0m/s; green – 0.3 m/s; yellow – 0.55 m/s; orange – 0.7 m/s; red – 1 m/s). Arrow size depicts the strength of the current, while arrow direction represents the direction of the surface current. The presence of a westerly current sweeping south of Puerto Rico (PR) further into the Caribbean (A). The formation and presence of a circular current off the coast of Colombia (CO), Panama (PA), and Costa Rica (CR) (B-E). No distinct currents lead directly to the Honduran coast (A - F).

Discussion

An uncharacterized foraging aggregation of juvenile hawksbill sea turtles resides off the northwestern coast of Roatán, Honduras, within the SBWEMR (Dunbar et al. 2016). The current study is the first to characterize a Honduran foraging aggregation and suggest juvenile recruitment patterns based on rookery contribution estimates. MtDNA analyses suggested the presence of fourteen 736-bp haplotypes within the SBWEMR juvenile aggregation.

Typical of foraging aggregations, the presence of various haplotypes suggests the SBWEMR aggregation is of mixed stock composition, as has been found elsewhere in the wider Caribbean (Bass 1999). Elevated haplotype diversity of our foraging aggregation in comparison to baseline stocks, suggested that our aggregation contained a greater number of haplotypes than each of the baseline rookeries. Four haplotypes (EiA24, EiA42, EiA80, EiA95) unique to our foraging aggregation, have yet to be associated with specific nesting rookeries. However, haplotype EiA24 has been associated with foraging aggregations in the Cayman Islands (Blumenthal et al. 2009), but foraging aggregations associated with haplotypes EiA42, EiA80, and EiA95 have not yet been published. Initially haplotype EiA83 was only associated with foraging aggregations in Florida and Tobago (Wood et al. 2013, Gorham et al. 2014, Cazabon-Mannette et al. 2016). However, due to an expansion in sample size of nesting turtles, this haplotype was recently associated with a nesting rookery in Antigua (Levasseur et al. 2019). These results suggest the presence of additional uncharacterized rookeries that may contribute to the SBWEMR aggregation.

Fixation estimates among individual nesting rookeries indicated significant genetic variation among nesting sites. Although genetic variation between Costa Rica and both Tobago and Puerto Rico were relatively low, due to substantial geographic distance, all three rookeries were considered distinct and separate (Gonzalez-Garza et al. 2015).

Bayesian mixed stock analysis estimated rookery contributions using equal weighted priors and priors weighted for rookery size. Bayesian mixed stock analysis with equal weighted priors estimated rookery contributions from Colombia, Costa Rica, and Puerto Rico. Bayesian mixed stock analysis with priors weighted for rookery size, also estimated rookery contributions from Colombia, Costa Rica, and Puerto Rico, but with smaller confidence intervals, as seen with several other studies conducted in the Caribbean (Bass et al. 2004, Naro-Maciel et al. 2007). Relatively large confidence intervals have been difficult to avoid, since haplotype data from several potential source rookeries remain unavailable, and several haplotypes are broadly shared among distant rookeries (Putman et al. 2013). Although large confidence intervals are typical of mixed stock analyses, since wide-ranging confidence intervals are present (Blumenthal et al. 2009, Monzon-Arguello et al. 2010, Monzón-Argüello et al. 2011, Proietti et al. 2014), additional information is required to corroborate mixed stock analysis interpretations. As seen in studies by Putman et al. (2013) and Blumenthal et al. (2009), the inclusion of ocean surface current data may provide clearer interpretations of hatchling dispersals and rookery contributions.

Long distance dispersals of hatchlings by ocean surface currents have been documented (Browne et al. 2010, Mansfield et al. 2014, Cazabon-Mannette et al. 2016) . The results of our study also suggest that long distance dispersal may be influenced by existing surface currents. There are a number of well-known ocean currents that flow through the Atlantic and Caribbean. However, once within the Caribbean, the fine-scale movements of ocean surface currents are highly specific within our region of study. For our study, simulated surface current data acquired from the OSCAR database indicated a direct current south of Puerto Rico moving west towards Central America. Although this current begins to dissipate before reaching the coasts of Central America, a slight northerly current may aid in the continued drift of post-hatchlings towards the Mesoamerican Reef basin (Figure 4A). In addition, larger juveniles nearing the age of neritic recruitment may shift from drift dispersal behavior to active swimming prior to settling into neritic foraging grounds. Putman et al. (2013) suggest that with larger body size, swimming becomes a larger component of net velocity in dispersal, and juvenile turtles are able to move more independently of currents. This behavioral change may aid in the recruitment of juveniles from Puerto Rico to the SBWEMR as the westerly current declines. While some post-hatchlings have been known to migrate long distances to foraging grounds (Bowen et al. 2007, Grossman et al. 2007), some juveniles have settled into neritic foraging habitats closer to their beaches of estimated origin (Browne et al. 2010, Cazabon-Mannette et al. 2016). The close proximity of the SBWEMR to Colombia and Costa Rica, and the presence of currents leading from these regions towards the SBWEMR provide some support for our results, suggesting relatively short distance post-hatchling dispersals from Colombia and Costa Rica. OSCAR simulated data suggest the presence of a circular current off the coast of Colombia, Panama, and Costa Rica (Figure 4B, C, D, & F)). However, over time, the current shifts northward towards Honduras.

Drift patterns of post-hatchlings carried by this current could possibly transport turtles towards Honduran waters and towards the SBWEMR.

Time period of dispersal may also influence rookery contributions and haplotype frequencies. As currents leading towards the Mesoamerican Reef vary over time, dispersal of post-hatchlings and genetic characterization of the SBWEMR foraging aggregation may likewise vary. A study by Bjorndal et al. (2008) of green turtles in the Bahamas over a 12-year period indicated that haplotype frequencies of foraging aggregations changed over time. These changes were attributed to the shifting of ocean currents during the oceanic stage, leading to recruitment of post-hatchlings and juveniles from different rookies. Although temporal shifts in haplotype frequencies were not observed with hawksbills in a study by Velez-Zuazo et al. (2008) in Puerto Rico, their results were likely due to both a shorter 3-year study period and small sample size. Understanding the consequences of changes through time on dispersal of post-hatchlings is important to effectively estimate all contributions from various regions, and to develop meaningful management strategies.

Although Colombia, Costa Rica, and Puerto Rico have the highest estimated contributions of the entire baseline stock, the overall contribution from the baseline stock to the SBWEMR juvenile aggregation remains relatively small. Several haplotypes found within the SBWEMR aggregation were removed from the analysis due to their absence from the baseline stock. Our preliminary results suggest the need for additional rookery data. Several accounts of regular nesting populations have been reported on Utila and Guanaja (Dunbar et al. 2019), and mainland Honduras (Meylan 1999), although these nesting rookeries have not yet been genetically characterized. Recent tagging reports in

2019 from work on Utila (Dunbar pers. comm.), suggest that several turtles nesting on Utila were at one-point forging juveniles within the SBWEMR. These additional reports pose the idea of Utila as a potential contributor to the SBWEMR foraging aggregation. However, until additional information can be collected, implementation of management units that include the SBWEMR foraging aggregation remains difficult. Although foraging aggregations, such as that in the SBWEMR, have distant rookery contributions, several potential contributing rookeries remain uncharacterized. However, with information garnered from this study, protection of rookeries in Colombia, Costa Rica, and Puerto Rico may be essential for continued recruitment of juvenile foraging turtles into this area of the Western Caribbean.

Acknowledgments

We would like to thank the Department of Earth and Biological Science and the Protective Turtle Ecology Center for Training, Outreach, Research, Inc. (ProTECTOR, Inc.) for funding this work. We gratefully acknowledge Alberto Abreu-Grobois, Kate Levasseur, Michelle Cazabon-Mannette, and Robin LeRoux for their involvement in procuring recent haplotype records. We extend our gratitude to the Roatan Dive Center for their continued collaboration and support during our field work in Honduras. We are grateful to the many ProTECTOR, Inc. Interns and Volunteers who helped with sample collection. Finally, we express our gratitude to Jimmy Miller for providing logistical support and to Lidia Salinas for securing permits for work in Honduras. This project was permitted under the department of Fisheries (DIGEPESCA/SAG – Honduras) permit No. 251-10, the Institute for Forest Conservation (ICF-Honduras) permit No. DE-MP-055-2016 and ASG-ICF-139-2018, and Loma Linda University IACUC protocol No. 8120038 and 8150049.

References

Bass, A. L. (1999). Genetic analysis to elucidate the natural history and behavior of hawksbill turtles (*Eretmochelys imbricata*) in the wider Caribbean: A review and re-analysis. *Chelonian Conservation and Biology* **3**(2): 195-199.

Bass, A. L., S. P. Epperly and J. J. C. G. Braun-McNeill (2004). Multi-year analysis of stock composition of a loggerhead turtle (Caretta caretta) foraging habitat using maximum likelihood and Bayesian methods. **5**(6): 783-796.

Bass, A. L., D. A. Good, K. A. Bjorndal, J. I. Richardson, Z. M. Hillis, J. A. Horrocks and B. W. Bowen (1996). Testing models of female reproductive migratory behaviour and population structure in the Caribbean hawksbill turtle, Eretmochelys imbricata, with mtDNA sequences. *Molecular Ecology* **5**(3): 321-328.

Baumbach, D. S., E. C. Anger, N. A. Collado and S. G. Dunbar (2019). Identifying Sea Turtle Home Ranges Utilizing Citizen-Science Data from Novel Web-Based and Smartphone GIS Applications. *Chelonia Conservation and Biology* **18**(2): 133-144.

Berube, M. D., S. G. Dunbar, K. Ruetzler and W. K. Hayes (2012). Home Range and Foraging Ecology of Juvenile Hawksbill Sea Turtles (*Eretmochelys imbricata*) on Inshore Reefs of Honduras. *Chelonian Conservation and Biology* **11**(1): 33-43.

Bjorndal, K. A. and A. B. J. M. E. Bolten (2008). Annual variation in source contributions to a mixed stock: implications for quantifying connectivity. **17**(9): 2185-2193.

Bjorndal, K. A. and J. C. B. Jackson (2003). Roles of Sea Turtles in marine ecosystems: Reconstructing the Past. <u>The Biology of Sea Turtles</u>. Boca Raton, CRC Press. **II:** 259-273.

Blumenthal, J. M., F. A. Abreu-Grobois, T. J. Austin, A. C. Broderick, M. W. Bruford, M. S. Coyne, G. Ebanks-Petrie, A. Formia, P. A. Meylan, A. B. Meylan, et al. (2009). Turtle groups or turtle soup: dispersal patterns of hawksbill turtles in the Caribbean. *Molecular Ecology* **18**(23): 4841-4853.

Blumenthal, J. M., T. J. Austin, C. D. L. Bell, J. B. Bothwell, A. C. Broderick, G. Ebanks-Petrie, J. A. Gibb, K. E. Luke, J. R. Olynik, M. F. Orr, et al. (2009). Ecology of Hawksbill Turtles, *Eretmochelys imbricata*, on a Western Caribbean Foraging Ground. *Chelonian Conservation and Biology* **8**(1): 1-10.

Bolker, B. M., T. Okuyama, K. A. Bjorndal and A. B. Bolten (2007). Incorporating multiple mixed stocks in mixed stock analysis: 'many-to-many' analyses. *Molecular Ecology* **16**(4): 685-695.

Bowen, B. W., A. L. Bass, A. GarciaRodriguez, C. E. Diez, R. van Dam, A. Bolten, K. A. Bjorndal, M. M. Miyamoto and R. J. Ferl (1996). Origin of hawksbill turtles in a Caribbean feeding area as indicated by genetic markers. *Ecological Applications* **6**(2): 566-572.

Bowen, B. W., W. S. Grant, Z. Hillis-Starr, D. J. Shaver, A. Bjorndal, A. B. Bolten and A. L. Bass (2007). Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. *Molecular Ecology* **16**(1): 49-60.

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

Browne, D. C., J. A. Horrocks and F. A. Abreu-Grobois (2010). Population subdivision in hawksbill turtles nesting on Barbados, West Indies, determined from mitochondrial DNA control region sequences. *Conservation Genetics* **11**(4): 1541-1546.

Camiñas, J. A. and C. O. J. F. f. r. De Málaga (2004). Sea turtles of the Mediterranean Sea: population dynamics, sources of mortality and relative importance of fisheries impacts. **738**: 27-84.

Carrion-Cortez, J., C. Canales-Cerro, R. Arauz and R. Riosmena-Rodriguez (2013). Habitat Use and Diet of Juvenile Eastern Pacific Hawksbill Turtles (Eretmochelys imbricata) in the North Pacific Coast of Costa Rica. *Chelonian Conservation and Biology* **12**(2): 235-245.

Cazabon-Mannette, M., D. Browne, N. Austin, A. Hailey and J. Horrocks (2016). Genetic structure of the hawksbill turtle rookery and foraging aggregation in Tobago, West Indies. *Journal of Experimental Marine Biology and Ecology* **485**: 94-101.

Diaz-Fernandez, R., T. Okayama, T. Uchiyama, E. Carrillo, G. Espinosa, R. Marquez, C. Diez, H. J. C. C. Koike and Biology (1999). Genetic sourcing for the hawksbill turtle, Eretmochelys imbricata, in the northern Caribbean region. **3**(2): 296-300.

Dickerson, D., C. Theriot, M. Wolters, C. Slay, T. Bargo and W. Parks (2007). Effectiveness of relocation trawling during hopper dredging for reducing incidental take of sea turtles. 2007 World Dredging Conference.

Dunbar, S. G., D. S. Baumbach, C. T. Hayes, M. K. Wright and L. Salinas (2017). Activities of the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR) in Honduras. Annual Report of the 2015 and 2016 Seasons.

Dunbar, S. G., D. S. Baumbach, M. K. Wright, C. T. Hayes, J. Holmberg, J. Crall and C. V. Stewart (2017). HotSpotter: less manipulating, more learning, and better vision for turtle photo identification. 37th Annual Symposium on Sea Turtle Biology and Conservation, Las Vegas, Neavada, USA.

Dunbar, S. G., C. T. Hayes and D. S. Baumbach (2016). Impacts of Recreational Diving on Hawksbill Sea Turtles (*Eretmochelys imbricata*) in the Sandy Bay West End Marine Reserve, Honduras. Annual Report of the 2014 Summer Research Season.

Dunbar, S. G., L. Salinas and L. Stevenson (2008). In-Water Observations of Recently Released Juvenile Hawksbills (*Eretmochelys imbricata*). *Marine Turtle Newsletter* **121**: 5-9.

Dunbar, S. G., M. K. Wright, E. C. Hyatt, R. T. Gammariello, D. S. Baumbach and L. Salinas (2019). ProTECTOR, Inc. National Report of Activities for the 2018 Research Season. Annual Report of the 2018 Summer Research Seaon.

Duran, N., S. G. Dunbar, R. A. Escobar and T. G. Standish (2015). High frequency of multiple paternity in a solitary population of olive ridley sea turtles in Honduras. *Journal of Experimental Marine Biology and Ecology* **463**: 63-71.

Ferreira, R. L., F. R. Ceia, T. C. Borges, J. A. Ramos and A. B. Bolten (2018). Foraging niche segregation between juvenile and adult hawksbill turtles (Eretmochelys imbricata) at Príncipe island, West Africa. *Journal of Experimental Marine Biology and Ecology* **498**: 1-7.

Finkbeiner, E. M., B. P. Wallace, J. E. Moore, R. L. Lewison, L. B. Crowder and A. J. Read (2011). Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. *Biological Conservation* **144**(11): 2719-2727.

Galtier, N., B. Nabholz, S. Glémin and G. Hurst (2009). Mitochondrial DNA as a marker of molecular diversity: a reappraisal. *Molecular Ecology* **18**(22): 4541-4550.

Gaos, A. R., R. L. Lewison, M. P. Jensen, M. J. Liles, A. Henriquez, S. Chavarria, C. M. Pacheco, M. Valle, D. Melero and V. Gadea (2017). Natal foraging philopatry in eastern Pacific hawksbill turtles. *Royal Society Open Science* **4**(8): 170153.

Gaos, A. R., R. L. Lewison, M. J. Liles, V. Gadea, E. Altamirano, A. V. Henríquez, P. Torres, J. Urteaga, F. Vallejo and A. Baquero (2016). Hawksbill turtle terra incognita: conservation genetics of eastern Pacific rookeries. *Ecology and Evolution* **6**(4): 1251-1264.

Godley, B. J., J. M. Blumenthal, A. C. Broderick, M. S. Coyne, M. H. Godfrey, L. Hawkes and M. J. Witt (2008). Satellite tracking of sea turtles: Where have we been and where do we go next? *Endangered Species Research* **3**.

Gonzalez-Garza, B., A. Stow, L. Felipe Sanchez-Teyer and O. Zapata-Perez (2015). Genetic variation, multiple paternity, and measures of reproductive success in the critically endangered hawksbill turtle (Eretmochelys imbricata). *Ecology and Evolution* **5**(24): S758-S769.

Gorham, J. C., D. R. Clark, M. J. Bresette, D. A. Bagley, C. L. Keske, S. L. Traxler, B. E. Witherington, B. M. Shamblin and C. J. Nairn (2014). Characterization of a Subtropical Hawksbill Sea Turtle (*Eretmocheyles imbricata*) Assemblage Utilizing Shallow Water Natural and Artificial Habitats in the Florida Keys. *Plos One* **9**(12): 16.

Grossman, A., C. Bellini, A. Fallabrino, A. Formia, J. M. Mba, J. N. Mba and C. J. M. T. N. Obama (2007). Second TAMAR-tagged hawksbill recaptured in Corisco Bay, West Africa. **116**(26).

Guimarães, S. M., D. C. Tavares and C. Monteiro-Neto (2017). Incidental capture of sea turtles by industrial bottom trawl fishery in the Tropical South-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **98**(6): 1525-1531.

Harrison, E., P. von Weller and B. Nahill (2017). ENDANGERED SOUVENIRS: Hawksbill Sea Turtle Products For Sale in Latin America & the Caribbean. J. Urteaga, S. G. Dunbar and J. Azanza-Ricardo, Too Rare to Wear.

IUCN. "IUCN Red List of threatened species." Retrieved 2020, 2020, from www.iucnredlist.org.

Jackson, J. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson and J. A. Estes (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**(5530): 629-637.

Karl, S. A., B. W. Bowen and J. C. Avise (1992). Global Population Genetic-Structure and Male-Mediated Gene Flow in the Green Turtle (Chelonia-Mydas) - RFLP Analysis of Anonymous Nuclear Loci. *Genetics* **131**(1): 163-173.

Lahanas, P. N., K. A. Bjorndal, A. B. Bolten, S. E. Encalada, M. M. Miyamoto, R. A. Valverde and B. W. Bowen (1998). Genetic composition of a green turtle (Chelonia mydas) feeding ground population: evidence for multiple origins. *Marine Biology* **130**(3): 345-352.

Lee, P. L. M. (2008). Molecular ecology of marine turtles: New approaches and future directions. *Journal of Experimental Marine Biology and Ecology* **356**(1-2): 25-42.

Leroux, R. A., P. H. Dutton, F. Alberto Abreu-Grobois, C. J. Lagueux, C. L. Campbell, E. Delcroix, J. Chevalier, J. A. Horrocks, Z. Hillis-Starr, S. Troeng, et al. (2012). Re-examination of Population Structure and Phylogeography of Hawksbill Turtles in the Wider Caribbean Using Longer mtDNA Sequences. *Journal of Heredity* **103**(6): 806-820.

Levasseur, K. E., S. P. Stapleton, M. C. Fuller and J. M. J. M. E. P. S. Quattro (2019). Exceptionally high natal homing precision in hawksbill sea turtles to insular rookeries of the Caribbean. **620**: 155-171.

Limpus, C. J. (1992). Estimation of tag loss in marine turtle research. *Wildlife Research* **19**(4): 457-469.

Manel, S., O. E. Gaggiotti and R. S. Waples (2005). Assignment methods: matching biological questions techniques with appropriate. *Trends in Ecology & Evolution* **20**(3): 136-142.

Mansfield, K. L., J. Wyneken, W. P. Porter and J. J. P. o. t. R. S. B. B. S. Luo (2014). First satellite tracks of neonate sea turtles redefine the 'lost years' oceanic niche. **281**(1781): 20133039.

Meylan, A. B. (1999). International Movements of Immature and Adult Hawksbill Turtles (*Eretmochelys imbricata*) in the Caribbean Region. *Chelonian Conservation and Biology* **3**(2): 189 - 194.

Meylan, A. B. (1999). Status of the Hawksbill Turtle(Eretmochelys imbricata) in the Caribbean Region. *Chelonian Conservation and Biology* **3**(2): 177-184.

Meylan, A. B. and M. Donnelly (1999). Statust justification for listing the hawksbill turtle (*Eretmochelys imbricata*) as critically endangered on the 1996 IUCN Red List of Threatened Animals. *Chelonian Conservation and Biology* **3**: 200 - 224.

Meylan, A. J. N. (1998). Hawksbill turtles still endangered. **391**(6663): 117.

Monzón-Argüello, C., N. Loureiro, C. Delgado, A. Marco, J. Lopes, M. Gomes and A. Abreu-Grobois (2011). Príncipe island hawksbills: genetic isolation of an eastern Atlantic stock. *Journal of Experimental Marine Biology and Ecology* **407**(2): 345-354.

Monzon-Arguello, C., C. Rico, A. Marco, P. Lopez and L. F. Lopez-Jurado (2010). Genetic characterization of eastern Atlantic hawksbill turtles at a foraging group indicates major undiscovered nesting populations in the region. *Journal of Experimental Marine Biology and Ecology* **387**(1-2): 9-14.

Mortimer, J. A. and M. Donnelly (2008). "Marine Turtle specialist group IUCN red list status assessment: Hawksbill turtle (*Eretmochelys imbricata*)."

Naro-Maciel, E., J. H. Becker, E. H. S. M. Lima, M. Â. Marcovaldi and R. DeSalle (2007). Testing Dispersal Hypotheses in Foraging Green Sea Turtles (Chelonia mydas) of Brazil. *Journal of Heredity* **98**(1): 29-39.

Naro-Maciel, E., M. Le, N. N. FitzSimmons, G. J. M. P. Amato and Evolution (2008). Evolutionary relationships of marine turtles: a molecular phylogeny based on nuclear and mitochondrial genes. **49**(2): 659-662.

Natoli, A., K. P. Phillips, D. S. Richardson and R. W. Jabado (2017). Low genetic diversity after a bottleneck in a population of a critically endangered migratory marine turtle species. *Journal of Experimental Marine Biology and Ecology* **491**: 9-18.

Nishizawa, H., J. Okuyama, O. Abe, M. Kobayashi and N. J. M. T. N. Arai (2012). Mitochondrial DNA variation in hawksbill turtles (Eretmochelys imbricata) nesting on Ishigaki Island, Japan. **132**: 1-2.

Norman, J. A., C. Moritz and C. J. Limpus (1994). Mitochondrial DNA Control Region Polylmorphisms Genetic Markers for Ecological Studies of Marine Turtles. *Molecular Ecology* **3**(4): 363-373.

Pella, J. and M. Masuda (2001). Bayesian methods for analysis of stock mixtures from genetic characters. *Fishery Bulletin*(1).

Proietti, M. C., J. Reisser, L. F. Marins, C. Rodriguez-Zarate, M. A. Marcovaldi, D. S. Monteiro, C. Pattiaratchi and E. R. Secchi (2014). Genetic Structure and Natal Origins of Immature Hawksbill Turtles (Eretmochelys imbricata) in Brazilian Waters. *Plos One* **9**(2): 12.

ProTECTOR (2015, June 9, 2015). "How to Draw Blood From a Juvenile Sea Turtle." ProTECTOR Sea Turtle Blood Sampling. from https://www.youtube.com/watch?v=qdjDKwivkdA.

Putman, N. F., F. A. Abreu-Grobois, A. C. Broderick, C. Ciofi, A. Formia, B. J. Godley, S. Stroud, T. Pelembe, P. Verley and N. Williams (2014). Numerical dispersal simulations and genetics help explain the origin of hawksbill sea turtles in Ascension Island. *Journal of Experimental Marine Biology and Ecology* **450**: 98-108.

Putman, N. F. and E. J. P. o. t. R. S. B. B. S. Naro-Maciel (2013). Finding the ‘lost years’ in green turtles: insights from ocean circulation models and genetic analysis. **280**(1768): 20131468.

Rees, A. F., C. Carreras, A. C. Broderick, D. Margaritoulis, T. B. Stringell and B. J. Godley (2017). Linking loggerhead locations: using multiple methods to determine the origin of sea turtles in feeding grounds. *Marine Biology* **164**(2): 30.

Reich, K. J., K. A. Bjorndal and A. B. Bolten (2007). The 'lost years' of green turtles: using stable isotopes to study cryptic lifestages. *Biology Letters* **3**: 712 - 714.

RMP (2015). "Our History - Roatán Marine Park." 2015.

Sarmiento-Ramírez, J. M., E. Abella-Pérez, A. D. Phillott, J. Sim, P. Van West, M. P. Martín, A. Marco and J. J. P. o. Diéguez-Uribeondo (2014). Global distribution of two fungal pathogens threatening endangered sea turtles. **9**(1): e85853.

Spotila, J. R. (2004). Sea turtles: A complete guide to their biology, behavior, and conservation, JHU Press.

Trujillo-Arias, N., D. F. Amorocho, D. López-Álvarez and L. M. J. B. d. I. M. y. C.-I. Mejía-Ladino (2014). Phylogeographic relations of some feeding and nesting of hawksbill turtle rookeries (Eretmochelys imbricata) in the Caribbean and Pacific of Colombia. **43**(1): 159-182.

Vargas, S. M., M. P. Jensen, S. Y. Ho, A. Mobaraki, D. Broderick, J. A. Mortimer, S. D. Whiting, J. Miller, R. I. Prince and I. P. Bell (2015). Phylogeography, genetic diversity, and management units of hawksbill turtles in the Indo-Pacific. *Journal of Heredity* **107**(3): 199-213.

Velez-Zuazo, X., W. D. Ramos, R. P. van Dam, C. E. Diez, A. Abreu-Grobois and W. O. McMillan (2008). Dispersal, recruitment and migratory behaviour in a hawksbill sea turtle aggregation. *Molecular Ecology* **17**: 839 - 853.

Wallace, B. P., A. D. DiMatteo, A. B. Bolten, M. Y. Chaloupka, B. J. Hutchinson, F. A. Abreu-Grobois, J. A. Mortimer, J. A. Seminoff, D. Amorocho, K. A. Bjorndal, et al. (2011). Global Conservation Priorities for Marine Turtles. *Plos One* **6**(9): 14.

Witzell, W. (1983). Synopsis of biological data on the hawksbill turtle, Eretmochelys imbricata (Linnaeus, 1766), Food & Agriculture Org.

Wood, L. D., R. Hardy, P. A. Meylan and A. B. Meylan (2013). Characterization of a hawksbill turtle (Eretmochelys imbricata) foraging aggregation in a high-latitude reef community in southeastern Florida, USA. *Herpetological Conservation and Biology* **8**(1): 258-275.

CHAPTER THREE

HAWKSBILL UTILIZATION AND HABITAT SUITABILITY OF A MARINE RESERVE IN ROATÁN, HONDURAS

Marsha K. Wright[1,2,3], Lance Pompe[3,4], Deepak Mishra [5], Dustin S. Baumbach[1,2,3] Lidia Salinas [6], and Stephen G. Dunbar[1,2,3,6]

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

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

[3]Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92350

[4]Health Geoinformatics Laboratory, School of Public Health, Loma Linda University, Loma Linda, CA 92350

[5]Department of Geography, University of Georgia, Athens, GA 30602

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

**Corresponding author: Marsha Wright mkwright@llu.edu*

Abstract

Marine protected areas (MPAs) have been established to decrease the negative impacts of human activities. Several sea turtle species reside within MPAs, however, habitat suitability for sea turtles within many MPAs remains unknown. Habitat modeling and species mapping have become essential tools in determining areas suitable for species inhabitance. MaxEnt is a popular machine-learning program that uses presence-only occurrence data and is considered to be the best modeling method in discriminating between suitable and unsuitable habitats. Using MaxEnt, we created species distribution models (SDM) from presence-only occurrence points of juvenile hawksbills and three environmental variables: boat traffic intensities, prey item distributions, and benthic characterizations, within the Sandy Bay West End Marine Reserve (SBWEMR) in Roatán, Honduras. Area under the receiving operator curve (AUC) values indicated high model accuracy. Jackknife evaluations indicated algal prey items *Dictyota spp.* and *K. limminghei* had the greatest influence on species distribution, followed by boat traffic intensity, *G. neptuni* sponge counts, and lastly benthic characterizations. Areas of suitability shifted based on time of day and ranged from a low probability of presence (0.0) to a high probability of presence (0.8). Regardless of time of day, the SBWEMR is mainly classified as moderately suitable, with least suitable habitat prevalent in the most northeastern region of the reserve and the southwestern tip of the reserve. High suitability was evident within the mid-region of the reserve. Although the reserve overall is at most moderately suitable, the SBWEMR remains an important local recruitment and foraging ground for juvenile hawksbills. Hawksbills have been considered resilient, continually functioning beneath their operational limits. However, with continued depletion of essential habitats over time, areas of habitat suitable for hawksbill inhabitance may decrease below levels sufficient for continued hawksbill presence.

*Keywords***:** species distribution model, MaxEnt, *Eretmochelys imbricata,* SBWEMR, Bay Islands of Honduras

Introduction

Sea turtles are marine reptiles that can be found in tropical and subtropical regions of the world. They utilize wide areas of the ocean, spanning over 110 countries and territories (Bjorndal et al. 2003). According to the International Union for Conservation of Nature (IUCN), although all species of sea turtles were once abundant, all seven species are currently classified as either data deficient, vulnerable, endangered, or critically endangered (www.iucnredlist.org). Declines in sea turtle populations can be attributed to anthropogenic activities, such as exploitation of eggs, accidental by-catch, exposure to pathogens or pollutants, and the destruction or alteration of nesting beaches and foraging areas (Jackson et al. 2001, Marcovaldi et al. 2007, Finkbeiner et al. 2011, Gaos et al. 2012, Guimarães et al. 2017). Currently, the hawksbill sea turtle (*Eretmochelys imbricata*) is classified as critically endangered (IUCN 2020). Over the past several decades, hawksbill populations have decreased approximately 80% due to threats specific to hawksbills (Bowen et al. 2007, Mortimer et al. 2008). In addition to the typical threats to sea turtles, hawksbills are victims of turtle harvesting, specifically targeted for the tortoiseshell trade. Trade of hawksbill products have been prohibited by the Convention on International Trade in Endangered Species of Wild Fauna and Flora

(CITES) since 1977. However, the hawksbill carapace, frequently referred to as “bekko” in Asia, has been a popular trade product used to create decorative items (Canin 1989). Due to the unsustainable harvest of hawksbills, estimates suggest that more than 4 million turtles have been killed globally within the past 150 years (Miller et al. 2019). In order to replenish populations numbers, conservation strategies require the adequate protection of this critically endangered species, and the habitat in which individuals reside.

Whether they be terrestrial or aquatic, protected areas have been implemented to reduce the negative impacts of human activities on species survival, to preserve remaining individuals, and to ultimately replenish and restore populations (Wang 2019). Specifically, marine protected areas (MPAs) have been implemented to decrease the negative impacts of human-driven activities on marine life (Lubchenco et al. 2003). Effective management of MPAs requires consistent observation and monitoring of human pressure (Geldmann et al. 2014) and species presence (Sánchez-Carnero et al. 2016). Sea turtle presence has been recorded within the bounds of several protected areas (Rouphael et al. 2013, Gorham et al. 2014, Herren et al. 2018, Selby et al. 2019), however, current management practices of few protected areas have been assessed or reformed to ensure policies benefit sea turtles and their vital habitats (Fernandes et al. 2017, Hayes et al. 2017). Typically, assessments of sea turtle use in protected areas are limited to nesting regions (Witt et al. 2008, Christianen et al. 2014) or corridors used during internesting periods (Witt et al. 2008). Few studies assess both sea turtle distribution and suitability of foraging areas located within protected zones. Several studies suggest the establishment of new MPAs or the extension of existing MPAs due to sea turtle presence (Hays et al. 2014, Lea et al. 2016, Dawson et al. 2017, Fuentes et al. 2018), but do not further assess essential habitat characteristics and the suitability of existing areas, nor do they suggest a reformation of management strategies to ensure these habitat qualities are maintained.

Habitat modeling and species mapping have become essential tools in predicting species distributions and identifying suitable regions for species inhabitance (Hooker et al. 2011). Species distribution models (SDM) utilize species occurrence data and corresponding environmental variables to make applications in ecology and conservation. Environmental variables can be divided into three categories: regulators, which control species ecophysiology; disturbances, which are any disruptions that affect the environmental system; and resources, which are compounds that provide energy (Guisan et al. 2000, Guisan et al. 2005). SDMs have been used to predict the influx of invasive species (Gassó et al. 2012), to identify spatial patterns of species diversity (de la Estrella et al. 2012), to estimate global distribution of species (Yesson et al. 2012), to map the geographical range shifts of species (Gotelli et al. 2015), and to predict the impact of climate change on species distributions (Briscoe et al. 2016). Overall, SDMs can be used to estimate suitability of various regions for species inhabitance, and to predict and map the extent of a species across either terrestrial or aquatic landscapes. Within marine environments, SDMs have been used to identify critical habitats of migratory species, such as fin whales (*Balaenoptera physalus*), striped dolphins (*Stenella coeruleoalba*) (Panigada et al. 2008), harbour porpoises (*Phocoena phocoena*) (Embling et al. 2010), bottlenose dolphins (*Tursiops truncatus*), grey seals (*Halichoerus grypus*), and harbour seals (*Phoca vitulina*) (Bailey et al. 2009). However, studies utilizing SDMs to assess suitability of foraging areas for sea turtles in existing marine protected areas are lacking.

The Sandy Bay West End Marine Reserve (SBWEMR) is a marine protected area off the northwestern coast of Roatán, Honduras. The reserve was initially created to protect the reef and its inhabitants from destructive human practices (RMP 2015). However, as human population density, tourism, and aquatic-based activities in the region increase (Ministry of Tourism, unpublished data), continued restructuring of management practices with respect to sea turtle survivability has not taken place. Using species distribution modeling, we aimed to assess the suitability of the SBWEMR by combining hawksbill occurrence data with environmental variables likely influencing hawksbill distribution throughout the reserve. With MaxEnt, we sought to create our model from presence-only hawksbill occurrence points and three environmental categories; resource, regulator and disturbance. Specifically, we endeavored to asses three different environmental variables within the SBWEMR: boat traffic intensities, prey item distributions, and benthic characterizations. We also aimed to evaluate which environmental variables have the greatest effect on hawksbill distribution and assess which regions of the SBWEMR are most suitable for hawksbill use.

Methods

Study Site

Roatán is a Bay Island of Honduras located approximately 55 km north of mainland Honduras. The SBWEMR is a marine protected area located off the northwestern coast of the island (16˚21’ 44’’ N, 86˚25’ 06’’ W) (Figure 1). The reserve lies within the Mesoamerican Barrier Reef and is made up of barrier, fringing, patch, and sloping reefs ranging in depths of approximately 5 – 40 m (Gonzalez 2013).

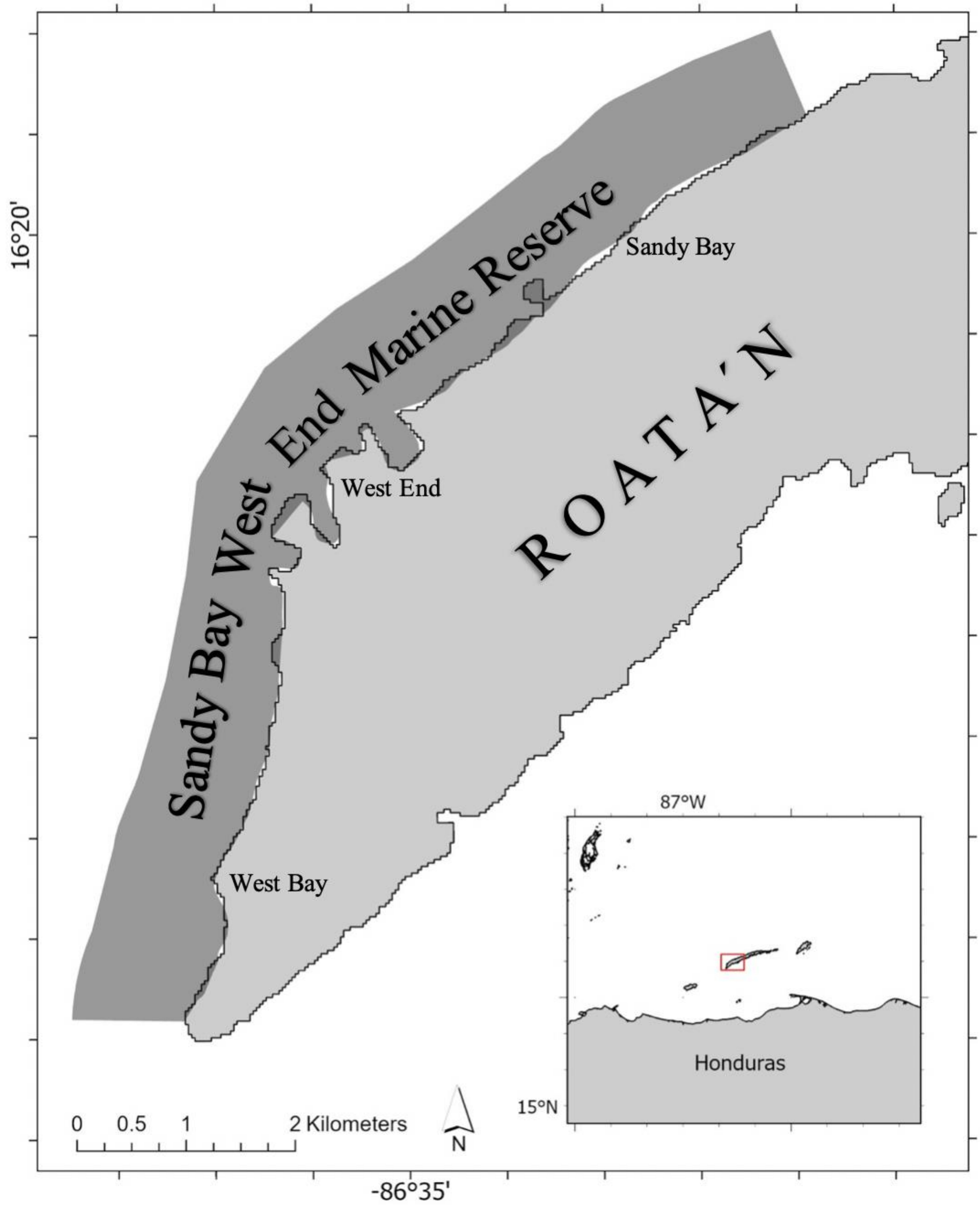

Figure 1. The Sandy Bay West End Marine Reserve (SBWEMR). The protected area is located off the Northwestern coast of Roatán, Honduras and spans 13 km of coastline, extending 1 km from shore.

The reserve encompasses 13 km of Roatán's coastline, stretching from the westernmost tip of the island in West Bay through West End to Sandy Bay, extending approximately 1 km offshore (RMP 2015). A detailed description of the benthic environment in the SBWEMR is provided in Hayes et al. (2017) and Baumbach et al. (2019).

Species Distribution Model

MaxEnt is a popular machine-learning program used to create species distribution models and map habitat suitability of regions varying in area from worldwide to entire continents, countries, and smaller regions (de la Estrella et al. 2012, Santos et al. 2013, Coxen et al. 2017, dos Santos et al. 2017). Since MaxEnt allows the use of presence-only occurrence data, continuous and categorical environmental variables, and is considered to be the best modeling method in discriminating between suitable and unsuitable habitats, it was the program chosen for this study (Merow et al. 2013). The model was created using presence-only occurrence points of juvenile hawksbills and three environmental variable predictors: boat traffic intensities, prey item distributions, and benthic characterizations. Boat traffic has been shown to alter activity patterns, increase stress, and lead to physical injury in various marine animals and was chosen as a disturbance variable (Bracciali et al. 2012, Niemi et al. 2014, Shimada et al. 2017). Prey item distribution was chosen as a resource variable since prey item abundance and distribution influences species presence and distribution (Pyke 1984). Benthic composition was chosen as a regulator variable since sea turtle presence can be associated with various benthic habitat types (Wood et al. 2013, Walcott et al. 2014). Hawksbill occurrence records were acquired from in-water turtle surveys, and environmental variables were sampled via in-water habitat surveys, boat traffic surveys, and remote sensing.

Species Occurrence Data

Sea Turtle Surveys

Hawksbill occurrence data were collected through a series of in-water surveys while SCUBA diving. Surveys took place throughout the SBWEMR from June to September 2016 – 2018. In-water surveys lasted approximately one hour and were undertaken randomly in approximately 0.9 km^2 area blocks of the 13 km^2 reserve. Surveys were completed in each block in the morning (8:30 – 10:30) and afternoon (14:30 – 16:30) time periods, where 2 – 5 divers traversed the area in a transect pattern, similar to the strip transect method described by Baumbach et al. (2019). Upon sighting of a hawksbill turtle, the location was recorded based on the dive site latitude and longitude. Upon sighting of a hawksbill turtle, the location was recorded based on the dive site latitude and longitude (Garmin – GPSMAP 64s).

Environmental Data

Boat Traffic Assessment

Boat traffic throughout the SBWEMR was quantified through a series of boat count surveys, conducted from the shore similar to those performed by La Manna et al. (2010). Surveys were completed throughout the entire SBWEMR, along approximately 13 km of coastline, and were conducted 2 – 3 times per week from July to September 2016 – 2018. We conducted counts for 20 minutes during the morning (8:30 – 10:30) and afternoon (14:30 – 16:30) time periods, indicating the number of boats that remained stationary or traveled through an ~ 1 km^2 area. We termed the number of boats traveling through a region in one hour ‘boat intensity’ and calculated boat intensity by the equation:

$$(B_M - B_A) \times 3 = {}^{boats}/_{hour} \tag{1}$$

where B_M equals the number of boats that moved through an ~ 1 km^2 area in the twenty-minute period and B_A equals the number of boats that remained stationary in the same twenty-minute period. Since the difference of moving and stationary boats was calculated during a twenty-minute observation period, the difference was multiplied by three to estimate the number of boats moving through an ~ 1km^2 area per hour.

Prey Item Distribution

In order to characterize prey item distributions, we utilized area and line transect surveys. Area transects were used to estimate percent cover of potential algal prey items *Dictyota spp.*, *Halimeda opuntia*, *Lobophora variegate*, and *Kallymenia limminghei*, and line surveys were used specifically to quantify presence of the sponge *Geodia neptuni*. For area transects, a 30 m transect line was placed randomly along the reef and 6, 1 m^2 quadrats were placed consecutively along the transect line every 5 m, with the quadrat centered on the transect line. Photographs of each quadrat were taken, edited, and transferred to the Coral Point Count with Excel extensions (CPCe, Ver. 4.1, National Coral Reef Institute, Fort Lauderdale, FL)(Kohler et al. 2006). To calculate the percent cover of potential algal prey items, a simple area analysis was completed using CPCe’s tracing function to outline all occurrences of each algal species in the quadrat photograph.

In order to quantify *G. neptuni* presence throughout the SBWEMR, in-water *G. neptuni* sponge counts were conducted by line transects, as described by Baumbach et al. (2019).

Remote Sensing Benthic Data

Image Capture

A 4-band (B, G, R, NIR) multispectral scene of QuickBird satellite data with 2.44 m spatial resolution was obtained from Satellite Imaging Corporation (formerly known as Digital Globe Inc., Colorado, USA). The image was captured by the satellite on 15 March 2004. The satellite data was radiometrically and geometrically corrected by the vendor to remove radiometric noise and geometric distortions. The georectification was performed with a nearest-neighbor interpolation which resulted in a RMSE error of ± 1 pixel.

Image Processing - Atmospheric Correction

Raw digital numbers (DNs) or pixel values were converted to top-of-atmosphere (TOA) radiance using QuickBird provided calibration coefficients. The land areas were masked using a near-infrared (NIR) band-based binary mask. Cloud cover and cloud shadows were also removed using a different binary mask. The image was processed through a first-order single scattering albedo atmospheric correction to remove Rayleigh and aerosol scattering. Aerosol scattering component was derived from an optically deep-water area covering 50 × 50 pixels window. Band-specific Rayleigh and aerosol scattering components were subtracted from the TOA radiance which subsequently converted to remote sensing reflectance (R_{rs}). The details of the atmospheric correction procedure can be found in Mishra et al. (2005).

Benthic Habitat Mapping

Lyzenga (1978) bathymetric model was recalibrated using *in situ* and principal component (PC) transformed QuickBird R_{rs} data (PC1) representing a uniform reflectance bottom type (i.e., seagrass substrate type) in this study. The bathymetric map was used in Lee et al. (1994)'s radiative transfer model which decomposes total R_{rs} to R_{rs} by water column and R_{rs} by benthic substrate. Water column inherent optical properties (i.e. band-wise absorption and backscattering coefficients) were derived from the optically deep-water window using empirical models proposed by Lee et al. (1998). Finally, water depth, absorption, and backscattering parameters were used to derive the bottom albedo or benthic reflectance image. The benthic reflectance image was clustered to classify the benthic habitat types using the Iterative Self Organizing Data (ISODATA) algorithm to derive 100 clusters. The 100 clusters were grouped into five bottom types (seagrass with sand, dense seagrass, coral, coral with sand, and sand) for accuracy assessment. The details of the water column correction and benthic habitat mapping procedure can be found in Mishra et al. (2006).

Model and Map Compilation

Environmental Layer Creation

We used ArcGIS Pro (ESRI, Redlands, CA) to create 12 spatial data layers for insertion into MaxEnt; 11 environmental spatial data layers (Table 1) and a single background layer, depicting the area of the study site. Benthic environmental data acquired from remote sensing (dense seagrass, seagrass with sand, sand, coral with sand, coral) were imported into ArcGIS Pro in raster format and converted to American

Standard Code for Information Interchange (ASCII). Environmental data collected from field surveys (boat traffic intensity, *Dictyota spp*., *L. variegate*, *K. limminghei*, *H. opuntia*, *G. neptuni*) were imported into ArcGIS in table format and joined to a vector layer of the SBWEMR. Each individual environmental variable vector layer was transformed to raster with identical coordinate projections, extent, and spatial resolution (Table 2). Multicollinearity tests were performed in ArcGIS Pro using band collection statistics spatial analyst tool. Correlation coefficients values for *H. opuntia* and *L. variegata* prey item variables were > ± 0.85, indicating multicollinearity. Therefore, the corresponding layers were excluded from the model (Table 3).

Table 1. Environmental Variable Layers. Eleven environmental variables were assessed for use in our study. Nine (bolded) variables selected through a correlation test, were used to create a model corresponding to the morning and afternoon time periods. Relative percent (%) contribution of each variable to the MaxEnt model creation is provided.

Environmental Variable	Unit	% Contribution Morning	% Contribution Afternoon
Dense Seagrass	0 (absent); 1 (present)	6.7	2.7
Seagrass with Sand	0 (absent); 1 (present)	1.4	4.3
Sand	0 (absent); 1 (present)	23.9	4.2
Coral with Sand	0 (absent); 1 (present)	3.3	4.1
Coral	0 (absent); 1 (present)	5.6	5.2
Boat Traffic Intensity	boats/hr.	4.8	18.5
Dictyota spp.	%/m^2	35.5	39.1
Lobophora variegate	%/m^2	-	-
Kallymenia limminghei	%/m^2	2.6	1.6
Halimeda opuntia	%/m^2	-	-
Geodia neptuni	#/km^2	16.3	20.3

Table 2. ArcGIS Layer Descriptions. The characteristics of each environmental variable layer were identical. Each layer had the same extent, geographic and projected coordinate system, projection and spatial resolution.

Extent	*Top*	1807495.9877 m
	Bottom	1798510.7877 m
	Right	548154.8243 m
	Left	542157.2243 m
Geographic Coordinate System		GCS Clarke 1866
Projected Coordinate System		UTM Zone 16 Northern Hemisphere
Projection		Transvers Mercator
Spatial Resolution		2.8 m

Table 3. Environmental Variable Correlation Matrix. Correlation values calculated using Band Collection Statistics in ArcGIS. "DS' is dense seagrass, "CS" is coral with sand, "SS" is seagrass with sand, "CL" is coral, "SN" is sand, "KM" is Kallymenia, "LB" is Lobophora, "HM" is Halimeda, "GN" is Geodia, "DT" is Dictyota, "BTM" is boat traffic intensity in the morning, "BTA" is boat traffic intensity in the afternoon.

	DS	**CS**	**SS**	**CL**	**SN**	**KM**	**LB**	**HM**	**GN**	**DT**	**BTM**	**BTA**
DS	1											
CS	-0.127	1										
SS	-0.083	-0.139	1									
CL	-0.139	-0.099	-0.116	1								
SN	-0.158	-0.172	-0.153	-0.231	1							
KM	0.009	0.127	-0.081	0.069	*-0.002	1						
LB	0.005	0.133	-0.080	0.067	-0.016	0.981	1					
HM	-0.006	0.131	-0.065	0.050	-0.048	0.743	0.858	1				
GN	-0.012	0.091	-0.018	0.026	-0.065	0.300	0.469	0.815	1			
DT	-0.005	0.133	-0.070	0.052	-0.044	0.785	0.888	0.996	0.758	1		
BTM	-0.036	-0.278	0.079	-0.190	**-0.002	-0.439	-0.469	-0.466	-0.345	-0.468	1	
BTA	-0.022	-0.266	0.082	-0.184	-0.016	-0.395	-0.421	-0.418	-0.275	-0.425	0.971	1

Note : If two variables had ≥ ± 0.85, only one varible was selected for the model. All correlations were significant at the 0.01 level, unless otherwise stated (*correlation is significant at the 0.05 level; ** correlation is not significant).

MaxEnt Conditions and Model Creation

To create species distribution models and map habitat suitability within the SBWEMR, we used MaxEnt version 3.4.1. In-water turtle surveys provided 94 occurrence points in the morning and 81 in the afternoon, 75 % of which were used for model training and 25 % as test data. To avoid overfitting the model, the regularization value was kept as 0.5 for both morning and afternoon models. To reduce the effects of spatial autocorrelation, bootstrapping replication run type was used for 10 replicate runs, and iterations were fixed at 1,000. Remotely sensed environmental variable layers were classified as categorical, while the remaining environmental variables were classified as continuous. All other programmable values were kept at default. Linear, quadratic, product, threshold, and hinge features were used to generate both the morning and afternoon models. The threshold value was chosen using the minimum training presence. Area under the receiving operator curve (AUC) values were used to assess model accuracy and predictability, and jackknifing method was used to indicate the importance of each environmental variable on species distribution via gain. Probability of hawksbill presence (PHP) in relation to each predictor variable was indicated with response curves for continuous variables and response bar graphs for categorical variables. PHP was classified as low (0.0 – 0.2), slightly moderate (0.2 – 0.4), moderate (0.4 – 0.6), and high (0.6 – 1.0). We imported final outputs of both the morning and afternoon models into ArcGIS Pro and clipped each output to display the suitability of geographic region within the SBWEMR. Suitability of habitat within the SBWEMR was classified as unsuitable (0.0 – 0.2), moderately suitable (0.2 – 0.4), suitable (0.4 – 0.6), and highly suitable (0.6 – 1.0).

Results

Model Performance and Variable Input

Models created to predict species distribution in both the morning and afternoon exhibited high accuracy. Area under the receiving operator curve (AUC) values were 0.84 in the morning and 0.79 in the afternoon. Overall percent contribution of each environmental variable to the model's creation varied between the morning and afternoon (Table 1). In the morning model, jackknife evaluation of regularized training gain indicated *Dictyota spp.* percent cover had the greatest influence on species distribution, followed by *G. neptuni* sponge count, boat traffic intensity, *K. limminghei* percent cover, and lastly benthic characterization (Figure 2A). Estimates of testing gain in the morning model implied that *Dictyota spp.* percent cover had the greatest influence on species distribution, followed by the benthic variable sand, boat traffic intensity, *G. neptuni* sponge count, and lastly the remaining benthic variables. However, dense seagrass presented a negative gain, suggesting that this benthic variable is a poor choice for further prediction of species distribution (Figure 2B). Estimates of regularized training gain in the afternoon suggested that boat traffic had the greatest influence on species distribution, followed by *G. neptuni* sponge count, *Dictyota spp*. percent cover, *K. limminghei* percent cover, and lastly benthic characterization (Figure 3A). In the afternoon model, jackknifing estimates of test gain revealed that boat traffic intensity had the greatest influence on species distribution, followed by *Dictyota spp.* percent cover, *G. neptuni* sponge count, *K. limminghei* percent cover, and lastly benthic makeup (Figure 3B).

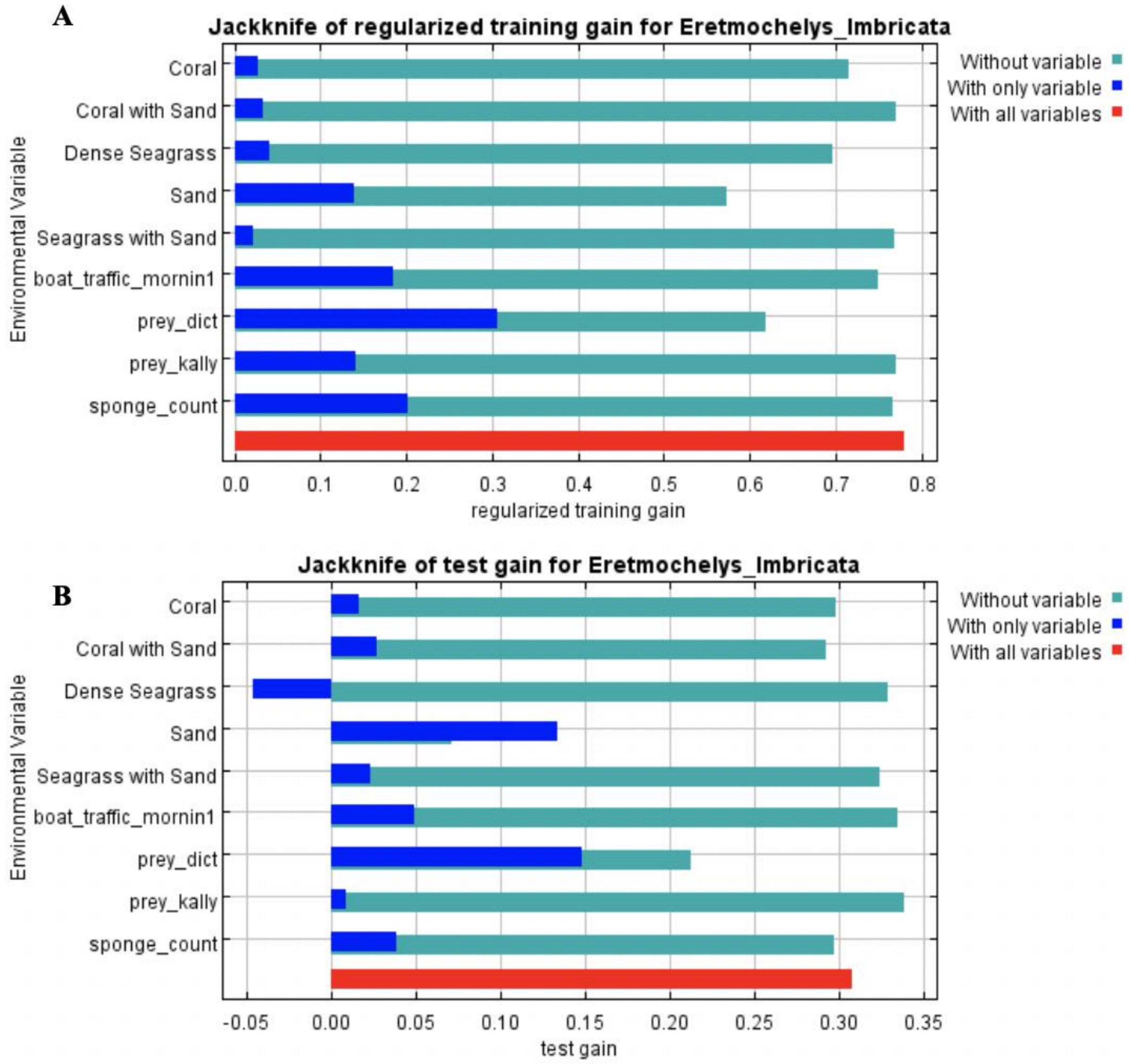

Figure 2. Jackknifing estimates depicting variable importance on hawksbill distribution in the morning. Jackknife of regularized training gain (A), Jackknife of test gain (B). Teal bars represent testing gain when variable is omitted, dark blue bars represent testing gain of variable when used in isolation, and red bars represent testing gain with all variables present.

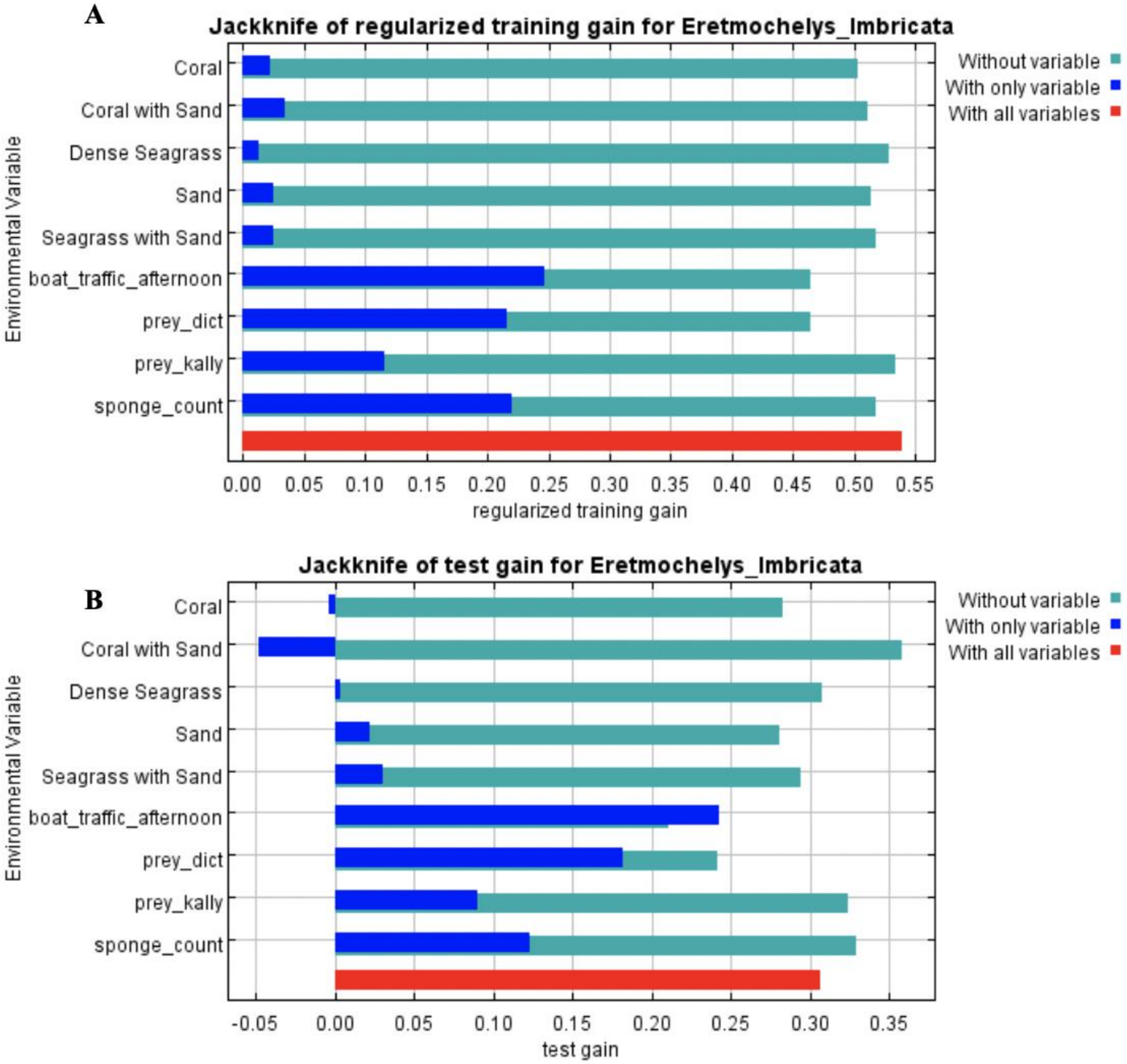

Figure 3. Jackknifing estimates depicting variable importance on hawksbill distribution in the afternoon. Jackknife of regularized training gain (A), Jackknife of test gain (B). Teal bars represent testing gain when variable is omitted, dark blue bars represent testing gain of variable when used in isolation, and red bars represent testing gain with all variables present.

However, specific variables, such as coral with sand and coral, presented a negative gain, suggesting that these benthic variables are poor predictor of species distribution (Figure 3B). Response curves for PHP based on boat traffic intensity indicated an increase in the PHP as boat traffic intensity increased in both the morning and afternoon. However, in the morning, PHP decreased and plateaued after reaching an intensity of 50 boats/hour (Figure 4A & 4B). Response curves for PHP based on *Dictyota spp.* (Figure 5A & B) and *K. limminghei* (Figure 6A & B) percent cover indicated a decrease in the PHP as percent cover increased in both the morning and afternoon. In contrast, response curves for PHP based on sponge count indicated an increase in the probability of hawksbill presence as *G. neptuni* sponge count increased in both the morning (Figure 7A) and afternoon (Figure 7B). Unlike response curves for continuous variables, general trends of response bar graphs for categorical variables varied depending on the time of day. In the morning model, an increase in occurrence potential was evident in the presence of coral, dense seagrass, and sand, while a decrease in occurrence potential was evident in the presence of seagrass with sand, and coral with sand (Figure 8A). However, regardless of the presence or absence of benthic variables, the morning model suggested slightly moderate to high PHP when associated with all categorical environmental variables. In the afternoon model, an increase in occurrence potential was evident in the presence of all variables, except coral and sand (Figure 8B). However, regardless of the presence or absence of benthic variables, the afternoon model also suggested a slightly moderate to high PHP when associated with all categorical environmental variables.

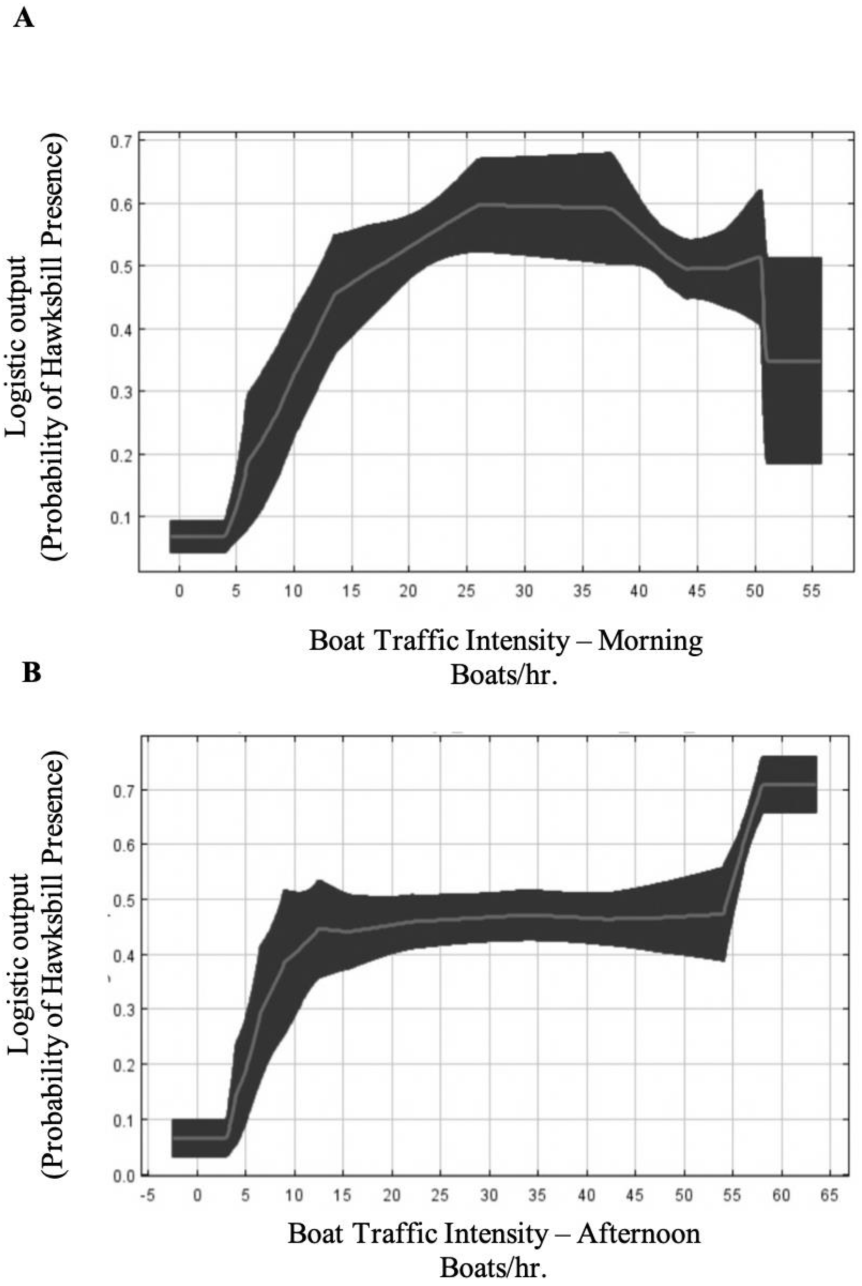

Figure 4. Response curves of probability of hawksbill presence (PHP) in relation to boat traffic intensity in the morning (A) and afternoon (B). Response curves indicate the dependence of predicted suitability on boat traffic intensity. In both figures, boat traffic intensity (boats/hour) is depicted on the x-axis and logistic output (probability of presence) is depicted on the y-axis. Grey outline indicates one standard deviation.

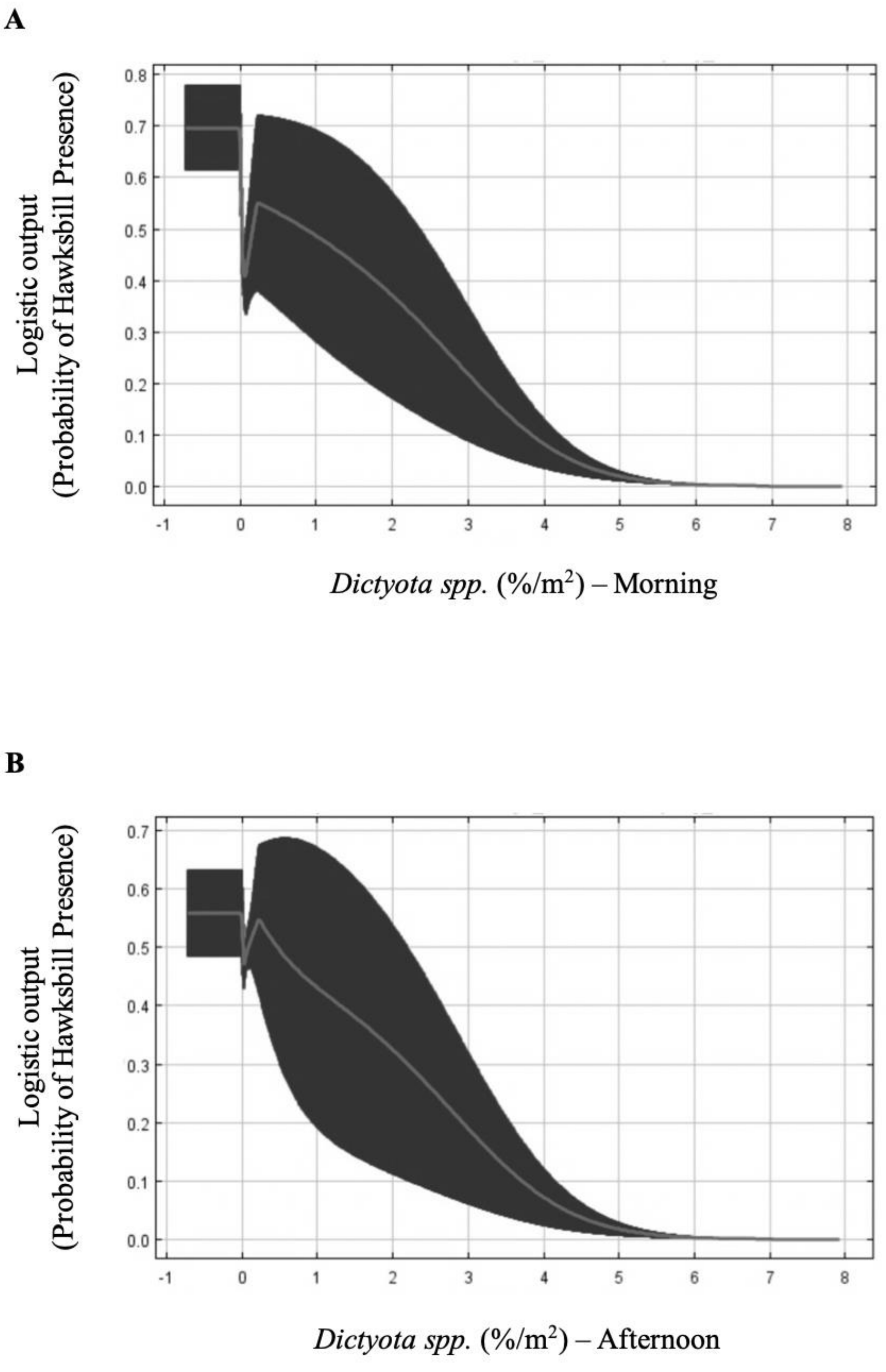

Figure 5. Response curves for probability of hawksbill presence (PHP) in relation to potential prey item, *Dictyota spp*. in the morning (A) and afternoon (B). Response curves indicate the dependence of predicted suitability on *Dictyota spp*. percent cover. In both figures, *Dictyota spp*. percent cover is depicted on the x-axis and logistic output (probability of presence) is depicted on the y-axis. Grey outline indicates one standard deviation.

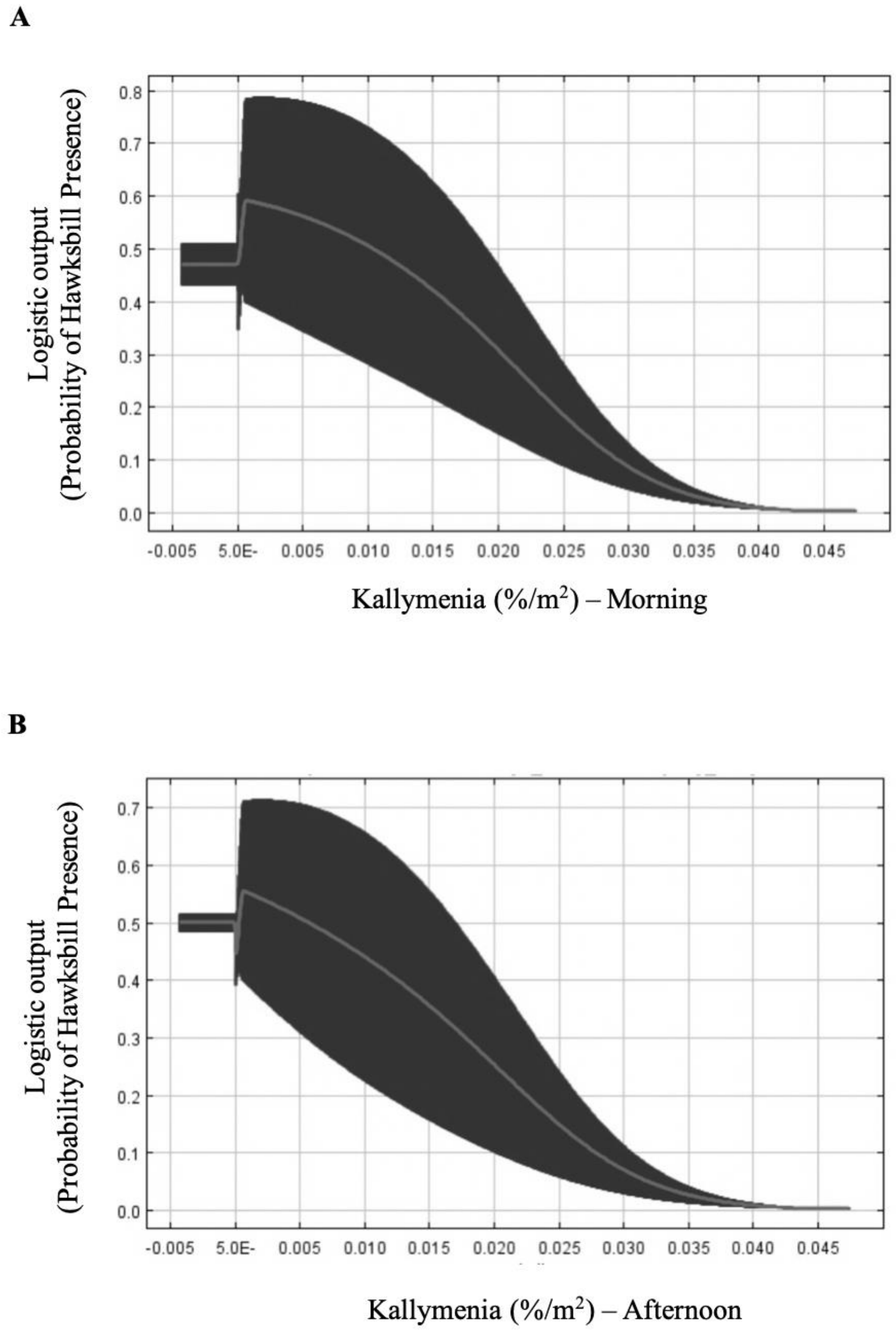

Figure 6. Response curves for probability of hawksbill presence (PHP) in relation to potential prey item, *K. limminghei* in the morning (A) and afternoon (B). Response curves indicate the dependence of predicted suitability on *K. limminghei* percent cover. In both figures, *K. limminghei* percent cover is depicted on the x-axis and logistic output (probability of presence) is depicted on the y-axis. Grey outline indicates one standard deviation.

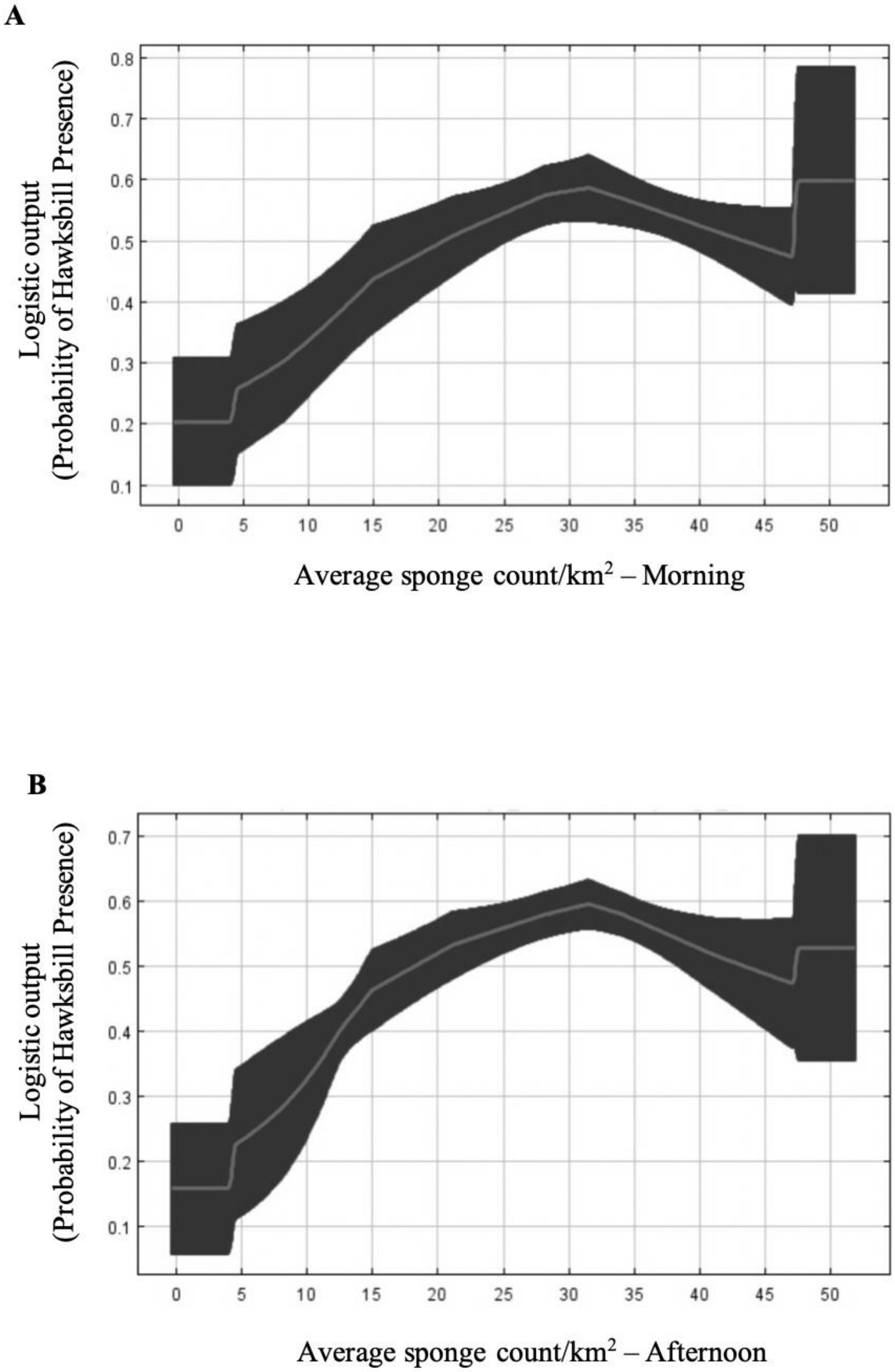

Figure 7. Response curves of hawksbill probability of presence (PHP) in relation to potential prey item, *G. neptuni* in the morning (A) and afternoon (B). Response curves indicate the dependence of predicted suitability on *G. neptuni* count per squared kilometer. In both figures *G. neptuni* count per squared kilometer is depicted on the x-axis and logistic output (probability of presence) is depicted on the y-axis. Grey outline indicates one standard deviation.

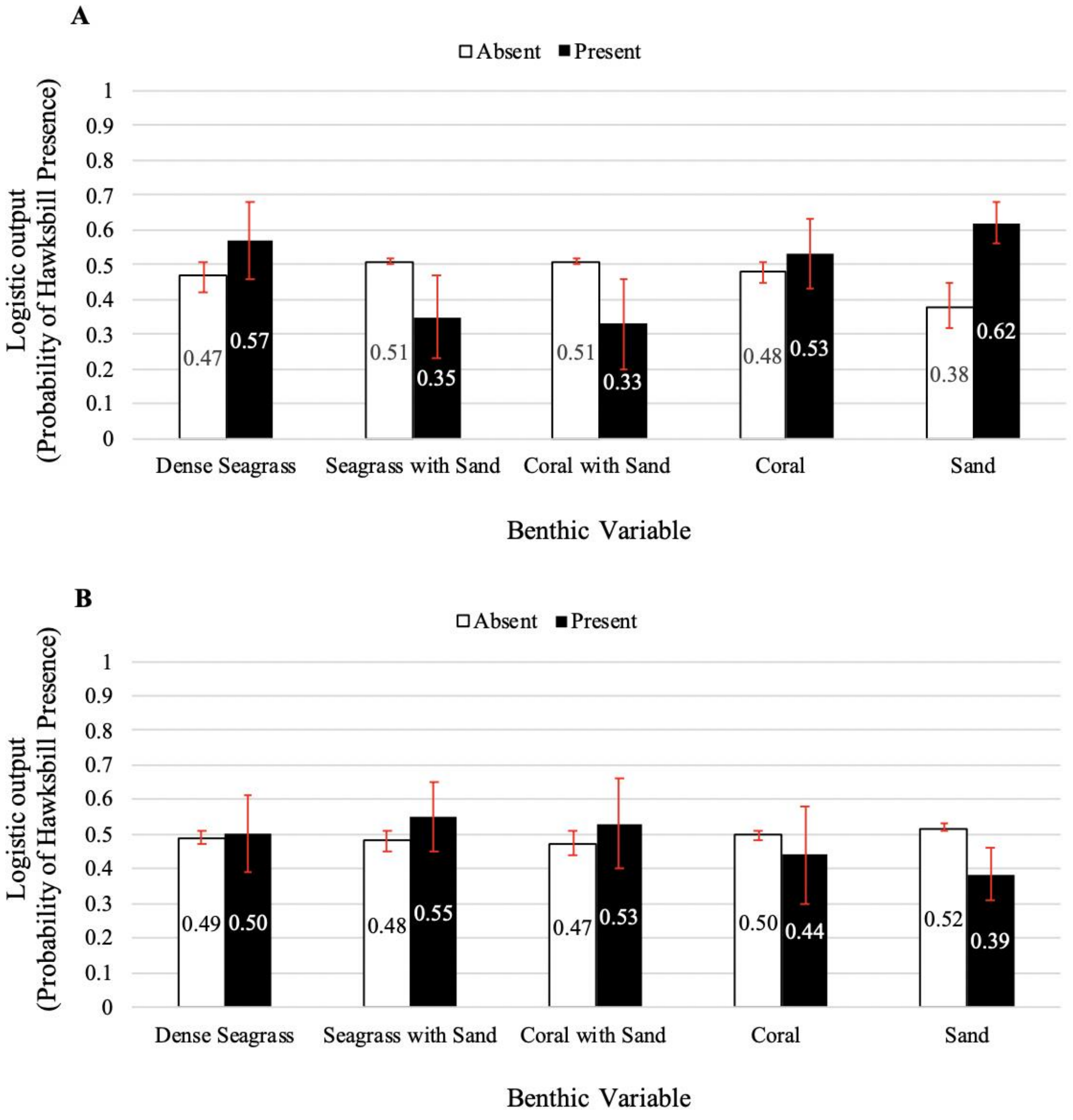

Figure 8. Response bar graphs of hawksbill probability of presence (PHP) in relation to benthic makeup in the Morning (A) and Afternoon (B). (Note: X-axis "0" values correspond to absence of the benthic type, while "1" values correspond to presence of the benthic type; MaxEnt runs (black) and the mean +/- one standard deviation (grey, two shades for categorical variables)).

Hawksbill Distribution Model

Using the environmental parameters associated with hawksbill occurrence data, MaxEnt logistic output indicated regions of varying suitability within the SBWEMR in both the morning and afternoon. Areas of suitability shifted based on time of day and ranged from unsuitable (0.0) to highly suitable (0.8). Regardless of time of day, the majority of the SBWEMR can be classified as moderately suitable at best, with least suitable habitat most evident in the northeastern most region of the reserve. High suitability was evident within a small area of the mid-region of the reserve in both the morning (Figure 9) and afternoon simulations (Figure 10).

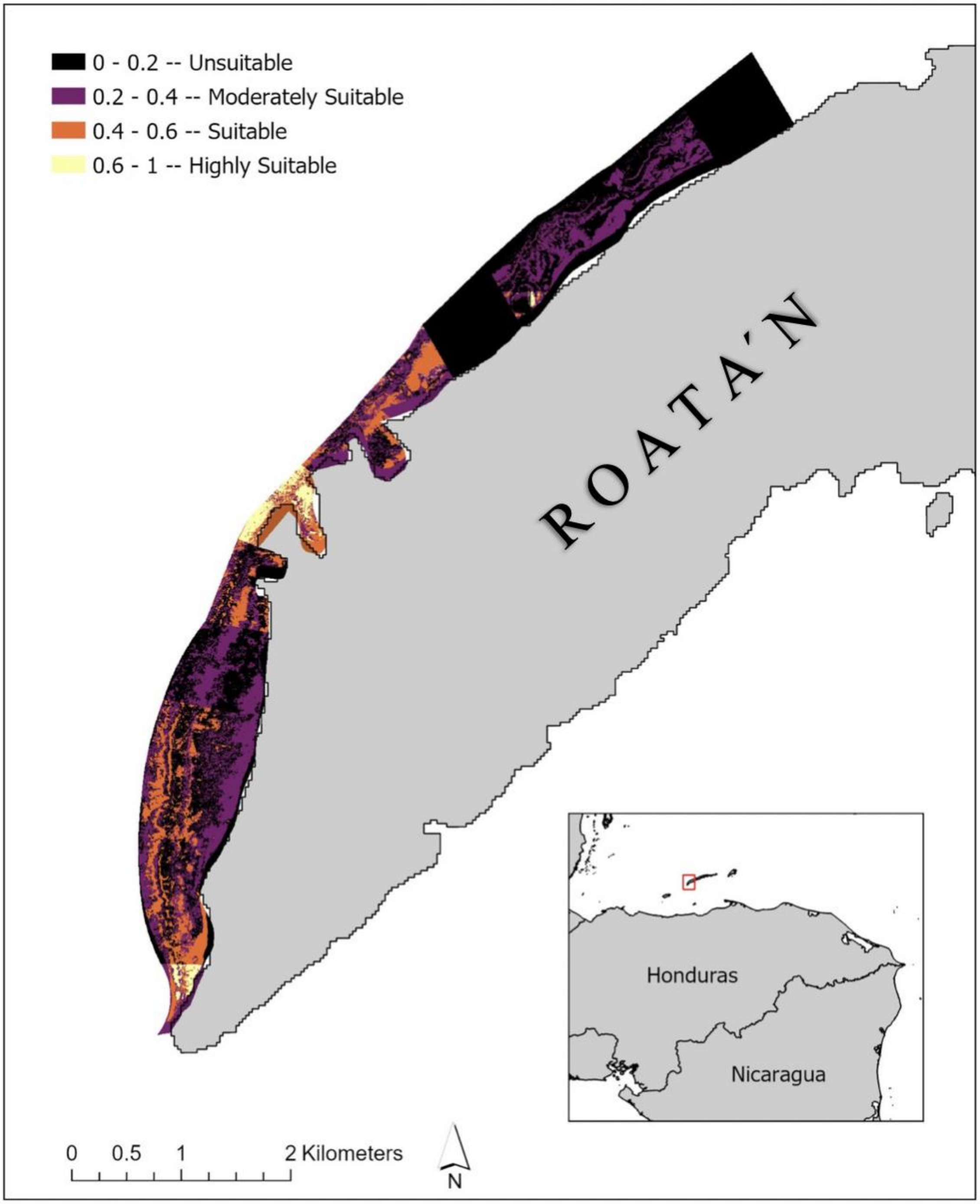

Figure 9. Predicted habitat suitability of the SBWEMR in the morning. MaxEnt logistic output depicted varying suitability throughout the SBWEMR. Suitability was classified as either unsuitable (0 – 0.2), moderately suitable (0.2 – 0.4), suitable (0.4 – 0.6), or highly suitable (0.6 – 1).

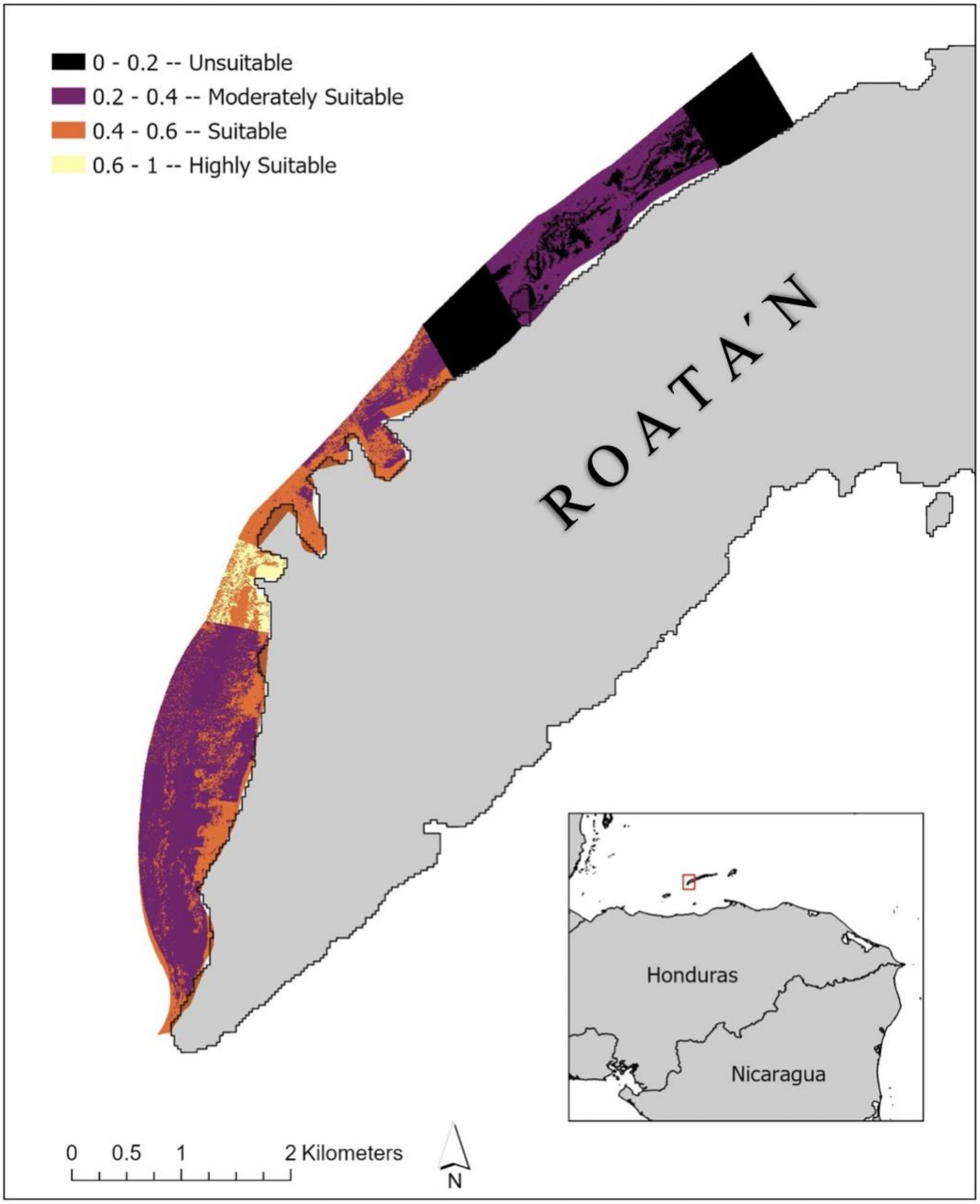

Figure 10. Predicted habitat suitability of the SBWEMR in the afternoon. MaxEnt logistic output depicted varying suitability throughout the SBWEMR. Suitability was classified as either unsuitable (0 – 0.2), moderately suitable (0.2 – 0.4), suitable (0.4 – 0.6), or highly suitable (0.6 – 1).

Discussion

Species distribution models (SDMs) have previously been used in sea turtle conservation efforts (Duncan 2012, Guo 2014, Varo- Cruz et al. 2016). However, aside from Hart et al. (2013) and Selby et al. (2019), few models assess hawksbill distributions in association with several environmental factors in marine protected areas. Furthermore, the suitability of a protected area for hawksbill inhabitance is often overlooked. Our study is the first to assess the distribution of foraging juvenile hawksbills in Caribbean Honduras and to use MaxEnt to evaluate the suitability of an MPA for continued hawksbill presence, although several models have focused on the suitability of nesting sites (Lichstein et al. 2002, Santos et al. 2006, Pike et al. 2013).

In our model, prey item predictors, *G. neptuni*, *K. limminghei* and *Dictyota spp.*, had the greatest influence on suitability. However, with respect to algal prey item percent cover (*K. limminghei* and *Dictyota spp.)*, we noted a negative correlation, with PHP decreasing as percent cover of *K. limminghei* and *Dictyota spp.* increased. Although algal prey items are a potential source of nutrients and are found in the diets of hawksbills foraging off the coast of other regions, such as Australia (Bell 2013) and Costa Rica (Santoro et al. 2015), our results suggest that hawksbills foraging within the reserve may not be heavily reliant on these algal species to obtain nutritional requirements. Initial focal follows of foraging hawksbills, in the SBWEMR by Baumbach et al. (2015), suggested hawksbill diet was composed of the algal species *Dictyota spp.*, *H. opuntia*, *L. variegate*, and *K. limminghei*. However, further work by Baumbach et al. (unpublished data) suggested that ingestion of other algal species was incidental during attempts to ingest *K. limminghei*, and that *K. limminghei*, although present in hawksbill diets, makes up only a small proportion of their diet. Algae has been found in the diet of some hawksbills foraging off the coasts of the Dominican Republic (León et al. 2002), Puerto Rico (Van Dam et al. 1997), and other regions of Roatán (Berube et al. 2012), yet our model suggests that algae may not be a large component of hawksbill diets in the SBWEMR. This conclusion aligns well with the established, mainly spongivorous foraging ecology of hawksbills in the Caribbean (León et al. 2002, Blumenthal et al. 2009). Studies in the Pacific and Indian oceans have shown that hawksbill diets can be comprised mainly of algae (Limpus et al. 2009, Bell 2013) and hard corals (Obura et al. 2010), however, shifts to primarily algal diets were likely due to the decimation of sponge prey items within the foraging ranges of hawksbills. According to the optimal foraging theory, prey item selectivity and foraging patterns may vary based on prey item availability (Pyke 1984). Still, according to Rincon-Diaz et al. (2011), hawksbill prey item selection is not always associated with abundance. In some cases, selectivity may be strong for rare items. This may be indicative of higher PHP in regions of low algal percent cover in the SBWEMR.

In our models, sponge counts of *G. neptuni* had the second greatest positive influence on suitability. Unlike algal prey item percent cover, PHP positively correlated with *G. neptuni* distribution. Since increasing presence of *G. neptuni* in the reserve indicated increasing PHP, our findings continue to support the positive influence of sponge availability on hawksbill presence and distribution. With respect to resource environmental variables, the model output suggests that regions of high *G. neptuni* counts and low *K. limminghei* and *Dictyota spp.* are considered regions of moderate to high suitability for hawksbill presence within the SBWEMR. We suggest that PHP was higher in regions of high *G. neptuni* count and low *K. limminghei* and *Dictyota spp,* since home range and core use areas are influenced by prey item availability and preference. In-water observations, esophageal lavage, and stable isotope analyses performed by Baumbach et al. (unpublished data) indicated that hawksbill diets within the SBWEMR are predominantly comprised of *Geodia neptuni* (68.8 %) when compared to the alga *K. limminghei* (18.8%), supporting the results of our model.

In addition to prey item availability, the presence of predators and other disturbances may influence home range extent and species distributions, limiting habitat use, species ranges and abundance (Heithaus et al. 2002, Wood et al. 2017). Our model indicated that increasing boat traffic intensity positively correlated with an increase in PHP. Furthermore, our model outputs suggested regions with higher boat traffic intensities were “suitable” habitats within the reserve. These results contradict the general theory of predator avoidance. However, rather than a positive effect on sea turtle presence, we suggest that boating has a no effect on sea turtle distribution, and rather that the influence of prey item distribution dictates hawksbill presence independent of boat traffic intensity. Recent underwater auditory studies performed by Tyson et al. (2017), indicated that in-water hawksbill behavior does not appear to be affected by sounds emitted from boat traffic. Other studies suggest that when nonintrusive, turtles become accustomed to disturbances, unaware of their potential threats (von Brandis et al. 2010, Nanninga et al. 2017). These results are supported by recent studies in Roatán by Wright et al. (in prep), where hawksbills remained undisturbed and showed no obvious stress response to boats passing overhead during feeding events. Although boats do not pose a consumptive risk to aquatic species, Frid et al. (2002) proposed that any human-caused disturbance stimulus may be considered a form of predation. Since antipredatory behavior can be exhibited as a response to loud noises and fast approaching objects, boat presence could be considered a form of predation. Foraging behaviors and distribution of fishes (Payne et al. 2015, Magnhagen et al. 2017, Ivanova et al. 2018), humpback whales (*Megaptera novaeangliae*)(Blair et al. 2016), and dolphins (Pirotta et al. 2015) have all been reported to be altered by boat presence. However, our results help demonstrate the ability of hawksbills to coexist with boat traffic, seemingly undisturbed by increasing boat traffic intensity.

While our model was able to predict habitat suitability, there were nevertheless, several limitations and assumptions to the model. SDMs are limited, since they are unable to analyze compounding effects and ecological processes that define the relationship between a species and the environmental variables (Elith et al. 2009). In addition, the small spatial extent of our study site also limited the number and type of environmental variables that could be applied to the model. The range of spatial resolution and extent of coverage for many available layers are broad, with a single resolution unit equivalent to approximately 1˚(Yesson et al. 2012), 25 km (Ferrier et al. 2002), or other similar resolutions that are greater than the spatial scale of the SBWEMR in its entirety. Although spatial resolution could be resampled to fit the scope of our study site, the small degree in change of these environmental variables would render the layer insignificant in our small study area. Studies by Lowen et al. (2016) also indicated that model performance does not increase by resampling spatial resolution. In any case, our model outputs may be used to identify regions of ecological importance within the SBWEMR. In addition, AUC values obtained in our study were greater than 0.75, indicating each model contained useful information (Elith et al. 2006) and were able to predict habitat suitability greater than chance (AUC = 0.5).

According to our model outputs, regions of low suitability are clustered mainly in the northeastern region of the reserve. Based on the relationship of resource variables with hawksbill presence in the reserve, strategies to improve suitability should focus on resource replenishment. Competition for space is typical between sponge and algal species. In spatially limited regions, competitors affect growth capabilities of sponges (González-Rivero et al. 2011, Singh et al. 2016). In the presence of increased anthropogenic nutrients, sponge and algal cover has increased in coral reefs. However, elevated nutrients levels are only beneficial for sponges in the absence of contact with algae. In the presence of elevated nutrient concentrations, algae competitively inhibit sponge growth (Easson et al. 2014). Therefore, management of anthropogenic nutrients within the SBWEMR is essential.

Although testing gain data suggested our model had a poor ability to estimate suitability if extrapolated and used to test other regions, training data were able to assess suitability within the SBWEMR. If fine-tuned further by the addition of subsequent environmental variables and more precise occurrence points, a model with sufficient extrapolation capability may potentially map hawksbill distribution and habitat suitability along the entire coast of Roatán. With the information garnered from further model manipulations, we may be able to identify regions that require implementation of habitat rehabilitation strategies. Hawksbills have been considered a resilient species, with some studies suggesting they continually function beneath their operational limits with respect to routine foraging activities (von Brandis et al. 2010). Although hawksbills have also been known to supplement their diets with additional prey items (Berube et al. 2012), continued depletion of suitable habitat overtime may reduce resource items below sustainable levels for hawksbill inhabitance. To ensure adequate supply of potential resource items, specifically sponges, hawksbill foraging areas should be monitored for anthropogenic runoff and other pollutants that may potentially inhibit the growth of important resource items. Furthermore, MPAs in the wider Caribbean that are adjacent to coastal developments and increasing human populations should be monitored for pollutants, and eutrophying outputs, and should be managed accordingly.

Acknowledgements

We thank the Loma Linda University Department of Earth and Biological Science and the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR, Inc.) for funding this work. We acknowledge the Health Geoinformatics Laboratory in the School of Public Health at Loma Linda University for their assistance with ArcGIS. We also extend our gratitude to Mary and Gary Miller at the Roatan Dive Center, and Rafael Brioso, Paolo Shikanai, Kathy Berner and their dive center staff at Splash Inn for their collaboration and continuing support of our field work in Honduras. We are grateful to ProTECTOR, Inc. Interns (Tori Bolin, Zoe Aguila, Lindsay Marston, and Samantha Read) and ProTECTOR Inc. Volunteers (Skylar Kuhn Razvan Orban, Sebastian Tulai, and Voicu Tulai), all of whom assisted with data collection. Finally, we express our gratitude to both Jimmy Miller and Lidia Salinas for providing logistical support in Honduras. This project was permitted under the department of Fisheries (DIGEPESCA/SAG – Honduras) permit No. 251-10, the Institute for Forest Conservation (ICF-Honduras) permit No. DE-MP-055-2016 and ASG-ICF-139-2018, and Loma Linda University IACUC protocol No. 8120038 and 8150049.

References

Bailey, H. and P. M. Thompson (2009). Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area. *Marine Ecology Progress Series* **378**: 279-287.

Baumbach, D., C. Hayes, M. K. Wright, M. Macpui, L. A. Salinas and S. G. Dunbar (2015). Potential Hawksbill Prey Item Distribution Among Dive Sites in a Marine Protected Area in Roatán, Bay Islands, Honduras. 35th Annual Symposium on Sea Turtle Biology and Conservation, Dalaman, Mugla, Turkey.

Baumbach, D. S., E. C. Anger, N. A. Collado and S. G. Dunbar (2019). Identifying Sea Turtle Home Ranges Utilizing Citizen-Science Data from Novel Web-Based and Smartphone GIS Applications. *Chelonia Conservation and Biology* **18**(2): 133-144.

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

Berube, M. D., S. G. Dunbar, K. Ruetzler and W. K. Hayes (2012). Home Range and Foraging Ecology of Juvenile Hawksbill Sea Turtles (*Eretmochelys imbricata*) on Inshore Reefs of Honduras. *Chelonian Conservation and Biology* **11**(1): 33-43.

Bjorndal, K. A. and J. C. B. Jackson (2003). Roles of Sea Turtles in marine ecosystems: Reconstructing the Past. The Biology of Sea Turtles. Boca Raton, CRC Press. **II:** 259-273.

Blair, H. B., N. D. Merchant, A. S. Friedlaender, D. N. Wiley and S. E. Parks (2016). Evidence for ship noise impacts on humpback whale foraging behaviour. *Biology Letters* **12**(8): 20160005.

Blumenthal, J. M., T. J. Austin, C. D. L. Bell, J. B. Bothwell, A. C. Broderick, G. Ebanks-Petrie, J. A. Gibb, K. E. Luke, J. R. Olynik, M. F. Orr, et al. (2009). Ecology of Hawksbill Turtles, *Eretmochelys imbricata*, on a Western Caribbean Foraging Ground. *Chelonian Conservation and Biology* **8**(1): 1-10.

Bowen, B. W., W. S. Grant, Z. Hillis-Starr, D. J. Shaver, A. Bjorndal, A. B. Bolten and A. L. Bass (2007). Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. *Molecular Ecology* **16**(1): 49-60.

Bracciali, C., D. Campobello, C. Giacoma and G. Sara (2012). Effects of nautical traffic and noise on foraging patterns of Mediterranean damselfish (*Chromis chromis*). *Plos One* **7**(7): e40582.

Briscoe, N. J., M. R. Kearney, C. A. Taylor and B. A. Wintle (2016). Unpacking the mechanisms captured by a correlative species distribution model to improve predictions of climate refugia. *Global Change Biology* **22**(7): 2425-2439.

Canin, J. (1989). International Trade in Sea Turtle Products. Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology, Jekyll Island, Georgia, NOAA Technical Memorandum NMFS-SEFC-232.

Christianen, M. J., P. M. Herman, T. J. Bouma, L. P. Lamers, M. M. van Katwijk, T. van der Heide, P. J. Mumby, B. R. Silliman, S. L. Engelhard and M. van de Kerk (2014). Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. *Proceedings of the Royal Society B: Biological Sciences* **281**(1777): 20132890.

Coxen, C. L., J. K. Frey, S. A. Carleton, D. P. J. G. e. Collins and conservation (2017). Species distribution models for a migratory bird based on citizen science and satellite tracking data. **11**: 298-311.

Dawson, T. M., A. Formia, P. D. Agamboué, G. M. Asseko, F. Boussamba, F. Cardiec, E. Chartrain, P. D. Doherty, J. M. Fay and B. J. Godley (2017). Informing marine protected area designation and management for nesting olive ridley sea turtles using satellite tracking. *Frontiers in Marine Science* **4**: 312.

de la Estrella, M., R. G. Mateo, J. J. Wieringa, B. Mackinder and J. Muñoz (2012). Legume diversity patterns in West Central Africa: influence of species biology on distribution models. *Plos One* **7**(7): e41526.

dos Santos, L. A., M. F. Mendes, A. P. Krüger, M. L. Blauth, M. S. Gottschalk and F. R. J. P. o. Garcia (2017). Global potential distribution of Drosophila suzukii (Diptera, Drosophilidae). **12**(3): e0174318.

Duncan, R. (2012). Development of a Species Distribution Model for the East Pacific Green Sea Turtle using Ecological Geoprocessing Tools, Texas A & M University.

Easson, C. G., M. Slattery, D. M. Baker and D. J. Gochfeld (2014). Complex ecological associations: competition and facilitation in a sponge–algal interaction. *Marine Ecology Progress Series* **507**: 153-167.

Elith, J., C. H. Graham*, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick and A. J. E. Lehmann (2006). Novel methods improve prediction of species' distributions from occurrence data. **29**(2): 129-151.

Elith, J. and J. R. Leathwick (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual review of ecology, evolution, and systematics* **40**: 677-697.

Embling, C. B., P. A. Gillibrand, J. Gordon, J. Shrimpton, P. T. Stevick and P. S. Hammond (2010). Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*). *Biological Conservation* **143**(2): 267-279.

Fernandes, A., A. C. V. Bondioli, M. Solé and A. Schiavetti (2017). Seasonal Variation in the Behavior of Sea Turtles at a Brazilian Foraging Area. *Chelonia Conservation and Biology* **16**(1): 93-102.

Ferrier, S., G. Watson, J. Pearce and M. Drielsma (2002). Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. *Biodiversity and Conservation* **11**(12): 2275-2307.

Finkbeiner, E. M., B. P. Wallace, J. E. Moore, R. L. Lewison, L. B. Crowder and A. J. Read (2011). Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. *Biological Conservation* **144**(11): 2719-2727.

Frid, A. and L. Dill (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**(1).

Fuentes, M. M., A. J. Gillis, S. A. Ceriani, T. L. Guttridge, M. P. V. Z. Bergmann, M. Smukall, S. H. Gruber and N. Wildermann (2018). Informing marine protected areas in Bimini, Bahamas by considering hotspots for green turtles (*Chelonia mydas*). *Biodiversity and Conservation* **28**(1): 1-15.

Fuentes, M. M., I. R. Lawler and E. J. W. R. Gyuris (2007). Dietary preferences of juvenile green turtles (Chelonia mydas) on a tropical reef flat. **33**(8): 671-678.

Gaos, A. R., R. L. Lewison, B. P. Wallace, I. L. Yanez, M. J. Liles, W. J. Nichols, A. Baquero, C. R. Hasbun, M. Vasquez, J. Urteaga, et al. (2012). Spatial ecology of critically endangered hawksbill turtles *Eretmochelys imbricata*: implications for management and conservation. *Marine Ecology Progress Series* **450**: 181-U198.

Gassó, N., W. Thuiller, J. Pino and M. Vilà (2012). Potential distribution range of invasive plant species in Spain. *NeoBiota* **12**: 25.

Geldmann, J., L. N. Joppa and N. D. Burgess (2014). Mapping change in human pressure globally on land and within protected areas. *Conservation Biology* **28**(6): 1604-1616.

Gonzalez, I. (2013). Roatan Bay Islands Honduras Dive Guide: 60 of Roatan's Best Dives

González-Rivero, M., L. Yakob and P. J. Mumby (2011). The role of sponge competition on coral reef alternative steady states. *Ecological Modelling* **222**(11): 1847-1853.

Gorham, J. C., D. R. Clark, M. J. Bresette, D. A. Bagley, C. L. Keske, S. L. Traxler, B. E. Witherington, B. M. Shamblin and C. J. Nairn (2014). Characterization of a Subtropical Hawksbill Sea Turtle (*Eretmocheyles imbricata*) Assemblage

Utilizing Shallow Water Natural and Artificial Habitats in the Florida Keys. *Plos One* **9**(12): 16.

Gotelli, N. J. and J. Stanton- Geddes (2015). Climate change, genetic markers and species distribution modelling. *Journal of Biogeography* **42**(9): 1577-1585.

Guimarães, S. M., D. C. Tavares and C. Monteiro-Neto (2017). Incidental capture of sea turtles by industrial bottom trawl fishery in the Tropical South-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **98**(6): 1525-1531.

Guisan, A. and W. J. E. l. Thuiller (2005). Predicting species distribution: offering more than simple habitat models. **8**(9): 993-1009.

Guisan, A. and N. E. Zimmermann (2000). Predictive habitat distribution models in ecology. *Ecological Modelling* **135**(2-3): 147-186.

Guo, J. (2014). Modelling Loggerhead Sea Turtle (Caretta Caretta) Nesting Habitat: Evaluation of the Species Distribution Model by Species-environment and Abundance-occupancy Relationships, University of Twente Faculty of Geo-Information and Earth Observation (ITC).

Hart, K. M., A. R. Sartain, Z. M. Hillis-Starr, B. Phillips, P. A. Mayor, K. Roberson, R. A. Pemberton, J. B. Allen, I. Lundgren and S. Musick (2013). Ecology of juvenile hawksbills (Eretmochelys imbricata) at Buck Island Reef National Monument, US Virgin Islands. *Marine Biology* **160**(10): 2567-2580.

Hayes, C. T., D. S. Baumbach, D. Juma and S. G. Dunbar (2017). Impacts of recreational diving on hawksbill sea turtle (*Eretmochelys imbricata*) behaviour in a marine protected area. *Journal of Sustainable Tourism* **25**(1): 79-95.

Hays, G. C., J. A. Mortimer, D. Ierodiaconou and N. Esteban (2014). Use of Long-Distance Migration Patterns of an Endangered Species to Inform Conservation Planning for the World's Largest Marine Protected Area. *Conservation Biology* **28**(6): 1636-1644.

Heithaus, M., A. Frid and L. Dill (2002). Shark-inflicted injury frequencies, escape ability, and habitat use of green and loggerhead turtles. *Marine Biology* **140**(2): 229-236.

Herren, R. M., D. A. Bagley, M. J. Bresette, K. G. Holloway-Adkins, D. Clark and B. E. Witherington (2018). Sea Turtle Abundance and Demographic Measurements in a Marine Protected Area in the Florida Keys, USA. *Herpetological Conservation and Biology* **13**(1): 224-239.

Hooker, S. K., A. Cañadas, K. D. Hyrenbach, C. Corrigan, J. J. Polovina and R. R. Reeves (2011). Making protected area networks effective for marine top predators. *Endangered Species Research* **13**(3): 203-218.

IUCN (2020). "IUCN Red List of threatened species." Retrieved 2020, 2020, from www.iucnredlist.org.

Ivanova, S. V., S. T. Kessel, J. Landry, C. O'Neill, M. F. McLean, M. Espinoza, S. Vagle, N. E. Hussey and A. T. Fisk (2018). Impact of vessel traffic on the home ranges and movement of shorthorn sculpin (*Myoxocephalus scorpius*) in the nearshore environment of the high Arctic. *Canadian Journal of Fisheries and Aquatic Species* **75**(12): 2390-2400.

Jackson, J. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson and J. A. Estes (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**(5530): 629-637.

Kohler, K. E., S. M. J. C. Gill and Geosciences (2006). Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. **32**(9): 1259-1269.

La Manna, G., S. Clo, E. Papale and G. Sara (2010). Boat traffic in Lampedusa waters (Strait of Sicily, Mediterranean Sea) and its relation to the coastal distribution of common bottlenose dolphin (Tursiops truncatus). *Ciencias Marinas* **36**(1): 71-81.

Lea, J. S. E., N. E. Humphries, R. G. von Brandis, C. R. Clarke and D. W. Sims (2016). Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. *Proceedings of the Royal Society B-Biological Sciences* **283**(1834): 8.

Lee, Z., K. L. Carder, S. K. Hawes, R. G. Steward, T. G. Peacock and C. O. Davis (1994). Model for the interpretation of hyperspectral remote-sensing reflectance. *Applied Optics* **33**(24): 5721-5732.

Lee, Z., K. L. Carder, C. D. Mobley, R. G. Steward and J. S. Patch (1998). Hyperspectral remote sensing for shallow waters. I. A semianalytical model. *Applied Optics* **37**(27): 6329-6338.

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

Lichstein, J. W., T. R. Simons, S. A. Shriner and K. E. J. E. m. Franzreb (2002). Spatial autocorrelation and autoregressive models in ecology. **72**(3): 445-463.

Limpus, C. J. and L. Fien (2009). A biological review of Australian marine turtles, Environmental Protection Agency.

Lowen, J., C. McKindsey, T. Therriault and C. DiBacco (2016). Effects of spatial resolution on predicting the distribution of aquatic invasive species in nearshore marine environments. *Marine Ecology Progress Series* **556**: 17-30.

Lubchenco, J., S. R. Palumbi, S. D. Gaines and S. Andelman (2003). Plugging a Hole in the Ocean: The Emerging Science of Marine Reserves. *Ecological Applications* **13**(sp1): 3-7.

Lyzenga, D. R. (1978). Passive remote sensing techniques for mapping water depth and bottom features. *Applied Optics* **17**(3): 379-383.

Magnhagen, C., K. Johansson and P. Sigray (2017). Effects of motorboat noise on foraging behaviour in Eurasian perch and roach: a field experiment. *Marine Ecology Progress Series* **564**: 115-125.

Marcovaldi, M. A., G. G. Lopez, L. S. Soares, A. J. Santos, C. Bellini and P. C. Barata (2007). Fifteen years of hawksbill sea turtle (*Eretmochelys imbricata*) nesting in Northern Brazil. *Chelonian Conservation and Biology* **6**(2): 223-228.

Merow, C., M. J. Smith and J. A. J. E. Silander Jr (2013). A practical guide to MaxEnt for modeling species’ distributions: what it does, and why inputs and settings matter. **36**(10): 1058-1069.

Miller, E. A., L. McClenachan, Y. Uni, G. Phocas, M. E. Hagemann and K. Van Houtan (2019). The historical development of complex global trafficking networks for marine wildlife. *Science Advances* **5**(3): eaav5948.

Mishra, D., S. Narumalani, D. Rundquist and M. Lawson (2006). Benthic habitat mapping in tropical marine environments using QuickBird multispectral data. *Photogrammetric Engineering Remote Sensing* **72**(9): 1037-1048.

Mishra, D. R., S. Narumalani, D. Rundquist and M. Lawson (2005). High-resolution ocean color remote sensing of benthic habitats: a case study at the Roatan Island, Honduras. *IEEE Transactions on Geoscience and Remote Sensing* **43**(7): 1592-1604.

Mortimer, J. A. and M. Donnelly (2008). "Marine Turtle specialist group IUCN red list status assessment: Hawksbill turtle (*Eretmochelys imbricata*)." 2016.

Nanninga, G. B., I. M. Côté, R. Beldade and S. C. Mills (2017). Behavioural acclimation to cameras and observers in coral reef fishes. *Ethology* **123**(10): 705-711.

Niemi, M., M. Auttila, A. Valtonen, M. Viljanen and M. Kunnasranta (2014). Haulout patterns of Saimaa ringed seals and their response to boat traffic during the moulting season. *Endangered Species Research* **22**(2): 115-124.

Obura, D., A. Harvey, T. Young, M. Eltayeb and R. von Brandis (2010). Hawksbill turtles as significant predators on hard coral. *Coral Reefs* **29**(3): 759-759.

Panigada, S., M. Zanardelli, M. MacKenzie, C. Donovan, F. Mélin and P. S. Hammond (2008). Modelling habitat preferences for fin whales and striped dolphins in the

Pelagos Sanctuary (Western Mediterranean Sea) with physiographic and remote sensing variables. *Remote Sensing of Environment* **112**(8): 3400-3412.

Payne, N. L., D. E. van der Meulen, I. M. Suthers, C. A. Gray and M. D. Taylor (2015). Foraging intensity of wild mulloway *Argyrosomus japonicus* decreases with increasing anthropogenic disturbance. *Marine Biology* **162**(3): 539-546.

Pearson, R. G. (2007). Species' distribution modeling for conservation educators and practitioners. *Synthesis. American Museum of Natural History* **50**: 54-89.

Pike, D. A. J. G. E. and Biogeography (2013). Climate influences the global distribution of sea turtle nesting. **22**(5): 555-566.

Pirotta, E., N. D. Merchant, P. M. Thompson, T. R. Barton and D. Lusseau (2015). Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. *Biological Conservation* **181**: 82-89.

Pyke, G. H. (1984). Optimal foraging theory: a critical review. *Annual Review of Ecology Systematics* **15**(1): 523-575.

Rincon-Diaz, M. P., C. E. Diez, R. P. Van Dam and A. M. J. J. o. H. Sabat (2011). Foraging selectivity of the hawksbill sea turtle (Eretmochelys imbricata) in the Culebra Archipelago, Puerto Rico. **45**(3): 277-283.

RMP (2015). "Our History - Roatán Marine Park." 2015.

Rouphael, T., A. Abdulla, O. Attum, N. Marshall and U. Ghazali (2013). Do marine protected areas in the Red Sea afford protection to dugongs and sea turtles? *Journal of Biodiversity and Endangered Species* **1**: 1-6.

Sánchez-Carnero, N., D. Rodríguez-Pérez, E. Couñago, F. Le Barzik and J. Freire (2016). Species distribution models and local ecological knowledge in marine protected areas: The case of Os Miñarzos (Spain). *Ocean & Coastal Management* **124**: 66-77.

Santoro, M., J. Morales, F. Bolaáos, G. Chaves and M. De Stefano (2015). Helminths of hawksbill turtle (*Eretmochelys imbricata*) from the Pacific coast of Costa Rica. *Helminthologia* **52**(1): 67-70.

Santos, K. C., C. Tague, A. C. Alberts, J. J. C. C. Franklin and Biology (2006). Sea turtle nesting habitat on the US Naval Station, Guantanamo Bay, Cuba: a comparison of habitat suitability index models. **5**(2): 175-187.

Santos, S. M., R. Lourenco, A. Mira and P. J. P. O. Beja (2013). Relative effects of road risk, habitat suitability, and connectivity on wildlife roadkills: the case of tawny owls (Strix aluco). **8**(11).

Selby, T. H., K. M. Hart, B. J. Smith, C. G. Pollock, Z. Hillis-Starr and M. K. Oli (2019). Juvenile hawksbill residency and habitat use within a Caribbean marine protected area. *Endangered Species Research* **40**: 53-64.

Shimada, T., C. Limpus, R. Jones and M. Hamann (2017). Aligning habitat use with management zoning to reduce vessel strike of sea turtles. *Ocean & Coastal Management* **142**: 163-172.

Singh, A. and N. L. Thakur (2016). Influence of spatial competitor on the growth and regeneration of the marine sponge Cinachyrella cf. cavernosa (Porifera, Demospongiae). *Hydrobiologia* **768**(1): 111-123.

Tyson, R. B., W. E. Piniak, C. Domit, D. Mann, M. Hall, D. P. Nowacek and M. M. Fuentes (2017). Novel Bio-Logging Tool for Studying Fine-Scale Behaviors of Marine Turtles in Response to Sound. *Frontiers in Marine Science* **4**: 219.

Van Dam, R. and C. Diez (1997). Predation by hawksbill turtles on sponges at Mona Island, Puerto Rico. Proceedings of the 8th international coral reef symposium.

Varo- Cruz, N., J. A. Bermejo, P. Calabuig, D. Cejudo, B. J. Godley, L. F. López-Jurado, S. K. Pikesley, M. J. Witt, L. A. J. D. Hawkes and Distributions (2016). New findings about the spatial and temporal use of the Eastern Atlantic Ocean by large juvenile loggerhead turtles. **22**(4): 481-492.

von Brandis, R. G., J. A. Mortimer and B. K. Reilly (2010). In-water observations of the diving behaviour of immature hawksbill turtles, *Eretmochelys imbricata*, on a coral reef at D'Arros Island, Republic of Seychelles. *Chelonia Conservation and Biology* **9**(1): 26-32.

Walcott, J., S. Eckert, H. Oxenford and J. J. E. S. R. Horrocks (2014). Use of a towed camera system to investigate benthic habitat use by inter-nesting female hawksbill sea turtles. **24**(2): 159-170.

Wang, Y. (2019). On Dilemmas and Solutions for the Issues of HIgh Seas Marine Protected Areas During the BBNJ Negotiation *Applied Ecology and Environmental Research* **17**(4): 8615-8629.

Witt, M. J., A. C. Broderick, M. S. Coyne, A. Formia, S. Ngouessono, R. J. Parnell, G.-P. Sounguet and B. J. Godley (2008). Satellite tracking highlights difficulties in the design of effective protected areas for Critically Endangered leatherback turtles *Dermochelys coriacea* during the inter-nesting period. *Oryx* **42**(02): 296-300.

Wood, L. D., B. Brunnick and S. L. Milton (2017). Home range and movement patterns of subadult hawksbill sea turtles in Southeast Florida. *Journal of Herpetology* **51**(1): 58-67.

Wood, L. D., R. Hardy, P. A. Meylan and A. B. Meylan (2013). Characterization of a hawksbill turtle (Eretmochelys imbricata) foraging aggregation in a high-latitude reef community in southeastern Florida, USA. *Herpetological Conservation and Biology* **8**(1): 258-275.

Yesson, C., M. L. Taylor, D. P. Tittensor, A. J. Davies, J. Guinotte, A. Baco, J. Black, J. M. Hall- Spencer and A. D. Rogers (2012). Global habitat suitability of cold-water octocorals. *Journal of Biogeography* **39**(7): 1278-1292.

CHAPTER FOUR

INFLUENCE OF BOAT TRAFFIC ON THE DISTRIBUTION AND BEHAVIOR OF JUVENILE HAWKSBILLS FORAGING IN A MARINE PROTECTED AREA IN ROATÁN, HONDURAS

Marsha K. Wright[1,2,*], Dustin S. Baumbach[1,2], Nancy Collado[3], Shahnaj Binte Safi[3], and Stephen G. Dunbar[1,2]

[1]*Protective Turtle Ecology Center for Training, Outreach and Research, Inc. (ProTECTOR, Inc.), Loma Linda, CA 92350, sdunbar@llu.edu*

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

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

**Corresponding author: Marsha Wright mkwright@llu.edu*

Abstract

Marine protected areas (MPAs) have been implemented to reduce disturbances and negative impacts of human activities on marine life. However, many marine protected areas do not address specific threats, particularly those of boat traffic and the behavioral alterations and physical injury to marine organisms that may result. Studies have shown that boating pressure can alter activity patterns, increase stress, and lead to physical injury in various aquatic animals. The Sandy Bay West End Marine Reserve (SBWEMR), a marine protected area in Roatán, Honduras, has been identified as a recruiting ground and foraging area for the critically endangered hawksbill sea turtle. While direct capture by the public is forbidden, managing increasing boat traffic and its effect on hawksbill distribution and behavior are not addressed in the reserve's management plans. We aimed to quantify the amount of boat traffic moving throughout the SBWEMR and evaluate the effect of boat traffic on the presence, distribution, and behavior of juvenile hawksbills. For the purpose of this study, we divided the SBWEMR into 3 zones corresponding to three major coastal towns: West Bay, West End, and Sandy Bay. Boat traffic throughout each zone was quantified through a series of above-water and in-water surveys, while hawksbill behavior and presence in each zone were evaluated through in-water surveys using SCUBA. Spearman correlation suggested a significant positive correlation between boat intensity and hawksbill presence, although no significant correlation was evident between boat intensity and behavior. Although data suggest that boat traffic may not disrupt or negatively alter in-water behavior, hawksbills are prone to the additional hazards of boat collisions and propeller strikes. In order to reduce the risks of injury and mortality, efforts should be made to continually monitor, regulate, and enforce vessel speeds in MPAs where hawksbills reside.

Keywords: sea turtles, vessel traffic, Sandy Bay West End Marine Reserve, *Eretmochelys imbricata*

Introduction

Human activities have disturbed marine organisms for centuries. Populations of numerous marine species have declined due to varying anthropogenic activities, resulting in pollution, habitat destruction, accidental bycatch, and direct take (Lercari et al. 2007, Mortimer et al. 2008). Marine protected areas (MPAs) have been implemented to decrease the negative impacts of these human activities on marine life (Lubchenco et al. 2003). Approximately 16,924 MPAs have been created around the world to promote the goal of long-term conservation of marine life UNEP-WCMC and IUCN (2020). However, the protective significance of many established MPAs is often less than intended, as they lack sufficient funding, governance, enforcement, and proper resources to achieve their specified conservation goals. These parks may provide a false sense of protection and are, at times, referred to as 'paper parks'(Rife et al. 2013). In some cases, MPAs have been established simply to meet quotas or political agendas (Jameson et al. 2002). Although there is evidence to suggest many MPAs are lacking in effectiveness, properly managed MPAs have shown great improvement in protecting aquatic animals from threats of extractive and destructive human activities, such as overfishing (Bohnsack 1998), bottom trawling (Lindholm et al. 2004), poison fishing (Barber et al.

1998, Neuwinger 2004), and dynamite fishing (Guard et al. 1997). However, many management strategies solely address the threat of overfishing or other forms of direct take by regulating catch limits or implementing no-take zones. Many protected areas do not address the threat of boat traffic. Additionally, several MPAs overlook behavioral alterations and physical injuries that occur to organisms within areas of unregulated boating (Hilborn 2015).

Studies have shown that boating activities can alter activity patterns, increase stress, and lead to physical injury in various aquatic animals. Bracciali et al. (2012) discovered that foraging behavior of the Mediterranean damselfish (C*hromis chromis*) was significantly altered by boat presence, with feeding frequencies reduced and escape reaction time increased in the presence of boat noise. Haulout patterns of ringed seals (*Phoca hispida saimensis*) during molting seasons were also altered in the presence of boat traffic. Niemi et al. (2014) found that rather than remaining on land, as they typically do during the molting process, ringed seals (*Phoca hispida saimensis*) in Finland were more likely to retreat to the water in the presence of boats. In the case of dolphins, Pirotta et al. (2015) concluded that foraging behaviors of Atlantic bottlenose dolphins (*Tursiops truncatus*) were altered not only by the sound of boats, but also by the physical presence of boats. In addition to behavioral changes, boat traffic can also lead to physical injury. Aquatic reptiles, such as crocodiles and turtles, are susceptible to injurious boat strikes that may potentially be fatal (Orós et al. 2005, Grant et al. 2010, Shimada et al. 2017). In regions where boat traffic and boat speeds are regulated, disruption of, and collisions with, marine organisms have decreased (Grant et al. 2010).

However, many marine protected areas still do not address the potential issues of unregulated boat traffic (Bulté et al. 2010, Thurstan et al. 2012).

The Sandy Bay West End Marine Reserve (SBWEMR) was established in 1989 to protect the fringing reefs and their inhabitants from excessive hunting practices, development projects, degradation by sand and coral mining, and other practices that contributed to the depletion of local marine life (Colwell 1999). Not long before the establishment of the reserve, Central American governments began promoting tourism as an avenue of economic development. The Honduran government established certain incentives to attract foreign investors to begin tourism development in the region (Stonich 1998). Tourism has now grown to supply approximately 16% of the nation's gross domestic product (Turner 2015). However, certain consequences can be paired with the growth of tourism, including consequences of ecological concern. According to the National Marine Manufacturers Association (NMMA), an increase in boating led to the exportation of over 400 million dollars' worth of recreational boats and marine engines from the United States to the Caribbean region, in 2011 alone (NMMA 2011).

In the SBWEMR, popular tourist attractions and activities include diving, fishing, and recreational sports, which require the use of boats and other motorized transportation (Stonich 1998). In addition to its location within a tourist destination, the SBWEMR has also been identified as a foraging ground for the critically endangered hawksbill sea turtle (Dunbar et al. 2014, Hayes et al. 2016, Baumbach et al. 2019). Although some hawksbill foraging aggregations are comprised of both adult and juvenile turtles (Limpus 1992, Zuñiga-Marroquin et al. 2017, Bell et al. 2018), the SBWEMR appears to be an important foraging ground mostly for juvenile hawksbills. While direct turtle capture by the public is prohibited, the effect of boat traffic on hawksbills and the need for management of increasing boat traffic has not been addressed within the reserve. As a result of economic development in Roatán and subsequent income from tourism, the coastline of the SBWEMR is now highly developed and is comprised of multiple dive centers, hotels, and marinas, all of which produce boat traffic. A study by Hayes et al. (2016) in the SBWEMR suggested that increased pressure from turtle-diver interactions during SCUBA diving activities, may negatively impact hawksbill behavior, yet neither the effect of boating pressure on hawksbill distribution and presence, nor the effect of boating pressure on hawksbill behavior have been assessed.

Critically endangered species, such as the hawksbill sea turtle, require active implementation and enforcement of effective conservation strategies. To restore hawksbill population numbers, efforts must be made to understand how human activities, such as boating, might alter hawksbill presence and behavior. Multiple studies have taken place on hawksbills in the Caribbean, yet few studies focus on the influence of boat traffic on hawksbill distribution and behavior. We aimed to quantify the amount of boat traffic moving throughout the SBWEMR and evaluate the effect of boat traffic on the presence, distribution, and behavior of juvenile hawksbills within the SBWEMR foraging aggregation.

Methods

Study Site

Roatán is a Bay Island of Honduras and is located approximately 55 km north of mainland Honduras. The Sandy Bay West End Marine Reserve (SBWEMR) is a marine protected area located off the northwestern coast of the island (16˚21’ 44’’ N, 86˚25’ 06’’ W) (Figure 1). The reserve lies within the Mesoamerican Barrier Reef and is made up of barrier, fringing, patch, and sloping reefs, ranging in depths of approximately 5 – 40 m (Gonzalez 2013). The reserve has been referred to as an “Entrepreneurial MPA,” since it was initially established in 1989 by a single dive resort and, at the time, was supported by a sole monetary contributor (Colwell 1998, Forest 1998). At the time of its initial establishment, the reserve only encompassed 6 km of Roatán’s coastline, primarily in the Sandy Bay area. Over the years, the boundaries of the marine reserve have been extended to include 13 km of the coastline, stretching from the westernmost tip of the island in West Bay, to Sandy Bay, and extends approximately 1 km offshore (RMP 2015). For the sake of this study, we divided the SBWEMR into three zones corresponding with the three major coastal towns bordering the reserve: West Bay, West End, and Sandy Bay (Figure 1). The three zones of the SBWEMR were further divided into fourteen sectors. The West Bay zone was divided into four sectors, while both the West End and Sandy Bay zones were divided into five sectors each. Each sector was approximately 0.9 km^2 (Figure 1).

Boat Traffic Assessment

Boat traffic in the SBWEMR was quantified through a series of above-water and in-water boat count surveys. Boat count surveys were conducted above water and took place 2 – 3 times per week from July to September 2016 – 2018. The number of boats that passed through a sector and the number of boats that remained stationary in the sector were counted.

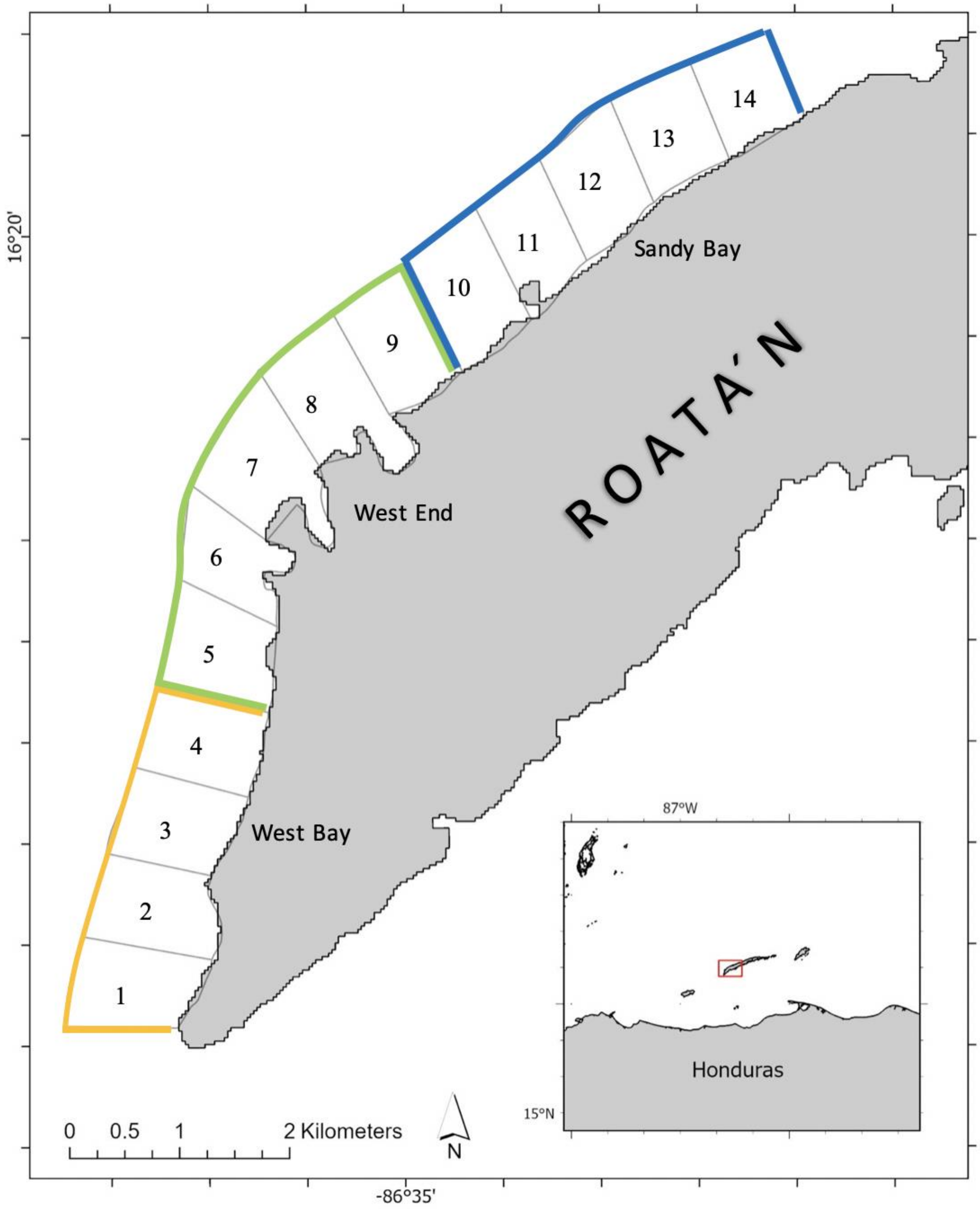

Figure 1. Study Site. The Sandy Bay-West End Marine Reserve (SBWEMR) is located on the west side of the island. The park extends 1 km from the shore and encompasses 13 km of coastline, containing the coasts of three main towns: West Bay, West End, and Sandy Bay. The reserve was divided into 3 zones: West Bay, West End, and Sandy Bay. Each zone was then divided into additional sectors: West Bay, indicated by a yellow boundary (sectors 1-4); West End, indicated by a green boundary (sectors 5-9); Sandy Bay indicated by a blue boundary (sectors 10-14).

We termed the number of boats traveling through a sector in one hour ‘boat intensity’ and calculated boat intensity by the equation:

$$(B_M - B_A) \times 3 = {}^{boats}/_{hour} \tag{1}$$

where B_M equals the number of boats that moved through the sector in the twenty-minute period and B_A equals the number of boats that remained stationary in the same twenty-minute period. Since the difference of moving and stationary boats was calculated during a twenty-minute observation period, the difference was multiplied by three to estimate the number of boats moving through a sector during a sixty-minute period.

In-water boat counts took place during in-water surveys. During approximately one-hour-long in-water surveys, the number of boats heard during the dive was recorded. Although type and size were not recorded, we calculated boat intensity for each sector where surveys were completed. Boat traffic intensities calculated at the sector level were then averaged to calculate boat traffic intensity at the zone level.

Hawksbill Presence and Distribution (In-Water Surveys)

Hawksbill presence in the SBWEMR was evaluated from June to September 2016 – 2018 through in-water surveys using SCUBA. In-water surveys and boat counts were conducted simultaneously by two groups; however, in-water surveys lasted approximately one hour and were performed in-water in the morning (8:30 – 10:30) and afternoon (14:30 – 16:30). During each survey, 2 – 5 divers traversed each sector in a transect pattern, similar to the strip transect method described by Baumbach et al. (2019). Upon sighting a turtle, the location, depth, behavior at sighting, and tag number were noted. When possible, each hawksbill was photographed for photo-identification purposes (Dunbar et al. 2017, Dunbar et al. 2017) and captured for individual work-up. Standard measurements (curved carapace length (CCL), curved carapace width (CCW), and weight were recorded for each turtle following methods by Dunbar et al. (2008) and Berube et al. (2012). Hawksbill sighting values used for data analyses were indicated as sightings per effort.

Behavioral Observations

During in-water surveys, hawksbill behaviors were recorded using a Canon G16 camera in a Fantasea Line FG16 underwater housing. Once in sight, divers remained at least 4.5 m from each turtle to ensure behaviors were not additionally altered by diver presence (Meadows 2004, Hayes et al. 2016). Hawksbill behaviors were recorded for as long as possible, usually 10 minutes or more. Using Jwatcher (Blumstein et al. 2006), hawksbill behaviors were reviewed to calculate the duration of five behaviors: swimming, resting, surfacing, investigating, and eating. We acquired behavior definitions from Dunbar et al. (2008) and Stimmelmayr et al. (2010). Briefly, swimming was characterized as constant movement through the water column, and resting was characterized as the cessation of movement, remaining stationary on the seafloor (reef, sand, rubble, etc.) without investigating or eating. Surfacing was characterized as floating at the water’s surface, which typically included breathing events. Investigating was characterized as frequent pauses to examine nearby material, and eating was characterized as biting, chewing, and/or ingesting prey while stationary or suspended in the water column.

Data Analysis

One-way analysis of variance (ANOVA) was used to assess the variation in hawksbill sightings and boat traffic intensities among the three years, three zones, and two time periods. Pairwise t-tests were used to further indicate significance in hawksbill sightings between the morning and afternoon and among the three years, once adjusted for year and zone. Using Spearman correlation, the relationship between boat traffic intensity and hawksbill sightings was assessed overall and for each year. A separate one-way ANOVA was used to measure variation in behavioral states across time, and a separate Spearman correlation was used to estimate the relationship between boat traffic intensity and time spent in each behavior. Spearman correlation was also used to assess the relationship between duration of each behavioral state and size: CCL and weight.

Results

Boat Traffic Assessment

Boat traffic was quantified in the SBWEMR over a period of ten weeks from June to September in 2016 – 2018. During above-water surveys, a total of 6,999 boats were counted over the span of the three-year period. However, total boat counts varied from year to year. In 2016, taxi boats had the highest counts (43 %), followed by dive boats (35 %), recreational boats (17 %), and non-motorized boats (5 %). In both 2017 and 2018, dive boats had the highest counts (40 %; 36 %), followed by taxi boats (33 %; 32 %), recreational boats (21 %; 24 %), and non-motorized boats (6 %; 7 %). Although boat traffic intensity was highest in 2016, followed by 2017 and 2018, results demonstrated that boat traffic intensity was not significantly different among all three years (F = 2.54, df = 2, $p = 0.085$). However, boat traffic intensity was significantly higher in 2016 when compared to 2017 ($t = -3.08$, $p = 0.002$), when we adjusted for zone. Boat traffic intensity in 2018 was not significantly different from boat traffic intensities in both 2016 ($t = -1.43$, $p = 0.155$) and 2017 ($t = 1.64$, $p = 0.103$). When analyzed by zone, boat traffic intensity was significantly different among the three zones ($F = 33.26$, df = 2, $p < 0.0001$) (Table 1). The overall mean of boat traffic intensity was significantly higher in West Bay and West End compared to Sandy Bay (Table 1 and Figure 2A). In all three years, there was also no significant difference in boat traffic intensity between the morning and afternoon time periods ($F = 2.091$, df = 1, $p > 0.01$).

During in-water surveys, a total of 1,203 boats were counted. Results showed that boat traffic intensity was not significantly different among all three years ($F = 0.32$, df = 2, $p = 0.726$). In all three years, there was no significant difference in boat traffic intensity between the morning and afternoon time periods ($F = 2.29$, df = 1, $p = 0.141$). Boat traffic intensity was significantly different among the three zones ($F = 6.468$, df = 2, $p = 0.005$) and the overall mean of boat traffic intensity was significantly higher in West Bay and West End compared to Sandy Bay (Table 2 and Figure 2B).

Hawksbill Presence and Distribution (In-Water Surveys)

A total of 242 in-water surveys were completed from June to September 2016 – 2018 (Table 3). During these surveys, a total of 180 juvenile hawksbill sightings were recorded (Table 4). One-way ANOVA demonstrated that hawksbill sightings were significantly different among the three zones ($F= 5.57$, df = 2, $p = 0.005$) and the three years ($F = 3.48$, df = 2, $p = 0.036$). Hawksbill sightings in West Bay and West End were significantly greater than Sandy Bay. However, hawksbill sightings were not significantly different between morning and afternoon time periods (F = 3.328, df = 1, p = 0.072). Once adjusted for year and zone, hawksbill presence in the afternoon was significantly lower than in the morning (t = -2, p = 0.049). Hawksbill presence in 2016 was significantly lower than hawksbill presence in 2017 (t = 2.1, p =0.033) and 2018 (t = 2.69, p = 0.0089), adjusting for year and zone. Spearman correlation results indicated a significant positive correlation between boat intensity and hawksbill presence (rho = 0.31, p = 0.0038) (Figure 3). However, when each year was assessed separately, a significantly positive correlation between boat intensity and hawksbill presence was evident only in 2016 (rho = 0.64, p < 0.001) (Figure 4). In-water boat traffic intensity and hawksbill presence were also significantly positively correlated (rho = 0.947, p < 0.0001) (Figure 5).

Behavioral Observation

A total of 557 minutes of hawksbill (n = 37) behaviors were recorded during in-water surveys from June to September 2017 – 2018. Since ‘resting’ observations were absent, only four behavioral states were used for analysis: swimming, foraging, eating, and surfacing. Hawksbills spent the most time swimming (160 minutes; 33.4 %), followed by investigating (158 minutes; 33 %), eating (141 minutes, 29.5 %), and at the surface (20 minutes, 4.1 %). Overall, time spent in each behavior was significantly different (f = 17.46, df = 3, p < 0.001). There was a moderately positive association between time spent eating and CCL (rho = 0.64, p = 0.001) and weight (rho = 0.53, p = 0.01) (Figure 6A & B).

Table 1: One-way ANOVA of Boat Intensity by zone for above-water counts.

Variable	Means	S.E	Df	F-Value	P-Value
Sandy Bay	8.87	2.62	2	33.26	P<0.0001
West End	33.27	2.62			
West Bay	37.67	2.92			

Table 2: One-Way ANOVA of Boat Intensity by zone for in-water Counts.

Variable	Means	DF	F-Value	P-Value
West Bay	6.5	2	6.468	0.005
West End	8.7			
Sandy Bay	4.2			

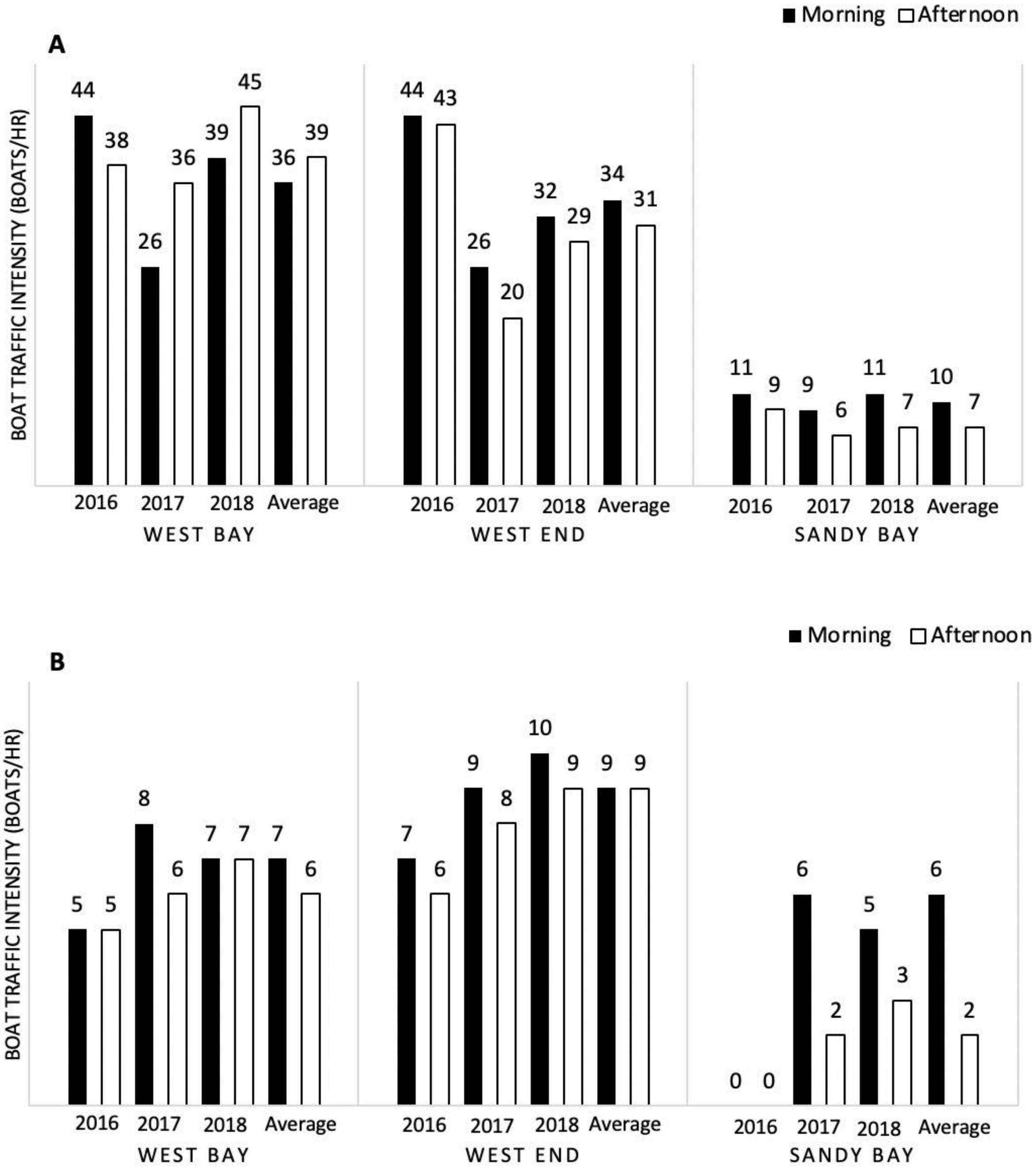

Figure 2. Mean Boat Traffic Intensity. **A)** Above-water boat count surveys were used to estimate boat traffic intensity (boats/hour) in West Bay, West End, and Sandy Bay. Mean boat traffic intensities from 2016, 2017, and 2018 are displayed side by side. Average boat traffic intensity from all three years combined is displayed last for each zone. **B)** In-water boat count surveys were used to estimate boat traffic intensity (boats/hour) in West Bay, West End, and Sandy Bay. Mean boat traffic intensities from 2016, 2017, and 2018 are displayed side by side. Average boat traffic intensity from all three years combined is displayed last in each zone.

Table 3. In-Water Observation Surveys (2016-2018). In-water observations surveys were conducted in the morning and afternoon in the Sandy Bay, West End, and West Bay zones. The total number or surveys completed in each zone in the morning and afternoon during the entire study is shown. The total number of surveys completed in each zone is also shown.

	West Bay	West End	Sandy Bay
Morning	49	45	21
Afternoon	53	58	16
Total	102	103	37

Table 4. In-water sightings (2016-2018). In-water hawksbill sighting were recorded in the morning and afternoon in the Sandy Bay, West End, and West Bay zones. The total number of hawksbills observed in each zone in the morning and afternoon during the entire study is shown. The total number of hawksbills observed in each zone is also shown.

	West Bay	West End	Sandy Bay
Morning	39	39	16
Afternoon	39	42	5
Total	78	81	21

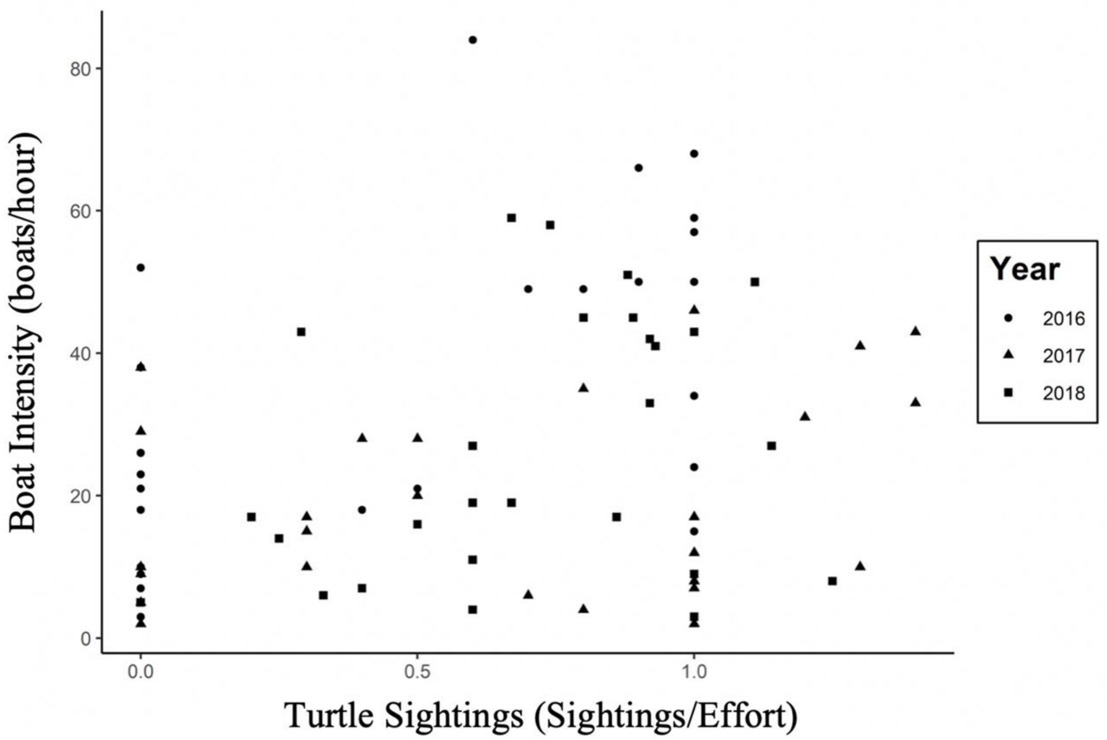

Figure 3. Spearman Correlation - Overall. Spearman correlation between boat traffic intensity and hawksbill sightings in all three study years. Although moderate, overall, a positive correlation between boat traffic intensity and hawksbill presence is evident (rho = 0.31; p = 0.0038).

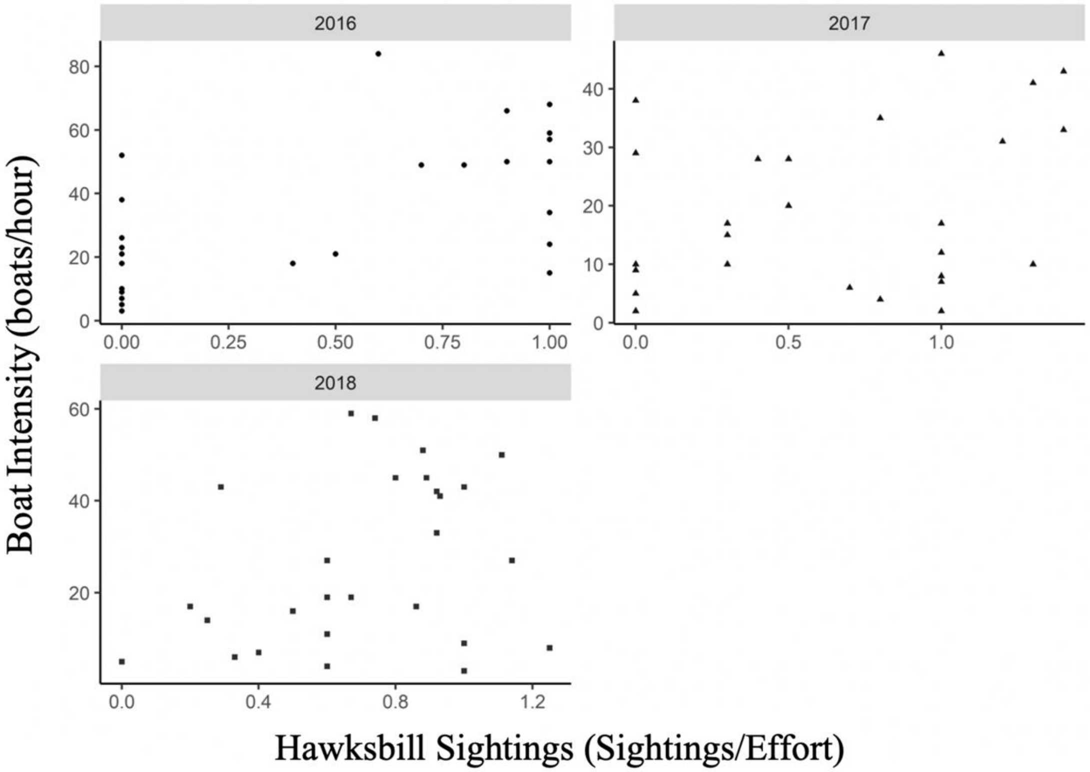

Figure 4. Spearman Correlation – Individual Years. Spearman correlation between boat traffic intensity and hawksbill sightings in 2016, 2017, and 2018, displayed individually. A positive correlation between boat traffic intensity and hawksbill presence is evident in each year, however, a significantly positive correlation between boat intensity and hawksbill presence is evident only in 2016 (P<0.001).

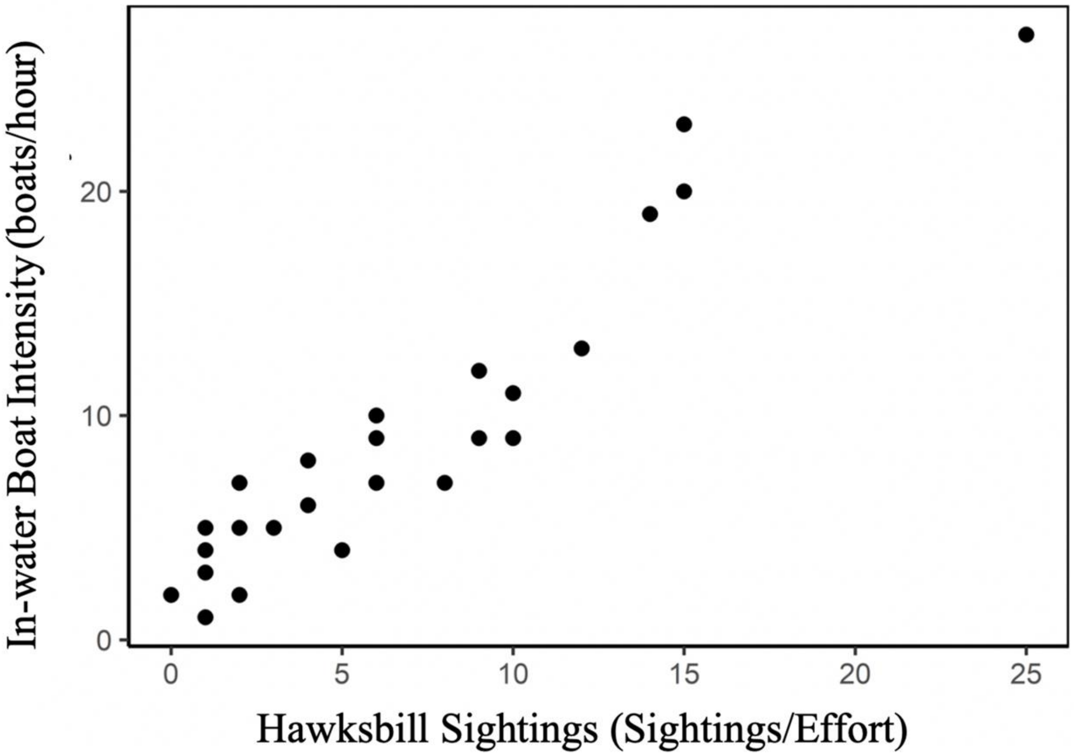

Figure 5. Spearman Correlation – In-water Boat Traffic. Spearman correlation between boat traffic intensity and hawksbill sightings in all years combined. A significantly positive correlation between in-water boat intensity and hawksbill presence is evident ($P < 0.001$).

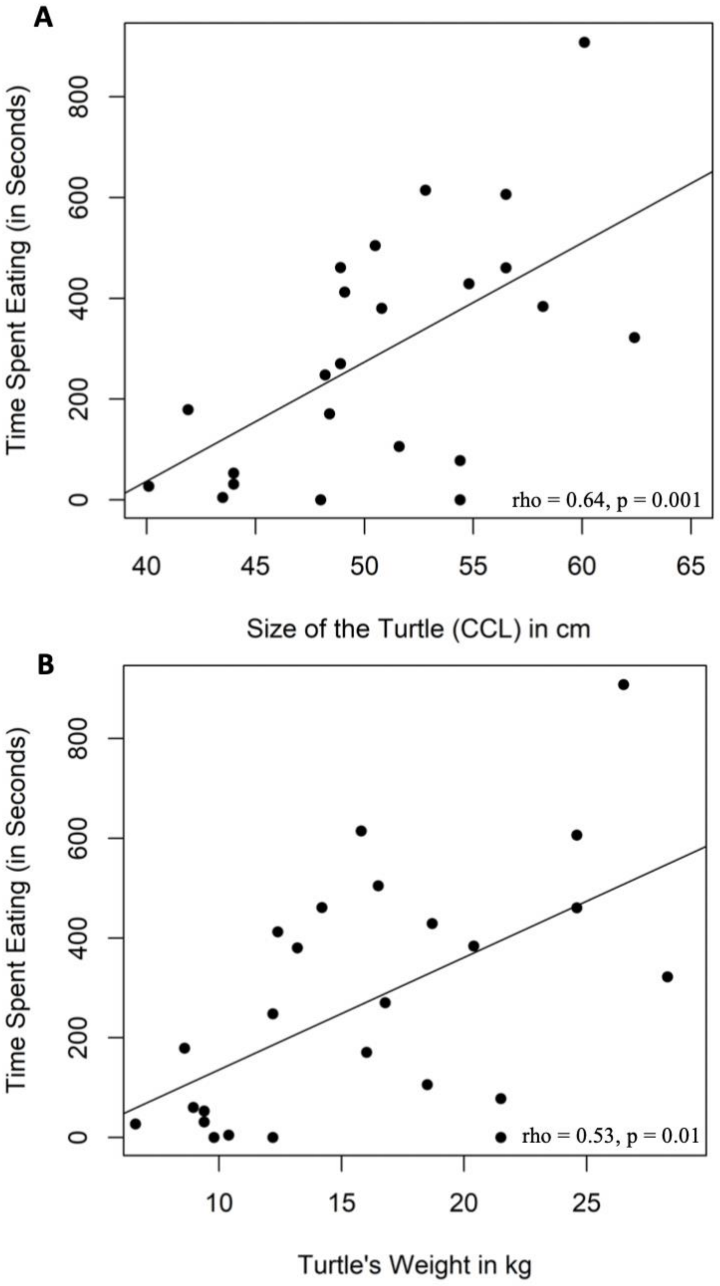

Figure 6. Duration of Hawksbill Eating Behavior. **A)** Time spent eating according to curved carapace length (CCL). A moderately positive association between time spent eating and CCL is evident (rho = 0.64; p = 0.001). Time spent eating increases with CCL. **B**) Time spent eating according to weight (kg). a moderately positive association between time spent eating and weight (rho = 0.53; p = 0.01). Time spent eating increases with weight.

Spearman correlation indicated a non-significant negative relationship between boat intensity and time spent in each behavior for each zone; swimming (rho = -0.15, p = 0.41), eating (rho = 0.05, p = 0.77), surfacing (rho = -0.34, p = 0.07), and foraging (rho = -0.28, p = 0.12) (Table 5). Although occurrences of boat dodges by hawksbills were not captured with the Canon G16, three instances were counted during personal observations.

Table 5: Correaltion between behavior and time. Spearman correlation suggested there was no significant correlation between boat intensity and time spent in each behavior.

Variable	Rho	P-Value
Swimming	-0.2	0.41
Eating	0.05	0.77
Surfacing*Surfaced	-0.3	0.07
Investigating/Foraging	-0.3	0.12

Discussion

One purpose of marine protected areas (MPAs) is to decrease the negative influences of human activities on marine life and the marine environment. Although many MPAs have imposed fishing quotas and have established no-entry zones (Christie et al. 2007, McCook et al. 2010, Thurstan et al. 2012, Hilborn 2015), few regulate boat traffic where it is permitted (Ashe et al. 2010). The SBWEMR was established to protect the local reef from detrimental human activities, yet, to date, the reserve has no regulations on boat traffic or vessel speeds (RMP 2015). With the steadily increasing influx of visitors and the increasing economic incentives for tourism in Roatán, development on the island has progressed at a rapid pace. Over the years, the number of tourists visiting the island has increased from 900 in 1969 to over 1 million in 2014 (Ministry of Tourism, unpublished data). Appealing to tourists in the region, businesses and individuals in the tourism industry have increased access to water sports, transportation, and other recreational activities all within the marine environment. As human activities continue to develop in coastal areas, boat numbers will continue to rise in coastal habitats (McCarthy 2004, Halpern et al. 2008), such as the SBWEMR. Constant movement of boat traffic throughout the reserve potentially disrupts the quality of life for the critically endangered hawksbill, which forages within the reserve. We sought to quantify boat traffic within the reserve and assess if boat presence alters hawksbill presence, distribution, or behavior.

Calculated boat traffic intensity was highest in zones associated with densely populated towns. The West Bay and West End zones correspond to the towns of West Bay and West End, which are popular destinations for tourists. Numerous hotels, hostels, rental properties, dive shops, restaurants, bars, shops, and other attractions are located in these towns. In contrast, Sandy Bay is sparsely populated by tourists and in 2015, only two dive centers were located in the area (Ministry of Tourism, unpublished data). Boat traffic intensity by boat type also varied depending on location. Although a taxi boat system runs throughout the entire SBWEMR, fewer taxi boats travel to Sandy Bay compared to West Bay and West End. These results may also be attributed to the lower popularity of the Sandy Bay region among tourists and visitors (MKW, pers. ob.). In Sandy Bay, there are fewer popular attractions and less popular beaches, several of which are characterized by muddy substrate and abundant sea grass shallows. High dive boat and taxi boat intensities were evident in West Bay and West End zones and can likely be best attributed to an abundance of dive centers in these areas and the numbers of tourists traveling to and from West End to West Bay. As of 2015, approximately 24 dive centers were located in West End and West Bay combined (Ministry of Tourism, unpublished data), which together consists of only approximately 8.5 km of coastline. In addition to differences in boat types, boat traffic intensity also varied according to year. Tourism is a large contributor to economic development in this region and the amount of boat traffic in the SBWEMR may be directly affected by the number of tourists traveling to Roatán and, more specifically, the western side of the island, each year. Since a fluctuation in the number of tourists visiting Roatán each year has been evident in previous tourism surveys (Ministry of Tourism, unpublished data), the same variation in visitation could explain the fluctuations in boat traffic during our years of study. The same has been seen in other coastal areas around the world, including Norway (Madsen et al. 2009), Australia’s Great

Barrier Reef (Harriott 2002), and Tanzania (Masalu 2000), where an increase in tourism has been linked to an increase in boating activities.

Behavioral responses to variation in boat traffic intensity were also assessed in hawksbills foraging in the SBWEMR. Similar to studies by von Brandis et al. (2010) and Van Dam et al. (1997) where hawksbills spent less time at the surface than in other activities, hawksbills foraging in the reserve also spent less time at the surface than foraging, swimming and eating. In a previous study on hawksbill behavior in Roatan, but outside the SBWEMR, Dunbar et al. (2008) indicated that hawksbills spent more time swimming and foraging than eating. The same behavioral comparison was evident in juvenile hawksbills foraging in the SBWEMR, confirming that hawksbills often initiate exploratory activities, as also seen in studies by Wood et al. (2017). Taken independently, the similarity of these behavioral comparisons of SBWEMR hawksbills to those of other foraging aggregations suggests that hawksbill behaviors within the reserve are similar to typical sea turtle behaviors. However, when behavioral durations were correlated to boat traffic intensity, although not statistically significant, a negative correlation of swimming, surfacing, and foraging was apparent in relation to elevated boat traffic intensity. Similar results were evident in the study by Hayes et al. (2016), where the duration of in-water behaviors, such as swimming, eating, and foraging decreased in the presence of an unnatural pressure, such as diver interaction. A threat to the duration of foraging due to unnatural pressures could negatively impact hawksbill survivability, decreasing detection and access to needed nutrients. However, in nutritionally favorable habitats, a threat to foraging durations may not negatively impact hawksbill survivability, since foraging efforts have been recorded to decrease, while somatic growth rates increase (Van Dam et al. 1997, Diez et al. 2002). These results suggest that turtles are able to locate adequate food faster, spending more time eating and less time searching (Schoener et al. 1971). However, in unfavorable habitats, a reduction in time spent foraging could hinder prey acquisition and decrease somatic growth rates (Diez et al. 2002, Bjorndal et al. 2016). In addition, a decrease in surfacing activity was unique to our study, indicating that boat traffic intensity may impose an additional hindrance to hawksbill behavior at the surface.

According to Frid et al. (2002), any human-caused disturbance stimuli should be considered a form of predation. Prey initiate anti-predator behavioral changes to generalized threat stimuli, ranging from loud noises to fast approaching objects. Therefore, although not consumptive, boats may potentially be considered a type of predator. However, studies by Hammerschlag et al. (2015) suggest that hawksbills lack anti-predator responses in the presence of predators, specifically consumptive predators. A study by Hammerschlag et al. (2015) assessing predator-prey interactions between tiger sharks (*Galeocerdo cuvier*) and loggerhead turtles (*Caretta caretta*) across an open environment, suggests that, although the preferred habitat of sea turtles off the coast of Florida largely overlaps with the home range of sharks in the area, sea turtles do not initiate risk avoidance behaviors in response to predator presence. A subsequent study by Hammerschlag et al. (2016) assessing the predator-prey relationship between tiger sharks (*Galeocerdo cuvier*) and green turtles (*Chelonia mydas*) in Australia support the findings of Hammerschlag et al. (2015) in Florida. Again, in Australian waters, sea turtles did not exhibit anti-predatorial responses to increased predator presence. In addition, according to a study by Foley et al. (2007), although the overlap of shark and sea turtle home ranges increased during nesting seasons, sea turtles did not commence predator avoidance behaviors. Instead, increased predator presence resulted in increased sea turtle mortality, since sea turtle consumption by sharks increased as the number of sharks in the area increased (Foley et al. 2007).

The absence of behavioral changes in the presence of predators, such as sharks, may be due to the inability of turtles to predict predation risk, since predation is not consistent throughout spatial and temporal scales (Kauffman 2010). In addition, turtles have been known to become accustomed to nonintrusive disturbances (von Brandis et al. 2010, Nanninga et al. 2017). Hawksbills within the SBWEMR remained undisturbed and demonstrated no visible physical response to boats passing overhead during feeding events. Although fine-scale behavioral responses were not assessed, our results of in-water hawksbill behaviors in response to boat presence are supported by recent underwater auditory studies performed by Tyson et al. (2017), in which in-water behaviors of free swimming green turtles (*Chelonia mydas*) classified as pitch, roll, and heading, were unaffected by sound emitted from passing boat traffic. However, previous encounters with stressors, such as boat strikes or near misses, may elicit a learned avoidance response.

In response to destructive disturbances, such as boat strikes, turtles may adjust behaviors prior to surfacing events. After releasing captured juvenile hawksbills in a non-protected area off eastern Roatán, Dunbar et al. (2008) recorded an alteration in surfacing behavior. During surfacing events, turtles slowed their ascent speed and remained in the water column approximately 1 m below the surface before rapidly reaching the surface, quickly respiring, and immediately descending from the surface.

von Brandis et al. (2010) also noted a change in behavior in hawksbills in a non-protected area, as turtles seemed “wary” prior to breaking the surface. This behavioral mechanism may allow turtles to scan prior to reaching the surface, and has been suggested as a method of predator or threat avoidance (Van Dam et al. 1997, Nowacek et al. 2001, Martin 2003). However, once at the surface, turtles are scarcely able to detect the direction of approaching threats and, depending on approach speed, may be unable to quickly submerge in sufficient time to avoid injury (Hazel et al. 2007).

Often unable to detect approaching boats and retreat in a timely manner, sea turtles are victims of boat collisions and propeller strikes. As a result, several instances of injury and mortality have been recorded in sea turtle species, more so in regions of unregulated boating (Lutcavage et al. 1997, Orós et al. 2005, Deem et al. 2006, Chaloupka et al. 2008, Casale et al. 2010, Phu et al. 2019). Although within a protected area, several instances of boat collision injuries and reoccurring strikes have been documented off the coast of Mabul Island (Phu et al. 2019). Apart from the implementing of boating regulations in unprotected areas, the restructuring of current management strategies to include boating regulations are important to ensure quality of life for sea turtles. Although instance of boat strikes were not directly addressed in our study, most incidences of boat strikes are recorded in areas that are in close proximity to commercial and tourism ports, or characterized by dense motorized boat operations (Davenport et al. 2006, Denkinger et al. 2013). Hazel et al. (2007) showed that regulation of vessel speed within a reserve is necessary to avoid collisions with sea turtles. According to Thurstan et al. (2012), boat traffic is a high impact risk factor for wildlife and habitats within marine reserves. If unregulated and unmonitored, inappropriate boating without restrictions can reduce the ability of animals to avoid boat collisions. Activities involving boat traffic can only be characterized as low impact factors if carefully controlled.

Although our results suggest that boat traffic does not directly disrupt the behaviors of hawksbill foraging in the SBWEMR, the potential for boat strikes remains evident. Further analysis of boat strike prevalence in the SBWEMR and subsequent altered hawksbill behavior is needed. Efforts should be made to continually monitor and regulate vessel speeds throughout the SBWEMR for conservation of the critically endangered hawksbills in the area to be effective. Furthermore, to avoid injury and potential mortality, boat traffic quantity and speed should be regulated in MPAs where sea turtles are present.

Acknowledgements

We would like to thank the Department of Earth and Biological Sciences and the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR, Inc.) for funding this work. We extend our gratitude to Roatán Dive Center for their assistance during this project, and to Splash Inn Dive Center for their continuing collaboration and support of our field work in Honduras. We are grateful to the many ProTECTOR, Inc. Interns (Daniel Trujillo, Justin Cruz LeDuc, Shannon Byrd, Samantha Read, Lindsay Marston, and Ashley Morrow) and Volunteers (Caitlin Love and Skylar Kuhn) who have helped with sample collection over the years. Finally, we express our gratitude to Jimmy Miller for providing logistical support in Roatán, and to ProTECTOR, Inc. Country Coordinator, Lidia Salinas for securing permits for work in Honduras. This project was permitted under the department of Fisheries (DIGEPESCA/SAG – Honduras) permit No. 251-10, the Institute for Forest Conservation (ICF-Honduras) permit No. DE-MP-055-2016 and ASG-ICF-139-2018, and Loma Linda University IACUC protocol No. 8120038 and 8150049.

References

Aguirre, A. A., S. C. Gardner, J. C. Marsh, S. G. Delgado, C. J. Limpus and W. J. Nichols (2006). Hazards associated with the consumption of sea turtle meat and eggs: a review for health care workers and the general public. *EcoHealth* **3**(3): 141-153.

Ashe, E., D. Noren and R. Williams (2010). Animal behaviour and marine protected areas: incorporating behavioural data into the selection of marine protected areas for an endangered killer whale population. *Animal Conservation* **13**(2): 196-203.

Bailey, H. and P. M. Thompson (2009). Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area. *Marine Ecology Progress Series* **378**: 279-287.

Barber, C. V. and V. R. Pratt (1998). Poison and profits: cyanide fishing in the Indo-Pacific. *Environment: Science and Policy for Sustainable Development* **40**(8): 4-9.

Bas, A. A., A. A. Ozturk and B. Ozturk (2015). Selection of critical habitats for bottlenose dolphins (*Tursiops truncatus*) based on behavioral data, in relation to marine traffic in the Istanbul Strait, Turkey. *Marine Mammal Science* **31**(3): 979-997.

Bass, A. L. (1999). Genetic analysis to elucidate the natural history and behavior of hawksbill turtles (*Eretmochelys imbricata*) in the wider Caribbean: A review and re-analysis. *Chelonian Conservation and Biology* **3**(2): 195-199.

Bass, A. L., S. P. Epperly and J. J. C. G. Braun-McNeill (2004). Multi-year analysis of stock composition of a loggerhead turtle (Caretta caretta) foraging habitat using maximum likelihood and Bayesian methods. **5**(6): 783-796.

Bass, A. L., D. A. Good, K. A. Bjorndal, J. I. Richardson, Z. M. Hillis, J. A. Horrocks and B. W. Bowen (1996). Testing models of female reproductive migratory behaviour and population structure in the Caribbean hawksbill turtle, Eretmochelys imbricata, with mtDNA sequences. *Molecular Ecology* **5**(3): 321-328.

Baumbach, D., C. Hayes, M. K. Wright, M. Macpui, L. A. Salinas and S. G. Dunbar (2015). Potential Hawksbill Prey Item Distribution Among Dive Sites in a Marine Protected Area in Roatán, Bay Islands, Honduras. 35th Annual Symposium on Sea Turtle Biology and Conservation, Dalaman, Mugla, Turkey.

Baumbach, D. S., E. C. Anger, N. A. Collado and S. G. Dunbar (2019). Identifying Sea Turtle Home Ranges Utilizing Citizen-Science Data from Novel Web-Based and Smartphone GIS Applications. *Chelonia Conservation and Biology* **18**(2): 133-144.

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

Bell, I. and M. P. Jensen (2018). Multinational genetic connectivity identified in western Pacific hawksbill turtles, *Eretmochelys imbricata*. *Wildlife Research* **45**(4): 307-315.

Berube, M. D., S. G. Dunbar, K. Ruetzler and W. K. Hayes (2012). Home Range and Foraging Ecology of Juvenile Hawksbill Sea Turtles (*Eretmochelys imbricata*) on Inshore Reefs of Honduras. *Chelonian Conservation and Biology* **11**(1): 33-43.

Bjorndal, K. A. and A. B. J. M. E. Bolten (2008). Annual variation in source contributions to a mixed stock: implications for quantifying connectivity. **17**(9): 2185-2193.

Bjorndal, K. A., M. Chaloupka, V. S. Saba, C. E. Diez, R. P. van Dam, B. H. Krueger, J. A. Horrocks, A. J. B. Santos, C. Bellini, M. A. G. Marcovaldi, et al. (2016). Somatic growth dynamics of West Atlantic hawksbill sea turtles: a spatio-temporal perspective. *Ecosphere* **7**(5): e01279-n/a.

Bjorndal, K. A. and J. C. B. Jackson (2003). Roles of Sea Turtles in marine ecosystems: Reconstructing the Past. The Biology of Sea Turtles. Boca Raton, CRC Press. **II:** 259-273.

Blair, H. B., N. D. Merchant, A. S. Friedlaender, D. N. Wiley and S. E. Parks (2016). Evidence for ship noise impacts on humpback whale foraging behaviour. *Biology Letters* **12**(8): 20160005.

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

Blumenthal, J. M., F. A. Abreu-Grobois, T. J. Austin, A. C. Broderick, M. W. Bruford, M. S. Coyne, G. Ebanks-Petrie, A. Formia, P. A. Meylan, A. B. Meylan, et al. (2009). Turtle groups or turtle soup: dispersal patterns of hawksbill turtles in the Caribbean. *Molecular Ecology* **18**(23): 4841-4853.

Blumenthal, J. M., T. J. Austin, C. D. L. Bell, J. B. Bothwell, A. C. Broderick, G. Ebanks-Petrie, J. A. Gibb, K. E. Luke, J. R. Olynik, M. F. Orr, et al. (2009). Ecology of Hawksbill Turtles, *Eretmochelys imbricata*, on a Western Caribbean Foraging Ground. *Chelonian Conservation and Biology* **8**(1): 1-10.

Blumstein, D. T., J. C. Daniel and C. S. Evans (2006). JWatcherTM 1.0 An Introductory User's Guide. *Last Modified* **9**.

Bohnsack, J. A. (1998). Application of marine reserves to reef fisheries management. *Australian Journal of Ecology* **23**(3): 298-304.

Bolker, B. M., T. Okuyama, K. A. Bjorndal and A. B. Bolten (2007). Incorporating multiple mixed stocks in mixed stock analysis: 'many-to-many' analyses. *Molecular Ecology* **16**(4): 685-695.

Bowen, B. W., A. L. Bass, A. GarciaRodriguez, C. E. Diez, R. van Dam, A. Bolten, K. A. Bjorndal, M. M. Miyamoto and R. J. Ferl (1996). Origin of hawksbill turtles in a Caribbean feeding area as indicated by genetic markers. *Ecological Applications* **6**(2): 566-572.

Bowen, B. W., W. S. Grant, Z. Hillis-Starr, D. J. Shaver, A. Bjorndal, A. B. Bolten and A. L. Bass (2007). Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. *Molecular Ecology* **16**(1): 49-60.

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

Bracciali, C., D. Campobello, C. Giacoma and G. Sara (2012). Effects of nautical traffic and noise on foraging patterns of Mediterranean damselfish (*Chromis chromis*). *Plos One* **7**(7): e40582.

Bracciali, C., D. Campobello, G. Giacoma and G. Sará (2012). Effects of Nautical Traffic and Noise on Foraging Patterns of Mediterranean Damselfish (*Chromis chromis).* *Plos One* **7**(7): 1 - 11.

Bräutigam, A. and K. L. Eckert (2006). Turning the tide: exploitation, trade and management of marine turtles in the Lesser Antilles, Central America, Colombia and Venezuela. Cambridge, Traffic International.

Briscoe, N. J., M. R. Kearney, C. A. Taylor and B. A. Wintle (2016). Unpacking the mechanisms captured by a correlative species distribution model to improve predictions of climate refugia. *Global Change Biology* **22**(7): 2425-2439.

Brown, J. J. and G. W. Murphy (2010). Atlantic sturgeon vessel-strike mortalities in the Delaware Estuary. *Fisheries* **35**(2): 72-83.

Browne, D. C., J. A. Horrocks and F. A. Abreu-Grobois (2010). Population subdivision in hawksbill turtles nesting on Barbados, West Indies, determined from mitochondrial DNA control region sequences. *Conservation Genetics* **11**(4): 1541-1546.

Bulté, G., M. A. Carrière and G. Blouin- Demers (2010). Impact of recreational power boating on two populations of northern map turtles (*Graptemys geographica*). *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**(1): 31-38.

Camiñas, J. A. and C. O. J. F. f. r. De Málaga (2004). Sea turtles of the Mediterranean Sea: population dynamics, sources of mortality and relative importance of fisheries impacts. **738**: 27-84.

Canin, J. (1989). International Trade in Sea Turtle Products. Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology, Jekyll Island, Georgia, NOAA Technical Memorandum NMFS-SEFC-232.

Canin, J. (1991). International trade aspects of the Japanese Hawksbill shell ('Bekko') industry. *Marine Turtle Newsletter* **54**: 17-21.

Carrion-Cortez, J., C. Canales-Cerro, R. Arauz and R. Riosmena-Rodriguez (2013). Habitat Use and Diet of Juvenile Eastern Pacific Hawksbill Turtles (Eretmochelys imbricata) in the North Pacific Coast of Costa Rica. *Chelonian Conservation and Biology* **12**(2): 235-245.

Casale, P., M. Affronte, G. Insacco, D. Freggi, C. Vallini, P. Pino d'Astore, R. Basso, G. Paolillo, G. Abbate and R. Argano (2010). Sea turtle strandings reveal high anthropogenic mortality in Italian waters. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**(6): 611-620.

Cazabon-Mannette, M., D. Browne, N. Austin, A. Hailey and J. Horrocks (2016). Genetic structure of the hawksbill turtle rookery and foraging aggregation in Tobago, West Indies. *Journal of Experimental Marine Biology and Ecology* **485**: 94-101.

Chaloupka, M., T. M. Work, G. H. Balazs, S. K. Murakawa and R. Morris (2008). Cause-specific temporal and spatial trends in green sea turtle strandings in the Hawaiian Archipelago (1982–2003). *Marine Biology* **154**(5): 887-898.

Christianen, M. J., P. M. Herman, T. J. Bouma, L. P. Lamers, M. M. van Katwijk, T. van der Heide, P. J. Mumby, B. R. Silliman, S. L. Engelhard and M. van de Kerk (2014). Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. *Proceedings of the Royal Society B: Biological Sciences* **281**(1777): 20132890.

Christie, P. and A. T. White (2007). Best practices for improved governance of coral reef marine protected areas. *Coral Reefs* **26**(4): 1047-1056.

Colwell, S. (1998). Dive-tourism and private stewardship of small-scale coral reef marine protected areas. Proceedings of the international tropical marine ecosystems management symposium.

Colwell, S. (1999). Dive-Tourism and Private Stewardship of Small-Scale Coral Reef Marine Protected Areas. International Tropical Marine Ecosystems Management Symposium (ITMEMS), Townsville, Australia.

Coxen, C. L., J. K. Frey, S. A. Carleton, D. P. J. G. e. Collins and conservation (2017). Species distribution models for a migratory bird based on citizen science and satellite tracking data. **11**: 298-311.

Cruz, G. A. and M. Espinal (1987). National Report for Honduras. Western Atlantic Turtle Symposium II. Mayagüez, Puerto Rico**:** WATS2-047.

Davenport, J. and J. L. Davenport (2006). The impact of tourism and personal leisure transport on coastal environments: A review. *Estuarine, Coastal and Shelf Science* **67**(1–2): 280-292.

Dawson, T. M., A. Formia, P. D. Agamboué, G. M. Asseko, F. Boussamba, F. Cardiec, E. Chartrain, P. D. Doherty, J. M. Fay and B. J. Godley (2017). Informing marine protected area designation and management for nesting olive ridley sea turtles using satellite tracking. *Frontiers in Marine Science* **4**: 312.

de la Estrella, M., R. G. Mateo, J. J. Wieringa, B. Mackinder and J. Muñoz (2012). Legume diversity patterns in West Central Africa: influence of species biology on distribution models. *Plos One* **7**(7): e41526.

Deem, S. L., E. S. Dierenfeld, G. P. Sounguet, A. R. Alleman, C. Cray, R. H. Poppenga, T. M. Norton and W. B. Karesh (2006). Blood values in free-ranging nesting leatherback sea turtles (*Dermochelys coriacea*) on the coast of the Republic of Gabon. *Journal of Zoo Wildlife Medicine* **37**(4): 464-472.

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

Diaz-Fernandez, R., T. Okayama, T. Uchiyama, E. Carrillo, G. Espinosa, R. Marquez, C. Diez, H. J. C. C. Koike and Biology (1999). Genetic sourcing for the hawksbill turtle, Eretmochelys imbricata, in the northern Caribbean region. **3**(2): 296-300.

Dickerson, D., C. Theriot, M. Wolters, C. Slay, T. Bargo and W. Parks (2007). Effectiveness of relocation trawling during hopper dredging for reducing incidental take of sea turtles. 2007 World Dredging Conference.

Diez, C. E. and R. P. van Dam (2002). Habitat effect on hawksbill turtle growth rates on feeding grounds at Mona and Monito Islands, Puerto Rico. *Marine Ecology Progress Series* **234**: 301-309.

Dobbs, K., L. Fernandes, S. Slegers, B. Jago, L. Thompson, J. Hall, J. Day, D. Cameron, J. Tanzer and F. MacDonald (2007). Incorporating marine turtle habitats into the marine protected area design for the Great Barrier Reef Marine Park, Queensland, Australia. *Pacific Conservation Biology* **13**(4): 293-302.

dos Santos, L. A., M. F. Mendes, A. P. Krüger, M. L. Blauth, M. S. Gottschalk and F. R. J. P. o. Garcia (2017). Global potential distribution of Drosophila suzukii (Diptera, Drosophilidae). **12**(3): e0174318.

Dunbar, S. G., D. S. Baumbach, C. T. Hayes, M. K. Wright and L. Salinas (2017). Activities of the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR) in Honduras. <u>Annual Report of the 2015 and 2016 Seasons</u>.

Dunbar, S. G., D. S. Baumbach, M. K. Wright, C. T. Hayes, J. Holmberg, J. Crall and C. V. Stewart (2017). HotSpotter: less manipulating, more learning, and better vision for turtle photo identification. 37th Annual Symposium on Sea Turtle Biology and Conservation, Las Vegas, Neavada, USA.

Dunbar, S. G., C. T. Hayes and D. S. Baumbach (2016). Impacts of Recreational Diving on Hawksbill Sea Turtles (*Eretmochelys imbricata*) in the Sandy Bay West End Marine Reserve, Honduras. <u>Annual Report of the 2014 Summer Research Season.</u>

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

Dunbar, S. G., L. Salinas and L. Stevenson (2008). In-Water Observations of Recently Released Juvenile Hawksbills (*Eretmochelys imbricata*). *Marine Turtle Newsletter* **121**: 5-9.

Dunbar, S. G., M. K. Wright, E. C. Hyatt, R. T. Gammariello, D. S. Baumbach and L. Salinas (2019). ProTECTOR, Inc. National Report of Activities for the 2018 Research Season. <u>Annual Report of the 2018 Summer Research Seaon</u>.

Duncan, R. (2012). Development of a Species Distribution Model for the East Pacific Green Sea Turtle using Ecological Geoprocessing Tools, Texas A & M University.

Duran, N., S. G. Dunbar, R. A. Escobar and T. G. Standish (2015). High frequency of multiple paternity in a solitary population of olive ridley sea turtles in Honduras. *Journal of Experimental Marine Biology and Ecology* **463**: 63-71.

Dutton, D. L., P. H. Dutton, M. Chaloupka and R. H. Boulon (2005). Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biological Conservation* **126**(2): 186-194.

Easson, C. G., M. Slattery, D. M. Baker and D. J. Gochfeld (2014). Complex ecological associations: competition and facilitation in a sponge–algal interaction. *Marine Ecology Progress Series* **507**: 153-167.

Elith, J., C. H. Graham*, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick and A. J. E. Lehmann (2006). Novel methods improve prediction of species' distributions from occurrence data. **29**(2): 129-151.

Elith, J. and J. R. Leathwick (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual review of ecology, evolution, and systematics* **40**: 677-697.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee and C. J. Yates (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17**(1): 43-57.

Embling, C. B., P. A. Gillibrand, J. Gordon, J. Shrimpton, P. T. Stevick and P. S. Hammond (2010). Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*). *Biological Conservation* **143**(2): 267-279.

Fernandes, A., A. C. V. Bondioli, M. Solé and A. Schiavetti (2017). Seasonal Variation in the Behavior of Sea Turtles at a Brazilian Foraging Area. *Chelonia Conservation and Biology* **16**(1): 93-102.

Ferreira, R. L., F. R. Ceia, T. C. Borges, J. A. Ramos and A. B. Bolten (2018). Foraging niche segregation between juvenile and adult hawksbill turtles (Eretmochelys imbricata) at Príncipe island, West Africa. *Journal of Experimental Marine Biology and Ecology* **498**: 1-7.

Ferrier, S., G. Watson, J. Pearce and M. Drielsma (2002). Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. *Biodiversity and Conservation* **11**(12): 2275-2307.

Finkbeiner, E. M., B. P. Wallace, J. E. Moore, R. L. Lewison, L. B. Crowder and A. J. Read (2011). Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. *Biological Conservation* **144**(11): 2719-2727.

Foley, A., K. Singel, R. Hardy, R. Bailey, S. J. F. Schaf and J. F. L. Wildlife Research Institute, Jacksonville, Florida, USA (2007). Distributions, relative abundances, and mortality factors for sea turtles in Florida from 1980 through 2007 as determined from strandings.

Forest, N. B. (1998). Assessment of coastal regulations and implementation: case study of Roatan, Bay Islands, Honduras.

Frid, A. and L. Dill (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**(1).

Fuentes, M. M., A. J. Gillis, S. A. Ceriani, T. L. Guttridge, M. P. V. Z. Bergmann, M. Smukall, S. H. Gruber and N. Wildermann (2018). Informing marine protected areas in Bimini, Bahamas by considering hotspots for green turtles (*Chelonia mydas*). *Biodiversity and Conservation* **28**(1): 1-15.

Gabriella, L. M. and S. Gianluca (2019). A false sense of protection: recreational uses and illegal behaviour in a Mediterranean Marine Protected Area and implications for management. *Integrated Environmental Assessment and Management*.

Gallo, B. M., S. Macedo, B. d. B. Giffoni, J. H. Becker and P. C. Barata (2006). Sea turtle conservation in Ubatuba, southeastern Brazil, a feeding area with incidental capture in coastal fisheries. *Chelonia Conservation and Biology* **5**(1): 93-101.

Galtier, N., B. Nabholz, S. Glémin and G. Hurst (2009). Mitochondrial DNA as a marker of molecular diversity: a reappraisal. *Molecular Ecology* **18**(22): 4541-4550.

Gaos, A. R., R. L. Lewison, M. P. Jensen, M. J. Liles, A. Henriquez, S. Chavarria, C. M. Pacheco, M. Valle, D. Melero and V. Gadea (2017). Natal foraging philopatry in eastern Pacific hawksbill turtles. *Royal Society Open Science* **4**(8): 170153.

Gaos, A. R., R. L. Lewison, M. P. Jensen, M. J. Liles, A. Henriquez, S. Chavarria, C. M. Pacheco, M. Valle, D. Melero and V. Gadea (2018). Rookery contributions, movements and conservation needs of hawksbill turtles at foraging grounds in the eastern Pacific Ocean. *Marine Ecology Progress Series* **586**: 203-216.

Gaos, A. R., R. L. Lewison, M. J. Liles, V. Gadea, E. Altamirano, A. V. Henríquez, P. Torres, J. Urteaga, F. Vallejo and A. Baquero (2016). Hawksbill turtle terra incognita: conservation genetics of eastern Pacific rookeries. *Ecology and Evolution* **6**(4): 1251-1264.

Gaos, A. R., R. L. Lewison, B. P. Wallace, I. L. Yanez, M. J. Liles, W. J. Nichols, A. Baquero, C. R. Hasbun, M. Vasquez, J. Urteaga, et al. (2012). Spatial ecology of critically endangered hawksbill turtles *Eretmochelys imbricata*: implications for management and conservation. *Marine Ecology Progress Series* **450**: 181-U198.

Gassó, N., W. Thuiller, J. Pino and M. Vilà (2012). Potential distribution range of invasive plant species in Spain. *NeoBiota* **12**: 25.

Geldmann, J., L. N. Joppa and N. D. Burgess (2014). Mapping change in human pressure globally on land and within protected areas. *Conservation Biology* **28**(6): 1604-1616.

Godley, B. J., J. M. Blumenthal, A. C. Broderick, M. S. Coyne, M. H. Godfrey, L. Hawkes and M. J. Witt (2008). Satellite tracking of sea turtles: Where have we been and where do we go next? *Endangered Species Research* **3**.

Gonzalez, I. (2013). Roatan Bay Islands Honduras Dive Guide: 60 of Roatan's Best Dives

Gonzalez-Garza, B., A. Stow, L. Felipe Sanchez-Teyer and O. Zapata-Perez (2015). Genetic variation, multiple paternity, and measures of reproductive success in the critically endangered hawksbill turtle (Eretmochelys imbricata). *Ecology and Evolution* **5**(24): S758-S769.

González-Rivero, M., L. Yakob and P. J. Mumby (2011). The role of sponge competition on coral reef alternative steady states. *Ecological Modelling* **222**(11): 1847-1853.

Gorham, J. C., D. R. Clark, M. J. Bresette, D. A. Bagley, C. L. Keske, S. L. Traxler, B. E. Witherington, B. M. Shamblin and C. J. Nairn (2014). Characterization of a Subtropical Hawksbill Sea Turtle (*Eretmocheyles imbricata*) Assemblage Utilizing Shallow Water Natural and Artificial Habitats in the Florida Keys. *Plos One* **9**(12): 16.

Gotelli, N. J. and J. Stanton- Geddes (2015). Climate change, genetic markers and species distribution modelling. *Journal of Biogeography* **42**(9): 1577-1585.

Grant, P. B. C. and T. R. Lewis (2010). High Speed Boat Traffic: A risk to crocodilian populations. *Herpetological Conservation and Biology* **5**(3): 456-460.

Greenland, J. A. and C. J. Limpus (2007). Marine wildlife stranding and mortality database annual report 2006, II Cetacean and pinniped, Brisbane, Environmental Protection Agency. **18:** 2011.

Grossman, A., C. Bellini, A. Fallabrino, A. Formia, J. M. Mba, J. N. Mba and C. J. M. T. N. Obama (2007). Second TAMAR-tagged hawksbill recaptured in Corisco Bay, West Africa. **116**(26).

Guard, M. and M. Masaiganah (1997). Dynamite Fishing in Southern Tanzania, Geographical Variation, Intensity of use and possible solutions. *Marine Pollution Bulletin* **34**(10): 758-762.

Guimarães, S. M., D. C. Tavares and C. Monteiro-Neto (2017). Incidental capture of sea turtles by industrial bottom trawl fishery in the Tropical South-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **98**(6): 1525-1531.

Guisan, A. and W. J. E. l. Thuiller (2005). Predicting species distribution: offering more than simple habitat models. **8**(9): 993-1009.

Guisan, A. and N. E. Zimmermann (2000). Predictive habitat distribution models in ecology. *Ecological Modelling* **135**(2-3): 147-186.

Guo, J. (2014). Modelling Loggerhead Sea Turtle (Caretta Caretta) Nesting Habitat: Evaluation of the Species Distribution Model by Species-environment and Abundance-occupancy Relationships, University of Twente Faculty of Geo-Information and Earth Observation (ITC).

Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'agrosa, J. F. Bruno, K. S. Casey, C. Ebert and H. E. Fox (2008). A global map of human impact on marine ecosystems. *Science* **319**(5865): 948-952.

Hammerschlag, N., I. Bell, R. Fitzpatrick, A. J. Gallagher, L. A. Hawkes, M. G. Meekan, J. D. Stevens, M. Thums, M. J. Witt and A. Barnett (2016). Behavioral evidence suggests facultative scavenging by a marine apex predator during a food pulse. *Behavioral Ecology and Sociobiology* **70**(10): 1777-1788.

Hammerschlag, N., A. C. Broderick, J. W. Coker, M. S. Coyne, M. Dodd, M. G. Frick, M. H. Godfrey, B. J. Godley, D. B. Griffin and K. Hartog (2015). Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape. *Ecology* **96**(8): 2117-2126.

Harriott, V. J. (2002). Marine tourism impacts and their management on the Great Barrier Reef, Citeseer.

Harrison, E., P. von Weller and B. Nahill (2017). ENDANGERED SOUVENIRS: Hawksbill Sea Turtle Products For Sale in Latin America & the Caribbean. J. Urteaga, S. G. Dunbar and J. Azanza-Ricardo, Too Rare to Wear.

Hart, K. M., A. R. Sartain, I. Fujisaki, H. L. Pratt, D. Morley and M. W. Feeley (2012). Home range, habitat use, and migrations of hawksbill turtles tracked from Dry Tortugas National Park, Florida, USA. *Marine Ecology Progress Series* **457**: 193 - 207.

Hart, K. M., A. R. Sartain, Z. M. Hillis-Starr, B. Phillips, P. A. Mayor, K. Roberson, R. A. Pemberton, J. B. Allen, I. Lundgren and S. Musick (2013). Ecology of juvenile hawksbills (Eretmochelys imbricata) at Buck Island Reef National Monument, US Virgin Islands. *Marine Biology* **160**(10): 2567-2580.

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

Hayes, C. T., D. S. Baumbach, D. Juma and S. G. Dunbar (2017). Impacts of recreational diving on hawksbill sea turtle (*Eretmochelys imbricata*) behaviour in a marine protected area. *Journal of Sustainable Tourism* **25**(1): 79-95.

Hays, G. C. (2004). Good news for sea turtles. *Trends in Ecology & Evolution* **19**(7): 349-351.

Hays, G. C., J. A. Mortimer, D. Ierodiaconou and N. Esteban (2014). Use of Long-Distance Migration Patterns of an Endangered Species to Inform Conservation Planning for the World's Largest Marine Protected Area. *Conservation Biology* **28**(6): 1636-1644.

Hazel, J. (2009). Turtles and vessels: threat evaluation and behavioural studies of green turtles in near-shore foraging grounds, James Cook University.

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

Heithaus, M., A. Frid and L. Dill (2002). Shark-inflicted injury frequencies, escape ability, and habitat use of green and loggerhead turtles. *Marine Biology* **140**(2): 229-236.

Herren, R. M., D. A. Bagley, M. J. Bresette, K. G. Holloway-Adkins, D. Clark and B. E. Witherington (2018). Sea Turtle Abundance and Demographic Measurements in a Marine Protected Area in the Florida Keys, USA. *Herpetological Conservation and Biology* **13**(1): 224-239.

Hilborn, R. (2015). Marine Protected Areas miss the boat. *Science* **350**(6266): 1326-1326.

Hill, J. E., C. M. King, K. R. Stewart, F. V. Paladino and P. H. Dutton (2018). Genetic Differentiation of Hawksbill Turtle Rookeries on St. Croix, US Virgin Islands. *Chelonia Conservation and Biology* **17**(2): 303-308.

Hooker, S. K., A. Cañadas, K. D. Hyrenbach, C. Corrigan, J. J. Polovina and R. R. Reeves (2011). Making protected area networks effective for marine top predators. *Endangered Species Research* **13**(3): 203-218.

IUCN (2020). "IUCN Red List of threatened species." Retrieved 2020, 2020, from www.iucnredlist.org.

Ivanova, S. V., S. T. Kessel, J. Landry, C. O'Neill, M. F. McLean, M. Espinoza, S. Vagle, N. E. Hussey and A. T. Fisk (2018). Impact of vessel traffic on the home ranges and movement of shorthorn sculpin (*Myoxocephalus scorpius*) in the nearshore environment of the high Arctic. *Canadian Journal of Fisheries and Aquatic Species* **75**(12): 2390-2400.

Jackson, J. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson and J. A. Estes (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**(5530): 629-637.

Jameson, S. C., M. H. Tupper and J. M. Ridley (2002). The three screen doors: can marine "protected" areas be effective? *Marine Pollution Bulletin* **44**(11): 1177-1183.

Karl, S. A., B. W. Bowen and J. C. Avise (1992). Global Population Genetic-Structure and Male-Mediated Gene Flow in the Green Turtle (Chelonia-Mydas) - RFLP Analysis of Anonymous Nuclear Loci. *Genetics* **131**(1): 163-173.

Kohler, K. E., S. M. J. C. Gill and Geosciences (2006). Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. **32**(9): 1259-1269.

La Manna, G., S. Clo, E. Papale and G. Sara (2010). Boat traffic in Lampedusa waters (Strait of Sicily, Mediterranean Sea) and its relation to the coastal distribution of common bottlenose dolphin (Tursiops truncatus). *Ciencias Marinas* **36**(1): 71-81.

Lahanas, P. N., K. A. Bjorndal, A. B. Bolten, S. E. Encalada, M. M. Miyamoto, R. A. Valverde and B. W. Bowen (1998). Genetic composition of a green turtle (Chelonia mydas) feeding ground population: evidence for multiple origins. *Marine Biology* **130**(3): 345-352.

Lea, J. S. E., N. E. Humphries, R. G. von Brandis, C. R. Clarke and D. W. Sims (2016). Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. *Proceedings of the Royal Society B-Biological Sciences* **283**(1834): 8.

Lee, P. L. M. (2008). Molecular ecology of marine turtles: New approaches and future directions. *Journal of Experimental Marine Biology and Ecology* **356**(1-2): 25-42.

Lee, Z., K. L. Carder, S. K. Hawes, R. G. Steward, T. G. Peacock and C. O. Davis (1994). Model for the interpretation of hyperspectral remote-sensing reflectance. *Applied Optics* **33**(24): 5721-5732.

Lee, Z., K. L. Carder, C. D. Mobley, R. G. Steward and J. S. Patch (1998). Hyperspectral remote sensing for shallow waters. I. A semianalytical model. *Applied Optics* **37**(27): 6329-6338.

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

Lercari, D. and E. A. Chavez (2007). Possible causes related to historic stock depletion of the totoaba, *Totoaba macdonaldi* (Perciformes : Sciaenidae), endemic to the Gulf of California. *Fisheries Research* **86**(2-3): 136-142.

Leroux, R. A., P. H. Dutton, F. Alberto Abreu-Grobois, C. J. Lagueux, C. L. Campbell, E. Delcroix, J. Chevalier, J. A. Horrocks, Z. Hillis-Starr, S. Troeng, et al. (2012). Re-examination of Population Structure and Phylogeography of Hawksbill Turtles in the Wider Caribbean Using Longer mtDNA Sequences. *Journal of Heredity* **103**(6): 806-820.

Levasseur, K. E., S. P. Stapleton, M. C. Fuller and J. M. J. M. E. P. S. Quattro (2019). Exceptionally high natal homing precision in hawksbill sea turtles to insular rookeries of the Caribbean. **620**: 155-171.

Lewison, R. L. and L. B. Crowder (2007). Putting longline bycatch of sea turtles into perspective. *Conservation Biology* **21**(1): 79-86.

Lichstein, J. W., T. R. Simons, S. A. Shriner and K. E. J. E. m. Franzreb (2002). Spatial autocorrelation and autoregressive models in ecology. **72**(3): 445-463.

Limpus, C. J. (1992). Estimation of tag loss in marine turtle research. *Wildlife Research* **19**(4): 457-469.

Limpus, C. J. and L. Fien (2009). A biological review of Australian marine turtles, Environmental Protection Agency.

Lindholm, J., P. Auster and P. Valentine (2004). Role of a large marine protected area for conserving landscape attributes of sand habitats on Georges Bank (NW Atlantic). *Marine Ecology Progress Series* **269**: 61-68.

Lowen, J., C. McKindsey, T. Therriault and C. DiBacco (2016). Effects of spatial resolution on predicting the distribution of aquatic invasive species in nearshore marine environments. *Marine Ecology Progress Series* **556**: 17-30.

Lubchenco, J., S. R. Palumbi, S. D. Gaines and S. Andelman (2003). Plugging a Hole in the Ocean: The Emerging Science of Marine Reserves. *Ecological Applications* **13**(sp1): 3-7.

Lusseau, D., D. E. Bain, R. Williams and J. C. Smith (2009). Vessel traffic disrupts the foraging behavior of southern resident killer whales Orcinus orca. *Endangered Species Research* **6**(3): 211-221.

Lutcavage, M. E., P. Plotkin, B. Witherington and P. L. Lutz (1997). Human Impacts on Sea Turtle Survival. The Biology of Sea Turtles. **1:** 387-409

Lyzenga, D. R. (1978). Passive remote sensing techniques for mapping water depth and bottom features. *Applied Optics* **17**(3): 379-383.

Madsen, J., I. Tombre and N. E. Eide (2009). Effects of disturbance on geese in Svalbard: implications for regulating increasing tourism. *Polar Research* **28**(3): 376-389.

Magnhagen, C., K. Johansson and P. Sigray (2017). Effects of motorboat noise on foraging behaviour in Eurasian perch and roach: a field experiment. *Marine Ecology Progress Series* **564**: 115-125.

Mancini, A., J. Senko, R. Borquez-Reyes, J. G. Póo, J. A. Seminoff and V. Koch (2011). To poach or not to poach an endangered species: elucidating the economic and social drivers behind illegal sea turtle hunting in Baja California Sur, Mexico. *Human Ecology* **39**(6): 743-756.

Manel, S., O. E. Gaggiotti and R. S. Waples (2005). Assignment methods: matching biological questions techniques with appropriate. *Trends in Ecology & Evolution* **20**(3): 136-142.

Mansfield, K. L., J. Wyneken, W. P. Porter and J. J. P. o. t. R. S. B. B. S. Luo (2014). First satellite tracks of neonate sea turtles redefine the 'lost years' oceanic niche. **281**(1781): 20133039.

Marcovaldi, M. A., G. G. Lopez, L. S. Soares, A. J. Santos, C. Bellini and P. C. Barata (2007). Fifteen years of hawksbill sea turtle (*Eretmochelys imbricata*) nesting in Northern Brazil. *Chelonian Conservation and Biology* **6**(2): 223-228.

Martin, C. S. (2003). The Behaviour of Free-living Marine Turtles: Underwater Activities, Migrations and Seasonal Occurences, University of Wales Swansea.

Masalu, D. C. (2000). Coastal and marine resource use conflicts and sustainable development in Tanzania. *Ocean and Coastal Management* **43**(6): 475-494.

McCarthy, E. (2004). International Regulation of Underwater Sound: Establishing Rules and Standards to Address Ocean Noise Pollution. Boston, MA, Kluwer Academic Publishers.

McCook, L. J., T. Ayling, M. Cappo, J. H. Choat, R. D. Evans, D. M. De Freitas, M. Heupel, T. P. Hughes, G. P. Jones and B. Mapstone (2010). Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. *Proceedings of the National Academy of Sciences* **107**(43): 18278-18285.

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

Merow, C., M. J. Smith and J. A. J. E. Silander Jr (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. **36**(10): 1058-1069.

Meylan, A. B. (1999). International Movements of Immature and Adult Hawksbill Turtles (*Eretmochelys imbricata*) in the Caribbean Region. *Chelonian Conservation and Biology* **3**(2): 189 - 194.

Meylan, A. B. (1999). Status of the Hawksbill Turtle(Eretmochelys imbricata) in the Caribbean Region. *Chelonian Conservation and Biology* **3**(2): 177-184.

Meylan, A. B. and M. Donnelly (1999). Statust justification for listing the hawksbill turtle (*Eretmochelys imbricata*) as critically endangered on the 1996 IUCN Red List of Threatened Animals. *Chelonian Conservation and Biology* **3**: 200 - 224.

Meylan, A. J. N. (1998). Hawksbill turtles still endangered. **391**(6663): 117.

Miksis-Olds, J. L., P. L. Donaghay, J. H. Miller, P. L. Tyack and J. A. Nystuen (2007). Noise level correlates with manatee use of foraging habitats. *The Journal of the Acoustical Society of America* **121**(5): 3011-3020.

Miller, E. A., L. McClenachan, Y. Uni, G. Phocas, M. E. Hagemann and K. Van Houtan (2019). The historical development of complex global trafficking networks for marine wildlife. *Science Advances* **5**(3): eaav5948.

Milliken, T. and H. Tokunaga (1987). The Japanese sea turtle trade, 1970-1986, Center for Environmental Education.

Mishra, D., S. Narumalani, D. Rundquist and M. Lawson (2006). Benthic habitat mapping in tropical marine environments using QuickBird multispectral data. *Photogrammetric Engineering Remote Sensing* **72**(9): 1037-1048.

Mishra, D. R., S. Narumalani, D. Rundquist and M. Lawson (2005). High-resolution ocean color remote sensing of benthic habitats: a case study at the Roatan Island, Honduras. *IEEE Transactions on Geoscience and Remote Sensing* **43**(7): 1592-1604.

Monzón-Argüello, C., N. Loureiro, C. Delgado, A. Marco, J. Lopes, M. Gomes and A. Abreu-Grobois (2011). Príncipe island hawksbills: genetic isolation of an eastern Atlantic stock. *Journal of Experimental Marine Biology and Ecology* **407**(2): 345-354.

Monzon-Arguello, C., C. Rico, A. Marco, P. Lopez and L. F. Lopez-Jurado (2010). Genetic characterization of eastern Atlantic hawksbill turtles at a foraging group indicates major undiscovered nesting populations in the region. *Journal of Experimental Marine Biology and Ecology* **387**(1-2): 9-14.

Mortimer, J. A. and M. Donnelly (2008). "Marine Turtle specialist group IUCN red list status assessment: Hawksbill turtle (*Eretmochelys imbricata*)." 2016.

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

Nanninga, G. B., I. M. Côté, R. Beldade and S. C. Mills (2017). Behavioural acclimation to cameras and observers in coral reef fishes. *Ethology* **123**(10): 705-711.

Naro-Maciel, E., J. H. Becker, E. H. S. M. Lima, M. Â. Marcovaldi and R. DeSalle (2007). Testing Dispersal Hypotheses in Foraging Green Sea Turtles (Chelonia mydas) of Brazil. *Journal of Heredity* **98**(1): 29-39.

Naro-Maciel, E., M. Le, N. N. FitzSimmons, G. J. M. P. Amato and Evolution (2008). Evolutionary relationships of marine turtles: a molecular phylogeny based on nuclear and mitochondrial genes. **49**(2): 659-662.

Natoli, A., K. P. Phillips, D. S. Richardson and R. W. Jabado (2017). Low genetic diversity after a bottleneck in a population of a critically endangered migratory marine turtle species. *Journal of Experimental Marine Biology and Ecology* **491**: 9-18.

Neuwinger, H. D. (2004). Plants used for poison fishing in tropical Africa. *Toxicon* **44**(4): 417-430.

Niemi, M., M. Auttila, A. Valtonen, M. Viljanen and M. Kunnasranta (2014). Haulout patterns of Saimaa ringed seals and their response to boat traffic during the moulting season. *Endangered Species Research* **22**(2): 115-124.

Nishizawa, H., J. Okuyama, O. Abe, M. Kobayashi and N. J. M. T. N. Arai (2012). Mitochondrial DNA variation in hawksbill turtles (Eretmochelys imbricata) nesting on Ishigaki Island, Japan. **132**: 1-2.

NMMA (2011). Recreational Boating Statistical Abstract. Chicago, Illinois, National Marine Manufacture Association.

Norman, J. A., C. Moritz and C. J. Limpus (1994). Mitochondrial DNA Control Region Polylmorphisms Genetic Markers for Ecological Studies of Marine Turtles. *Molecular Ecology* **3**(4): 363-373.

Nowacek, S. M., R. S. Wells and A. R. Solow (2001). Short- term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* **17**(4): 673-688.

Obura, D., A. Harvey, T. Young, M. Eltayeb and R. von Brandis (2010). Hawksbill turtles as significant predators on hard coral. *Coral Reefs* **29**(3): 759-759.

Orós, J., A. Torrent, P. Calabuig and S. Déniz (2005). Diseases and causes of mortality among sea turtles stranded in the Canary Islands, Spain (1998–2001). *Dis Aquat Organ* **63**(1): 13-24.

Panigada, S., M. Zanardelli, M. MacKenzie, C. Donovan, F. Mélin and P. S. Hammond (2008). Modelling habitat preferences for fin whales and striped dolphins in the Pelagos Sanctuary (Western Mediterranean Sea) with physiographic and remote sensing variables. *Remote Sensing of Environment* **112**(8): 3400-3412.

Payne, N. L., D. E. van der Meulen, I. M. Suthers, C. A. Gray and M. D. Taylor (2015). Foraging intensity of wild mulloway *Argyrosomus japonicus* decreases with increasing anthropogenic disturbance. *Marine Biology* **162**(3): 539-546.

Pella, J. and M. Masuda (2001). Bayesian methods for analysis of stock mixtures from genetic characters. *Fishery Bulletin*(1).

Phillips, A. and W. C. Union (2002). Management guidelines for IUCN category V protected areas: Protected landscapes/seascapes, IUCN--the World Conservation Union.

Phillips, S. J. and M. Dudík (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**(2): 161-175.

Phillips, S. J., M. Dudík and R. E. Schapire (2017). Maxent software for modeling species niches and distributions (Version 3.4. 1). *Biodiversity Informatics*.

Phu, J. L. and P. Palaniappan (2019). Recaptured Wild Green Turtles (Chelonia mydas) with Newly Documented Boat Strike Injuries in Mabul Island, Sabah, Malaysia. *Chelonia Conservation and Biology* **18**(2): 265-272.

Pike, D. A. J. G. E. and Biogeography (2013). Climate influences the global distribution of sea turtle nesting. **22**(5): 555-566.

Pirotta, E., N. D. Merchant, P. M. Thompson, T. R. Barton and D. Lusseau (2015). Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. *Biological Conservation* **181**: 82-89.

Poiner, I. and A. N. M. Harris (1996). Incidental capture, direct mortality and delayed mortality of sea turtles in Australia's Northern Prawn Fishery. *Marine Biology* **125**(4): 813-825.

Proietti, M. C., J. Reisser, L. F. Marins, C. Rodriguez-Zarate, M. A. Marcovaldi, D. S. Monteiro, C. Pattiaratchi and E. R. Secchi (2014). Genetic Structure and Natal Origins of Immature Hawksbill Turtles (Eretmochelys imbricata) in Brazilian Waters. *Plos One* **9**(2): 12.

ProTECTOR (2015, June 9, 2015). "How to Draw Blood From a Juvenile Sea Turtle." ProTECTOR Sea Turtle Blood Sampling. from https://www.youtube.com/watch?v=qdjDKwivkdA.

Putman, N. F., F. A. Abreu-Grobois, A. C. Broderick, C. Ciofi, A. Formia, B. J. Godley, S. Stroud, T. Pelembe, P. Verley and N. Williams (2014). Numerical dispersal simulations and genetics help explain the origin of hawksbill sea turtles in Ascension Island. *Journal of Experimental Marine Biology and Ecology* **450**: 98-108.

Putman, N. F. and E. J. P. o. t. R. S. B. B. S. Naro-Maciel (2013). Finding the ‘lost years’ in green turtles: insights from ocean circulation models and genetic analysis. **280**(1768): 20131468.

Pyke, G. H. (1984). Optimal foraging theory: a critical review. *Annual Review of Ecology Systematics* **15**(1): 523-575.

Rees, A. F., C. Carreras, A. C. Broderick, D. Margaritoulis, T. B. Stringell and B. J. Godley (2017). Linking loggerhead locations: using multiple methods to determine the origin of sea turtles in feeding grounds. *Marine Biology* **164**(2): 30.

Reich, K. J., K. A. Bjorndal and A. B. Bolten (2007). The 'lost years' of green turtles: using stable isotopes to study cryptic lifestages. *Biology Letters* **3**: 712 - 714.

Rife, A. N., B. Erisman, A. Sanchez and O. Aburto- Oropeza (2013). When good intentions are not enough… Insights on networks of “paper park” marine protected areas. *Conservation Letters* **6**(3): 200-212.

Rincon-Diaz, M. P., C. E. Diez, R. P. Van Dam and A. M. J. J. o. H. Sabat (2011). Foraging selectivity of the hawksbill sea turtle (Eretmochelys imbricata) in the Culebra Archipelago, Puerto Rico. **45**(3): 277-283.

RMP (2015). "Our History - Roatán Marine Park." 2015.

Rouphael, T., A. Abdulla, O. Attum, N. Marshall and U. Ghazali (2013). Do marine protected areas in the Red Sea afford protection to dugongs and sea turtles? *Journal of Biodiversity and Endangered Species* **1**: 1-6.

Sánchez-Carnero, N., D. Rodríguez-Pérez, E. Couñago, F. Le Barzik and J. Freire (2016). Species distribution models and local ecological knowledge in marine protected areas: The case of Os Miñarzos (Spain). *Ocean & Coastal Management* **124**: 66-77.

Santoro, M., J. Morales, F. Bolaáos, G. Chaves and M. De Stefano (2015). Helminths of hawksbill turtle (*Eretmochelys imbricata*) from the Pacific coast of Costa Rica. *Helminthologia* **52**(1): 67-70.

Santos, K. C., C. Tague, A. C. Alberts, J. J. C. C. Franklin and Biology (2006). Sea turtle nesting habitat on the US Naval Station, Guantanamo Bay, Cuba: a comparison of habitat suitability index models. **5**(2): 175-187.

Santos, S. M., R. Lourenco, A. Mira and P. J. P. O. Beja (2013). Relative effects of road risk, habitat suitability, and connectivity on wildlife roadkills: the case of tawny owls (Strix aluco). **8**(11).

Sarmiento-Ramírez, J. M., E. Abella-Pérez, A. D. Phillott, J. Sim, P. Van West, M. P. Martín, A. Marco and J. J. P. o. Diéguez-Uribeondo (2014). Global distribution of two fungal pathogens threatening endangered sea turtles. **9**(1): e85853.

Schoener, T. W. J. A. r. o. e. and systematics (1971). Theory of feeding strategies. **2**(1): 369-404.

Schofield, G., R. Scott, A. Dimadi, S. Fossette, K. A. Katselidis, D. Koutsoubas, M. K. S. Lilley, J. D. Pantis, A. D. Karagouni and G. C. Hays (2013). Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate. *Biological Conservation* **161**: 101-109.

Selby, T. H., K. M. Hart, B. J. Smith, C. G. Pollock, Z. Hillis-Starr and M. K. Oli (2019). Juvenile hawksbill residency and habitat use within a Caribbean marine protected area. *Endangered Species Research* **40**: 53-64.

Shimada, T., C. Limpus, R. Jones and M. Hamann (2017). Aligning habitat use with management zoning to reduce vessel strike of sea turtles. *Ocean & Coastal Management* **142**: 163-172.

Singh, A. and N. L. Thakur (2016). Influence of spatial competitor on the growth and regeneration of the marine sponge Cinachyrella cf. cavernosa (Porifera, Demospongiae). *Hydrobiologia* **768**(1): 111-123.

Spotila, J. R. (2004). Sea turtles: A complete guide to their biology, behavior, and conservation, JHU Press.

Stimmelmayr, R., V. Latchman and M. Sullivan (2010). In-water observations of hawksbill (*Eretmochelys imbricata*) and green (*Chelonia mydas*) turtles in St. Kitts, Lesser Antilles. *Marine Turtle Newsletter*(127): 17.

Stonich, S. C. (1998). Political ecology of tourism. *Annals of Tourism Research* **25**(1): 25-54.

Thurstan, R. H., J. P. Hawkins, L. Neves and C. M. Roberts (2012). Are marine reserves and non-consumptive activities compatible? A global analysis of marine reserve regulations. *Marine Policy* **36**(5): 1096-1104.

Troeng, S., P. H. Dutton and D. Evans (2005). Migration of hawksbill turtles Eretmochelys imbricata from Tortuguero, Costa Rica. *Ecography* **28**(3): 394-402.

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

Trujillo-Arias, N., D. F. Amorocho, D. López-Álvarez and L. M. J. B. d. I. M. y. C.-I. Mejía-Ladino (2014). Phylogeographic relations of some feeding and nesting of hawksbill turtle rookeries (Eretmochelys imbricata) in the Caribbean and Pacific of Colombia. **43**(1): 159-182.

Turner, R. (2015). Travel & Tourism Economic Impact 2015 Honduras. London, World Travel & Tourism Council.

Tyson, R. B., W. E. Piniak, C. Domit, D. Mann, M. Hall, D. P. Nowacek and M. M. Fuentes (2017). Novel Bio-Logging Tool for Studying Fine-Scale Behaviors of Marine Turtles in Response to Sound. *Frontiers in Marine Science* **4**: 219.

UNEP-WCMC and IUCN (2020). "Marine Protected Planet [On-line]." 2020.

Van Dam, R. and C. Diez (1997). Predation by hawksbill turtles on sponges at Mona Island, Puerto Rico. Proceedings of the 8th international coral reef symposium.

Van Dam, R. P. and C. E. Diez (1997). Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. *Coral Reefs* **16**(2): 133-138.

Van Dam, R. P. and C. E. Diez (1997). Surfacing behavior of the marine turtle *Eretmochelys imbricata*. *Journal of Herpetology* **31**(2): 313-316.

Vargas, S. M., M. P. Jensen, S. Y. Ho, A. Mobaraki, D. Broderick, J. A. Mortimer, S. D. Whiting, J. Miller, R. I. Prince and I. P. Bell (2015). Phylogeography, genetic diversity, and management units of hawksbill turtles in the Indo-Pacific. *Journal of Heredity* **107**(3): 199-213.

Varo- Cruz, N., J. A. Bermejo, P. Calabuig, D. Cejudo, B. J. Godley, L. F. López-Jurado, S. K. Pikesley, M. J. Witt, L. A. J. D. Hawkes and Distributions (2016). New findings about the spatial and temporal use of the Eastern Atlantic Ocean by large juvenile loggerhead turtles. **22**(4): 481-492.

Velez-Zuazo, X., W. D. Ramos, R. P. van Dam, C. E. Diez, A. Abreu-Grobois and W. O. McMillan (2008). Dispersal, recruitment and migratory behaviour in a hawskbill sea turtle aggregation. *Molecular Ecology* **17**: 839 - 853.

von Brandis, R. G., J. A. Mortimer and B. K. Reilly (2010). In-water observations of the diving behaviour of immature hawksbill turtles, *Eretmochelys imbricata*, on a coral reef at D'Arros Island, Republic of Seychelles. *Chelonia Conservation and Biology* **9**(1): 26-32.

Walcott, J., S. Eckert, H. Oxenford and J. J. E. S. R. Horrocks (2014). Use of a towed camera system to investigate benthic habitat use by inter-nesting female hawksbill sea turtles. **24**(2): 159-170.

Wallace, B. P., A. D. DiMatteo, A. B. Bolten, M. Y. Chaloupka, B. J. Hutchinson, F. A. Abreu-Grobois, J. A. Mortimer, J. A. Seminoff, D. Amorocho, K. A. Bjorndal, et al. (2011). Global Conservation Priorities for Marine Turtles. *Plos One* **6**(9): 14.

Wang, Y. (2019). On Dilemmas and Solutions for the Issues of HIgh Seas Marine Protected Areas During the BBNJ Negotiation *Applied Ecology and Environmental Research* **17**(4): 8615-8629.

Witt, M. J., A. C. Broderick, M. S. Coyne, A. Formia, S. Ngouessono, R. J. Parnell, G.-P. Sounguet and B. J. Godley (2008). Satellite tracking highlights difficulties in the design of effective protected areas for Critically Endangered leatherback turtles *Dermochelys coriacea* during the inter-nesting period. *Oryx* **42**(02): 296-300.

Witzell, W. (1983). Synopsis of biological data on the hawksbill turtle, Eretmochelys imbricata (Linnaeus, 1766), Food & Agriculture Org.

Witzell, W. N. (1999). Distribution and relative abundance of sea turtles caught incidentally by the US pelagic longline fleet in the western North Atlantic Ocean, 1992-1995. *Fishery Bulletin* **97**(1): 200-211.

Wood, L. D., B. Brunnick and S. L. Milton (2017). Home range and movement patterns of subadult hawksbill sea turtles in Southeast Florida. *Journal of Herpetology* **51**(1): 58-67.

Wood, L. D., R. Hardy, P. A. Meylan and A. B. Meylan (2013). Characterization of a hawksbill turtle (Eretmochelys imbricata) foraging aggregation in a high-latitude reef community in southeastern Florida, USA. *Herpetological Conservation and Biology* **8**(1): 258-275.

Wood, L. D., S. L. Milton and T. L. Maple (2017). Foraging Behavior of Wild Hawksbill Turtles (*Eretmochelys imbricata*) in Palm Beach County, Florida, USA. *Chelonian Conservation and Biology* **16**(1): 70-75.

Yesson, C., M. L. Taylor, D. P. Tittensor, A. J. Davies, J. Guinotte, A. Baco, J. Black, J. M. Hall- Spencer and A. D. Rogers (2012). Global habitat suitability of cold-water octocorals. *Journal of Biogeography* **39**(7): 1278-1292.

Zuñiga-Marroquin, T. and A. Espinosa de los Monteros (2017). Genetic characterization of the Critically Endangered hawksbill turtle (*Eretmochelys imbricata*) from the Mexican Pacific region. *Latin American Journal of Aquatic Research* **45**(3): 555-562.

CHAPTER FIVE

CONCLUSIONS

The Sandy Bay West End Marine Reserve (SBWEMR) is a protected area that lies off the northwestern coast of Roatán, Honduras. An aggregation of juvenile hawksbills has been found foraging within the reserve. In this dissertation, I sought to estimate connections between this protected aggregation and international nesting rookeries, to assess the suitability of the SBWEMR as a recruitment zone for foraging juvenile hawksbills, and to further assess the influence of boat traffic on hawksbill distribution and behavior. My work is the first to assess population genetics of foraging hawksbills in Honduras. It is also the first to assess the suitability of a marine protected area in Honduras, evaluating the influence of three environmental variable predictors: boat traffic intensity, prey item distribution, and benthic classification, on foraging hawksbill inhabitance.

In Chapter 1, the extent of hawksbill decline, and the importance of effective protected areas were reviewed. I discussed the challenge of establishing protected areas for a migratory species, and explained how molecular markers and species distribution models can be used to connect populations and pinpoint essential characteristics of suitability. I also briefly explained how protected areas are often established without limits on recreational activities. In return, unregulated activities, such as boating, have negatively influenced behavior and have caused injury and mortality of several marine species.

In Chapter 2, I report the use of mitochondrial DNA (mtDNA) haplotype analysis to estimate the contributions of several wider Caribbean rookeries to the SBWEMR foraging aggregation. Since longer haplotypes allow greater genetic differentiation, I used haplotypes 736 bps in length. Fourteen different haplotypes were identified from our sampling within the foraging aggregation, indicating a mixed stock with several potential rookery contributions. Through mixed stock analysis, I was able to apply weighted priors for rookery size and distance to assess percent contribution of wider Caribbean rookeries. Mixed stock analyses showed greatest contributions from Colombia, Puerto Rico, and Costa Rica, regardless of rookery size or distance. Haplotype composition of baseline rookeries lacked several unique haplotypes present within the SBWEMR aggregation, indicating the need for further rookery characterizations. Buoy dispersal and surface current analyses were used to support contribution estimates and indicated general potential dispersal patterns of juveniles to the reserve. Due to the paucity of buoy drifter data, I relied on surface current assessment data from the Ocean Surface Current Analysis Real-time (OSCAR) global surface current database. Simulated surface currents presented two distinct currents that may contribute to post-hatchling dispersal patterns. The first suggested the presence of a westerly current sweeping south of Puerto Rico towards Central America, and the second suggested the presence of a circular current that cyclically formed and dissipated off the coast of Colombia, Panama, and Costa Rica. Together, these two patterns support dispersal patterns from Colombia, Costa Rica, and Puerto Rico, as indicated by mixed stock analyses.

In Chapter 3, with a better understanding of the origins of this foraging aggregation, I set out to assess the suitability of the reserve for continued hawksbill inhabitance. I assessed the suitability of the SBWEMR, combining hawksbill occurrence data and three environmental predictor variables: boat traffic intensity, prey item distribution, and benthic characterization. Using MaxEnt, I evaluated which environmental factors had the greatest effect on hawksbill distribution within the reserve, and which regions of the reserve were most suitable for hawksbill use. The presence or absence of benthic variables alone (sand, dense seagrass, seagrass with sand, coral, and coral with sand) did not appear to influence overall habitat suitability. Instead, resource environmental variables (*G. neptuni*, *K. limminghei*, and *Dictyota spp.*) had the greatest influence on probability of hawksbill presence and subsequently habitat suitability, followed by the disturbance variable, boat traffic intensity. When assessed individually, *G. neptuni* was the only resource variable that had a positive influence on habitat suitability. The disturbance environmental variable (boat traffic intensity) had the second greatest influence on habitat suitability. Contrary to my hypothesis, the model indicated that increasing boat traffic intensity positively correlated with an increase in probability of hawksbill presence. Furthermore, model outputs suggested that regions of higher boat traffic intensities were "suitable" habitat within the reserve. However, due to additional analyses reported in Chapter 4, I suggested that boating has a neutral effect on sea turtle distribution and that the influence of prey item distribution dictates hawksbill presence. According to the model output, the SBWEMR is mostly classified as moderately to highly suitable, with regions of low suitability clustered mainly in the northernmost region of the reserve.

In Chapter 4, I further assessed boat traffic and its effect on the presence, distribution, and behavior of hawksbills foraging within the SBWEMR. Through a series of in-water and above-water boat counts, boat traffic intensity within the SBWEMR was calculated and correlated to hawksbill presence. Through in-water observation, I assessed and categorized hawksbill activities into four different behaviors: swimming, surfacing, investigating, and eating. Variation in time spent in each behavior was correlated with boat traffic intensity. I found boat traffic intensity significantly higher in West Bay and West End, compared to Sandy Bay. In addition, hawksbill sightings were significantly greater in West Bay and West End, compared to Sandy Bay. Spearman correlation indicated a positive correlation between boat traffic intensity and hawksbill presence. However, in-water behavioral analyses suggested that hawksbill behavior was not affected by increased boat traffic intensity. A negative, although non-significant, correlation between boat traffic intensity and behavior durations was apparent. However, several personal in-water observations during feeding events, demonstrated hawksbills were behaviorally indifferent to passing boats.

The SBWEMR is essential neritic habitat for juvenile hawksbills who utilize the region for foraging needs. Results of this dissertation indicated that the reserve is an important local foraging location for juveniles originating from Colombia, Costa Rica, and Puerto Rico. Suitability of the reserve for hawksbill inhabitance is greatly impacted by resource variables within the region. Therefore, to increase suitability in the northernmost region of the reserve, a decrease in anthropogenic runoff contributing to excessive algal growth is needed. Although boating may not negatively influence hawksbill presence or alter in-water behavior, impending threats of boat collisions and propeller strikes pose a continuous risk to individuals of the foraging aggregation when surfacing to breathe. Since hawksbills within the reserve are found at greater numbers in areas of high boat traffic, I recommend that boating within the reserve be monitored, and vessel speed be carefully regulated.

Future Work

For future work, I suggest small adjustments to the current work and several additional studies. Together this information will bolster my conclusions and further provide valuable information in regard to the origins of the reserve's inhabitants and its suitability, and provide further support for the importance of the Sandy Bay West End Marine Reserve. Supplemental studies will work to revise genetic analysis methods, to evaluate functional changes of hawksbills in response to stimuli, and to inform future conservation and management strategies.

To further assess and confirm natal origins, I suggest increasing the sample size used for analysis. Since the degree of differentiation between some contributing stocks varied around an F_{st} value of 0.35, I would suggest increasing the sample size of the foraging aggregation to 90 – 100 individuals. Increasing the sample size will ensure a more accurate estimation of stock contribution.

I would also suggest the completion of mixed stock analysis using shorter haplotype sequences (~ 400 – 500 bp in length). Although differentiation between stocks is not as apparent using these shorter sequences, several additional rookeries have been characterized using shorter sequences. Using these shorter haplotypes, the potential contributions of additional rookeries could be assessed.

Since the nesting rookery in Utila may be contributing to our foraging aggregation, I suggest genetic characterization of this rookery be undertaken and its inclusion in the baseline for mixed stock analysis. The analysis of this rookery may reveal the origin of unique haplotypes present in the SBWEMR foraging aggregation.

Although mtDNA haplotypes have been used wildly in sea turtle genetics, I would suggest a re-evaluation of this method of choice. Since evidence of recombination, paternal leakage, and introgression have been evident in humans, mammals, and some reptilian species, I would recommend an in-depth analysis on the precision of this molecular marker. Evidence of genetic alteration may indicate erroneous results from previous analyses.

To further assess the suitability of the SBWEMR, I propose the inclusion of several additional environmental predictor variables. Since the spatial resolution of most published variables were too large for the scope of the reserve, I suggest *in situ* analyses of habitat complexity, bottom current velocity, depth, slope, rugosity, and measures of species diversity. In addition, I suggest the implementation of more precise occurrence points in further suitability tests. Analysis of this additional information will help to further pinpoint potential habitat.

To further assess the influence of boat traffic intensity on sea turtle behavior, I suggest additional in-water observations, increasing the number of individuals sampled and the total minutes of observed behavior. With a larger sample size, supplementary analyses assessing changes in behavioral durations in response to boat traffic intensity could be controlled for size and weight to assess if responses vary based on maturity. In addition, I suggest instances of boat dodges be assessed and tallied during further in-water observations. This information can be used to inform conservations strategists of the imposing threat of boat traffic on hawksbills and greens in the reserve. In addition, I would suggest further utilizing citizen-scientists by creating a database using their logs of scarred or injured turtles. To further assess behavioral changes due to a boat collision or “near misses”, I suggest work to evaluate the depth at which turtles retreat after a dodge and a strike, the duration until the next surfacing interval, and changes in behavioral bouts.

To further assess habituation in sea turtles, I suggest efforts to evaluate hawksbill conditioning to a stimulus, such as boat traffic. Whether habituation becomes evident by a certain age, over a certain amount of time, or after a certain number of exposures is currently unknown.

The information garnered from these additional studies can be used to further the application of effective management strategies in SBWEMR. This information will be useful not only in SBWEMR, but in all coastal regions of sea turtle inhabitance around the world.

APPENDIX

Primer Data

LCM15382

5’-GCTTAACCCTAAGCATTGG-3’

H950

5’-GTCTCGGATTTAGGGGTTT-3’

EIIFP91

5’ -AGGCACATCGAATTGGTAAA-3’

Haplotype Data

EIA01

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTACTATTGTACATCTACTTATTTACCACTAGCATATGACCAGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTTACATAAACTGTTTAAACTACATGACTATTATACAGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATCGTCACAGTAATGGGTTA
TTTCTTAGTTCAGCTCATCACGAGAAATAAGCAATCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGC
CCATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATTGAATTGGTA
AAGTTCATTCATCTCTTTTTAAGAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATA
AGGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGC
CGAATTAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTA
ATGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATA
CTTTTTAGTTAAACCCCCCCACCC)

EIA02

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTACTATTGTACATCTACTTATTTACCACTAGCATATGACCAGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTTACATAAACTGTTTAAACTACATGACTATTATACAGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATCGTCACAGTAATGGGTTA
TTTCTTAGTTCAGCTCATCACGAGAAATAAGCAATCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGC
CCATTAATCTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATTGAATTGGTA
AAGTTCATTCATCTCTTTTTAAGAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATA
AGGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGC
CGAATTAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTA
ATGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATA
CTTTTTAGTTAAACCCCCCCACCC

EIA09

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCACTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACGGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATCGAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
CGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATCAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTA
ATGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATA
CTTTTTAGTTAAACCCCCCCACCC

EIA11

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACGGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATCGAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
CGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATCAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTA
ATGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATA
CTTTTTAGTTAAACCCCCCCACCC

EIA20

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACGGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATCAAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
CGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATCAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTA
ATGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATA
CTTTTTAGTTAAACCCCCCCACCCCCAT

EIA24

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACAGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATCGAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
GGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATTAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTAA
TGCTTGAAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATACT
TTTTAGTTAAACCCCCCCACCCCCAT

EIA41

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCACTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACAGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATCGAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
GGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATTAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTAA
TGCTTGAAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATACT
TTTTAGTTAAACCCCCCCACCCCCAT

EIA42

NNNNNNNNNNNNNNNGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATAT
CCGCAACACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGA
TTAATCTGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACAGGTA
ATAAGAATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATG
GGTTATTTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTT
CAGGCCCATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATCGAA
TTGGTAAAGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCT
GGCATAAGGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGAT
ACCTGCCGAATTAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTAT
TTAATTAATGCTTGGAAGACATATATTTTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACA
ACTATACTTTTTAGTTAAACCCCCCC

EIA43

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACAGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTCAGGCACATCGAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
CGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATCAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTA
ATGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATA
CTTTTTAGTTAAACCCCCCCACCCCCAT

EAI47

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACAGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTCAGGCACATCAAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
CGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATCAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTA
ATGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATA
CTTTTTAGTTAAACCCCCCCACCC

EIA63

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACGGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTCAGGCACATCGAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
CGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATCGATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTA
ATGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATA
CTTTTTAGTTAAACCCCCCCACCCCCAT

EIA80

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTTACATAAACTGTTTAAACTACATGACTATTATACGGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATCGAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
CGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATCGATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTA
ATGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATA
CTTTTTAGTTAAACCCCCCCACCC

EIA83

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACAGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATCGAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
GGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATTAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTAA
TGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATACT
TTTTAGTTAAACCCCCCCACCCCCAT

EIA95

ACGCAGAATAAGCGCCAACACATAAACTTACCTATATCCTCTACCGTGCCCAGCAGACCAATATCCGCAA
CACTTACCTATGTATTATTGTACATCTACTTATTTACCGCTAGCATATGACCGGTAGTACTGCTGATTAATC
TGACCTAAAACATAAAATTATTGGTTTCACATAAACTGTTTAAACTACATGACTATTATACAGGTAATAAG
AATGAAATGGTATAGGACATAATATTAAGTAATTATTCTCAAACATGAATATTGTCACAGTAATGGGTTAT
TTCTTAGTTCAGCTCATCACGAGAAATAAGCAACCCTTGTTAGTAAGATACAACATTACCAGTTTCAGGCC
CATTAATTTATGGCGTACATAACTGATCTATTCTGGCCTCTGGTTGTTTTTTCAGGCACATCGAATTGGTAA
AGTTCATTCATCTCTTTTTAAAAGGCCTCTGGTTAAATGAGTTCTATACATTAAATTTATAACCTGGCATAA
GGTGGTTTTACTTGCATATAGTAGTCTTTTTTTTCTCTTTGTGTTCTCAGGCCCACATAACTGATACCTGCC
GAATTAATGAAACTGAACCTACGTTTAAGATGATTGGTCGTGCAAGATAATCAATGGTATTATTTAATTAA
TGCTTGGAAGACATATATTCTTATAAAAACTCACAACAGTTATTTACAAGCCTAACCTATTACAACTATACT
TTTTAGTTAAACCCCCCCACCCCCAT

Buoy Data

Buoy Drifter data was acquired from National Oceanic and Atmospheric Administration (NOAA) as part of the Global Drifter Program at http://osmc.noaa.gov/Monitor/OSMC/OSMC.html.

Seventy drifters were located within the Caribbean between 2004 – 2017. Of these seventy, ten were associated within the Mesoamerican Reef basin (bold), but only three were present in the Mesoamerican Reef basin within 100 km of Roatán, Honduras between 2012 – 2017 (bold and underlined). The WMO ID of all drifter buoys are provided below.

13523
13581
13650
15647
41574
41606
41608
41624
41679
41681
41682
41683
41684
41686
41708
42502
42520
42552
42564
42653
43502
43516
43551
43552
43553
43555
43558
43559
43560
43561
43563
43564
43565
43566
43567
43569
43571
43572
3101514
1501581
1501605
1501609
3101532
3301528
4100678
4100679
4100682
4100683
4100684
4100685
4100686
4100708
4101580
4101600
4101740
4101741
4101746
4131581
4200520
4201525
4201583
4201584
4201588
4201590
5102559
5201639
5201640