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ECOLOGY AND CONSERVATION OF IMMATURE SEA TURTLES ACROSS MULTIPLE SCALES

A Dissertation Presented

by

LUCAS P. GRIFFIN

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
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Intercampus Marine Science Program

ECOLOGY AND CONSERVATION OF IMMATURE SEA TURTLES ACROSS MULTIPLE SCALES

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Andy J. Danylchuk, Graduate Program
Director, Intercampus Marine Science
Graduate Program

DEDICATION

To family.

And sea turtles.

ACKNOWLEDGMENTS

ABSTRACT

**ECOLOGY AND CONSERVATION OF IMMATURE SEA TURTLES ACROSS
MULTIPLE SCALES**

SEPTEMBER 2019

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Directed by: Professor Andy J. Danylchuk

Considering many sea turtle populations are a fraction of their historic size and anthropogenic threats within the marine environment are increasing, additional data are imperative to help mitigate anthropogenic disturbances and to build resilience into sea turtle populations. In this dissertation, I present three data chapters focused on immature sea turtle ecology and conservation. These chapters evaluate sea turtle ecology and conservation at varying scales, ranging from mitigating human-wildlife interactions at the individual level, to coastal movements and space use at the ecosystem level, and to large scale climate change impacts at the population level. Ultimately, these chapters provide a better understanding of immature turtle behavioral and spatial ecology within nearshore waters that are required for the continued conservation of turtles and their habitats.

In Chapter 2, following Chapter 1: General Introduction, I quantified the behavioral response of immature green turtles (*Chelonia mydas*) to disturbance by snorkelers in a popular ecotourism venture on Culebra Island, Puerto Rico, United States. Using a standardized disturbance stimulus, I evaluated whether turtles have individual-level responses to snorkeler disturbance. I found ninety percent of turtles disturbed by snorkelers initiated their fights at

distances of 3 m or less. Thus, I recommended snorkelers remain greater than 3 m distance from immature turtles. In addition, I found a significant intra-individual repeatability in behavioral responses to disturbance, suggesting, ecotourism activities may be disproportionally affecting individual turtles depending on their personality type. Finally, I suggest ecotourism activities be temporally and spatially stratified and better regulated to reduce missed foraging opportunities by immature turtles in important foraging areas.

In Chapter 3, I used acoustic telemetry to describe movement patterns and connectivity of immature green turtles on Culebra and Culebrita Islands, Puerto Rico and, secondly, to determine the spatial-temporal drivers of presence and absence of turtles. Network analysis revealed high fidelity within bays with little to no connectivity across the islands. Based on these findings, I provided evidence that habitat quality and availability in combination with predation risk (innate or learned) is likely driving different rates of somatic growth across the island. Using a presence-absence Bayesian model, results indicated turtles occupied areas of lagoon and seagrass habitats at night, and were rarely using areas of macroalgae habitat. The parameter estimates from the model enabled me to predict diel movement patterns and space use across the focal bay. While habitats within Culebra are still largely intact, coastal embayments are becoming increasingly threatened. Given that my research showed that turtles in Culebra exhibit high fidelity within the bays, it is imperative to protect these distinct habitats that serve as both shelter and foraging areas.

In Chapter 4, I examined the oceanic, atmospheric, and biological factors that may affect the increasing trend of cold-stunned immature Kemp's ridleys (*Lepidochelys kempii*) in Cape Cod Bay, Massachusetts, United States. Using cold-stunned data collected since the early 1980's and analytical methods, such as machine learning algorithms and Bayesian modeling, I

demonstrated higher cold-stunning years occurred when the Gulf of Maine has warmer seas surface temperature (SST) in late October through early-November. Hatchling numbers, a proxy for population abundance, was not identified as an important factor in predicting the number of annual cold-stunning strandings. Further, I predicted the potential annual cold-stunning counts out to 2031 based on the increasing Gulf of Maine SSTs and evaluated the population level effects of future cold-stunning events in the face of climate change. While cold-stunning at the population level may be minimal, I recommend the continued efforts to rehabilitate cold-stunned turtles to maintain population resilience for this critically endangered species.

For the fifth, and final chapter, I synthesized these findings in the context of contributions to the greater field of sea turtle conservation and management, propose future research directions, and re-visit caveats of these studies. Within this chapter, each data chapter is revisited to provide direct conservation applications to help mitigate anthropogenic disturbances. In Chapter 2, I suggest alternate ecotourism regulations and advocate for the spatial-temporal stratification of green turtle snorkel tours. In Chapter 3, I highlight the differential space use of green turtles within coastal habitats and advocate for the importance and protection of these habitats to ensure recruitment into adult populations. And finally, in Chapter 4, I advise for the recovery and rehabilitation of cold-stunned Kemp's ridley turtles to provide population resilience for this critically endangered species in a changing world.

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CHAPTER 1

GENERAL INTRODUCTION

Six of the seven species of sea turtles are classified as either critically endangered,

endangered, or vulnerable by the International Union for the Conservation of Nature (IUCN

2016). While conservation efforts, such as harvest and bycatch regulations, have led to

increasing sea turtle populations trends around the world (Hays et al., 2016, Mazaris et al.,

2017), sea turtle populations are still only a small fraction of their historic size. For example, in

the North Atlantic, green turtle (*Chelonia mydas*) populations were reduced as early as the 1800s

when adult turtles and their eggs were exploited to feed the large slave populations throughout

the Caribbean (Jackson 2001). Using harvest reports dating back to the 1600s, Jackson (1997)

conservatively estimated there were 33 to 39 million 50 kg adult green turtles between Grand

Cayman, Bermuda, Bahamas, Florida Keys, Costa Rica, and Isla Aves during the pre-colonial

period. Further, using these historic population estimates, Jackson et al. (2001) reported that by

the late 1990s the Caribbean green turtle populations were only 3-7% of their pre-colonial

abundance.

The critically endangered Kemp's ridley (*Lepidochelys kempii*), another example of an

exploited sea turtle species, has made a recovery from the brink of extinction. Using archived

footage from the primary Kemp's ridley nesting location located on Rancho Nuevo Beach,

Tamaulipas, Mexico, Bevan et al. (2016) estimated the population from 1947 and 1985 had

declined between 99.2 and 99.7%. This dramatic decline was due to both local harvest of eggs

(Hildebrand 1963, Adams 1966, Chavez et al. 1968, Marquez 1994) and a simultaneous

expansion of the Gulf of Mexico shrimping industry that caused considerable sea turtle bycatch

(Nance 1992). As these threats were curtailed, nesting populations began to increase at an exponential rate beginning in the mid 1980s. (NMFS et al. 2011). The Bi-National Recovery Plan predicted a growth of 19% per year from 2010-2020, with hopes that the predicted population increases would eventually lead to delisting the species by 2024 (NMFS et al. 2011). However, unexpectedly, in 2010, the growth of nesting Kemp's ridleys stopped and remained relatively static for unclear reasons (Caillouet et al. 2010, Caillouet et al. 2011, Caillouet et al. 2014, Crowder et al. 2011, Bevan et al. 2016, Gallaway et al. 2016, Kocmoud et al. 2019).

Considering sea turtle populations are only a fraction of their historic size, research is needed to fill fundamental knowledge gaps in turtle life history, especially in the face of persistent and emerging anthropogenic threats. One substantial gap in knowledge is centered around immature sea turtle ecology (Crouse et al. 1987, Hamann et al. 2010, Bjorndal et al. 2011, Rees et al. 2016, Wildermann et al. 2018). While immature turtles represent the most abundant life stage in turtle populations (Heppel et al. 1996, Casale and Heppell 2016), little is known of their in-water ecology since it is logistically difficult to investigate compared to nesting females on land (Wildermann et al. 2018). Wildermann et al. (2018) identified two major immature turtle research gaps, 1) the need for studies on population ecology and habitat use / behavior and, 2) the need for applied conservation research, with a focus on threats and management.

For my dissertation, I conducted research that evaluated sea turtle ecology and conservation at multiple scales, ranging from mitigating human-wildlife interactions at the individual level, to coastal movements and space use at the ecosystem level, and to large scale climate change impacts at the population level. This research used a number of novel techniques to reveal how immature sea turtles respond to disturbance, their environment, and a changing

climate. Collectively, my research provides a better understanding of immature turtle behavioral and spatial ecology within nearshore waters that are required for the continued conservation of turtles and their habitats.

1.1 Dissertation Format and Co-authorship

The five chapters in this dissertation contain three body chapters (2, 3, and 4) written in manuscript format. These three chapters are at various stages in the publication process in peer-reviewed journals, with chapters 2 and 4 already published, and chapter 3 in review. Although there are several co-authors for each of the four chapters, this dissertation represents my research. Below I list here the contributions of all authors by chapter title.

- Chapter 2. Individual-level behavioral responses of immature green turtles to snorkeler disturbance.

Griffin, L. P., Brownscombe, J. W., Gagné, T. O., Wilson, A. D. M., Cooke, S. J. & Danylchuk, A. J. 2017. Individual-level behavioral responses of immature green turtles to snorkeler disturbance. Oecologia, 183, 909–917.

I designed this study, conducted the data collection, data analyses, and manuscript preparation. Brownscombe, Gagné, contributed to data collection and manuscript preparation Wilson contributed to study design and manuscript preparation. Cooke contributed to manuscript preparation. Danylchuk secured funding for the research, and contributed to study design and manuscript preparation.

- Chapter 3. Movements, connectivity, and space use of immature green turtles within coastal habitats, Culebra, Puerto Rico: implications for conservation.

Griffin, L. P., Finn, J.T., Diez, C. & Danylchuk, A.J. *In Press*. Movements, connectivity, and space use of immature green turtles within coastal habitats, Culebra, Puerto Rico: implications for conservation. Endangered Species Research.

I designed this study, conducted the data collection, data analyses, and manuscript preparation. Finn contributed to data analyses and manuscript preparation. Diez and Danylchuk contributed to study design, data collection, and manuscript preparation. Danylchuk secured funding for the research.

- Chapter 4. Warming seas increase cold-stunning events for Kemp's ridley sea turtles in the northwest Atlantic.

Griffin, L. P., Griffin, C. R., Finn, J. T., Prescott, J. T., Faherty, M., Still, B. M. & Danylchuk, A. J. 2019. Warming seas increase cold-stunning events for Kemp's ridley sea turtles in the northwest Atlantic. PLoS ONE 14(1): e0211503. https://doi.org/10.1371/journal.pone.0211503

I designed this study, conducted data analyses, and manuscript preparation. Griffin, C, and Still contributed to study design and manuscript preparation. Finn contributed to data analyses and manuscript preparation. Prescott and Faherty contributed to data collection, study design, and

manuscript preparation. Danylchuk provided oversight and contributed to manuscript

preparation.

CHAPTER 2

INDIVIDUAL-LEVEL BEHAVIORAL RESPONSES OF IMMATURE GREENTURTLES TO

SNORKELER DISTURBANCE

2.1 Abstract

Despite many positive benefits of ecotourism, increased human encounters with wildlife may

have detrimental effects on wild animals. As charismatic megafauna, nesting and foraging sea

turtles are increasingly the focus of ecotourism activities. The purpose of our study was to

quantify the behavioral responses of immature green turtles (*Chelonia mydas*) to disturbance by

snorkelers, and to investigate whether turtles have individual-level responses to snorkeler

disturbance. Using a standardized disturbance stimulus in the field, we recorded turtle behaviors

pre- and post-disturbance by snorkelers. Ninety percent of turtles disturbed by snorkeler

(n = 192) initiated their flights at distances of ≤3 m. Using principal component analysis, we

identified two distinct turtle personality types, 'bold' and 'timid', based upon 145 encounters of

19 individually identified turtles and five disturbance response variables. There was significant

intra-individual repeatability in behavioral responses to disturbance, but bolder turtles had more

behavioral plasticity and less consistent responses than more timid individuals. Bolder

individuals with reduced evasion responses might be at a higher risk of shark predation, while

more timid turtles might have greater energetic consequences due to non-lethal predator effects

and repeated snorkeler disturbance. Over the longer term, a turtle population with a mix of bold

and timid individuals may promote more resilient populations. We recommend that snorkelers

maintain >3 m distance from immature green turtles when snorkeling, and that ecotourism

activities be temporally and spatially stratified. Further, turtle watching guidelines need to be

communicated to both tour operators and independent snorkelers to reduce the disturbance of turtles.

2.2 Introduction

Developing nations, regions, and communities typically cultivate ecotourism in hopes of creating environmentally sustainable economic prosperity while supporting wildlife conservation (Scheyvens 1999, Ashley and Roe 1998, Brooks et al. 2006, Gallagher and Hammerschlag 2011, Fennell 2014). Ecotourism can also generate funding and support for conservation activities and create socio-economic incentives to preserve and rehabilitate functioning ecosystems (Higginbottom et al. 2001, Cisneros-Montemayor et al. 2013). Despite these potential benefits, ecotourism may also increase human encounters with wildlife, causing detrimental effects such as avoidance, habituation, attraction, and cryptic responses (e.g., increased stress) (Higginbottom et al. 2001, Müllner et al. 2004, Piñeiro et al. 2012). Increased human encounters with wildlife may affect short- and long-term animal behaviors (Gabrielsen and Smith 1995, Green and Higginbottom 2001, Williams et al. 2006) and physiological responses (Knight and Cole 1995) as well as might result in habitat abandonment (Lusseau and Bejder 2007) and reduced reproductive success (Bejder 2005, Constantine and Bejder 2008).

Understanding how individual animals respond to disturbance provides resource managers with tools for developing conservation strategies (Conrad et al. 2011) as well as insight into ecological and evolutionary processes (Réale et al. 2010, Wolf and Weissing 2012). Yet, there can be much variation in behavioral plasticity between individual animals across taxa including mammals (Wilson et al. 1994, David et al. 2004, Svartberg et al. 2005, Martin and Réale 2008), insects (Bonte et al. 2007, Schuett et al. 2011), birds (Carere el al. 2005, Quinn and Cresswell 2005, Dingemanse et al. 2012), fishes (Dingemanse et al. 2007, Biro et al. 2010, Cote

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et al. 2010, Wilson et al. 2010) and reptiles (López et al. 2005, Highcock and Carter 2014, Kuo et al. 2015). Individual animals are often described as 'bold' when they demonstrate either high levels of exploratory behaviors (e.g., low anti-predator vigilance and short flight initiation distances) or short startle response durations following a disturbance (e.g., time duration of hiding). For example, Briffa et al. (2008) classified individual hermit crabs (*Pagurus bernhardus*) as 'bold' or 'timid' based upon the duration of their startle response (i.e., hiding within shell) when disturbed. When such behaviors are consistent across a range of situations, or through time, they are often referred to as representing animal 'personality' (Gosling 2001, Réale et al. 2007) or behavioral syndromes (Sih et al. 2004). Examining intraspecific behavior differences within a population is important for recognizing the possible presence of particularly sensitive individuals and developing comprehensive management plans. Nevertheless, few studies have incorporated how individual-level responses can be incorporated into management plans to mediate human effects.

The long-lived, globally threatened green turtle (*Chelonia mydas*) frequently inhabits coastal marine areas (Bolten 2003, Seminoff et al. 2015). Following their omnivorous oceanic phase, juvenile green turtles typically recruit to neritic (less than 200 m water depth) foraging grounds and shift to primarily herbivorous benthic feeding (Bolten 2003, Heppell et al. 2003, Jones and Seminoff 2013). Turtles use these areas as developmental habitats for decades until reaching sexual maturity (Bjorndal et al. 2000), then migrate hundreds to thousands of kilometers to natal areas to forage, mate and nest (Bowen and Karl 2007, Arthur et al. 2008). Sea turtles are relatively docile and easily located while nesting on beaches (Campbell 1999) and while foraging within neritic areas (Landry and Taggart 2010). As charismatic megafauna, ecotourism activities to observe sea turtle nesting and foraging are increasing, and it is argued

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that these encounters benefit conservation by raising awareness and appreciation for sea turtles (Tisdell and Wilson 2002, Ballantyne et al. 2011). Yet, others suggest that such tourist activities may disturb turtles, potentially reducing their survivorship and fitness (Landry and Taggart 2010, Hayes et al. 2016).

There are several reports of tourist activities adversely affecting green turtle behavior. Jacobson and Figueroa-Lopez (1994) reported that tourist activities (i.e., flashlights, flash cameras, physical blocking, touching) disturbed nesting green turtles on Costa Rican beaches, decreasing nesting success. Balazs et al. (1987) suggested that some green turtles in Hawaii shifted their feeding to evening periods in areas with high human activity during the day. In Hawaii, Meadows (2004) observed green turtles that were chased and touched by snorkelers exhibited changes in foraging activities and increased energy expenditures. Similarly, the presence of snorkel (Slater 2014, Kostas 2015) and SCUBA (Hayes et al. 2016) activity altered sea turtle behaviors when approached. Taquet et al. (2006) and Landry and Taggart (2010) cautioned against high ecotourism activities in neritic zones where sea turtles congregate. With increasing ecotourism worldwide (TIES 2006), there is a need to better understand the effects of ecotourism activities on sea turtles.

The primary goal of this study was to quantify the response of free-ranging wild immature green turtles to disturbance by snorkelers in the field using a standardized disturbance stimulus meant to mimic a tourist diving down to approach a turtle. The second aim of this study was to determine whether turtles exhibit consistent individual-level responses using their behavioral responses as a measure of boldness and by defining personality as repeatable individual differences in a single context that are consistent over time. These data may offer a measure of the sensitivity of immature green turtles to disturbance by tourists, and provide the

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foundation for management guidelines while simultaneously providing insight into ecological processes.

2.3 Methods

2.3.1 Study site

We conducted the study in Tamarindo Bay (18°19'04" N 65°19'02" W), located within the Luis Peña Channel Natural Reserve on the western side of Culebra Island, Puerto Rico. Tamarindo Bay is a shallow bay (1-10 m in depth) with expansive turtle grass (*Thalassia testudinum*) beds and is subject to high levels of ecotourism. Upwards of 30 000 tourists visit the bay each year, and four tour operators offer guided kayak and snorkel tours to view green turtles as they forage (Diego Morell Parea, Culebra Adventures, pers. comm. 2015). "High" and "low" tourist seasons are difficult to determine on Culebra Island, especially in regards to snorkel activity. While Culebra Island attracts non-Puerto Rico mainland residents during the winters, the summers are primarily Puerto Rico mainland residents on vacation. Based on input from local snorkel guides (Diego Morell Parea, Culebra Adventures, pers. comm. 2015) it is also difficult to parse out tourist seasons because local Puerto Rico tourists independently swim with turtles but engage less with local tour operators as non-residents would.

Typically, all green turtles observed are immature (estimated straight-line carapace length ranged between 40 and 60 cm); adults are rarely reported (Carlos Diez, Department of Natural and Environmental Resources, Commonwealth of Puerto Rico, pers. comm. 2014). Collectively, tour companies guide an average of 65 kayak / snorkel clients per day (Diego Morell Parea, Culebra Adventures, pers. comm. 2015), and we observed up to 30 tourists viewing a single turtle during a snorkel tour. In addition to tour groups, tourists often snorkel independently to

search for foraging green turtles. A main road leading from town easily accesses this beach and provides numerous public-parking options for high tourist days. There are no tourist accommodations at the beach, and beach access is never restricted.

2.3.2 Encounter and disturbance

To locate turtles, four snorkelers swam four 300 m-long transects parallel to the beach at approximately 7 m/min. Snorkelers were spaced evenly at 10, 40, 70, and 100 m from shore and snorkelers were rotated randomly throughout the study to avoid individual biases. Transects were swum twice a day between 0700 - 1000 hrs and 1600 - 1800 hrs, four days a week, from 25-June-2014 – 27-July-2014. Transects were performed twice a day to investigate if disturbance responses differed across diel phases. To limit tourist encounters, which could interfere with data collection, transect times were chosen in the morning and late afternoon. Upon encountering a green turtle, the observer maintained a 7-10 m distance from the turtle to record a) time, b) if turtle was alone or with one or more additional turtles within a 5 m radius (Y/N), c) type of movement (sedentary/mobile), and d) foraging rate (number of bites min_{-1} during a 1-min observation period). All observers had undergone in-water distance estimation practices for accuracy, precision, and standardization purposes.

After the initial pre-disturbance observation, we applied a standardized stimulus meant to mimic a tourist diving down to approach a turtle. This disturbance involved the observer diving to the seafloor approximately 4 m from the turtle and approaching the turtle from the right posterior. A GoPro HERO 3+ Black Edition camera (GoPro, Inc. San Mateo, CA, USA) was used to document the disturbance event and obtain an image of the right lateral facial scale pattern on the head for later individual identification (Schofield et al. 2008). Observers, without a recognition program, processed images of right lateral facial scale patterns to identify individual

turtles. Turtles were monitored for two minutes or until the observer had moved with the turtle a linear distance of 50 m (visually estimated), as the turtle moved away the observer recorded post-disturbance behaviors. We selected our disturbance behavior metrics based upon reported natural responses of sea turtles and other animals to predators and predator stimuli. Heithaus (2013) reported anti-predator behaviors by sea turtles when they encountered sharks. We are aware of no studies of flight-initiation-distance (FID) in sea turtles; however, Wang et al. (2010) and Bostwick et al. (2014) documented a flight response when a shark stimulus was introduced to captive-bred sea turtles. Yet, fleeing from a predator (FID) is a cost-benefit action. If an animal flees too soon, foraging and mating opportunities may be lost along with unnecessary energy expenditure. If an animal flees too late or not all, mortality may occur (Ydenberg and Dill 1986, Lima and Dill 1990). Consequently, we chose metrics that we associated with an animal's tendency to flee from a predator. Although sea turtles are not often categorized as social animals, grouping behavior or "foraging herds" has been documented for green turtles (Bresette et al. 2010, Heithaus 2013), which may potentially reduce predation risk as reported for other taxa (Pulliam and Caraco 1984).

FID (m) in 0.5 m increments was visually estimated and recorded as the distance when the turtle began to move away from the observer's approach. An abrupt-burst-response (Y/N) was noted if a turtle exhibited a sudden and severe startled response. The distance fled (m) was visually estimated as the linear distance the turtle swam away up to a maximum of 50 m. Latency to forage (sec) was measured as the time between the disturbance event and when the turtle resumed foraging up to a maximum of 120 sec. Flight to nearest neighbor (Y/N) was noted if the turtle ceased fleeing within a visually estimated 5 m radius of another individual or group of

turtles following the disturbance. Breached the surface to breathe (Y/N) was noted if the turtle went to the surface to breath following the disturbance.

2.3.3 Statistical analyses

All statistical analyses were conducted using R 3.1.3 (R Development Core Team 2015). Quantiles (0.90) and confidence intervals (0.95) were calculated for FID. The confidence intervals were calculated using the adjusted bootstrap method (N = 1000) with replacement. To show how traits vary with one another and to avoid autocorrelation issues associated with modeling individual response variables alone we performed principal component analysis. We used the *prcomp* function to reduce five behavior response variables for each individually-identified turtle (FID, distance fled, latency to forage, abrupt burst response, flight to a nearest neighbor) into one principal component (PC1). Breached the surface to breath response variable was excluded because we could not determine when a turtle had last surfaced to breath prior to disturbance. The PC1 was based on the correlation matrix of the five disturbance responses. The *p*-values were calculated from randomization tests, and variables with weights > 0.5 were considered major contributors to explaining overall variability in the model. The total collection of PC1 scores was repeatedly regressed to examine linear relationships with four pre-disturbance variables, including: session (AM/PM), if the turtle was in a group prior to disturbance, movement type, and foraging rate.

Using the PC1 scores of each encounter and individual identities as the random effect, we assessed temporal stability of post disturbance behavior tendencies of 19 identified individual turtles from 145 encounters. Due to the approximate Gaussian distribution of the PC1 scores, we fitted a linear mixed-effects model (LMM) to the distribution with individual turtle as the random effect to estimate repeatability (*rptR* package in R, Nakagawa and Schielzeth 2010).

Repeatability (r) was defined by the proportion of total variation in a behavior trait within and between individuals, and calculated as $r = \sigma_\alpha^2/(\sigma_\alpha^2 + \sigma_\varepsilon^2)$ where σ_α^2 was the between-group variance and $\sigma_{\varepsilon2}$ was the within-group variance (Bell et al. 2009, Nakagawa and Schielzeth 2010). If an individual's behavior is consistent across all repeated measurements, then $r = 1$. Conversely, if the behavior of an individual is random across all measurements, then $r = 0$ (Sokal and Rohlf 1981, Lessells and Boag 1987). Variance components in the LMM were estimated using restricted maximum likelihood (REML), and 95% confidence intervals and statistical significance (p-values) were estimated using a parametric bootstrap method (N = 1000) with replacement.

PC1 scores were averaged for individual turtles and also grouped into two personality types - timid (negative mean PC1 scores) or bold (positive mean PC1 scores). To examine if timid and bold turtles exhibited similar degrees of variation, we calculated from the PC1 scores, the mean standard deviation for each individual and conducted a one-way ANOVA with residuals weighted by number of encounters to compare the effect of personality type on the amount of variation in an individual turtle.

2.4 Results

2.4.1 Turtle encounters

We had 306 encounters with green turtles during our study, with 226 encounters occurring during morning surveys and 80 during late afternoon surveys. Prior to the disturbance, 78% of the turtle encounters were described as sedentary (n = 306) and 47% of turtle encounters were described as group formation (n = 306). Mean foraging rate prior to disturbance was 25.1 bites/min (± 9.86 bites/min SD, n = 254). Following the disturbance, 12% of turtles responded

with abrupt burst swimming (n = 192, representing total number of disturbance events when this

behavior was recorded), 66% of turtles breached the surface to breathe (n = 256), and 13% of

turtles fled to nearest neighbor post-disturbance (n = 237). FID averaged 1.7 m (± 1.02 m SD, n

= 192), and turtles fled an average of 24.2 m (± 18.84 m SD, n = 253), while latency to forage

averaged 61.9 sec (± 43.74 s SD, n = 242). Using the FID observations (n = 192), we

bootstrapped with replacement and estimated 1.6 − 1.8 m as the 95% confidence interval of the

mean minimum approaching distance of the population. Ninety percent of turtles disturbed by a

snorkeler initiated their flights at distances of ≤ 3 m (Fig. 1).

2.4.2 Individual-level behavioral response to disturbance

Using 145 turtle encounters with complete records, we were able to use video footage to

identify 19 individual turtles from their unique facial scale patterns. A turtle encounter was

considered a complete record when the individual turtle was identifiable (i.e., able to obtain an

image of the right lateral facial scale pattern on the head) and when the observer was able to

record all five disturbance response variables (FID, distance fled, latency to forage, abrupt burst

response, and flight to nearest neighbor) during the encounter. Encounters of individual turtles

ranged from 3 to 14 encounters per turtle ($\overline{X}$ = 7.6, ± 2.93 SD). The principal component analysis

reduced the five disturbance response variables into one significant component and explained

41.4 % of the variance ($p = 0.00$). Structure correlations were all positively correlated and were

highest for distance fled (factor loading = 0.86) and latency to forage (factor loading = 0.86),

followed by FID (factor loading = 0.54), abrupt burst response (factor loading = 0.48), and flight

to nearest neighbor (factor loading = 0.27). PC1 (Fig. 2) indicated a gradient of personality types

(i.e., timid and bold) between individuals in response to disturbance. Negative PC1 scores were

attributed to levels of "lower boldness" and positive PC1 scores were attributed to levels of

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"higher boldness". Overall, 53% (n = 10) of the identified turtles were considered bold (i.e., levels of higher boldness), showing short flight initiation distance, lower frequency to exhibit an abrupt burst response, short distances fled, short latency to forage, and lower frequency to take flight to nearest neighbor. Conversely, 47% (n = 9) of the identified turtles were considered timid (i.e., levels of lower boldness), showing the opposite behavior responses. There were no significant effects on PC1 scores by variables measured prior to disturbance (time of day, if the turtle was in a group, movement type, and foraging rate) (Table 1).

2.4.3 Repeatability measures

Using the 145 PC1 scores and individual turtle as the random effect, we calculated an overall significant repeatability value (r = 0.132, 95% CI: 0.001-0.253, p = 0.007), indicating repeatable tendencies exist at the individual level when responding to a snorkeler disturbance (Fig. 3). However, the repeatability value itself (r = 0.132) was low, indicating that while individuals display repeatable tendencies (p = 0.007), behavioral plasticity (variation) exists to some degree within individuals when responding to a snorkeler disturbance.

The two personality types, timid and bold, had a significant effect on the amount of variation in PC1 scores for an individual turtle (F (1, 17), = 7.01, p = 0.02). Individual turtles that were timid had a lower mean standard deviation score ($\overline{X}$= 1.14, ± 0.19 SD) than bold individual turtles ($\overline{X}$= 1.45, ± 0.41 SD) (Fig. 4).

2.5 Discussion

Viable sea turtle ecotourism operations depend on the opportunity for tourists to easily observe sea turtles; however, frequent disturbance of turtles by snorkelers has the potential to shift diurnal patterns in foraging behaviors as well as habitat use (Taquet et al. 2006, Landry and

Taggart 2010). Our study suggests that immature green turtles in the Luis Peña Channel Natural Reserve displayed consistent individual-level behavioral responses to tourist disturbances. Specifically, we were able to classify individual immature green turtles on a continuum from timid to bold based on their responses to snorkeler disturbance. The significant relationships between mean standard deviation scores and behavioral type assigned to individual turtles suggests that timid turtles had more consistent disturbance responses compared to bold turtles that displayed higher variability in disturbance responses across encounters. Further, the non-significant relationships between the PC1 scores and the variables measured prior to disturbance also suggest that extrinsic factors (i.e., time of day, if the turtle was in a group, movement type, and foraging rate) had no influence on disturbance response types.

2.5.1 Evidence of personality in immature green turtles

Defining personality as repeatable individual differences in a single context that are consistent over time (Réale et al. 2007) and using turtles' behavioral responses to disturbance as a measure of boldness, this study was able to demonstrate turtles exhibit consistent individual-level responses or personality. While repeatability in turtle behaviors was overall statistically significant within the context of disturbance response, the repeatability value was low which implies plasticity existed to some degree in how individual immature green turtles react to snorkelers. As Nakagawa and Schielzeth (2010) suggest, a repeatability value (r) may be low for two reasons (1) high within-individual variation or (2) low between-individual variation. For example, between-individual differences may be low if turtles do not act drastically different from one another in general, which might be true if a spectrum or continuum of responses exists as we suggest. Deriving a low repeatability value, as this study has, is likely due to a combination of the two. In addition, since individual turtles did not always respond in the same

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way to disturbance, this might reflect small individual differences in cue presentation (e.g., approach angle relative to the sun, swimming behavior of snorkeler), weather-related factors (e.g., more or less light/turbidity at time of disturbance), or perhaps the turtles' state prior to disturbance (i.e., length of time foraging or time since last breath, level of satiation). A potential confound of this study was the inability to assess energetic states through time which could influence turtles' perceived value of resources (i.e., boldness), a turtle's energetic state likely varies at a scale of weeks to months (Heithaus et al. 2007) which was similar to the time frame as our study.

2.5.2 Ecological implications

Our results suggest that individual-level behavior responses of immature green turtles may be attributed to differences in personality types. This is especially pertinent considering individual personality may drive an individual's sensitivity to non-consumptive disturbances. Ultimately, variation in the behaviors of turtles and other animals could influence both individual- and population-level processes as reported by Bejder et al. (2006) for dolphins. For example, bold turtles may adapt better over short- and long- term periods than timid turtles to non-life threatening tourist-based disturbances. In contrast, a timid turtle might have a greater long-term energetic consequence from repeated snorkeler disturbances as a result of reduced foraging opportunities and increased stress. At the population-level, snorkeler disturbance could shift the distribution of more sensitive turtles.

Sharks, a predator of sea turtles (Heithaus et al. 2007), could also potentially influence personality-dependent selection on immature green turtles through direct predation or non-lethal effects ("trait-mediated" or "risk effects") (Preisser et al. 2005, Heithaus et al. 2008, Creel and Christianson 2008, Creel 2011). While shark predation may target risk prone bold-individuals

who exhibit reduced antipredator behaviors (Geffroy et al. 2015), non-lethal effects motivated by shark presence may also affect turtle populations. Predator presence may require high energetic investment by turtles and missed foraging opportunities, especially for turtles in the best conditional state or with timid personalities that forego optimal but risky habitats (Werner and Peacor 2003, Preisser et al. 2005, Heithaus et al. 2007). In addition, persistent tourism disturbance may favor the selection of bold turtles, which could reduce antipredator behaviors and increase vulnerability to predators (Geffroy et al. 2015). Over the longer term, a turtle population with a mix of bold and timid individuals may promote more resilient populations as anthropogenic and predation pressures vary over time (Schindeler et al. 2010).

2.5.3 Conclusion

Considering that 90% of turtles in our study initiated flight response at ≤ 3 m, we recommend that snorkelers maintain > 3 m distance from immature green turtles when snorkeling. However, turtles at other sites may be less habituated to snorkelers than turtles at our study site, potentially requiring greater minimum approach distances. We also concur with the turtle watching guidelines proposed by Landry and Taggart (2010) that ecotourism activities be temporally and spatially stratified to reduce the effects of snorkelers on turtles. We encourage future studies to examine responses across seasons, which may account for any seasonal changes in turtle behavior or aggregation strategies and snorkel tourism disturbances. In addition, we were unable to account for any pre-existing conditioning some turtles may have to snorkeler disturbance in our study area. Thus, we further encourage additional research on the effects of snorkelers on green turtles across a wider diversity of sites with varying levels of snorkeler activity, including reference sites where green turtles are not affected by snorkelers. Ideally, future studies should also determine if green turtles become habituated to snorkelers and if adult

green turtles react differently to snorkelers than immature green turtles. In addition, measuring repeatability across multiple contexts, not just behavioral responses to disturbance, would strengthen the claim green turtles exhibit personality and provide further insight into the relationship between tourism, turtle personality, and predatory shark interactions. We suggest co-management between local government authorities, tour operators, and other stakeholder groups in the area to develop, communicate, and implement turtle watching guidelines. Effective management plans will help to ensure that economically viable sea turtle ecotourism operations persist.

Table 1 (a) One-way analysis of variance examining the effects of session (AM/PM), if the turtle was in a group (Y/N), and movement type (sedentary/mobile) on the PC1 scores, representing turtle behavioral responses to snorkeler disturbance, and (b) linear regression of the PC1 scores with foraging rate (bites/min) as a predictor.

a

Model	df	SS	MS	F	p
Session (AM/PM)	1	1.05	1.051	0.506	0.478
Residuals	143	296.98	2.077		
Total	144	298.03	3.128		
Group (Y/N)	1	7.17	7.17	3.525	0.0625
Residuals	143	290.86	2.034		
Total	144	298.03			
Movement Type (Sed./Mob.)	1	0.56	0.5564	0.267	0.606
Residuals	143	297.47	2.0802		
Total	144	298.03			

b

Response variable	Parameter	Estimate	SE	t-value	p-value
PC1 Scores	Intercept	0.45	0.37	1.17	0.25
	Forage rate	-0.02	0.01	-1.23	0.22
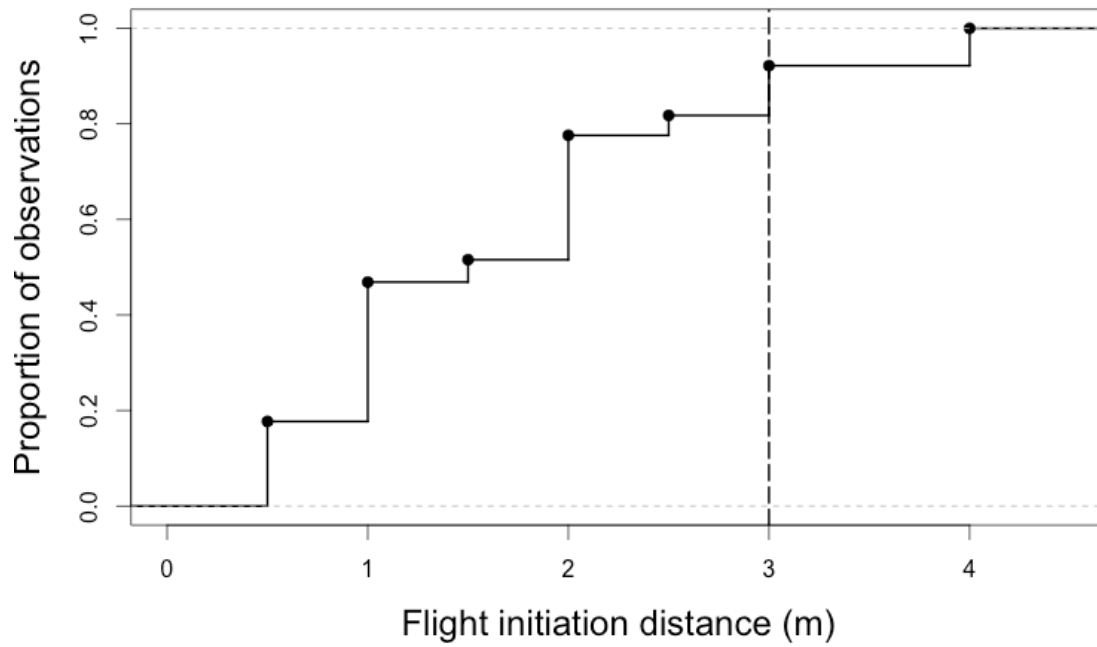
Fig. 1: Minimum green turtle flight initiation distance (FID) (n = 192 observations) expressed as cumulative proportion of observations, showing that 90% of flight initiations occurred at ≤ 3 m.
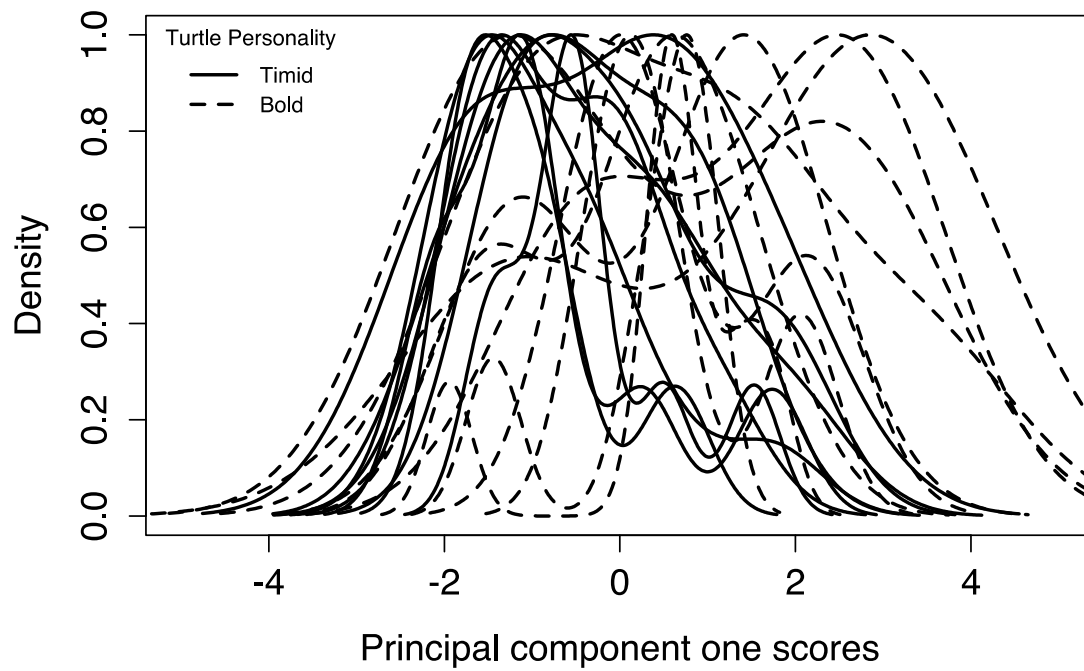
Fig. 2: Individual kernel densities (normalized) of PC1 scores of turtle disturbance responses (flight initiation distance, distance fled, latency to forage, exhibit abrupt burst response, and take flight to a nearest neighbor) of 19 turtles with timid turtles (n = 9) associated with negative means and bold turtles (n = 10) associated with positive means.
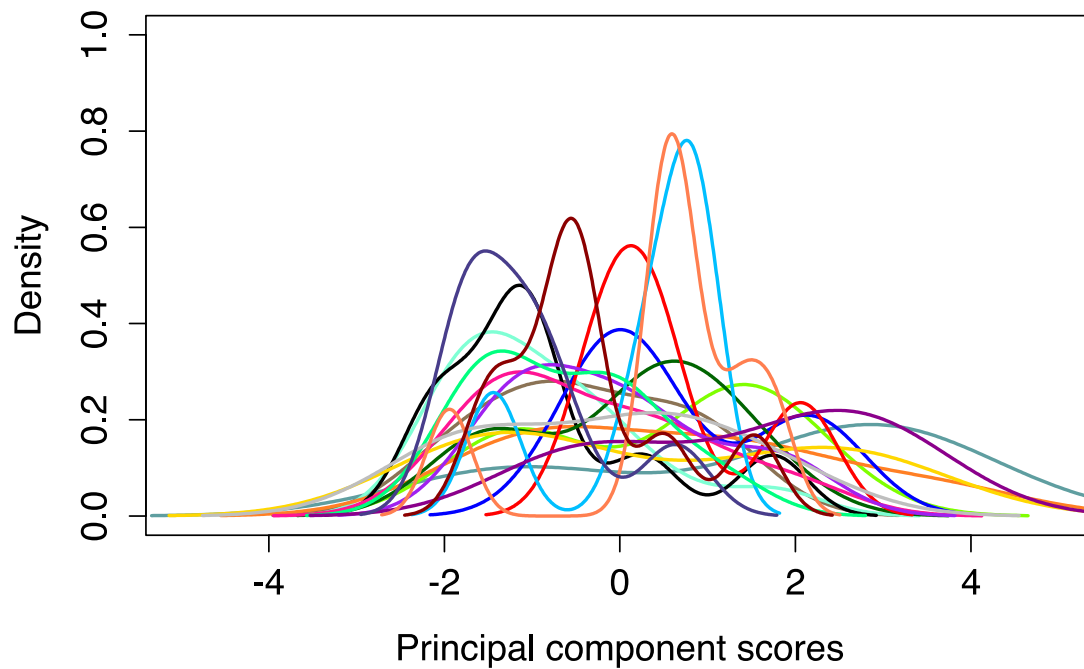
Fig. 3: Individual kernel densities (non-normalized) of PC1 scores of turtle disturbance responses (flight initiation distance, distance fled, latency to forage, exhibit abrupt burst response, and take flight to a nearest neighbor) of 19 turtles. Each kernel represents an individual turtle and the shape of kernels represents a measure of behavioral plasticity with wide, flat kernels associated with highly variable behavioral responses and narrower, peaked kernels associated with less variable responses of individual turtles to disturbance by snorkelers. Timid turtles (n = 9) had lower variable responses compared to bold turtles (n = 10).
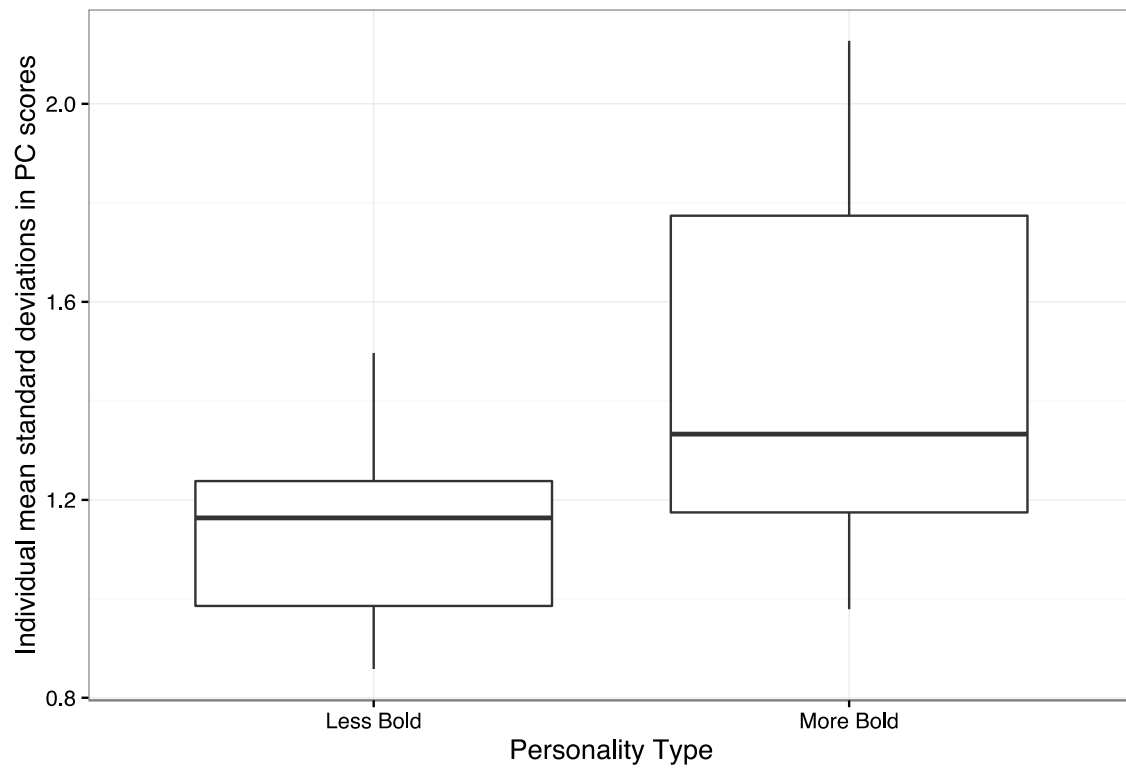
Fig. 4: Box plots of mean standard deviations of PC1 scores of disturbance responses of 19 turtles classified as timid (n = 9) or bold (n = 10), showing more consistent behavioral responses by timid turtles compared to bold turtles.

CHAPTER 3

MOVEMENTS, CONNECTIVITY, AND SPACE USE OF IMMATURE GREEN TURTLES

WITHIN COASTAL HABITATS, CULEBRA, PUERTO RICO: IMPLICATIONS FOR

CONSERVATION

3.1 Abstract

Juvenile green turtles occupy coastal marine habitats important for their ontogeny, however the details of their movement, connectivity, and space use in these developmental habitats are still poorly understood. Given that these areas are often threatened by human disturbance, additional information on green turtle spatial ecology is needed to meet conservation endpoints for this endangered species. For this study, we used fixed passive acoustic telemetry to 1) describe movement patterns and connectivity of immature green turtles within, outside, and across two bays, Manglar and Tortuga Bays, on Culebra and Culebrita Islands, Puerto Rico and 2) determine spatial-temporal drivers of presence and absence of turtles within Manglar Bay. Using network analysis to quantify their movement patterns, turtles in our study showed differential space use with little to no connectivity across the two bays. In addition, turtles exhibited high site fidelity with larger turtles leaving on brief trips. We applied a presence-absence Bayesian binomial model, on a subset of nine turtles at an hourly temporal scale, and showed that turtles within Manglar Bay occupied areas of lagoon and seagrass habitats at night, and were rarely using areas of macroalgae habitat. The parameter estimates from the model enabled us to predict the space use of turtles across Manglar Bay and the hourly probability distributions highlighted predictive diel movement patterns across the bay. Considering the importance of juvenile and subadult life-stages for population viability, we recommend continued protection of these critical juvenile turtle developmental habitats to ensure recruitment into the adult life stage.

3.2 Introduction

The globally threatened green turtle (*Chelonia mydas*) relies on shallow neritic foraging grounds for up to multiple decades until reaching or nearing sexual maturity (Bjorndal et al. 2000, Bolten 2003, Parker et al. 2011). Here, within these developmental areas, turtles will switch from their omnivorous oceanic foraging strategy to foraging largely on herbivorous seagrass and algae (Bjorndal et al. 1997, Heppell et al. 2002, Bolten 2003, Jones and Seminoff 2013). They are believed to occupy relatively small and specific home ranges but range size can vary due to habitat complexity (Mendonca 1983, Ogden et al. 1983, Brill et al. 1995, Whiting and Miller 1998, Seminoff et al. 2003, Makowski et al. 2006, Taquet et al. 2006, Hazel et al. 2009, Blumenthal et al. 2010, Lamont et al. 2015). For example, the home range of immature green turtles (50.9 – 82.5 cm straight carapace length, SCL) were > 16 km$_2$ in the Gulf of California where food resources are widely dispersed (Seminoff et al. 2002). Conversely, Brill et al. (1995) noted an average home range of < 3 km$_2$ for immature green turtles (< 65 cm carapace length) in Kaneohe Bay, Hawaii where both food resources and shelter were tightly clustered together. Makowski et al. (2006) reported 3 km$_2$ average home ranges for immature green turtles (27.9 – 48.1 cm SCL) in Florida with high use areas ranging between 0.18 and 1.17 km$_2$. Further, the size of an immature turtle may affect their home range size with larger immature turtles using deeper open waters and smaller immature turtles using shallow protected bays (Seminoff et al. 2003, Koch et al. 2007, Bresette et al. 2010). Overall, these studies suggest that immature green turtles inhabit well-defined habitats with high variability between home range sizes due to ecological differences in food and shelter resource availabilities, and to differences in body size (Makowski et al. 2006, Lamont et al. 2015).

Considering their complex life history, anthropogenic stressors may impact sea turtle

populations disproportionately across life-stages (Hamann et al. 2010, Wallace et al. 2010). Sea

turtles exhibit high levels of hatchling mortality and late age at sexual maturity (ASM), thus high

survival rates are critical for larger juveniles and adults if populations are to persist (Congdon et

al. 1997). While natural sea turtle mortality decreases with body size, there is an elevated

consequence for a population when larger individuals are removed just prior to reaching maturity

(Heppell et al. 2003). Within a stable stage distribution population (i.e., proportion of individuals

remain constant across both age class and time), large immature sea turtles will account for the

majority of the population, making their survivorship critical for population growth or decline

(Heppell 1998, Heppell et al. 2000). Consequently, protecting developmental habitats and

helping ensure recruitment of immature turtles to sexual maturity is essential for maintaining

population viability.

In Puerto Rico, the Culebra Archipelago provides important developmental feeding

habitats for immature green turtles (Collazo et al. 1992). Recognizing the area's importance, the

National Marine Fisheries Service designated Culebra as Resource Category I critical habitat for

the green turtle in 1998 (63 FR 46693, September 2, 1998), and federal management and

conservation measures are required within all coastal habitats within 3 nm (5.6 km) from

Culebra. Green turtles have been most intensively studied in two bays around Culebra, on the

eastern most side of Culebra in Manglar Bay and the on the small island of Culebrita (east of

Culebra) in Tortuga Bay (Collazo et al. 1992, Velez-Zuazo et al. 2010, Patrício et al. 2011,

Patrício et al. 2014, Patrício et al. 2016, Patrício et al. 2017). Although these two bays are in

close proximity, there are relatively few records of green turtles moving between the bays based

on a mark-recapture study with sampling occurring approximately twice during a given year

(Patrício et al. 2011). Immature green turtles spend decades in these near-shore developmental

habitats. Because these habitats are increasingly affected by anthropogenic disturbances, more

information is needed on turtle movements, connectivity, and space use within them.

Considering that the habitat composition and structure in these two bays are different,

understanding turtle movement and connectivity in relation to the bays may provide additional

insights on immature green turtle ecology. The purpose of this study was to 1) evaluate

movement patterns and connectivity of immature green turtles within, outside, and across two

bays: Manglar Bay on Culebra Island, and Tortuga Bay, on Culebrita Island, Puerto Rico, 2)

assess spatial-temporal drivers of presence and absences of turtles within Manglar Bay.

3.3 Methods

3.3.1 Turtle tagging study sites

The two study sites where turtles were tagged, Manglar Bay, Culebra Island (18° 19' 01'' N

and 65° 17' 24'' W), and Tortuga Bay, Culebrita Island, are 30 km east from the main island of

Puerto Rico. Both sites are shallow, ranging from 1-15 m deep but the two bays differ in

structure and habitat types (Fig. 5). Manglar Bay has deep lagoons (5 – 15 m) surrounded by

mangroves on the perimeter, shallow seagrass and macroalgal flats (0.5 – 2 m) intermixed, and a

linear reef outside the bay. Tortuga Bay has more uniform depth across a deep basin with a

shallow sandy perimeter. The bay consists primarily of colonized hard bottom, sand with

scattered seagrass and coral (Diez et al. 2010). A 2 km wide and 20 m deep channel, Culebrita

Strait, separates these two areas.

3.3.2 Turtle capture and tagging

Turtles were captured following procedures used by Diez et al. (2010) in collaboration

with the sea turtle surveys conducted annually by the Departamento de Recursos Naturales y

Ambientales de Puerto Rico and U.S. Fish and Wildlife Service. Turtles were captured using a 200 m x 5 m seine net (#18 nylon twine, 25 cm stretch mesh) deployed in shallow water areas no deeper than 5 m. With the net deployed, a boat carefully cruised the inner turtle foraging area of the bay, producing a disturbance that caused turtles to move towards the net. In smaller, shallower areas, swimmers snorkeled inside the capture area and chased turtles towards the net. A minimum of six swimmers snorkeled along the net, retrieving all entangled turtles. Each turtle was brought aboard the boat to measure mass, SCL (using Haglof 65 and 95 cm tree calipers), and have both front flippers tagged with two external tags (inconel and/or plastic tag). Digital pictures of the carapace and plastron were taken for each individual turtle and any abnormalities noted, such as fibropapillomatosis tumors.

Turtles were tagged with coded ultrasonic transmitters (Vemco V16-1L transmitters, 16 mm diameter, 54 mm length; 8.1 g in water; 60-180 s ping interval; 10 yr battery life) between March 2013 and March 2014.. Adapted from Fujisaki et al. (2012), transmitters were attached to right side caudal marginal scutes on the dorsal surface. To prepare the location, coarse sand paper (400 grit) was used to remove epibionts from the carapace surface and then wiped with isopropyl alcohol (70%) and dried and finally followed by application of acrylic paint. The transmitter was attached to the carapace by drilling two holes (8 mm) into the marginal scutes and then secured with stainless steel wire cable (cable strength, 27 kg) and embedded into a base of West Marine epoxy; with marine epoxy applied on top of the transmitter to cover and streamline it. Positioning was designed to minimize the risk of tag damage or loss by collisions with coral and to reduce hydrodynamic interference. Additionally, positioning ensured that the transmitter was submerged at all times, even when turtles surface.

3.3.3 Fixed passive receiver array

Movement patterns of tagged green turtles were monitored using a fixed passive acoustic receiver array (VR2W-69kHz receivers, Vemco Inc., Halifax, NS) comprised of 59 receivers. Individual receivers were secured to rebar (1 m) and anchored into a concrete block (23 kg). Receivers were strategically placed within bays, on the perimeter of bays, and around Culebra island to maximize the detections of animal movements. The fixed passive receiver array was originally developed to monitor the movements of multiple species (Finn et al. 2014, Brownscombe et al. 2019); thus, receivers were placed in a wide range of habitats ranging from shallow reef flats (< 3 m), enclosed embayments (< 15 m), and open water reef systems (< 45 m) (Fig. 5 and Fig. 6). Approximately, depths for receivers ranged from 1-45 m. Seven receivers were deployed in Manglar Bay, 25 receivers were positioned as a Vemco Positioning System (VPS) on the perimeter of Manglar Bay, two at Tortuga Bay, two in the channel between Manglar Bay and Tortuga Bay (Culebrita Strait), and 23 around Culebra island's perimeter (Fig. 6).

The VPS, a fine scale positioning system that enables the trilateration of detection data into positioning estimates, was designed for a shallow water marine fish (see Brownscombe et al. 2019) and did not generate ecologically relevant positioning data for green turtles in this study. However, employing anchored sync tags within the VPS originally deployed to assist fine scale positioning estimates of detections, we used the sync tag detections to generate multiple linear regressions (zero inflated binomial) to understand detection probabilities across distance. Although dependent on environmental conditions (e.g., wind, temperature, diel phase), our regressions, based on optimal environmental conditions, indicated our receivers roughly had a detection radius of 80 m at 50% detection efficiency. Detection probabilities were calculated for

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receivers (approximately 1-8 m depth) within the shallow VPS only and thus, were likely higher in deeper water.

3.3.4 Data processing

Detection data was exported from a VUE database (Vemco Inc., Halifax, NS) and analyzed in the R statistical environment (R Development Core Team 2018). Data was corrected for receiver clock drift, false detections created by simultaneous detection collisions, and for ricochet (multipath) detections or "echoes" created by complex bathymetry (Kessel et al. 2015). The first seven days of each transmitter detection log was removed to avoid potential tagging effects. Each detection log was examined with abacus plots, showing detections at each station across time, to determine if the transmitter fell off within the array which would result in many false detections for long periods of time. False detections within a detection log were identified when there were many consecutive detections on an individual receiver or on multiple closely placed receivers (if detection coverages overlapped). Detection logs were conservatively filtered accordingly for this potential issue.

3.3.5 Network analysis

Based in graph theory, network analysis is a valuable technique to examine acoustic telemetry movement data and to explore underlying ecological processes (Jacoby et al. 2012, Jacoby et al. 2016). For each deployed transmitter and their respective spatial network, we calculated detection number, days at liberty (defined here as the period between date of release and the date of the last detection, excluding the first seven days), residency index, station count, and number of paths. Data are reported as mean ± SD throughout, unless stated otherwise. Residency index was calculated by dividing the number of days detected by days at liberty

within the study area (Reubens et al. 2013). As a VPS generates high levels of simultaneous detections, due to its design to trilaterate approximate true positions, we decided to aggregate detections from the 25 VPS receivers based on general location (i.e., either associated with lagoon or reef type habitats) into either 'VPS Lagoon' receivers (n = 17) and 'VPS Reef' (n = 8). Specifically, station number was the number of stations an individual was detected on (i.e., receivers, including the VPS as VPS Lagoon and VPS Reef receiver aggregates) and a single path was defined as any unique node to node (station to station) movement. In addition, we calculated three network attributes; network density, average path length (APL), and mean betweeness (Bi_{mean}). The package igraph (Csardi and Nepusz 2006) was used to generate network metrics and network graphs. Network density refers to the degree of available routes in a network, ranging from 0-1, a higher density value indicates multiple routes were used and available for a given individual (Lédée et al. 2015, 2016). APL is the average shortest number of steps for all used paths between nodes (i.e., stations), this measure indicates on average how easily individuals may move through the network (Kurvers et al. 2014). Bi indicates a node's importance via its connection strength to other nodes, based on the number of paths that pass through a specific node (the focal station) when taking the shortest path length from one node to another (Jacoby et al. 2012). We used an ANCOVA to test if detection number, days at liberty, residency index, station count, and number of paths differed between size (SCL) and capture location (Manglar Bay and Tortuga Bay). In addition, we used linear models to test for an effect between size and network density, APL, and Bi_{mean} for Manglar Bay individuals only, as Tortuga Bay did not have extensive receiver coverage to calculate meaningful values.

3.3.6 Movements, connectivity, space use outside-, within-, and across- bays

Network analysis was further used to examine the movements, connectivity, and

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variation in space use across the study area. To examine these attributes across the study area and beyond just Manglar and Tortuga Bay, we used bipartite graphs (Dale and Fortin 2010). Here, these graphs are comprised of two different types of nodes, individuals and locations. Essentially, these bipartite graphs link individual turtles to the regions they visited. An important distinction is that these graphs are not spatially explicit and they highlight the relationships (i.e., visits) between the individuals and locations. They are particularly useful when attempting to examine the variation in space use patterns across individuals or groups of individuals (Urban and Keitt 2001, Fortuna et al. 2009, Jacoby et al. 2012, Finn et al. 2014, Heupel et al. 2019). The links between the individuals and locations, also referred to as the 'edges', are weighted by the number of detections at the given region. We aggregated the 26 stations (including the aggregated VPS receivers, see above) into eight areas that correspond to the area's geography, including: Honda, Dakity, Mosquito, Las Pelas, Manglar, San Ildefonso, Culebrita Strait, and Tortuga Bay (Fig. 6). By aggregating receivers into regions, we have also minimized issues surrounding detection efficiency (i.e., we have a high likelihood of detecting a passing individual within a region). To better observe space use patterns across the study area, the bipartite graphs were then plotted using the Fruchterman-Reingold force-directed layout algorithm (Fruchterman and Reingold 1991). This algorithm generates attractive and repulsive forces among all the regions or 'nodes' which are proportional to the weight of the edges connecting adjacent nodes (Tamassia 2013). Thus, if there was little or no attraction then nodes would arrange in an equidistant circle (Finn et al. 2014). However, when strong attractions / connections exist between nodes, the nodes and their heavily weighted edges would be tightly connected to one another, and thus, form possible 'network communities'.

3.3.7 Community network structuring

Potential network communities were identified across the eight receiver regions using six community detection algorithms. These algorithms cluster nodes into modules (i.e., potential communities) and are useful to examine the core space-use and the connectivity of different groups of individuals across the study area (Finn et al. 2014, Jacoby and Freeman 2016). The module clustering of nodes is based on the strength of the connections to one another. When groups of nodes have tight connections to one another (e.g., high number of visits between each other), they are referred to as communities. The applied algorithms to identify potential communities were: Leading-Eigenvector (Newman 2006), Walk-Trap (Pons and Latapy 2006), Fast-Greedy (Newman and Girvan 2004), Spin-Glass (Reichardt and Bornholdt 2006), Label-Propagation (Raghavan et al. 2007), and Multilevel (Blondel et al. 2008). Subsequently, modularity scores, used to assess the quality of potential network communities, were calculated for each community detection algorithm (Newman and Girvan 2004). These scores are the fraction of edges within selected modules (i.e., community) minus the fraction that would occur if the edges were randomly distributed across nodes (Finn et al. 2014). Thus, modularity scores range from 0-1, and the higher the modularity score for a community detection algorithm, the higher the quality of module divisions.

Each potential network community detected by an algorithm was assessed for significance by calculating the in-degree ($k_{i\,in}$) (number of links to nodes of the same module) and the out-degree ($k_{i\,out}$) (number of links to nodes outside its module) for each node within the given module. We used a Wilcoxon sum-rank test to see if nodes, within a given module, were more linked to one another than with other individual modules or the entire network (Song and Singh 2013). If a module is non-significant, $k_{i\,in}$ and $k_{i\,out}$ are about the same. If a module is

significant, and it has significantly more nodes linked within it than to nodes in other modules (high $k_{i\ in}$), it is labeled as a statistically significant community. If a module is significant and the nodes link more with nodes in other modules (high $k_{i\ out}$) then it is labeled as an 'anti-community'. Moving nodes from an anti-community module to another community would reduce modularity for the entire graph (Finn et al. 2014). Anti-communities are often corridors with many connections to other modules.

3.3.8 Spatial-temporal drivers within Manglar Bay

3.3.8.1 Data structuring

To examine turtle presence-absence distributions in Manglar Bay, we first created eight new receiver aggregates or 'regions' that specifically corresponded to the physical attributes of Manglar Bay and to nearby areas where turtles were regularly detected. Turtle presence or absence was binned by hour for each region. By aggregating receivers into regions and binning by hour, it is more likely we are capturing true presences and absences in Manglar Bay despite not formally incorporating detection efficiency. In addition, acoustic telemetry is a presence-only type of data, with term 'absence' referring to the lack of detection since it is impossible to definitively determine if a tagged animal is truly absent in this system. Here, binning the data provided better estimation of true absences.

3.3.8.2 Model covariates

Eight covariates were identified as potential predictors of green turtle presence and absence in Manglar Bay, including habitat variables (reef, lagoon, macroalgae, and seagrass), diel cycles (levels day vs. night), tide states (levels low, incoming, high, outgoing), tide height

(m), and tide daily range (m). All continuous variables were standardized to have a mean of 0 and a standard deviation of 1.

Using habitat data collected from the National Oceanic and Atmospheric Administration (NOAA) (https://products.coastalscience.noaa.gov/collections/benthic/e95usvi_pr/, Kendall et al. 2002), we generated relative habitat kernel density estimates (KDEs) (Sheather and Jones 1991) around Culebra Island for each type of habitat; specifically, reef, lagoon, macroalgae, and seagrass. Other habitats (e.g., linear reef, forereef, unconsolidated bottom, and sand) were assessed but were eliminated due to high collinearity and variance inflation factor (VIF) scores (i.e., these habitat types were highly correlated with one or more of the other habitat types) (Zuur 2009). KDE bandwidth sizes were generated for each unique habitat in the study area (ranging from 100 m to 1500 m), bandwidths incorporate both density and proximity of the focal habitat in the area. Using the habitat KDE bandwidth combinations, we derived all possible KDE point values for the derived eight Manglar Bay regions, and assessed the best bandwidth for each habitat using a series of random forest models (randomForest package, Liaw and Wiener 2002) with turtle presences binned at the hourly level as the response variable.

Diel cycle was included at two levels, day vs. night, with periods of day and night assigned using the maptools package (Bivand et al. 2013). Tide states, height, and daily range were derived from NOAA (https://tidesandcurrents.noaa.gov/noaatidepredictions.html).

3.3.8.3 Statistical models and validation

We modeled the hourly presence and absence of nine turtles within each region of Manglar Bay across 60 days between December 2013–February 2014, as a function of eight covariates and with four dependency structures (i.e., spatial and temporal) in a binomial regression with a trial size of nine. Only turtles with $< 50\%$ absences at the hour level were used.

The response variable, hourly presence, for each region ranged from 0-9. Selected habitat predictor variables, informed via random forest models, for the full model included: reef at 500 m bandwidth, lagoon at 300 m bandwidth, macroalgae at 100 m bandwidth, and seagrass at 200 m bandwidth. Fixed covariates were reef (continuous), lagoon (continuous), macroalgae (continuous), seagrass (continuous), diel period (categorical with two levels), tide states (categorical with four levels), tide height (continuous), tide daily range (continuous). The interaction terms were diel period (categorical with two levels) x seagrass, diel period x macroalgae, diel period x tide height, and tide height x tide daily range. Habitat covariates were selected based on the habitats available to turtles within Manglar Bay. Diel period was a covariate of interest to determine if space use changed across day and night periods. Covariates involving tidal cycles (states, height, and range) were examined since they may affect the availability of habitats or may provide a mechanism of transport for foraging green turtles (Brooks et al. 2009).

A Bayesian analysis framework with Integrated Nested Laplace Approximations (INLA) methodology (Rue et al. 2009) and binomial distribution was adopted to fit the data. INLA, able to handle large datasets, obtains the distribution of each parameter in a model while allowing for the incorporation of spatial and temporal dependency structures (i.e., autocorrelation) (Blangiardo and Cameletti 2015, Zuur et al. 2017). Autocorrelation, inherent to tracking data, presents a difficult and confounding caveat of estimating space use of tagged animals (Johnson et al. 2013, Fleming et al. 2015, Winton et al. 2018). When autocorrelation is ignored, the assumption that observations are independent is violated and has the potential to produce biased parameter estimates (Zuur et al. 2017). INLA now enables researchers to include dependency structures to deal with autocorrelation while reducing computational times (Bakka et al. 2018).

For example, outperforming more conventional methods that lacked formal incorporation of autocorrelation structures, Winton et al. (2018) used INLA to estimate the distribution and relative density of loggerhead sea turtles along the North Atlantic coast.

Here, to fit the model, INLA was applied using the R-INLA package (Rue et al. 2009). To incorporate a spatial dependency structure (i.e., account for autocorrelation) into the model as a random effect, we utilized a mesh and the stochastic partial differential equation (SPDE) approach (see Lindgren et al. 2011, Zuur et al. 2017). Essentially, the mesh, comprised of non-overlapping triangles (i.e., lines and vertices) provides a means to effectively approximate the spatial field across our study site which helps to reduce issues with autocorrelation (see Zuur et al. 2017). This spatial random effect was assumed to have a zero-mean prior Gaussian distribution with a Matérn covariance structure (Muñoz et al. 2013). Since approximation of the SPDE approach improves with finer meshes (i.e., more vertices) but increases computation, we generated multiple mesh sizes and ultimately selected a mesh with 2,155 vertices (Fig. 7). Finally, we used three dependency structures as random walk smoothers to help account for temporal autocorrelation issues, including: tide height, hour of the day, and study day.

Random walk smoothers change in shape depending on Penalized Complexity (PC) prior selection (Zuur et al. 2017). We ran the full candidate model with twenty-seven possible PC prior combinations to examine the effect and to select the best combination of informed PC priors for these trends. The best combination of PC priors was determined via Widely Applicable Information Criterion (WAIC) (Watanabe 2010). A lower WAIC value indicates an improved model by assessing the quality of fit vs. model complexity (Watanabe 2010).

We performed backward-stepwise model selection to choose the best combination of variables from the full candidate model, again, using WAIC and the selected random walk

informative PC priors. A posterior distribution was obtained for each included parameter, enabling probability statements about each focal parameter. Unlike frequentist analyses where confidence intervals and means are produced, the 0.025 and 0.975 quantiles of each posterior distribution (the credible interval) indicate the unknown parameter is 95% likely to fall within that range of values.

The final model was examined for homogeneity by plotting the residuals against fitted values and for potential patterns in residuals by plotting residuals versus each covariate in the model and each covariate not in the model. We plotted residuals versus spatial and temporal dependency structures (i.e., variograms and autocorrelation function plots) to assess existing potential issues with autocorrelation. To evaluate model performance and predictive accuracy, we generated a confusion matrix (i.e., a classification table that compares actual and predicted presences and absences to one another), calculated a dispersion statistic, compared the predicted and observed values using the full dataset, and, in addition, simulated from the posterior distributions of the regression parameters a thousand times to further assess under- or overdispersion (see Zuur et al. 2017).

3.3.8.4 Spatial-temporal predictions

Using the final model, we predicted the spatial-temporal distribution of turtles within and around Manglar Bay by hourly level. We derived 2,155 habitat point estimates from our original mesh's vertices (2,155 vertices) and from each habitat KDE; this mesh was originally generated via the SPDE approach. These point estimates were used to help predict turtle distribution across Manglar Bay at each hour. Further, we made spatially explicit delineations for each station region, used the mean tide height and tidal range, the median study day (296), and classified for each hourly predictive model as either day or night.

3.4 Results

Movement data were examined from 21 turtles captured from Manglar Bay via 26 transmitters, five turtles were re-captured and re-tagged with acoustic transmitters due to tag loss (March 2013, n = 8; December 2013, n = 14; March 2014, n = 4). From Tortuga Bay, 10 turtles were captured and tagged, no re-tagging occurred (December 2013, n = 8, March 2014, n = 2) (Table A.1, Appendix A). While some individuals were detected outside their respective bays, no individual captured in Manglar Bay was ever detected within Tortuga Bay and vice versa for turtles captured from Tortuga Bay. Individual turtle size at tagging (n = 36) ranged from 38 to 70 cm (straight-carapace-length [SCL]; 50.61 ± 7.84 cm) with no significant difference in size between the locations (Manglar Bay, 51.42 ± 8.14 cm, n=26; Tortuga Bay, 48.5 ± 6.93 cm, n=10). After removing the first seven days in each detection log (due to the anticipated tagging effects), days at liberty per transmitter ranged from 25 to 600 days (167.08 ± 148.57 d) with a mean residency index of 0.80 ± 0.26. There was no significant effect of size and capture location on detection number, days detected, days at liberty, or residency index; and no effect of size on network metrics (network density, APL, and Bi $_{mean}$) for turtles tagged in Manglar Bay. However, there was a significant effect of size ($F_{1,33}$ = 7.53, p = 0.01) and capture location ($F_{1,33}$ = 62.73, p < 0.001) on station count with larger turtles and turtles from Manglar Bay having higher station counts (Table A.2, Appendix A). There was no effect of size on number of paths but there was a significant effect of capture location on number of paths ($F_{1,33}$ = 31.26, p < 0.001) with greater number of paths exhibited by Manglar Bay turtles compared with Tortuga Bay turtles, potentially an artifact of the number of receivers and thus detection coverage.

3.4.1 Movements, connectivity, space use outside-, within-, and across- bays

Using the Fruchterman-Reingold force-directed layout algorithm, the bipartite graph shows heterogeneous space use across turtles captured in Manglar Bay (n = 21) and turtles captured in Tortuga Bay (n = 10) (Fig. 8). Turtles remained near their capture origin with only a few Manglar Bay individuals detected west of the bay in Mosquito, Dakity, and Honda Bay, and in the east to San Ildefonso and Culebrita Strait. While turtles were never detected across capture location bays, six turtles captured from Manglar Bay and two turtles captured from Tortuga Bay were detected in Culebrita Strait, but no individual here had more than 100 detections. Moreover, turtles tagged from Tortuga Bay were never detected on any receiver further away than Culebrita Strait.

3.3.2 Community network structuring

Network communities or 'modules' were found within the bipartite graph by six different community detection algorithms. Four of the six algorithms (Fast-Greedy, Spin-Glass, Label-Propagation, and Multilevel) produced identical module groups with the highest modularity score (0.197, Table 2). The four algorithms partitioned the bipartite graph into three modules (Fig. 9b); one of the three modules was found to be a significant community ($p < 0.001$) which partitioned all ten Tortuga Bay captured turtles with the Tortuga Bay node. The other two modules consisted of six Manglar Bay captured turtles partitioned with Las Pelas, Dakity, and Honda nodes ($p = 0.926$), and 15 turtles partitioned with Manglar, Mosquito, San Ildefonso nodes ($p = 0.062$). The two other algorithms (Leading Eigenvector and Walk-Trap) performed worse with modularity scores of 0.186 and 0.173, respectively. Both found five similar modules (Fig. 9a, Fig. 9c) to each other within the bipartite graph and both had one significant module, the Tortuga Bay community. There was a slight difference in placement of some Manglar Bay

individuals across the communities, and both algorithms created two modules that only consisted of one node or one turtle. No anti-communities, i.e., significantly more connections outside the module than within it (Finn et al. 2014), were found by any detection algorithm.

3.4.3 Spatial-temporal drivers within Manglar Bay

Using the model with the best fit based on the lowest WAIC value, the final model consisted of six fixed covariates; lagoon (continuous), macroalgae (continuous), seagrass (continuous), diel period (categorical with two levels), tide height (continuous), tide daily range (continuous), and two interaction terms; diel period (categorical with two levels) x seagrass and diel period x tide height. Green turtle presence and absence were largely explained by lagoon, macroalgae, the interaction between seagrass and diel period, and the random spatial and temporal effects (Table 3).

Juvenile green turtles were most likely to be present in areas with higher lagoon habitat values (lagoon, posterior mean = 1.22; 95% CI = [0.13, 2.31]), and in areas with higher seagrass habitat values at night (diel (night): seagrass, posterior mean = 0.29; 95% CI = [0.14, 0.45]). Turtles were less likely to be present in areas with higher macroalgae habitat values (macroalgae, posterior mean = -0.56; 95% CI = [-1.0, -0.10]). The predicted and observed values (presences and absences) across hour at each station region show heterogeneous space use across time (Fig. 10). While space use was variable across individual turtles (Fig. A.17, Appendix A), turtles largely followed a general spatiotemporal pattern within Manglar Bay. Turtles were most likely to be detected in the back portion of Manglar Bay (Region 1, R1 in Fig. 7) across all hours, with the highest probabilities between 07:00 hr and 17:00 hr. In addition, to the back portion of Manglar Bay, turtles were most likely to be detected in the western portion of Manglar Bay (Regions 5 and 6, Fig. 7) at night, between 19:00 hr and 06:00 hr. Turtles were more likely to be

detected in the eastern portion of the Manglar Bay (Regions 2, 3, and 4, Fig. 7) during daylight (between 08:00 hr and 17:00 hr). Turtles were rarely detected in the furthest western region (Region 8, Fig. 7), however, if they were detected here, it occurred most often during day time hours.

The final model correctly categorized 88% of the presences as determined by the confusion matrix (i.e., a classification table that compares actual and predicted presences and absences to one another), and the dispersion statistic derived via sum of squared Pearson residuals was 0.82, slightly underdispersed. Simulating from the posterior distributions of the regression parameters a thousand times, we observed an overestimation of zeros and an overestimation of nines (Fig. A.18, Appendix A). The simulation in combination with the dispersion statistic highlighted the potential misinterpretation of the variance structure. While computationally intense and difficult to implement, this model may have benefitted by using a zero-inflated binomial distribution (due to many absences) rather than a binomial distribution. While some autocorrelation still existed, it was largely corrected for with the SPDE approach and the hourly-station temporal dependency structure (Fig. A.19 and Fig. A.20, Appendix A).

Predicted probability distribution maps of green turtles were generated for each hour across Manglar Bay with the tide height and tidal range being held constant at their means, and using the median study day (296). The spatial maps were consistent with the model predictions, as higher and lower presences followed similar patterns as the predicted and observed values (presences and absences) across each hour and each station region (Fig. 10). Based on habitat features, turtle presence was estimated to be low in unobserved areas such as the reef but high in unobserved areas where seagrass and lagoon habitats existed. Further, diel period appears to be linked with spatial predictions, specifically, turtle probability distributions were condensed

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within the central and western portion of Manglar Bay at night and more dispersed towards the eastern portion of Manglar Bay during the day. Our model indicated turtles had the highest probabilities of detection in the back portion of Manglar Bay, also known as Region 1. Further, these probabilities in Region 1 were the highest between 07:00 hr and 17:00 hr. However, our predictive probability distribution maps (which account for habitat within the entire bay) showed the highest presences to be in the central part of the lagoon, in areas that were considered unobservable with our receivers.

3.5 Discussion

The main aims of this study were to examine movement patterns and connectivity of immature turtles within, outside, and across Manglar Bay on Culebra Island, and Tortuga Bay, on Culebrita Island, Puerto Rico, as well as determine the spatial-temporal drivers of presence and absence within Manglar Bay. As suggested by Patrício et al. (2011), juvenile green turtles around Culebra exhibit high site fidelity to specific bays with larger turtles leaving on brief trips. Further, the size distribution of tagged turtles in this study were similar to that reported by Patrício et al. (2014) and thus likely was representative of individuals that were not tagged. There was little overlap of space use outside respective bays for turtles captured in both Manglar and Tortuga Bay, further, no turtle was ever detected entering the opposing bay.

Our model incorporating habitat kernel densities indicated that turtles were more likely to be present in areas of lagoon habitat, seagrass at night, and less likely to be in macroalgae habitat. We used parameter estimates from the model to predict space use of nine turtles across Manglar Bay, our hourly probability distributions proved to be accurate and demonstrated turtles moving in predictive patterns across the bay. Here, acoustic telemetry in combination with novel analytical methods provide unique insights on their movement patterns such as space use,

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connectivity, and their spatial-temporal drivers. These methods included network analysis, community detection algorithms, and presence-absence Bayesian modeling while accounting for autocorrelation.

Within an ideal free distribution framework (Fretwell and Lucas 1969), each individual animal should arrange themselves across space, based on food supply, in a way that no individual has greater advantage than another, thus input matching is achieved via bottom-up processes (Milinksi and Parker 1991). However, through top-down processes, predation risk often heavily alters spatial distributions and ultimately impacts lifetime reproductive success based on the trade-off between energetic input and predation risk (Lima and Dill 1990, Moody et al. 1996). We suspect top-down processes related to predation risk occur within Culebra considering immature green turtles had differential space use, as indicated by network analysis, and never moved between Manglar Bay and Tortuga Bay, the two highest turtle density bays on Culebra that are only separated by 2 km. While anecdotal evidence suggests limited predator burdens (e.g., tiger sharks) around Culebra, predation risk and its non-lethal effects (trait-mediated or risk effects) is likely a major selective force in the evolution of behaviors which still drives spatial distributions of immature turtles around Culebra.

Furthermore, while genetic sampling suggested the recruitment origins for juvenile green turtles were similar across the two bays in Culebra (Patrício et al. 2017), somatic growth was significantly greater in Manglar Bay than in Tortuga Bay with minimum ages at maturity of 14 and 22 yr., respectively (Patrício et al. 2014). Since no differential recruitment (Patrício et al. 2017) or movement across bays exist, habitat quality and availability (Bjorndal et al. 2000) in combination with predation risk (innate or learned) is likely driving these different rates of somatic growth. Manglar Bay is comprised of macroalgae and the seagrass *Thalassia testudinum*,

the primary diet of green turtles in the Greater Caribbean (Bjorndal 1980), while Tortuga Bay is

predominantly covered by seagrasses *Syringodium filiforme* and *Halodule wrightii*. Residency

was high (0.80) for turtles regardless of size or location, supporting previous findings (Mendonca

1984, Brill et al. 1995, Makowski et al. 2006, and Colman et al. 2014) that immature green

turtles inhabit smaller but well-defined areas when ecological resources (i.e., food and shelter)

are tightly clustered. The compressed bipartite graphs and community plots show turtles in

Culebra use well-defined areas. However, there was an effect of turtle size and capture location

on station count, movement data showed larger individuals were more likely to exit the bay for

brief trips, which is consistent across other study areas (Seminoff et al. 2003, Koch et al. 2007,

Bresette et al. 2010). Potentially, as suggested by our data, predation risk and exploratory

behaviors decrease and increase with size, respectively.

3.5.1 Spatial-temporal drivers within Manglar Bay

Our results suggest turtles favored lagoon habitat, followed by seagrass habitat at the

night. Overall, turtles were much less likely to be present macroalgae habitat. Based on the

predicted hourly probability distribution maps, turtle's presence shifted from the central and

western portion of Manglar Bay at night towards the eastern portion during the day. We

anticipated turtles would be detected exiting and entering Manglar Bay for shelter and potentially

safer habitats during the night via the large channel at Region 4, however, we saw the nine

selected turtles largely remained within the lagoon during the night. Although, reef structure

exists around Culebra, which generally serves as resting habitat for turtles to reduce predation

risk (Ogden et al. 1983, Makowski et al. 2006, Taquet et al. 2006, Hazel et al. 2009), some

turtles within Culebra may find shelter in the protected lagoon as they would in exposed patch

reef system. In agreement with our findings, Blumenthal et al. (2010) also reported some green

turtles remaining within lagoon habitats at night. Further, turtles may be selecting seagrass at night for foraging opportunities if light conditions are suitable (Taquet et al. 2006).

3.5.2 Conclusion

Seagrass communities, the main diet of green sea turtles, are considered threatened globally (Waycott et al. 2009) and are highly vulnerable to human disturbances including urban and agriculture runoff off, coastal development, and dredging (Grech et al. 2012). Since Culebra Island, Puerto Rico, is classified as Resource Category I critical habitat for the green turtle (63 FR 46693, September 2, 1998) and largely protected through the Culebra National Wildlife Reserve, its coastal habitats are still relatively undisturbed, providing an excellent window into natural processes. While habitats within Culebra are still largely intact, multiple embayments are becoming increasingly threatened by sewage wastewater contamination and/or coastal development (e.g., mangrove clearing, high sediment loads). Further, plans for dredging for marinas are being proposed in these sensitive seagrass habitats. Considering, turtles in Culebra exhibit high fidelity within the bays, it is imperative to protect these distinct habitats that serve as both shelter and foraging areas. This is especially pertinent since the survival of immature turtles here in Culebra, could positively affect Caribbean wide nesting populations, specifically that of Costa Rica, Mexico, East Central Florida, and Suriname (Patrício et al. 2017). The protection of these essential juvenile turtle developmental habitats ensures the continued recruitment into recovering green turtle populations.

Table 2. Results from the six community detection algorithms applied to the bipartite graph (31 green turtles with 8 regions consisting of 48 out of the 59 receivers). These algorithms cluster the nodes (i.e., individuals and locations) into modules. Modularity, ranging from 0-1, indicates the community detection algorithms ability to partition the bipartite graph. Modularity is the fraction of edges within selected modules minus the fraction that would occur if edges were randomly distributed across nodes. Higher the modularity score, the better the algorithm performed at clustering. Significant modules ($p > 0.05$) under the Wilcoxon sum-rank test indicates there are significantly more connections with a module than outside of it and thus termed a 'community'.

Community detection algorithm	Modularity	Modules detected	Significant modules
Leading Eigenvector	0.186	5	1
Fast-Greedy	0.197	3	1
Spin-Glass	0.197	3	1
Label Propagation	0.197	3	1
Walktrap	0.173	5	1
Multilevel	0.197	3	1

Table 3 Results from final Bayesian presence and absence binomial model of nine green turtles within Manglar Bay across 60 days. Six covariates along with two interaction terms were included in the model. In addition, the model was fit with a spatial dependency structure to account for spatial autocorrelation (via the stochastic partial differential equation) and three random walk smoothers to account for temporal autocorrelation (tide height, hour of the day, and study day).

Predictor	Mean	SD	$Q_{0.025}$	$Q_{0.975}$
Intercept	-3.91	1.02	-5.91	-1.91
lagoon	1.22	0.56	0.13	2.31
macroalgae	-0.56	0.24	-1.0	-0.10
seagrass	0.41	0.29	-0.16	0.96
diel (night)	-0.29	0.09	-0.47	-0.12
tide height	-0.17	0.36	-0.87	0.53
tide range	0.05	0.07	-0.08	0.19
diel (night):seagrass	0.29	0.08	0.14	0.45
diel (night):tide height	-0.05	0.03	-0.10	0.00
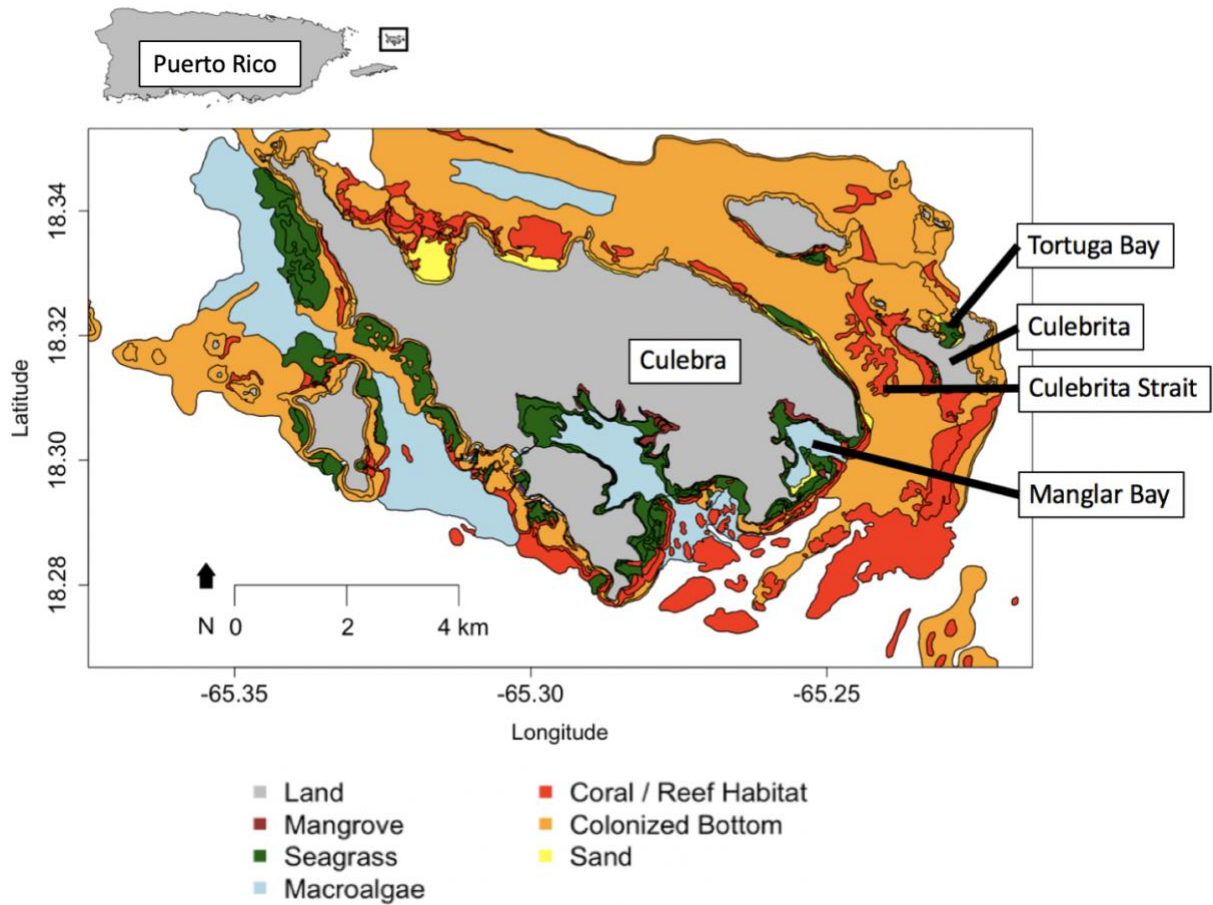
Fig. 5: Study site map of Culebra and Culebrita, Puerto Rico, including Manglar Bay, Tortuga Bay, and Culebrita Strait of Culebra, Puerto Rico. In addition, habitats of interest are displayed (https://products.coastalscience.noaa.gov/collections/benthic/e95usvi_pr/, Kendall et al. 2002).
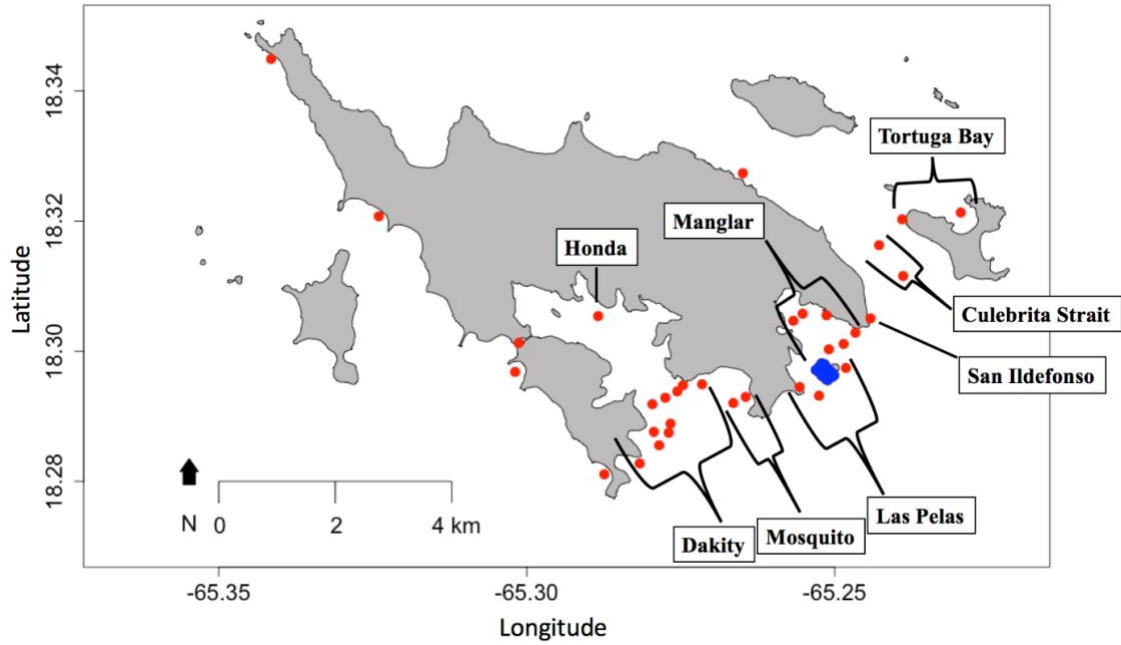
Fig. 6: Manglar and Tortuga Bays of Culebra, Puerto Rico with a total of 59 receivers (red and blue dots) deployed around Culebra island. Twenty-five receivers, as indicated by the blue dots, were positioned as a Vemco Positioning System (VPS) on the perimeter of Manglar Bay, based on receiver general VPS location they were categorized as either 'VPS Lagoon' receivers (n=17) or 'VPS Reef' (n=8). The corresponding receiver classified regions (i.e., Honda, Dakity, Mosquito, Las Pelas, Manglar, San Ildefonso, Culebrita Strait, and Tortuga Bay) used for the bipartite graphs are labeled.
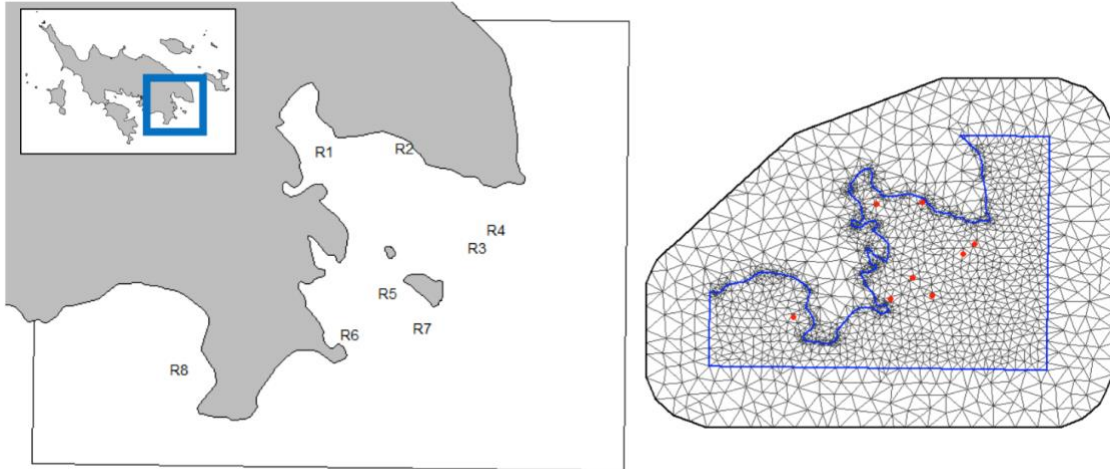
Fig. 7: Left: The Manglar Bay area with eight receiver aggregates or 'regions' specified. Right: The generated mesh, comprised of non-overlapping triangles, was used to approximate the spatial random field. Finer meshes leading to better approximations but longer computational times helps to reduce issues associated with autocorrelation. Our mesh contained 2,155 vertices which were used to account for spatial dependency within the presence-absence binomial model of nine turtles within Manglar Bay. The red dots represent the eight receiver aggregates or 'regions'.
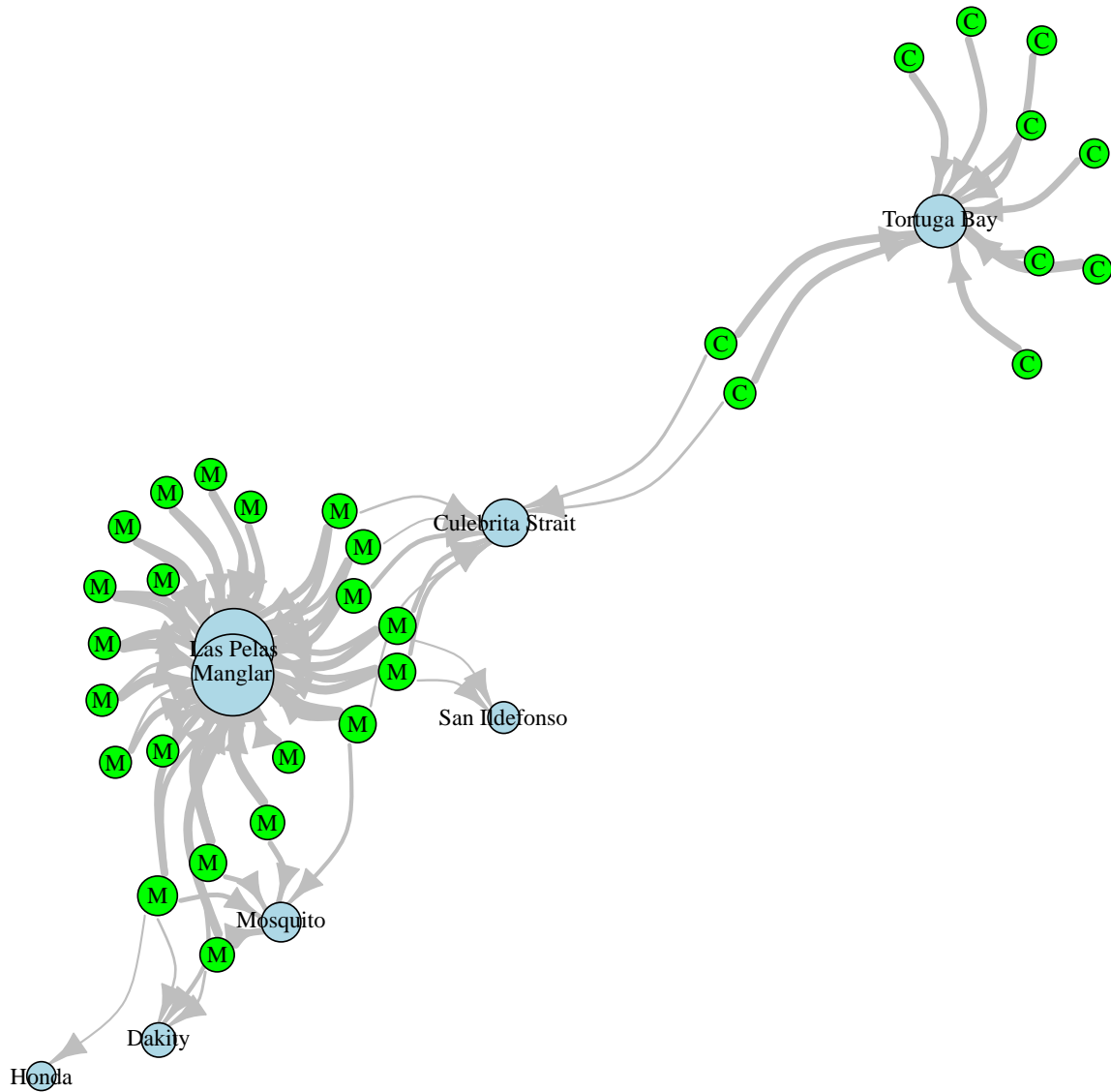
Fig. 8: Bipartite graph of turtle-region network in Culebra, Puerto Rico with Fruchterman-Reingold force-directed layout algorithm. The network displays the links (edges) between the turtles (green nodes) and regions visited (blue nodes). The width of edges is proportional to the number of detections at each region per individual and the diameter of each node is proportional to the node's degree (i.e., number of links to or from the node). The Fruchterman-Reingold force-directed layout algorithm balances attractive and repulsive forces among nodes which are proportional to the weight of edges connecting adjacent nodes (i.e., similar space use by individuals would be clustered together). Individuals are clustered closely together in their respective bays. Manglar Bay individuals are labeled with 'M' (Manglar) nodes and Tortuga Bay individuals are labeled with 'C' (Culebrita Island) nodes.
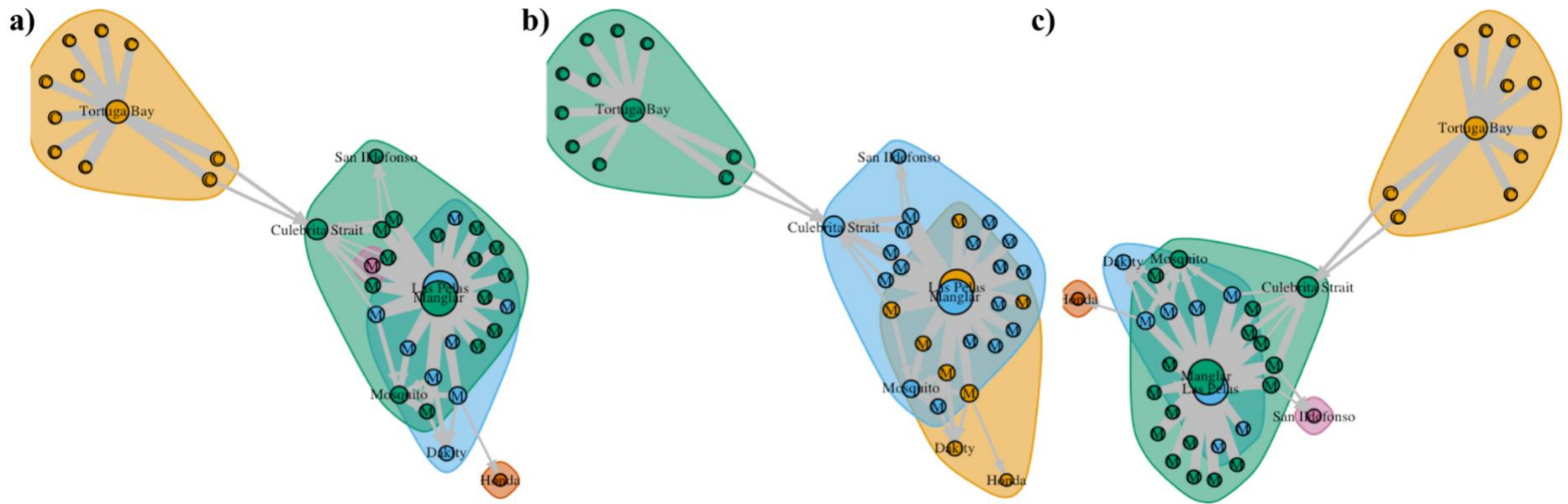
Fig. 9: Bipartite graphs with identified turtle community structuring (i.e., modules) via the six community detection algorithms a) Leading-Eigenvector, b) Fast-Greedy, Spin-Glass, Label-Propagation, and Multilevel and c) Walktrap algorithms. Fast-Greedy, Spin-Glass, Label-Propagation, and Multilevel had identical modules generated.
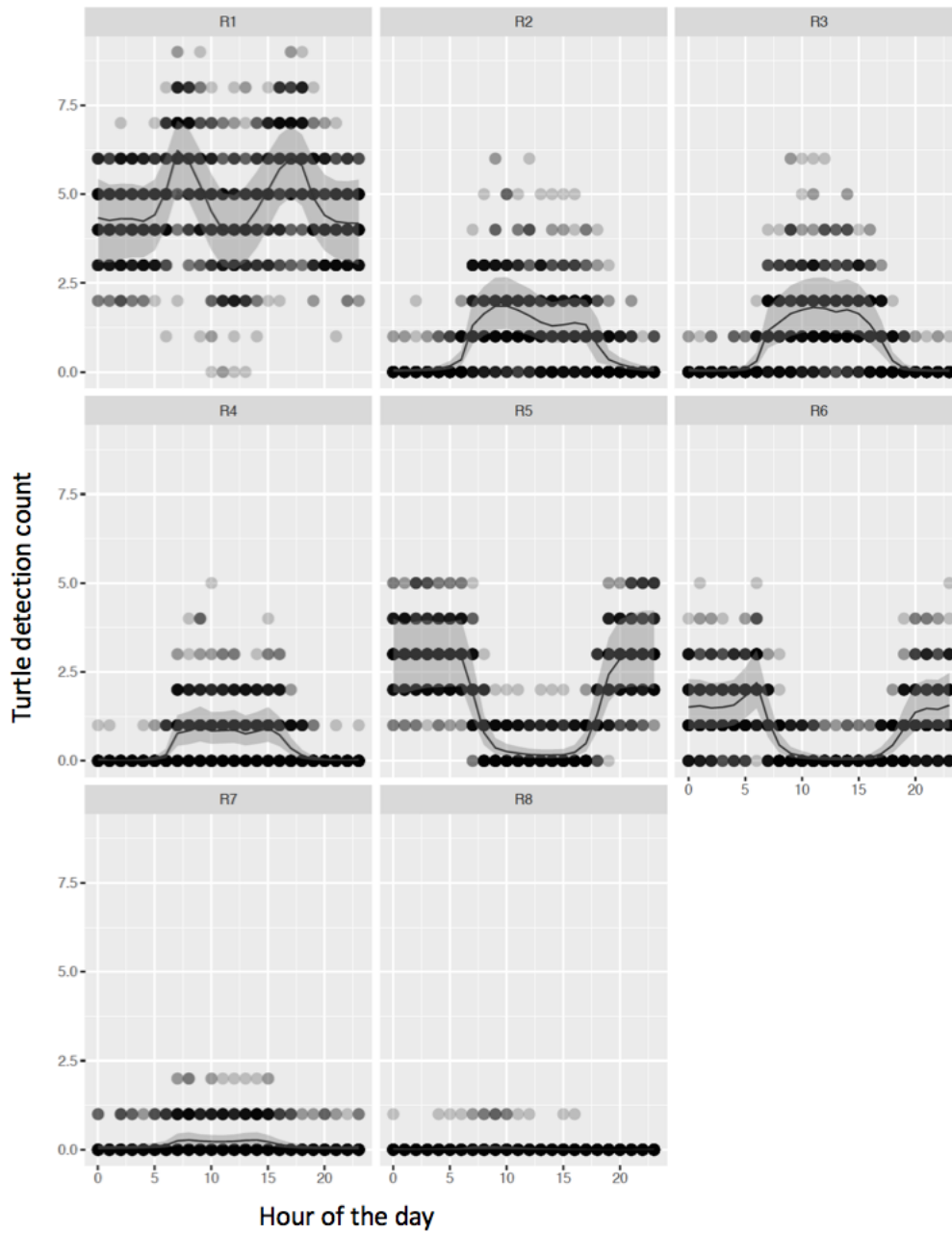
Fig. 10: Observed versus fitted values (presences and absences) segregated by region (labeled R1-R8) at the hour level for the Bayesian presence-absence binomial model of nine turtles within Manglar Bay across 60 days. The dots show the observed number of turtles (0-9) for each hour, and the black line with the gray credible interval shows the expected value for the number of turtles from the best model.
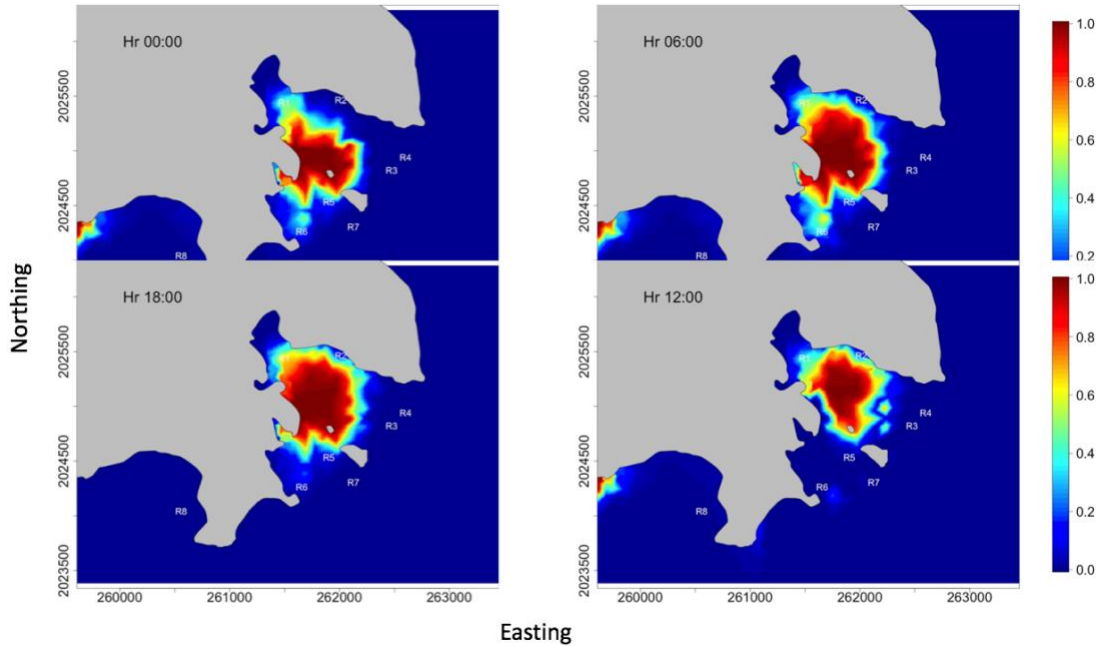
Fig. 11: Using the final Bayesian presence-absence binomial model parameter estimates, the spatial-temporal probability distribution of turtles within and around Manglar Bay at the hour level was produced, 0 (dark blue) being 0% probability of turtle presence and 1 (red) being 100% probability of turtle presence. Here, hours 0:00, 06:00, 12:00, and 18:00 are displayed. We derived 2,155 habitat point estimates from our original mesh (2,155 vertices) and from each habitat KDE, these point estimates were used to predict turtle distribution across Manglar Bay. Spatially explicit delineations for each station region were used and predictions were set to the mean tide height and tidal range, and the median study day (296). Each hour was also classified for each hourly predictive model as either day or night.

CHAPTER 4

WARMING SEAS INCREASE COLD-STUNNING EVENTS FOR KEMP'S RIDLEY SEA

TURTLES IN THE NORTHWEST ATLANTIC

4.1 Abstract

Since the 1970s, the magnitude of turtle cold-stun strandings have increased dramatically within the northwestern Atlantic. Here, we examine oceanic, atmospheric, and biological factors that may affect the increasing trend of cold-stunned Kemp's ridleys in Cape Cod Bay, Massachusetts, United States of America. Using machine learning and Bayesian inference modeling techniques, we demonstrate higher cold-stunning years occur when the Gulf of Maine has warmer sea surface temperatures in late October through early November. Surprisingly, hatchling numbers in Mexico, a proxy for population abundance, was not identified as an important factor. Further, using our Bayesian count model and forecasted sea surface temperature projections, we predict more than 2,300 Kemp's ridley turtles may cold-stun annually by 2031 as sea surface temperatures continue to increase within the Gulf of Maine. We suggest warmer sea surface temperatures may have modified the northerly distribution of Kemp's ridleys and act as an ecological bridge between the Gulf Stream and nearshore waters. While cold-stunning may currently account for a minor proportion of juvenile mortality, we recommend continuing efforts to rehabilitate cold-stunned individuals to maintain population resiliency for this critically endangered species in the face of a changing climate and continuing anthropogenic threats.

4.2 Introduction

Historically, sea turtle populations experienced wide-spread declines, primarily from by-catch and harvest of adults and eggs (Jackson 1997). While conservation measures have helped to increase sea turtle populations globally (Mazaris et al. 2017), both fine- and large-scale threats persist for all seven species of sea turtles, including bycatch, harvest, habitat degradation, pollution, tourism, and climate change. Of these, climate change may present the broadest threat for sea turtle conservation (Wallace et al. 2010 a, b, Butt et al. 2016). Predicted warmer temperatures and sea level rise may decrease hatchling success and available nesting habitats, and skew sex ratios (Butt et al. 2016, Laloë et al. 2017).

Less is understood about the potential effects of climate change on sea turtle cold-stunning events. As a result of prolonged exposure to cold water temperatures, hypothermic cold-stunned sea turtles can experience debilitating lethargic conditions that often lead to death (Morreale et al. 1992, Spotila et al. 1997, Innis et al. 2007, Keller et al. 2012). All sea turtle species are susceptible to becoming cold-stunned, however, the Kemp's ridley (*Lepidochelys kempii*), loggerhead (*Caretta carreta*), and green turtle (*Chelonia mydas*) are the most frequently cold-stunned species in the U.S., with cold-stun stranding events occurring at the upper limits of their ranges both in low and high latitudes (Turnbull et al. 2000). At lower latitudes, cold-stunning events are acute and triggered by extreme cold weather snaps, often during relatively mild winters (Witherington and Ehrhart 1989, Avens et al. 2012, Pirhalla et al. 2015, Roberts et al. 2014). At higher latitudes, cold-stunning events are associated with turtles not migrating south before the onset of late autumn storms and associated declining seasonal water temperatures (Burke et al. 1991, Coles and Musick 2000, Still et al. 2005, Bellido et al. 2010, Monzón-Argüello et al. 2012). In both regions, cold-stunning events occur when turtles appear to be

unexpectedly caught in areas with lower water temperatures and fail to depart from shallower colder nearshore waters. For example, in 2010, approximately 5,000 juvenile green turtles were cold-stunned and stranded across Florida (Avens et al. 2012), while in 2014, over 1,100 Kemp's ridleys stranded in Cape Cod Bay, Massachusetts.

Dependent on local wind and oceanic currents, cold-stunned sea turtles typically wash-up on beaches where, if found prior to death, they are recovered and sent to rehabilitation centers (Still et al. 2005). These recovery programs can be highly effective at reducing mortality rates of cold-stunned turtles. For example, in the large-scale 2010 Florida cold-stun event, only 20-22% of stranded turtles died that were recovered from St. Joseph Bay and Mosquito Lagoon, respectively (Avens et la. 2012, Provancha et al. 2012). Cold-stunned turtles recovered in more northerly areas, such as Massachusetts, are typically transported south to Georgia, Florida, or Texas for release (Hunt et al. 2016). It is challenging to predict large-scale cold-stunning events, making it difficult to adequately plan and budget for federal, state, and non-governmental organizations to mobilize their recovery efforts, especially in years when large numbers of turtles are cold-stunned.

The most common species to cold-stun in the northwest Atlantic is the Kemp's ridley, followed by loggerheads. Both species use the nearshore waters of the northeastern United States as developmental habitats, including New England, Long Island Sound, and Chesapeake Bay (Bleakney 1965, Lazell 1980, Shoop and Kenney 1992, Morreale et al. 2005, Still et al. 2005). Due to thermal constraints, these juvenile turtles must migrate south to warmer waters in fall (Musick et al. 1994, Epperly et al. 1995). Juvenile sea turtles become cold-stunned as sea surface temperatures drop to around 10 ℃, (Schwartz 1978, Witherington and Ehrhart 1989, Still et al. 2005) with death occurring at temperatures ranging from 5.0-6.5 ℃ (Schwartz 1978). The semi-

enclosed Cape Cod Bay, Massachusetts, acts as a natural catchment for turtles migrating south, and the bay accounts for most of the cold-stunned turtles in the northeastern U.S. (Still et al. 2005). In Cape Cod Bay, juvenile Kemp's ridleys (approximately three years old) typically cold-stun in November, while the larger bodied loggerheads can withstand colder water temperatures and typically cold-stun in December (Still et al. 2005). Within the past 40 years, over 4,700 Kemp's ridleys have stranded within Cape Cod. These cold-stunning events have intensified annually, requiring greater investment in recovery efforts (Still et al. 2005). Prior to 2009, only two years (i.e., 1999 and 2002) had over 100 sea turtles stranded, since 2009, over a hundred sea turtles commonly strand from cold-stunning each year in Cape Cod Bay.

Little is known about what factor(s) drive this increasing number of sea turtle strandings in Cape Cod Bay. A variety of potential factors have been identified to explain this increasing turtle cold-stunning trend, such as changing oceanic and atmospheric conditions, increasing sea surface temperatures, or recovering turtle nesting populations. The objectives of this study were to 1) identify what factors are affecting Kemp's ridley cold-stunning events in Cape Cod Bay, and 2) predict future rates of cold-stunning based on climate change projections.

4.3 Methods

4.3.1 Cold-stunned turtle data

Sea turtle cold-stunning data were provided by the Sea Turtle Stranding and Salvage Network (STSSN, https://www.greateratlantic.fisheries.noaa.gov/protected/stranding/disentanglements/turtle/stssn. html, Table B.6, Appendix B), which is coordinated by the National and Oceanic Atmospheric Administration (NOAA). This network is made up of trained stranding responders coordinated

locally and by state STSSN coordinators. STSSN has monitored Cape Cod Bay beaches since

1979. With stranding responders monitoring all potential stranding beaches from October-

January, we assumed a high probability of locating all stranded turtles for any given year. We

used the overall count of found Kemp's ridley stranded turtles per year from 1982-2016.

Stranding data from years prior to 1982 were omitted because of limited availability of sea

surface temperature (SST) data.

4.3.2 Environmental and biological data

Using the Optimal Interpolation Sea Surface Temperature database (OISST,

https://www.ncdc.noaa.gov/oisst) from NOAA, we calculated the average daily sea surface

temperature (SST) from 1982-2017 at 2.5 x 2.5 degrees with a spatial resolution of 0.25 degrees

for an area that spans across Cape Cod Bay, Gulf of Maine, and a portion of Georges Bank (Fig.

12). This nearly 50,000 km2 area encompasses the greater northern area of Cape Cod Bay and

Gulf of Maine, where Kemp's ridleys are likely to occur prior to migrating south in the fall. This

area was also chosen to capture the larger scale oceanic thermal conditions that may influence

the immigration and emigration of turtles into coastal areas of the northeastern U.S. To examine

the relationship between SSTs and cold-stunning events, we derived six aggregate SST statistics

at different time scales. These aggregate SST statistics include mean, maximum, minimum,

standard deviation of daily mean SSTs, number of days with daily mean SST below 10 ℃, and

number of days with daily mean SST above 20 ℃. Number of days with daily mean SST below

10 ℃ was chosen because the onset of cold-stun symptoms begins begin at 10 ℃ (Schwartz

1978, Witherington and Ehrhart 1989, Still et al. 2005). Number of days with daily mean SST

above 20 ℃ was chosen to capture periods of uncharacteristically warm SSTs.

In addition to SST derived statistics, we derived the sum of monthly North Atlantic

Oscillation (NAO) indices of each year between June and September. NAO indices, provided

from NOAA (https://www.ncdc.noaa.gov/teleconnections/nao/), are linked with pressure, wind,

and temperature conditions (Ottersen et al. 2001) that may influence turtle recruitment into

coastal areas of the northeastern U.S. We chose the months of June through September to

represent the period of summer recruitment by turtles into coastal areas

(http://www.seaturtlesightings.org/monthmap.html). In addition, the average annual monthly

NAO indices were lagged by two years, which infers the latitudinal position of the Gulf Stream

for a given year (Taylor and Stephens 1998). The annual average monthly Atlantic Multidecadal

Oscillation (AMO) indices, unsmoothed

(https://www.esrl.noaa.gov/psd/data/correlation/amon.us.data), were derived on an annual basis

and also lagged by 1, 2, and 3 years. AMO has been suggested to influence ocean circulation

patterns (Visbeck et al. 2003), which may affect emigration of juvenile Kemp's ridleys from the

Gulf of Mexico into the Gulf Stream or from the greater Atlantic into Cape Cod. Although the

majority of the Kemp's ridley population comes from the Rancho Nuevo area of Tamaulipas,

Mexico (Bevan et al. 2016), we used the annual number of hatchlings released from the

Tamaulipas index beaches (Rancho Nuevo, Playa Dos-Barra Del Tordo, Barra Ostionales-

Tepehuajes) to examine the role of hatchling numbers on cold-stunning events (hatchling data

pre-2015 provided by NMFS and USFWS, hatchling data from 2015 and after provided by

personal communication Peña, Table B.7, Appendix B). Nesting data were lagged by 2, 3, and 4

years because Kemp's ridleys found in Cape Cod are believed to be largely clustered across

these years of age (personal communication Avens). All data were examined for outliers and

collinearity. All statistical analyses were carried out using the software R (version 3.4.2) (R Core Team 2017).

4.3.3 Climate time windows

We used a sliding window approach (van de Pol et al. 2016, Bailey and van de Pol 2016) to determine the optimal climate time window for each of the six aggregate SST statistics (mean, maximum, minimum, standard deviation of daily mean SST, and number of days with daily mean SST below 10 ℃, and number of days with daily mean SST above 20 ℃). We also used the climwin package (Bailey and van de Pol 2016) to test multiple hypotheses about the relationship between the climate variables and the biological response. Using annual cold-stunning data as the biological response, the slidingwin function was used to test for and produce, via Akaike information criterion, the best possible climate time window for each aggregate SST statistic. Since the climate time windows were provided at a daily level (ordinal days), we collapsed time windows into half months. If the optimal day was between the 1_{st} and 14_{th} day of a month, it was considered as the early half of the month and if the optimal day was after the 14_{th} day of a month, it was considered as the late half of the month.

4.3.4 Random forest

We used random forest models from the randomForest package (Liaw and Wiener 2002) to identify the most important variables in relation to annual Kemp's ridley cold-stunning counts. Random forest models have relaxed assumptions (i.e., collinearity) and high explanatory power (Breiman 2001, Cutler et al. 2007). These random forest models, a type of machine learning algorithm, generate and fit hundreds to thousands of decision trees to a data set. However, each decision tree is a bootstrap sample of the total data set and each decision tree searches through a

random subset of the predictor variables at each node (decision) location. The best predictor variable for a specific node is chosen and the decision tree proceeds to the next node where a new random subset of predictor variables are evaluated. This is repeated for all subsequent nodes. The random forest model then assesses each variables' importance by evaluating the decreasing accuracy of trees when each variable is removed, this value is called the mean decrease in accuracy. We first ran the random forest model on all 11 explanatory variables to choose the top two variables that best explained cold-stunning counts. We then eliminated the collinear aggregate SST variables that had the lowest mean decrease in accuracy and subsequently ran the model again with the top non-collinear SST variables (minimum and standard deviation of daily mean SSTs, number of days with daily mean SST below 10 ℃, and number of days with daily mean SST above 20 ℃). Initial exploration indicated ~ 500 trees were sufficiently stable for random forest models; however, the number of trees was set to 2,000 for all random forest models to ensure optimal performance was reached.

4.3.5 Bayesian count model and validation

With a relatively small number of observations (n = 35 count years between 1982-2016), we decided to only use the two most important variables in our count model. Using the two most important variables as identified by our second random forest model, minimum of daily mean SSTs (2nd half of October thru the 1st half of November) and number of hatchlings (lagged by two, three, four years and averaged), we modeled annual Cape Cod Bay Kemp's ridley cold-stunning counts using a negative binomial distribution with approximate Bayesian inference models using Integrated Nested Laplace Approximations in the INLA package (Rue et al. 2009, Martins et al. 2013, www.r-inla.org). A Bayesian framework provides a posterior distribution for each parameter, and thus we can infer the unknown parameter is 95% likely to fall within a range

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of values around each posterior distribution as defined by the 0.025 and 0.975 quantiles. INLA, an alternative to Markov Chain Monte Carlo method, provides an efficient tool to obtain posterior distributions using numerical approximations (Rue et al. 2009).

Further, we modified variance estimates around each parameter using informative prior distributions to include measurement error of our selected covariates. Ignoring measurement error may severely bias parameter estimates and credible intervals, resulting in misinterpreting real covariate signals (Muff et al. 2015). When expert and prior knowledge exists about the uncertainty of the explanatory variables, it is possible to incorporate measurement error into the model via Bayesian analyses (Clayton 1992, Muff et al. 2015). We applied a heteroscedastic error structure (i.e., error changes from observation to observation) to the minimum of daily mean SSTs, which was derived from the OISST platform (mean $\pm$ SD = 0.19$\pm$ 0.02 °C). We applied a homoscedastic error structure (i.e., error remains a constant value across observations) to the number of hatchlings parameter. Since observation error was not reported for hatchlings released, we derived our informative prior for this parameter by calculating the standard deviation of the last 10 years of hatchlings released and then scaled each observation by this standard deviation. The counts of hatchlings released from the last 10 years were used because the trend appears to asymptote during this period; thus, the variation from observation to observation in these last 10 years may be indicative of some measurement error across the entire trend.

Multiple structures, including first-order autoregressive and first and second-order random walks, were applied and assessed, following Zuur et al. (2017), to address potential issues with temporal autocorrelation. However, all autocorrelation structures led the model to overfit the data, and we decided to exclude these structures. Further, we decided not to include

year as a covariate due to high collinearity (assessed via variance inflation factors) with the two parameters of minimum of daily mean SSTs and number of hatchlings.

We performed backwards step-wise model selection using Deviance Information Criterion (DIC, Spiegelhalter et al. 2002), and autocorrelation was assessed using the acf function from the stats package (R Core Team 2017). The final model was examined for overdispersion and homogeneity by plotting the residuals against fitted values, and for potential patterns in residuals by plotting residuals versus each covariate in the model and each covariate not in the model. In addition, we evaluated the models performance by assessing the fitted and observed values using the full dataset.

4.3.6 Prediction

The final model of annual Kemp's ridley cold-stunning counts as a function of minimum of daily mean SSTs (2_{nd} half of October thru the 1_{st} half of November) was then used to predict the potential future trend of Cape Cod Bay annual Kemp's ridley cold-stunning counts with warming sea surface temperatures. Predicted SSTs were derived specifically for our constructed study area using the observed minimum of daily mean SSTs rather than from global climate models that have multiple climatic scenarios. To generate estimates for potential future SSTs, we first calculated the slope of the observed minimum of daily mean SSTs and an intercept from the mean minimum of daily mean SSTs for the last 15 years. Using the calculated slope and intercept, we generated predicted temperatures for 15 years in advance of our study period. We set the measurement error for all 15 predicted temperature values to 0.5, generating additional uncertainty around these values.

Using both our future cold-stun predictions, as related to SST warming via climate change, and population estimates derived from Gallaway et al. (2016), we roughly estimated the

potential future population level effect of cold-stunning. Gallaway et al. (2016) reported the 2012 estimated Kemp's ridley female population at age two, three, and four were 32,060, 23,057, and 22,918, respectively. Female sex ratios were reported at 0.65 and 0.74 for in situ and protected nests, respectively. Using the averaged female population age estimate at age two, three, and four, and the averaged female sex ratios, as reported by Gallaway et al. (2016), we estimated the total number of turtles at age two, three, and four and then compared this estimate with our mean 2031 cold-stun prediction count. This assumes the population estimate of 2012 remains the same until 2031.

4.4 Results

With the wide variation in SSTs both seasonally and between years, we first used the sliding window approach to determine the optimal time window for examining the relationship between SST and cold-stunning events. The optimal climate time windows differed for the six aggregate SST statistics (Fig. 13). The earliest time window occurred from late June thru early August for number of days with daily mean SST > 20 ℃. The optimal time window for three of the SST statistics (mean, maximum, and standard deviation of the daily mean SSTs) occurred from early August thru the first half of October. The third time window occurred from late October thru early November for the minimum of the daily mean SSTs, and from late November thru early December for number of days with daily mean SST < 10 ℃.

Minimum of daily mean SSTs and number of hatchlings were the two most important variables associated with annual Kemp's ridley cold-stunning counts (Fig. 14) identified by the random forest models. Consequently, we removed the two SST variables mean and maximum of daily mean SSTs from the second random forest model due to collinearity.

Both minimum of daily mean SSTs and number of hatchlings along with their respective measurement error structures were included in the Bayesian count model (DIC 341.22). Using number of hatchlings alone as a covariate within the model produced a much higher DIC value of 380.55; however, using minimum of daily mean SSTs alone as a covariate produced a DIC value of 339.41. We decided to drop number of hatchlings from our final model based on the slightly lower DIC value and because number of hatchlings was found not to be important in original model (number of hatchlings, posterior mean = -0.02; 95% Credible Intervals (CI) = -0.3, 0.25]). Thus, using a negative binomial distribution, minimum of daily mean SSTs during late October thru early November was the variable that best explained annual cold-stunning counts. Annual Kemp's ridley cold-stunning events were more likely to be higher when the corresponding late fall SSTs were warmer (Fig.15, minimum of daily mean SSTs, posterior mean = 1.23; 95% Credible Intervals (CI) = 1.04, 1.41]).

Negative temporal autocorrelation at a lag of two was still present among the residuals, but it was minor and largely accounted for by using temperature as a covariate. Further, no obvious trend in the residuals existed, indicating little effect of temporal autocorrelation. The calculated overdispersion statistic was 1.02, indicating no overdispersion issues and the negative binomial was an adequate probability distribution. Common with count models, deviations from the expected increased with larger expected values, which occurred within this dataset in the later years. The observed values from the full dataset were heavily outside the final model's 95% CI; yet, the fitted trend appeared to closely match the trend in the observed data (Fig. 15).

Assuming SSTs within the Northwest Atlantic will continue to increase in the future, we generated predicted temperatures (mean ± SD = 17.36 ± 0.40 °C) for 15 years in advance of our study period using the slope and intercept of observed minimum of daily mean SSTs in the past

15 years. Since these predicted temperatures may vary, we incorporated a measurement error of 0.5 to all temperatures to incorporate more realistic uncertainty. Using these predicted temperatures and their associated measurement errors, we forecasted annual Kemp's ridley cold-stunning counts 15 years into the future. By 2031, the posterior mean predicted Kemp's ridleys cold-stunning count was 2,349 (95% CI = 1,328 - 3,933) (Fig. 16).

If the Kemp's ridleys age structure as reported by Gallaway et al. (2016) remains the same for the next 15 years, we estimate that approximately 1.8% of the juveniles (age classes two, three, and four) may cold-stun by 2031.

4.5 Discussion

Our study indicates that warming SST in the Gulf of Maine are associated with the increasing numbers of Kemp's ridley cold-stunned in Cape Cod Bay each year. The minimum of daily mean SSTs, alone, measured between late October thru early November, best explained the magnitude of annual Kemp's ridley cold-stunning events in Cape Cod Bay. However, maximum and mean of daily mean SSTs, both measured between August and early October, were collinear with minimum of daily mean SSTs. Thus, while warmer SSTs in late fall are indicative of higher annual cold-stunning counts, so are warmer SSTs in late summer and early fall. While our Bayesian count model found SST to be the most important variable in explaining the number of cold-stunned Kemp's ridleys, the model would be improved with a greater understanding of the small and large scale oceanic processes at work, such as eddies, currents, and thermoclines, which all operate on multiple spatial and temporal scales. However, our single covariate likely acts as a proxy for these processes, and our model does appear to explain the observed Kemp's ridleys cold-stunning trend. Surprisingly, the covariate number of hatchlings was not considered important in our full candidate count model, so we dropped this variable from the final model.

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Although the Kemp's ridley nesting population has increased over the years of our analyses, our results suggest the number of hatchlings released is not linked with the magnitude of cold-stunning events in Cape Cod Bay. Potentially, this statistical relationship between strandings and hatchlings was dampened due to variable hatchling survival (based on surface circulation patterns near nesting beaches) and due to the variable probability of turtles moving from the western Gulf of Mexico nesting beaches into the Atlantic (Putman et al. 2013). However, the hatchling indices do provide our best insight into the potential connection between population growth and cold stunning events.

Over the last decade, SSTs are warming 99% faster than the global ocean within the Gulf of Maine (Pershing et al. 2015). These warmer SSTs may be allowing Kemp's ridley to expand their northerly distribution along the northeast Atlantic continental shelf, as reported for many fish species (Kleisner et al. 2017). Although numbers of Kemp's ridley cold-stun strandings increased in both Cape Cod Bay and Long Island Sound since the 1970s, the magnitude of sea turtles cold-stunned have increased dramatically within Cape Cod Bay in comparison to Long Island Sound. This supports the hypothesis that the Kemp's ridley northerly neritic developmental grounds may have shifted more northward along the Atlantic coast, potentially in response to warming SSTs in the Gulf of Maine. Although Carr (1986, 1987) suggested that neonate and juvenile sea turtles disperse passively with wind and currents, Putman et al. (2012), Mansfield et al. (2014), and Putman and Mansfield 2015 demonstrated juvenile turtles are highly capable of active dispersal. Further, Mansfield et al. (2014), tracked neonate loggerheads with satellite telemetry and showed turtles may select for sea surface habitats based on thermal constraints. If these warmer thermal habitats are driving turtles to recruit to more northerly neritic developmental grounds, Cape Cod Bay may act as a natural catchment during the

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southerly migration in colder months. As suggested by Briscoe et al. (2017), if the warmer Gulf of Maine temperatures are acting as an ecological bridge that promotes higher levels of recruitment of organisms into nearshore waters from the Gulf Stream, numbers of cold-stunned Kemp's ridley turtles may well continue to increase over time as suggested by our mean prediction of 2,349 (95% CI = 1,328, 3,933) cold-stunned by 2031.

While we were unable to explain all outlier cold-stun years (1999, 2002, and 2014), we suggest Hurricane Arthur may have contributed to the high cold-stun count in 2014 (n = 1,188). Hurricane Arthur (1–5 July, 2014, https://www.nhc.noaa.gov/data/tcr/AL012014_Arthur.pdf), a category 2 hurricane (on Saffir-Simpson Hurricane Wind Scale) was an unusually early and severe hurricane to hit the northeast U.S. This storm may have 1) warmed waters, promoting sea turtle immigration into nearshore areas, or 2) generated enough wind and current to force sea turtles into nearshore waters (Monzón-Argüello et al. 2012). Since we were unable to assess this with our methods, we suggest future studies to consider anomalous hurricanes as potential predictors for atypically large cold-stunning events.

When evaluating the importance of cold-stunning recovery and rehabilitation efforts in the northeast U.S., it is important to consider the proportion of the Kemp's ridley population affected, and whether juvenile Kemp's ridleys in the Atlantic return to the Gulf of Mexico to reproduce. At the population level, cold-stunning may be affecting only a small fraction of the overall Kemp's ridley population. Assuming the Kemp's ridley age structure proportions reported by Gallaway et al. (2016) remain the same over time, we estimate that less than 2% of the juveniles within age classes two, three, and four may be cold-stunned in 2031. If there were no cold-stun recovery or rehabilitation efforts in 2031, cold-stunning deaths, estimated at 2,349 turtles, would only be a small fraction of mortality for the projected overall Kemp's ridley

population. Further, juvenile survivorship is often not considered as critical for population growth in comparison to the survivorship of larger sub-adult and adult turtles (Heppell 1998, Heppell et al. 2000, Heppell et al. 2002). However, depending on the future and variable Kemp's ridley population demographics, cold stunning events may eventually account for a larger proportion of the population if more turtles are recruiting northward. We also do not know to what extent juvenile Kemp's ridleys on the Atlantic coast return to the Gulf of Mexico to reproduce, but it has been suggested that turtles found on the Atlantic coast may have the navigational abilities to migrate back to the Gulf of Mexico (Meylan 1986, Musick and Limpus 1997, TEWG 2000). Despite the potentially small effect on the overall population, we believe that it is important to continue recovery and rehabilitation efforts for juvenile cold-stunned Kemp's ridleys in the northeast U.S. to bolster population resiliency. This increased resiliency is important considering the slowing trend of nesting Kemp's ridley females and continuing anthropogenic threats to turtles in the Gulf of Mexico (Caillouet, 2010, 2011, 2014, Crowder and Heppell, 2011, Bevan et al. 2016, Gallaway et al. 2016, Kocmoud et al. 2019). Thus, we recommend that all conservation efforts, including the rehabilitation of cold-stunned Kemp's ridleys, be continued for this critically endangered species.

4.5.1 Conclusion

Cold-stunning of Kemp's ridleys within Cape Cod Bay has continued to increase over the past 40 years. Our model indicated that years with warmer SSTs in the Gulf of Maine in late summer thru late fall produce higher numbers of cold-stun turtles on an annual basis. This is particularly alarming, considering the Gulf of Maine is predicted to continue to warm at a rapid rate in coming decades (Pershing et al. 2015). Surprisingly, hatchlings released, a proxy for population abundance, was not identified as important by our Bayesian count model. Our

predictions follow the observed trend and predict there may be as many as 2,349 Kemp's ridley turtles cold-stunned annually in Cape Cod Bay by 2031. Although cold-stunning likely only affects a small proportion of the overall population currently, we argue for the continuation of recovery and rehabilitation efforts to help maintain population resiliency of this critically endangered species. As we continue to observe warming SSTs in the northeast U.S. driven by climate change, managers need to be prepared for increasing numbers of Kemp's ridley cold-stun strandings to occur. Future studies should 1) determine when Kemp's ridleys typically immigrate into and emigrate out of coastal waters of the northeastern U.S., and 2) if juvenile Kemp's ridley turtles migrate back into the Gulf of Mexico to breed as adults.
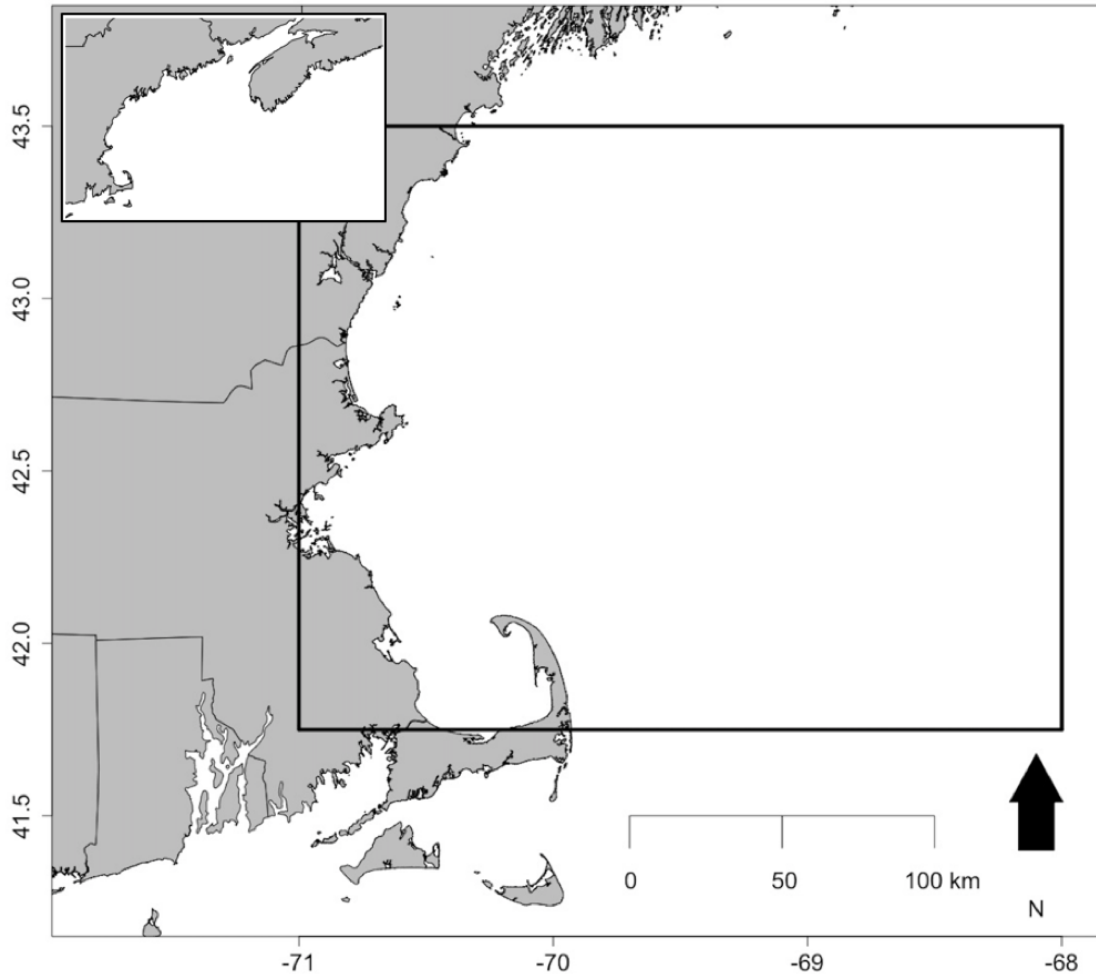
Fig. 12: Map of study area that spans across Cape Cod Bay, Gulf of Maine, and a portion of Georges Bank. Sea surface temperature compiled at 2.5 x 2.5 degrees with a special resolution of 0.25 degrees (black boxes) across the area, using the Optimal Interpolation Sea Surface Temperature database from NOAA.
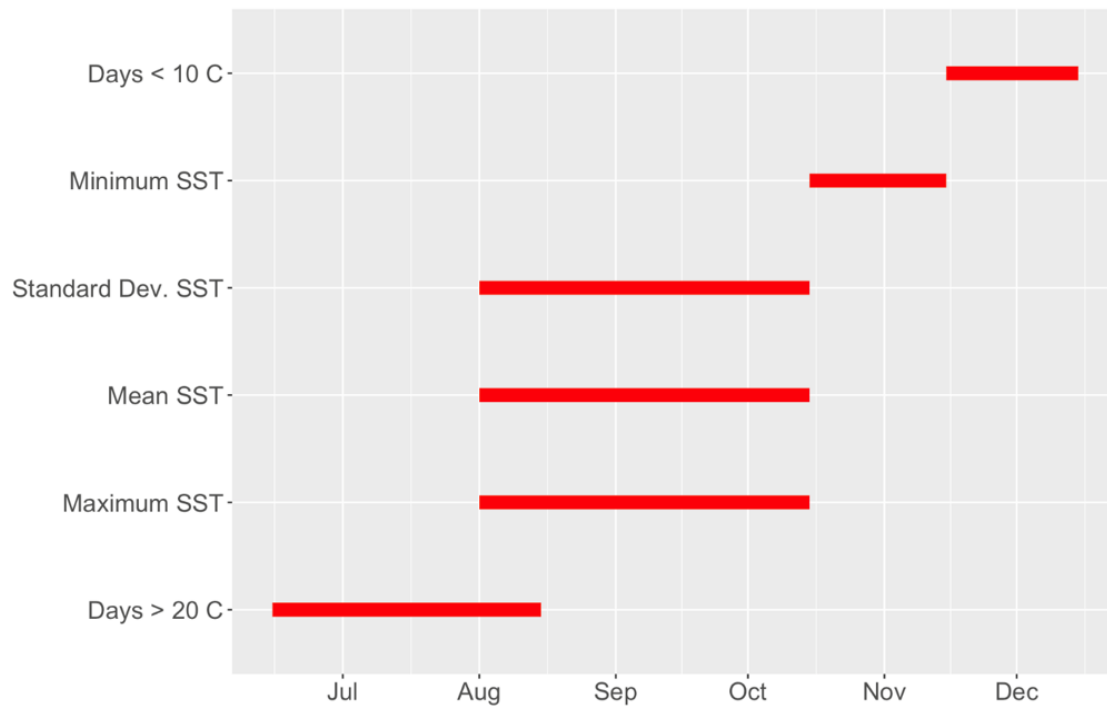
Fig. 13: Optimal climate time windows for selected variables. As identified by the climwin package for each aggregate SST statistic, including: mean, maximum, minimum, and standard deviation of the daily mean SSTs, number of days with daily SST below 10 ℃, and number of days with daily SST above 20 ℃.
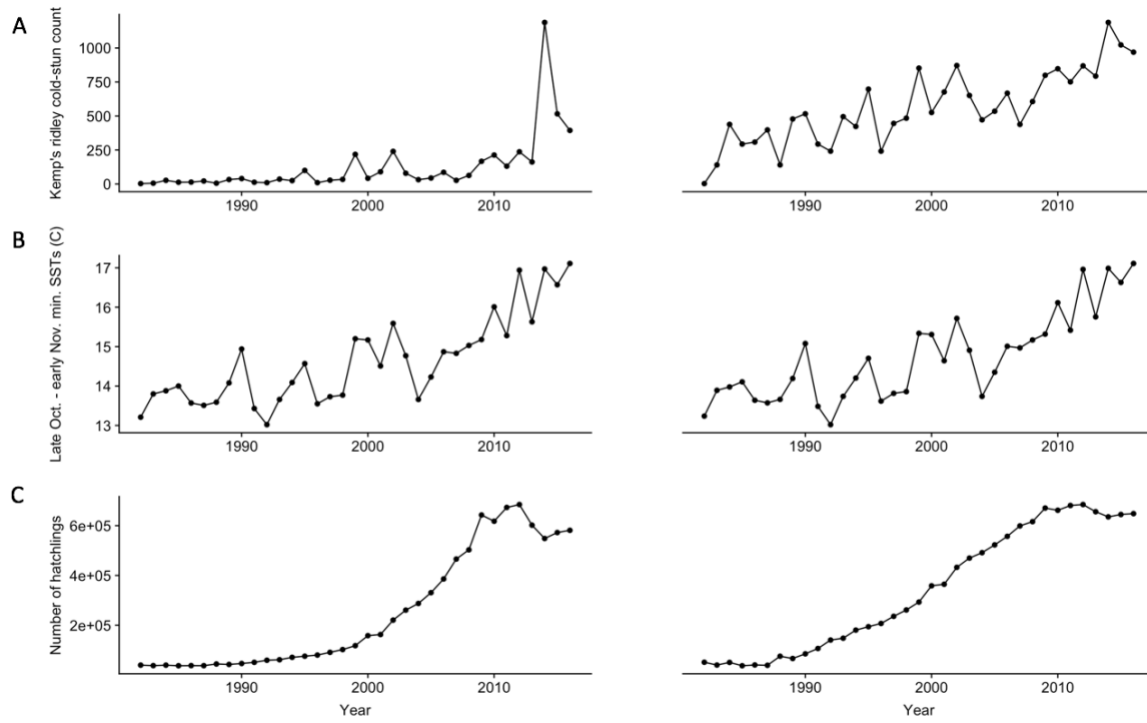
Fig. 14: Time series plots. Raw (left) and logged (right) time series (1982-2016) of A) annual Kemp's ridley cold-stun counts within Cape Cod Bay, B) minimum of the daily mean SST across late October thru early November within the study area, and C) number of hatchlings (lagged by two, three, four years and averaged).
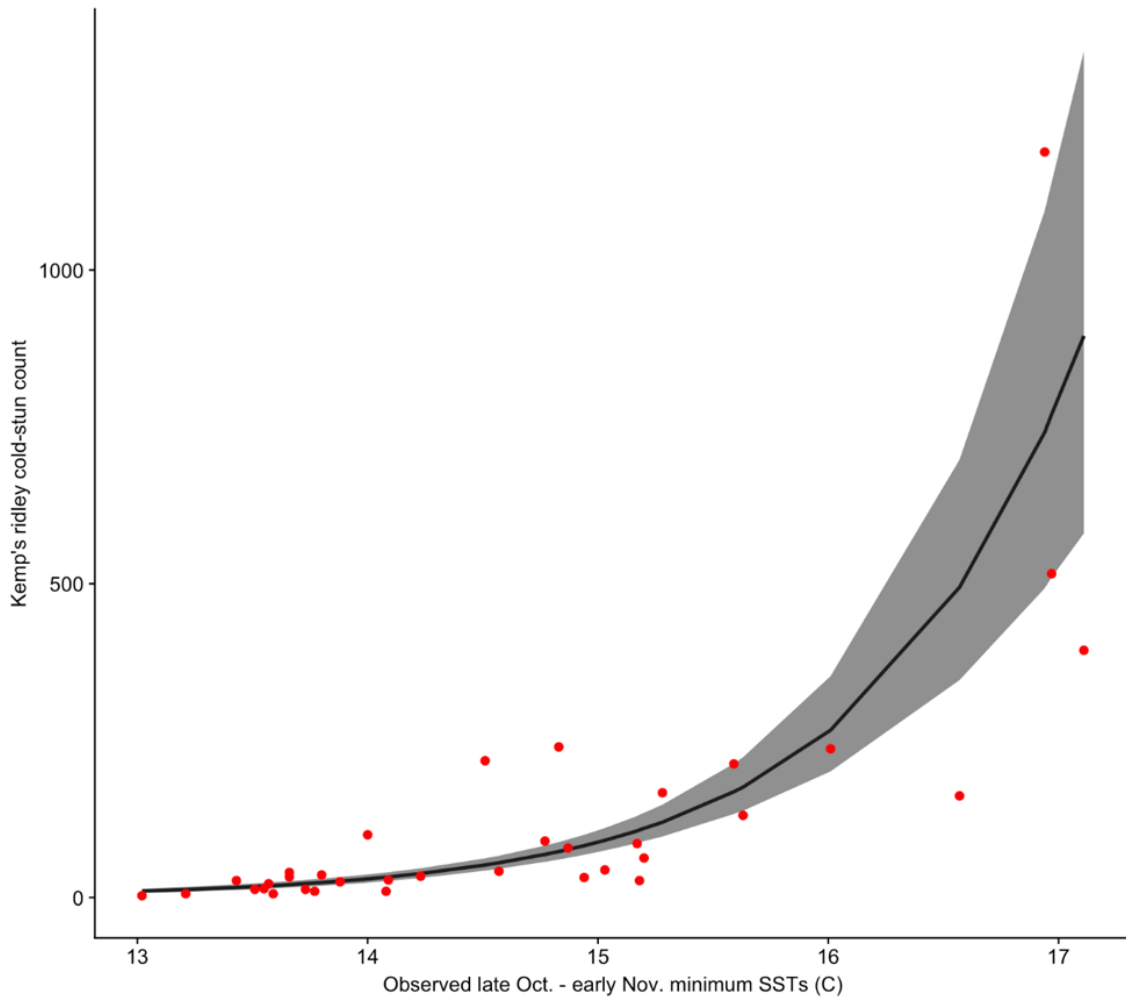
Fig. 15: Kemp's ridley cold-stun count versus minimum of the daily mean SST from late October thru early November. Included are posterior mean fitted values and 95% credible intervals.
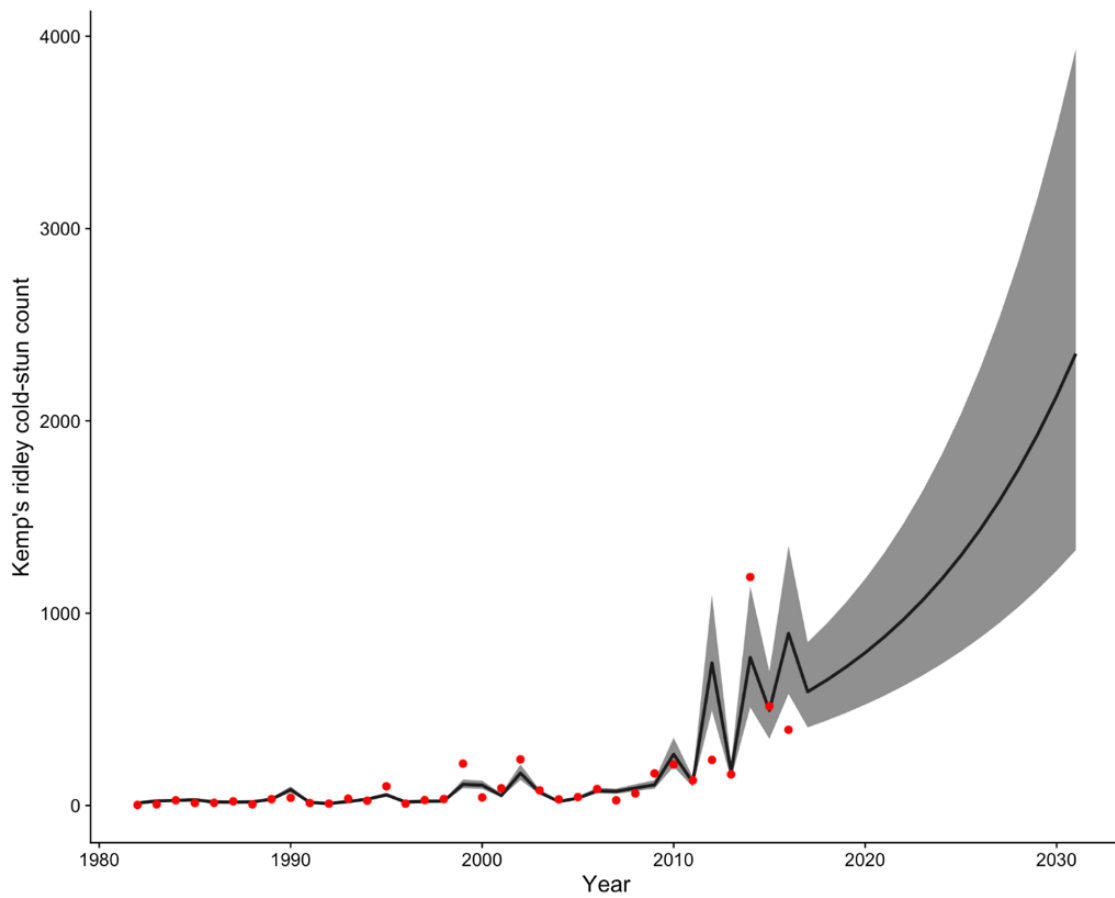
Fig. 16: Observed and predicted Kemp's ridley cold-stun count based on predicted future minimum of the daily mean SST (late October thru early November) within the study area.

CHAPTER 5

SYNTHESIS AND FUTURE RESEARCH DIRECTION

The overarching goal for my dissertation was to fill knowledge gaps surrounding immature sea turtles, a life history phase in which little is known about. Two major immature sea turtle research gaps are, 1) a lack of studies focused on population ecology and habitat use / behavior and, 2) a lack in applied conservation research focused on threats and management (Wildermann et al. 2018). With this dissertation, I provide both fundamental and applied research to address these two major research gaps. This research is necessary for resource managers to provide the best management solutions to mitigate past, current, and future threats. To do so, I conducted research across multiple scales ranging from mitigating direct human-wildlife interactions at the individual level (Chapter 2), to coastal movements and space use at the ecosystem level (Chapter 3), and to large scale climate change impacts at the population level (Chapter 4). Chapter 2 provides management suggestions for a snorkeler-turtle ecotourism venture while examining intra-individual repeatability at the individual level. Chapter 3 provides insight on the movements and connectivity of immature turtles within developmental habitats. Finally, Chapter 4 examines the potential population-level impacts climate change may have on the number of cold stunned immature turtles in the Northwest Atlantic. These findings have important implications for behavioral and spatial ecology as well as sea turtle conservation. Here, I synthesize these findings within a broader context and as contributions to the greater field of sea turtle ecology and conservation. In addition, I provide future research avenues and address any caveats of these studies.

5.1 Behavior and spatial ecology of sea turtles and implications for management and conservation

Conservation biology, focused on mitigating environmental damage arising from direct and indirect anthropogenic perturbations, has been traditionally examined at the population level (Soulè 1985). Whereas the field of conservation behavior, examined at the individual level, has been a relatively new and emerging field (Caro 2007, Berger-Tal et al. 2011). Chapter 2, focused on human-wildlife disturbance encounters, demonstrated turtles exhibit a range of intra-individual level behavior strategies in response to disturbance. Within a population, there are multiple behavior strategies that are determined by evolutionary processes in which behaviors producing the fittest offspring were selected (Krebs and Davies 1997). However, human disturbances may disproportionally affect individuals within a population with different behavior strategies (e.g. bold vs. timid individuals). The fitness value of certain behaviors may be altered, and if negatively impacted, the population of focus may decline, further, evolutionary outcomes may be altered if disturbances are generationally persistent (Norris 2004). Thus, behavior-based management practices, meant to preserve multiple behavior strategies at the individual level, are important when attempting to build resilience into animal populations (Berger-Tal et al. 2011). Not limited to this specific ecotourism venture, the spatial-temporal variation of ecotourism tours, not those involving sea turtles (e.g., whale shark, manatee, whale and dolphin tours), may be critical to avoid disproportionally affecting one behavior type over others (e.g., missed foraging opportunities for timid individuals).

Due to logistical constraints, I was only able to assess one location where snorkeler-turtle ecotourism was occurring. Ideally, this study would be replicated outside Culebra, Puerto Rico to other study sites, where similar snorkeler-turtle ventures exist, such as in Barbados and Hawaii (Landry and Taggart 2010). While I defined personality as repeatable individual differences in a

single context (i.e., disturbance response) that are consistent over time (Rèale et al. 2007), this study would have benefitted at exploring personality across multiple contexts such as exploratory and foraging behaviors. These contexts are difficult to assess with field observations and are often implemented in lab settings, making the approach of my study novel for exploring personality and behavior syndromes in the wild. Future research could include the use of accelerometer loggers to quantify the energy expenditure in response to disturbances as well as help to measure repeatable individual differences across multiple contexts (e.g., exploratory or foraging) over longer periods of time.

Extending animal behaviors to the ecosystem level, Chapter 3 examined the coastal movements and space use of immature green turtles within an important developmental habitat, Culebra, Puerto Rico. Within the coastal ecosystem, the interaction between biological and environmental parameters influenced green turtle movements (or lack of movements). Further, movement behaviors, including habitat selection, dispersal, and spatial distribution shape how individuals and populations interact with one another (Lima and Zollner 1996, Wang and Grimm 2007). Specifically, animal movements associated with maintaining a home range are closely linked with the acquisition of resources (e.g., food, shelter, mating). These movement data are also essential for informing management and conservation strategies (Cooke et al. 2004, Costa et al. 2012, Hays et al. 2016, Hays et al. 2019). For example, sea turtle management and, thus, conservation, has been improved with tracking information ranging from MPA development (Hitipeuw et al. 2007, Mèndez et al. 2013, Dawson et al. 2017) to by-catch reduction (Peckham et al. 2007, Howell et al. 2008, Howell et al. 2015, Casale et al. 2017). While tracking data have led to greater sea turtle protection and informed management, there is little information for the immature life phase which could benefit from fine scale tracking (Wildermann et al. 2018).

Chapter 3 fills important knowledge gaps on immature green turtle ecology with insights on their movements, space use, and their habitats. I determine turtles within Culebra exhibit high site fidelity within the embayments surrounding the island, suggesting resources (e.g., food, shelter) are tightly clustered in this system. In addition to high site fidelity, the differing somatic growth rates across the embayments (Patrício et al. 2014) suggest foraging and shelter habitat quality are different across the embayments. Ultimately, top-down processes related to predation risk (e.g., tiger sharks) may also be driving the heterogenous spatial distribution of immature turtles in Culebra. Examining the spatial-temporal drivers within Manglar Bay, I determined lagoon habitats were favored, followed by seagrass habitat at night. Overall turtles were much less likely to be present in macroalgage habitat. Further, based on model outputs and the observed movement patterns, these data indicate turtles within Culebra utilize lagoon habitats as shelter, an alternative to reef structure around the perimeter of the island.

The protection of habitats used by green turtles have a much greater impact than sea turtle conservation alone. Seagrass communities around the world are major primary producers, and provide shelter, food, and nursery grounds for a wide variety of marine organisms, including green sea turtles (Thayer et al. 1984). Further, seagrass communities are globally threatened (Waycott et al. 2009) and highly vulnerable to human disturbances (Grech et al. 2012). Herbivorous green turtles target specific plots of seagrass (Ogden 1980) and can continually crop these patches for up to a year (Bjorndal 1980). Green turtles typically crop the plant to the base, unlike other herbivores, which typically remove only small portions of plant tissue or uproot plants entirely (Moran and Bjorndal 2005). Turtle cropping eliminates dead growth and epiphytes that have attached to the leaves, preventing harmful algae colonization that creates hypoxic conditions and wasting disease in seagrass communities (Jackson et al. 2001). Further,

cropping promotes new mass growth from young shoots, which increases primary productivity

and nutrient content of seagrass leaves. Hughes (1994) speculated that declines in populations of

herbivores, such as turtles, may cause phase-shifting of benthic ecosystems to communities

dominated by macroalgae. Jackson et al. (2001) suggested that massive dieoffs of seagrass in

Florida Bay and Gulf of Mexico in the 1980's may have been linked with decreases in green

turtle populations. Considering green turtle populations are only a fraction of their historic size

and their importance in maintaining functional coastal ecosystems, continued conservation

strategies are needed for ecosystem and population resilience.

While acoustic telemetry is an effective tool to understand the movement ecology of a

given marine species (Hussey et al. 2015) there are many inherent challenges including tag

retention, receiver positioning, coverage, and detection efficiency, and analytics (Brownscombe

et al. 2019). When receivers are positioned in a tightly overlapping detection area, referred to as

a VEMCO Positioning System (VPS), the approximate true position of a given detection may be

determined via trilateration (Roy et al. 2014). However, VPSs are often limited in spatial extent

due to financial constraints and thus researchers typically rely on passive acoustic telemetry

array designs where a series of receivers are placed in areas of interest and provide presence-only

data. Results may be biased based on receiver placement, for example, if a turtle used a certain

habitat without a receiver in that area, one may incorrectly assume that habitat was not utilized.

Within Culebra, I would have placed additional receivers further away from the embayments,

particularly Manglar Bay, to definitively quantify whether turtles use those outer areas for shelter

or not. Ideally, these issues would largely be resolved by using a receiver grid layout rather than

selecting receiver positions by a point of interest method (Brownscombe et al. 2019). Further,

each receiver varies by detection range (e.g., 1 m – 1 km) and efficiency depending on

surrounding environmental characteristics (Kessel et al. 2014). Varying detection coverage and efficiency were not formally incorporated into analyses, while important, it was ultimately impossible with my chosen analyses. I attempted to mitigate these issues by aggregating receivers and detections by either space or time. While difficult to formally incorporate, there are methods being developed to incorporate detection efficiency (Brownscombe et al. In Review). Further, acoustic tag retention in Culebra was limited, detection data and a mark-and-recapture study in Culebra indicated turtles shed transmitters typically in several months' time. If these transmitters fell off within detection range of a receiver or multiple receivers, detection files often had hundreds to thousands of false-positive detections. Great care must be taken when examining detections due to false-positive detections. Tag retention may be improved by surgical implantation or attaching the transmitter to the underside of the flipper, similar to metal mark-and-recapture flipper tags. Future studies would benefit from careful receiver positioning, incorporation of detection coverages and efficiency, and improved tagging methodologies to improve tag retention. Further, the integration of accelerometer and depth loggers in combination with acoustic telemetry transmitters would provide greater insight into immature turtle space use, habitat utilization, and of the energetic states / behavior profiles (e.g., foraging vs. resting) associated with the seascape.

Current and future global climate change impacts may be one of the largest threats to animal populations (McCarty 2001, Garcia et al. 2014). Warmer temperatures and sea level rise are expected to decrease sea turtle hatchling success and available nesting habitats, and in-addition, skew sex ratios (Butt et al. 2016, Laloë et al. 2016). In Chapter 4, I demonstrate the increasing Gulf of Maine (GOM) sea surface temperatures (SSTs), due to climate change, are linked with the increasing annual Kemp's ridley cold stunning counts in the Northwest Atlantic.

One possible reason for the increased cold-stunned turtles may be because Kemp's ridley northerly neritic developmental grounds have shifted northward. As immature turtles migrate southward in the fall they are now more likely intercepted by Cape Cod Bay and subsequently exposed to cold temperatures and become cold stunned. Such range or phenology shifts, resulting from increased SSTs, are well documented for other GOM species (see Staudinger et al. 2019). Considering sea turtles are ectotherms and immature sea turtles have been shown to select habitats based on thermal constraints (Mansfield et al. 2014), it is not surprising immature Kemp's ridleys would shift north with warmer GOM SSTs.

In Chapter 4, using the Bayesian count model and forecasted SST projections, I predicted more than 2,300 Kemp's ridley turtles may cold-stun annually by 2031. At the population level, this may only be a fraction of the overall Kemp's ridley population, however, considering anthropogenic threats are increasing, I argue it is important for the continued rehabilitation of cold-stunned turtles. This is particularly important for Kemp's ridleys considering the slowing trend of nesting Kemp's ridley females in the Gulf of Mexico. In order to protect this critically endangered species management strategies must be proactive to build resilience into the population. Future research should focus on determining when immature Kemp's ridely turtle immigrate into and emigrate out of coastal waters of the northeastern U.S. and if they migrate back into the Gulf of Mexico to breed as adults. While this study does help to explain this upward trend in cold-stun counts, it could be improved by incorporating small and large scale oceanic processes such as eddies, currents, and thermoclines. In addition, our model does not integrate how many hatchlings pass the Florida straits and onto the Atlantic coast annually, I used the lagged hatchling indices as a proxy which is, currently, the most accurate indicator available.

5.2 Analytical advancements

In this dissertation, I applied novel analytical methods to address research gaps related to immature sea turtle ecology and conservation. These advanced methodologies included multivariate and Bayesian statistics, network analysis, and machine learning algorithms. In Chapter 2, principal component analysis, a multivariate tool to reduce variable dimensionality, was used to identify two distinct immature green turtle personality types, 'bold' and 'timid'. In Chapter 3, I used network analysis to examine regional connectivity and community structure among tagged immature green turtles. In addition, machine learning algorithms determined the optimal scale to evaluate habitat kernel densities. Selected habitats and their kernel densities were used in combination with a Bayesian presence-absence model to determine drivers of green turtle space use within Manglar Bay. This Bayesian presence-absence model also incorporated spatial and temporal autocorrelation structures. In Chapter 4, machine learning algorithms helped to identify the most important variables to model annual cold-stunned Kemp's ridley counts. The model was implemented within a Bayesian framework which allowed for measurement error to be included at the covariate level.

The collection of statistical tools used throughout this dissertation are not limited to sea turtle ecological studies. While these methods are complex, these type of analyses (e.g., multivariate, machine learning, Bayesian) have improved predictive power, ability to meet assumptions that are often violated, and, ultimately, a greater ability to explain the real underlying ecological processes than common analytical methods. As the field of ecology continues to advance, along with technological advances (e.g., the use of biologgers), statistical tools are evolving away from purely descriptive statistics to help answer questions at the individual, ecosystem, and population levels.

5.3 Summary

Overall, this dissertation has advanced our understanding of fundamental ecology and applied management of sea turtles and their habitats. To effectively protect and restore these threatened sea turtle populations, I argue sea turtle ecology and conservation must be examined at multiple scales. Here, within this dissertation, I examined human-wildlife interactions at the individual level, to coastal movements and space use at the ecosystem level, and to large scale climate change impacts at the population level. Each chapter provides direct management applications to help mitigate anthropogenic disturbances and to improve sea turtle conservation. These management suggestions include modifying ecotourism regulations, protecting coastal habitats, and for the recovery and rehabilitation of cold-stunned turtles. While these data and findings help to fill some of the many knowledge gaps in the immature sea turtle life history phase, they also contribute to the greater field of ecology. For example, these studies range from examining animal behavior respectabilities and personality in the wild, to drivers of animal movement, and to potential impacts of climate change. Throughout these chapters, novel statistical techniques, described in detail, were also used to improve our understanding of underlying ecological processes. These methods (e.g., multivariate, machine learning, Bayesian statistics) and their advantages over traditional analyses are not limited to questions regarding sea turtles but can also help to answer many other ecological questions. Ultimately, this dissertation fills fundamental and applied knowledge gaps and advocates to preserve sea turtle behaviors, habitats, and the individuals themselves to build population resiliency in an ever-changing world.

APPENDIX A

SUPPLEMENTAL: MOVEMENTS, CONNECTIVITY, AND SPACE USE OF IMMATURE

GREEN TURTLES WITHIN COASTAL HABITATS, CULEBRA, PUERTO RICO:

IMPLICATIONS FOR CONSERVATION

Table A.4 Tagging, detection, and network analysis data for the 26 transmitters deployed on 21 green turtles in Culebra, Puerto Rico.

ID	Tag	Date	SCL (cm)	Capture Location	Detection Number	Days Detected	Days at Liberty	Residency Index	Station Number	Paths	Network Density	Average Path Length	Mean Betweeness
TC01	26018	2013-12	43	Tortuga	1174	91	93	0.98	1	1	NA	NA	NA
TC02	26017	2013-12	47	Tortuga	1222	79	80	0.99	1	1	NA	NA	NA
TC03	26016	2013-12	46	Tortuga	1386	97	135	0.72	1	1	NA	NA	NA
TC04	26015	2013-12	38	Tortuga	107351	568	600	0.95	1	1	NA	NA	NA
TC05	26014	2013-12	42	Tortuga	2662	70	71	0.99	1	1	NA	NA	NA
TC06	26013	2013-12	50	Tortuga	6179	147	147	1	1	1	NA	NA	NA
TC07	26011	2013-12	47	Tortuga	1826	76	84	0.9	1	1	NA	NA	NA
TC08	26010	2013-12	56	Tortuga	10247	237	443	0.53	1	1	NA	NA	NA
TC09	26012	2014-03	58	Tortuga	3740	138	139	0.99	3	6	1	1.5	1
TC10	26026	2014-03	58	Tortuga	1953	96	420	0.23	2	4	2	1	0
TM01	30394	2013-03	44	Manglar	599	53	89	0.6	4	10	0.83	1.58	2.25
TM02	30396	2013-03	58	Manglar	11013	162	163	0.99	8	28	0.5	2.07	10.75
TM02	26002	2013-12	62	Manglar	26710	77	528	0.15	16	76	0.32	2.34	30.93
TM03	30398	2013-03	42	Manglar	756	71	100	0.71	6	25	0.83	1.37	3.58
TM03	26022	2013-12	49	Manglar	10026	105	105	1	11	76	0.69	1.5	13.34
TM05	30401	2013-03	46	Manglar	1831	66	109	0.61	4	11	0.96	1.33	1.5
TM06	30402	2013-03	44	Manglar	404	39	90	0.43	6	17	0.57	1.83	4.17
TM06	26023	2014-03	52	Manglar	2473	48	48	1	9	34	0.47	1.79	14.67
TM07	30431	2013-03	54	Manglar	14147	102	106	0.96	9	26	0.36	2.35	12.44
TM08	28754	2013-03	67	Manglar	2621	51	61	0.84	8	22	0.39	2.48	11.88
TM09	28757	2013-03	70	Manglar	8693	96	114	0.84	7	34	0.81	1.36	6.86
TM10	26003	2013-12	41	Manglar	1146	25	25	1	7	28	0.67	1.6	8.14
TM11	26004	2013-12	48	Manglar	5126	80	81	0.99	7	32	0.76	1.43	6.29
TM12	26005	2013-12	56	Manglar	8258	81	81	1	8	34	0.61	1.71	9.38
TM12	26031	2014-03	57	Manglar	4883	55	55	1	9	36	0.5	1.76	13.11
TM13	26006	2013-12	40	Manglar	9788	64	362	0.18	12	54	0.41	2.15	19.17
TM13	26029	2014-03	46	Manglar	6697	86	94	0.91	9	40	0.56	1.79	9.94
TM14	26007	2013-12	45	Manglar	3599	68	74	0.92	10	49	0.54	1.68	14.33
TM15	26008	2013-12	56	Manglar	9116	57	57	1	7	37	0.88	1.29	5.86
TM16	26009	2013-12	53	Manglar	16001	96	108	0.89	9	50	0.69	1.53	8.61
TM17	26019	2013-12	54	Manglar	143492	290	291	1	13	73	0.47	1.88	18.69
TM18	26020	2013-12	53	Manglar	11706	74	135	0.55	6	28	0.93	1.27	5.5
TM19	26021	2013-12	50	Manglar	23309	212	441	0.48	9	52	0.72	1.43	9
TM20	26024	2013-12	63	Manglar	16694	132	276	0.48	12	66	0.5	1.64	13.29
TM21	26025	2013-12	45	Manglar	29936	79	78	1.01	13	88	0.56	1.57	15.55

| TM22 | 26030 | 2014-03 | 42 | Manglar | 22087 | 129 | 132 | 0.98 | 8 | 32 | 0.57 | 1.66 | 10.5 |

Table A.5 ANCOVA results presented, ANCOVA used to test the in difference in detection number, days at liberty, residency index, station count, number of paths between size (SCL) and capture location (Manglar Bay and Tortuga Bay). In addition, linear model results presented below, which were used to test for an effect between size and network density, APL, and Bi mean for only Manglar Bay individuals, Tortuga Bay did not have extensive detection coverage to calculate meaningful values. Significant results ($p < 0.5$) are indicated with an asterisk.

Metric	Factor	df	F	p
Detection number				
	SCL	1,33	0.07	0.79
	Capture location	1,33	0.03	0.87
Days detected				
	SCL	1,33	0.34	0.56
	Capture location	1,33	3.52	0.07
Days at liberty				
	SCL	1,33	0.27	0.61
	Capture location	1,33	2.17	0.15
Residency index				
	SCL	1,33	0.46	0.50
	Capture location	1,33	0.08	0.78
Station count				
	SCL	1,33	7.53	0.01*
	Capture location	1,33	62.73	< 0.001 *
Paths				
	SCL	1,33	2.70	0.11
	Capture location	1,33	31.26	< 0.001 *
Network density				
	SCL	1,24	1.11	0.30
Average path length				
	SCL	1,24	1.72	0.20
Mean betweeness				
	SCL	1,24	1.56	0.22
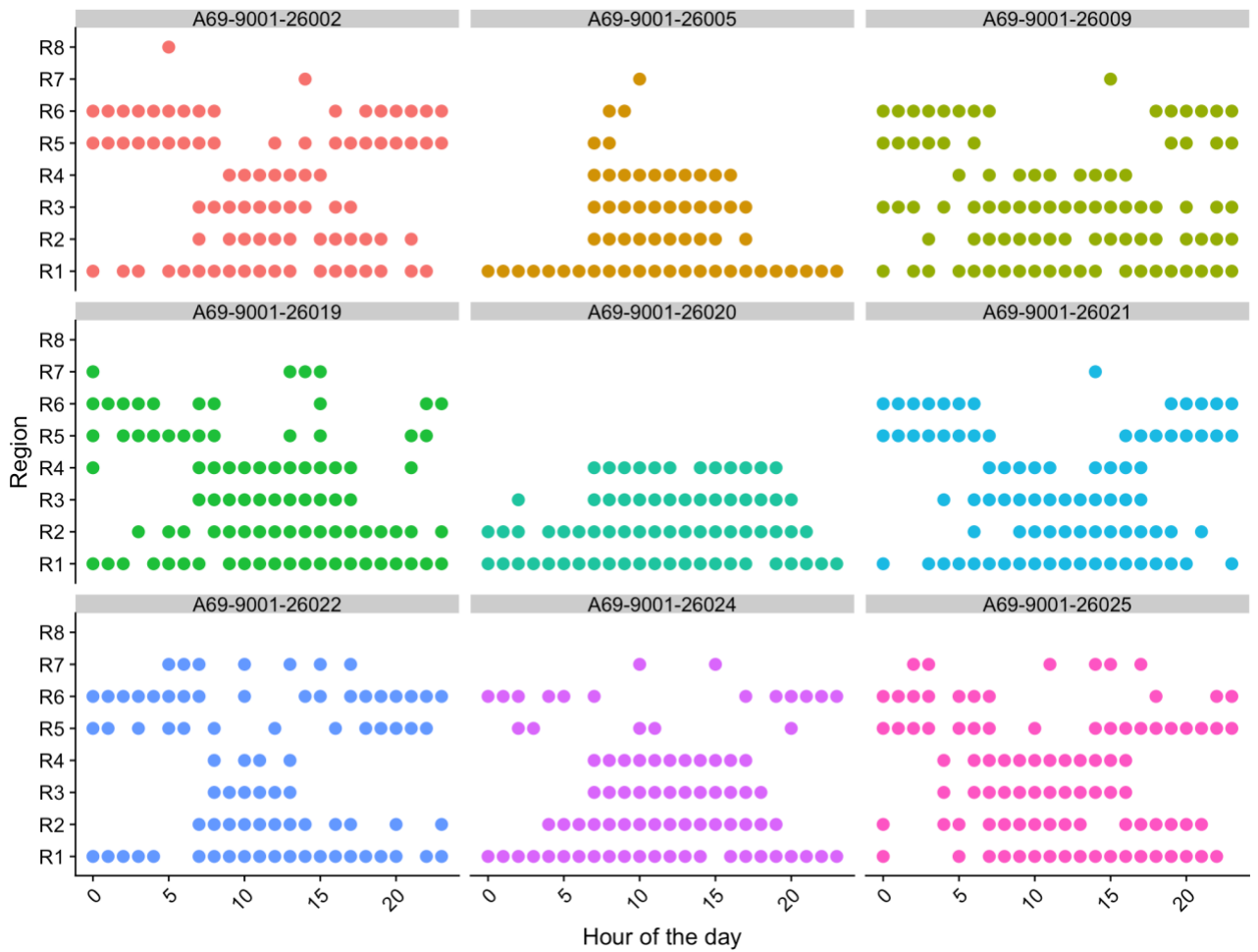
Fig. A.17: Individual turtle detections at the hour level across the Manglar Bay receiver aggregate regions. Only the regions at the hour level with the maximum observed detections are shown.
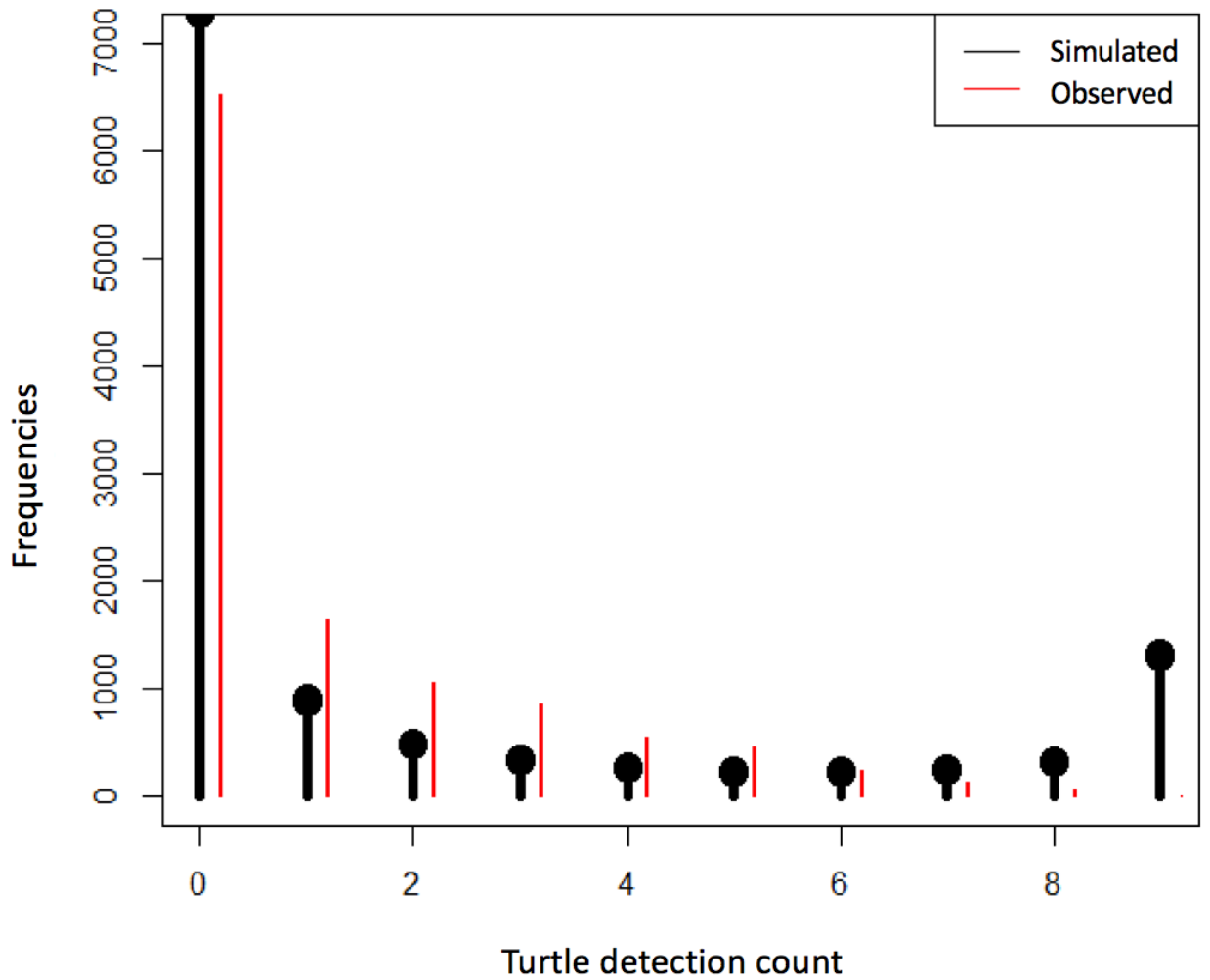
Fig. A.18: Observed turtle counts (red) versus simulated turtle counts (black) via our final Bayesian presence and absence binomial model of nine turtles within Manglar Bay across 60 days. The generated simulated data was derived from 1,000 simulations of the posterior distributions of our model's regression parameters.
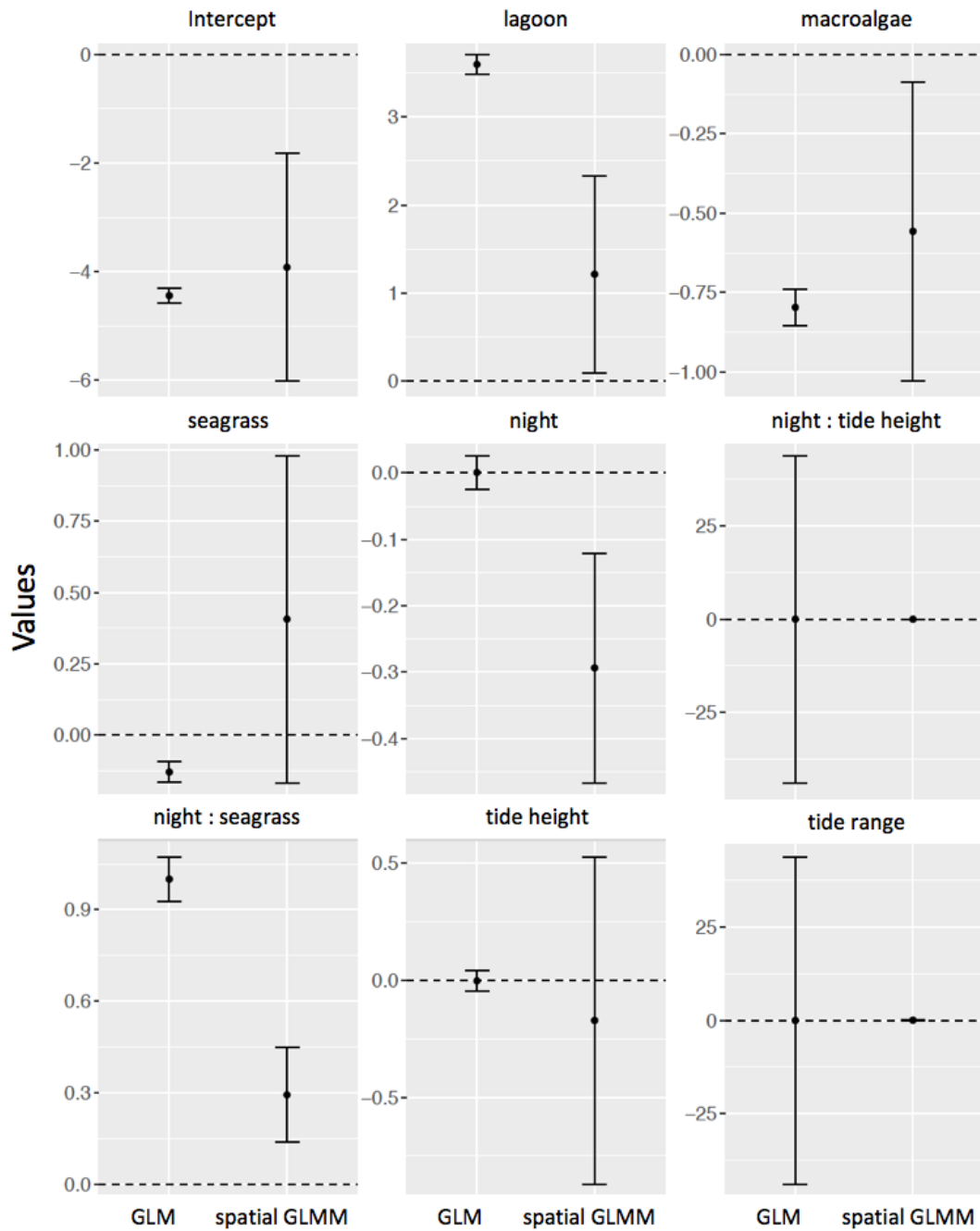
Fig. A.19: Using the results from final Bayesian presence and absence binomial model of nine turtles within Manglar Bay across 60 days, both GLM and GLMM with and without the spatial correlation structure is plotted.

a)
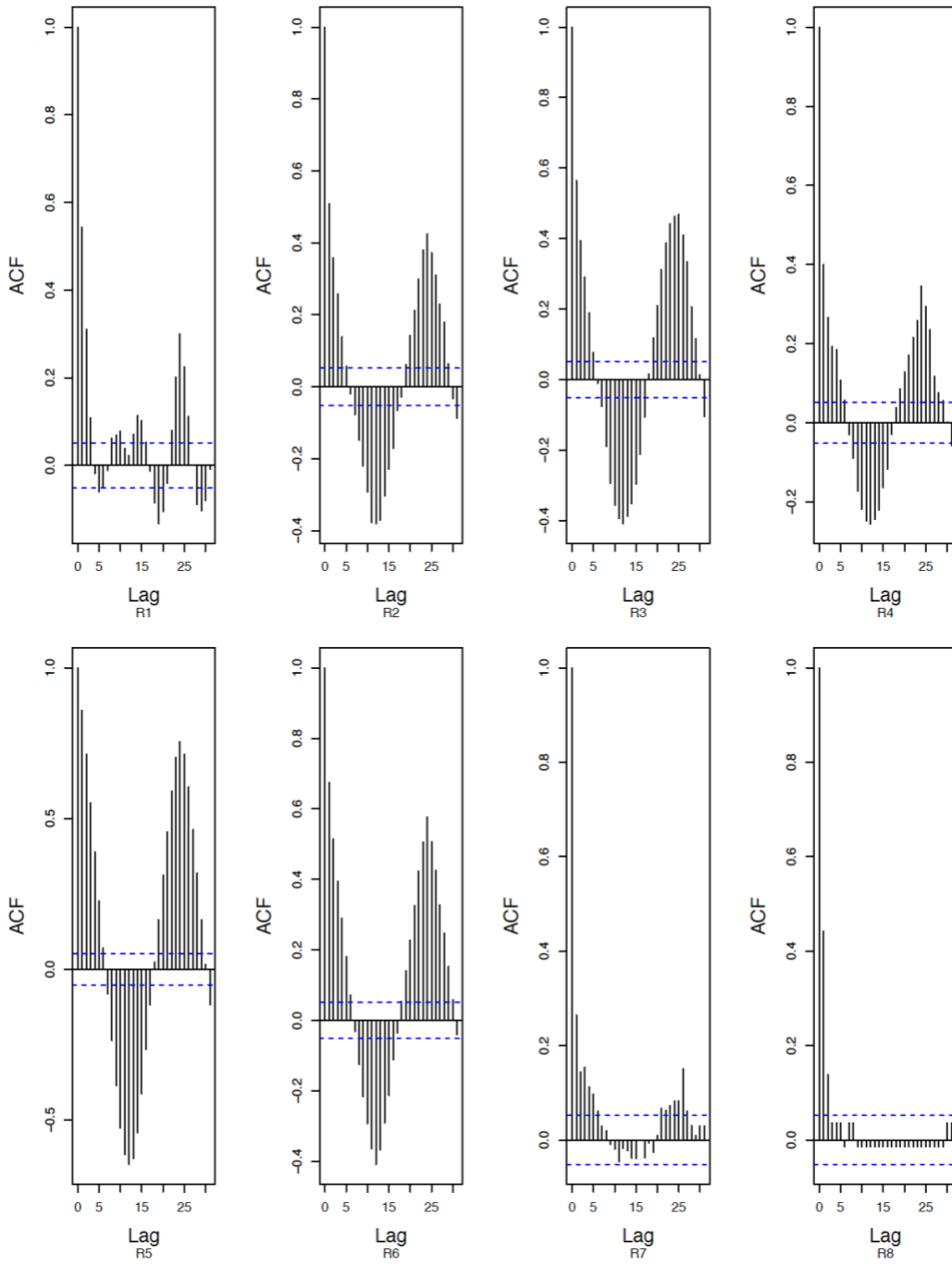
b)
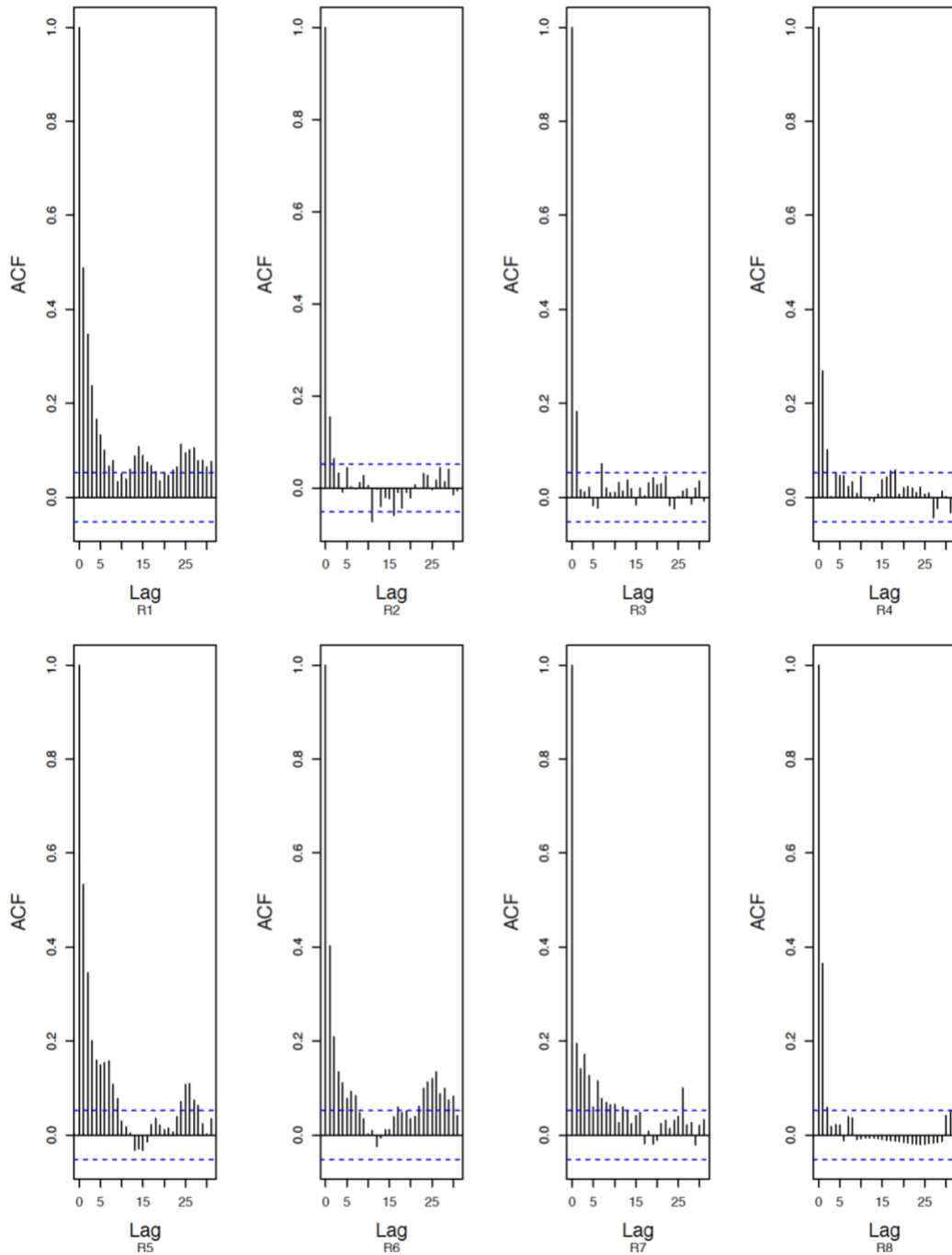
Fig. A.20: Autocorrelation function plots: a) derived from the raw data at each region (as indicated by R#) and b) from the final Bayesian presence and absence binomial model of nine turtles within Manglar Bay across 60 days (bottom) at each region (as indicated by R#) using three dependency structures as random walk smoothers, including: tide height, hour of the day, and study day.

APPENDIX B

SUPPLEMENTAL: WARMING SEAS INCREASE COLD-STUNNING EVENTS FOR

KEMP'S RIDLEY SEA TURTLES IN THE NORTHWEST ATLANTIC

Table B.6 Annual Kemp's ridley cold-stun stranding count (1982–2016) from Cape Cod, Massachusetts, USA.Sea turtle cold-stunning data provided by the Sea Turtle Stranding and Salvage Network.

Year	Turtle cold-stun stranding count
1982	3
1983	6
1984	27
1985	13
1986	14
1987	22
1988	6
1989	33
1990	40
1991	13
1992	10
1993	36
1994	25
1995	100
1996	10
1997	28
1998	34
1999	218
2000	42
2001	90
2002	240
2003	79
2004	32
2005	44
2006	86
2007	27
2008	63
2009	167
2010	213
2011	131
2012	237
2013	162
2014	1188
2015	516
2016	394

Table B.7Annual number of hatchlings released (1966–2018) from the Tamaulipas index beaches (Rancho Nuevo, Playa Dos-Barra Del Tordo, Barra Ostionales-Tepehuajes).Hatchling data pre-2015 provided by NMFS and USFWS 2015, hatchling data from 2015 and after provided by personal communication Peña.

Year	Hatchling count
1966	30555
1967	25305
1968	15750
1969	29820
1970	32970
1971	13755
1972	15330
1973	24675
1974	24675
1975	11100
1976	36100
1977	30100
1978	48009
1979	63996
1980	37378
1981	53282
1982	48007
1983	32921
1984	58124
1985	51033
1986	48818
1987	44634
1988	62218
1989	66802
1990	74339
1991	79749
1992	92116
1993	84605
1994	107687
1995	120038
1996	114842
1997	141770
1998	167168
1999	211355
2000	365479
2001	291268
2002	357313
2003	433719

2004	421684
2005	569963
2006	715002
2007	902290
2008	806079
2009	1025027
2010	663614
2011	630182
2012	927002
2013	688792
2014	519273
2015	613495
2016	769430
2017	887382
2018	729933

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