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Ecological and Oceanographic Influences on Leatherback Turtle Behavior and Scyphozoan Jellyfish Distributions in the Gulf of Mexico

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ECOLOGICAL AND OCEANOGRAPHIC INFLUENCES ON LEATHERBACK TURTLE BEHAVIOR AND SCYPHOZOAN JELLYFISH DISTRIBUTIONS IN THE GULF OF MEXICO

by

Katrina T. Aleksa

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ABSTRACT

ECOLOGICAL AND OCEANOGRAPHIC INFLUENCES ON LEATHERBACK TURTLE BEHAVIOR AND SCYPHOZOAN JELLYFISH DISTRIBUTIONS IN THE GULF OF MEXICO

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Leatherback turtles (*Dermochelys coriacea*) are a wide-ranging, oceanic species that feed exclusively on gelatinous zooplankton. Leatherback have been spotted in the Gulf of Mexico (GoM) for several decades and consistently had a high level of interactions with longline fisheries. However, no quantitative studies have been performed to address the spatiotemporal distribution of these turtles in the GoM. This research determines 1) leatherback movements and high-use areas in the GoM, 2) their association with oceanographic features, 3) the distribution and density of two abundant medusae in the northern GoM and any association with biophysical parameters, and 4) the body composition and energy density of a select leatherback prey, *Drymonema larsoni*.

Satellite telemetry data from 10 nesting and 6 in-water tagged leatherbacks were analyzed using a switching state-space model (SSSM) and a kernel density estimation to identify high-use areas. The SSSM revealed that foraging behavior was dominant in GoM and two high-use areas were present, one in the northeast GoM between Louisiana and the Florida panhandle, and the second in the southwest GoM along the Yucatán shelf waters in the Campeche Bay, Mexico. The leatherback positioning data were compared to physical oceanographic features (sea surface height anomalies, temperature and salinity fronts, ocean currents, divergence and convergence) to investigate their potential influence on turtle movement and space use. The turtle observations were found to be positively associated with sea surface lows and salinity fronts. Turtles also benefitted from their relationship with ocean currents more during migration than foraging behaviors.

The distribution and density of scyphozoan species (*Chrysaora quinquecirrha* and *Aurelia* spp.), potential leatherback prey items, were analyzed with generalized additive models (GAM) to determine the biophysical parameters that are associated with collection of these jellyfish in the northern GoM. These species were found to be associated with salinity, surface currents, temperature, chlorophyll *a* concentrations, and distance from shore. Visual observations of leatherback foraging in the northern GoM suggested a preferred prey item of *Drymonema larsoni*. This elusive species has been rarely studied, with only a few reports on its predation of *Aurelia* spp. A database search was conducted to determine the occurrence of *D. larsoni* in the northern GoM and how it compared to the biomass of *Aurelia* spp. *D. larsoni* specimens were also collected and processed to determine body composition and energy density. A high biomass of *Aurelia* spp. over consecutive years was linked to the presence of *D. larsoni* in the northern GoM. Sexually mature *D. larsoni* had a mean energy density of 0.19 kJ g WM^{-1} for the whole organism, and gonadal tissue had the highest amount of energy.

Overall, the research suggests that the GoM is a foraging destination for leatherback turtles with two high-use areas. The location and density of jellyfish prey coincided with the identified leatherback foraging, signifying support for sustained foraging efforts. The selective prey item, *D. larsoni*, has a similar energy density to selective prey in other known foraging locations, revealing the potential for high energy consumption in the GoM. Lastly, leatherback movements were associated with parameters that were descriptive of jellyfish density, suggesting space use was linked to the search for prey. These findings can be utilized for the conservation and management of leatherbacks in these waters.

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LIST OF ABBREVIATIONS

GoM	Gulf of Mexico
nGoM	northern Gulf of Mexico
SSSM	switching state-space model
ARS	area restricted search
GAM	generalized additive model
IUCN	International Union for Conservation of Nature and Natural Resources
NOAA	National Oceanic and Atmospheric Administration
STC	Sea Turtle Conservancy

CHAPTER I – General Introduction

Large charismatic megafauna are often what ignites the public's interest in the ocean. These majestic creatures invoke a wide range of emotions in humans from fear, to caring, to inspiration. This emotional tie drives the conviction to maintain and protect these species and their habitat. However, different goals exist when dealing with our desire for convenience in the uses of resources, both natural and manmade, and our desire to conserve the environment. In order to truly understand the anthropogenic pressures that influence marine organisms, we must uncover basic ecological information that is still lacking for so many of these threatened species.

Large, long-lived marine animals generally have extensive migration patterns which makes them hard to observe and requires the need for technological monitoring. Advancements in technology over the past decades has provided tools (satellite tags, hydroacoustic sampling, in situ imaging, and remote sensing data) that can measure GPS locations, dive depths, prey fields, and physical oceanographic features. Combining these datasets has led to an increase in the understanding of migratory pathways, foraging/ reproductive locations and behaviors, specific prey items, and behavioral influences of oceanographic features (Croll et al. 1998, Block et al. 2011). However, large gaps still exist in the data, both species wide and among inhabited locations. More studies have been conducted on marine species that exit the water (seals, sea lions, penguins, sea turtles), because the animals are more accessible for deployment of satellite tags. Certain genders or stages of life (e.g., mating, birthing, and nesting) are also easier to study due to proximity to coastlines and abundant numbers of individuals. A comprehensive approach that represents a demographically diverse sampling is required to describe important ecological dynamics that are directly related to the conservation of a species. Conversely, organisms that remain in the open ocean and have little to no contact with the coast are more elusive to sampling and consistent monitoring. Studying rare species leads to difficulties with spatial sampling and detectability; however, borrowing information or sharing data as well as using state variables like occupancy and species richness can provide reasonable inferences (MacKenzie et al. 2005). Therefore, data on only a few specimens can provide information on unknown behaviors and movements and provide insight to effects of rare species on the environment (Lyons et al. 2005). Ecological information about life histories helps to identify potential anthropogenic stressors, both strengthening our ability to manage and conserve vulnerable marine species.

1.1 Leatherbacks, Jellyfish, and the Gulf of Mexico

Leatherback turtles (*Dermochelys coriacea*) are the largest species of sea turtle and have the broadest distribution of any living reptile on the planet, yet population numbers are regionally variable due to human interactions. Leatherbacks are listed as an International Union for Conservation of Nature and Natural Resources (IUCN) vulnerable species and an endangered species under the U.S. Endangered Species Act. However, the threat level varies among oceanic basins and subpopulations (Wallace et al. 2013). For example, in the Pacific Ocean leatherbacks are critically endangered and continuing to decline, due to continued harvesting of adults and eggs, incidental capture/bycatch, and climate-induced changes to habitat and prey availability (Jones et al. 2012). Conversely, the leatherback population in the Northwestern Atlantic Ocean is recovering due to stable foraging habitats and safe guards established to protect nesting grounds (Bailey et al. 2012).

Similar to other long-lived, migratory marine animals, adult leatherbacks routinely return to the tropical nesting grounds during the summer and then migrate to distant foraging grounds using a number of behavioral and physiological adaptations. Individuals can travel up to tens of thousands of kilometers across ocean basins to reach successful foraging or nesting grounds within a single year (Eckert 2006, Eckert et al. 2012). Natal homing is common among all sea turtles, but due to the leatherbacks long oceanic migrations where landmarks are scarce, if present at all, advanced navigational skills enable them to locate productive foraging/mating grounds after traversing an ocean basin in seemingly straight lines (Lohmann et al. 1999). Such advanced navigational mechanisms include detecting and following the Earth’s magnetic field (Lohmann et al. 1999, Lohmann et al. 2008), detection of chemical cues (Lohmann et al. 2008, Endres and Lohmann 2012), and other sensory cues that allow them to follow oceanographic features such as discontinuities or oceanic fronts (Luschi et al. 2003, Eckert 2006, Benson et al. 2007). Foraging regions are located between tropical and temperate latitudes. As cold-blooded animals, leatherbacks are able to survive in temperate waters due to their thick layers of insulating fat, countercurrent circulatory systems, increased metabolic activity (maintaining a higher internal body temperature), and gigantothermy (reviewed by Eckert et al. 2012). In order to maintain these and other basic physiological demands (i.e. respiration, somatic growth), leatherbacks must be able to reliably and efficiently locate and forage on a sufficient amount of prey.

Leatherback turtle diets are entirely comprised of gelatinous zooplankton (Bjorndal 1997, Dodge et al. 2011), specifically cnidarian medusae and ctenophores, here after referred to as jellyfish, and to a lesser extent salps and pyrosomes. Jellyfish typically are considered a low energy, low nutrient food source, but energy content varies among species and tissue type. Water content in jellyfish commonly preyed upon by leatherbacks is ~96%, with protein making up the greatest percent of the organic material (~12.8%) followed by carbohydrates (~0.83%), and lipids (~0.32%; Doyle et al. 2007). Within a medusa, the oral arms contain the largest amount of nutrition, followed by the gonads and the bell (Doyle et al. 2007). For example, in the lion's mane jellyfish (*Cyanea capillata*) the mean gross energy density was found to be 7.81 KJ g Dry Mass (DM)$^{-1}$ for the oral arms, 7.19 KJ g DM^{-1} for the gonads and 2.16 KJ g DM^{-1} for the bell (Doyle et al. 2007). It has been suggested that 26% of the turtle's body mass must be consumed daily to meet their metabolic requirements (Jones et al. 2012). For an average adult leatherback (250-450 kg), this translates to 65-117 kg of jellyfish per day, leading to a lifetime consumptions of 1014 tons (Jones et al. 2012). Interestingly, leatherback hatchlings have been observed to eat 100% of their body mass per day, and adults have been reported consuming 50% or greater of their body mass per day (Heaslip et al. 2012). In the foraging grounds off Nova Scotia, the daily energy intake for a single adult leatherback feeding on *C. capillata* is estimated to be 66,018 kJ, leading to a daily consumption of 261 medusae, or 330kg (Heaslip et al. 2012). This high consumption rate in the foraging ground is nearly three times the basal metabolic energy requirement. These productive areas have been shown to allow for a ~33% increase in mass of turtles before they begin the southward migration back to tropical nesting locations (Heaslip et al. 2012). Therefore, locating these prey abundant foraging areas is critical to the survival of a leatherback turtle and the sustainability of the species itself.

Aggregations of jellyfish are often the result of physical oceanographic features. Jellyfish are typically found along convergence zones (fronts, upwelling, eddies), discontinuities (thermoclines, pycnoclines, nutriclines, haloclines), and gradients (hydrostatic pressure changes, turbulence; Graham et al. 2001, McClatchie et al. 2012, Luo et al. 2014, Greer et al. 2015). Certain species of jellyfish have the ability to form blooms. The formation of a bloom can be classified as a 'true bloom' by which jellyfish are increasing in biomass due to rapid population growth or an 'apparent bloom' where physical oceanic features concentrate the current population (Graham et al. 2001). Aggregations and blooms of jellyfish can be problematic to humans (i.e. clog fishing nets and industrial saltwater intakes, damage aquaculture stock, and detrimental to tourism), but to predators they provide valuable hot spots of foraging.

Located in the southeast region of North America, the Gulf of Mexico (GoM) spans approximately 600,000 miles^2 (1.5 million km^2), making it the ninth largest body of water in the world (Gulf of Mexico Program (GMP) 2014; www.epa.gov/gulfofmexico). Around sixty percent of the Gulf's water volume is located on the board intertidal and continental shelf regions, which represent depths up to 200m (GMP 2014). Fluvial input into the Gulf is massive, with over 60% of the continental United States draining into the basin through 33 river systems and 207 estuaries, as well as large contributions from Mexico and Cuba (GMP 2014). Strong nutrient input from the freshwater supply combined with diverse physical interactions and processes, including mixing water masses, shelf break circulations, eddy dynamics and the Loop Current, help to create a nutrient-rich, productive marine ecosystem. This supports a biodiverse marine environment with approximately 15,400 different species inhabiting the waters (Felder et al. 2009). Included in this list are five species of sea turtles and approximately 117 species of Medusozoans (Segura-Puertas et al. 2009, Jones and Seminoff 2013). This productive region is ideal for leatherback foraging because it can support a large biomass of gelatinous zooplankton. Within the Gulf of Mexico, potential jellyfish prey items that could support a leatherback population include several *Aurelia* spp., *Chrysaora quinquecirrha*, *Cyanea capillata*, *Drymonema larsoni*, *Pelagia noctiluca*, *Phyllorhiza punctata*, *Rhopilema verrilli,* and *Stomolophus meleagris* (Segura-Puertas et al. 2009). Unfortunately, data are lacking on the distribution, annual abundance, and ecology of the majority of these species, which limits investigations on predator-prey interactions.

This abundant biodiversity and productivity has led to an industrious exploitation of resources that can have adverse effects on the ecosystem. The GoM fisheries provide more shellfish, shrimp, and finfish annually than the combined efforts all along the eastern coast of the United States. Four of the Gulf’s fishing ports are in the top seven in the nation by weight of fishes landed, and eight of the fishing ports make the nation’s top twenty list for revenue (GMP 2014). Aside from direct fishing pressures, the biota are also taxed with habitat loss and pollution, such as oil spills and debris. The large megafauna are also faced with detrimental impacts of shipping traffic, boat strikes, and fisheries bycatch. These anthropogenic threats can be detrimental if left unchecked or are improperly managed.

1.2 Research Objectives

Sightings of leatherbacks in the GoM have occurred for decades, though no systemic ecological studies have been conducted on distribution or behavior, and the majority of information gathered from bycatch studies. Leatherbacks found in the GoM are from Caribbean nesting beaches located on the shores of Costa Rica, Panama, Trinidad, and French Guiana (Evans et al. 2007, Stewart et al. 2016), with the GoM utilized by a greater proportion of the nesting population in Costa Rica and Panama (Stewart et al. 2016). Bycatch records for the U.S. Atlantic coast show that the GoM has been regularly responsible for the highest number of interactions between leatherbacks and longline fisheries (Garrison and Stokes 2014). As studies have identified that these leatherbacks are from nesting stocks outside of the GoM, it would be presumed that the turtles are using this environment for post-nesting foraging behavior. Identifying the turtles' foraging landscape is crucial to understanding their ecology and protecting the species. Knowledge of the temporal and spatial distribution, turtle behavior, as well as food availability and selection will provide a better understanding of how the leatherbacks are utilizing the environment, and can promote successful management of the species alongside the extensive commercial fisheries.

This research represents the first quantitative look at leatherback movement and behavior in the GoM and their connection with potential prey species. Specific focus of the dissertation will address 1) Is foraging the main behavior expressed by leatherbacks in the GoM? 2) Do leatherbacks use the GoM non-uniformly in both space and time? 3) Are leatherback movements associated with ocean circulation and frontal features? 4) Will biological and physical oceanographic parameters be able to describe the distribution and density of scyphozoan jellyfish in the GoM? 5) Which parameters are most descriptive? 6) What is the body composition and energy density of a selected leatherback prey item, *Drymonema larsoni*? and 7) Would a difference in energy density explain help explain selective predation? Representing the first assessment of leatherback foraging within the Gulf of Mexico, these results can provide valuable information needed to establish a conservation and management plan for leatherbacks utilizing the GoM.

CHAPTER II – Space Use and Movements of Leatherback Turtles (*Dermochelys coriacea*) in the Gulf of Mexico

2.1 Introduction

Leatherback turtles (*Dermochelys coriacea*) are a large, migratory marine species that have the widest range of any reptile on the planet. Leatherbacks are listed as an IUCN vulnerable species and an endangered species under the U.S. Endangered Species Act; however, the threat level varies among oceanic basins and subpopulations (Wallace et al. 2013). Nesting beaches are found in tropical and sub-tropical regions, yet foraging areas reach latitudes as high as 71°N and 47°S, and reside across ocean basins, tens of thousands of kilometers away from nesting sites (Eckert et al. 2012). Female leatherbacks migrate between productive foraging areas and reproductive/nesting sites every 1-4 years, depending on the length of migration and food resources (James et al. 2005, Wallace et al. 2006, Benson et al. 2011). However, in the North Atlantic it has been shown that juvenile and adult turtles routinely make migrations out of temperate foraging areas when water temperatures drop during the winter and move southward covering a broad range of the ocean (James et al. 2005, Fossette et al. 2010b). Limited data on males reveal potential annual round-trip migrations for mating in the Western Atlantic (James et al. 2005).

Leatherbacks feed exclusively on gelatinous zooplankton and display specific feeding strategies to optimize their prey consumption. As visual predators (Heaslip et al. 2012, Wallace et al. 2015) leatherbacks can selectively feed on a particular prey (Houghton et al. 2006, Benson et al. 2007, Aleksa et al. in prep), as well as feed only on the most caloric-rich part of the prey when food is abundant and large (Scott Benson, pers. comm). Leatherbacks have also been observed to synchronize arrival to an area with times when food is most abundant (Eckert 2006). Within the foraging areas, leatherbacks perform Levy walk search behavior to locate patches of prey (Sims et al. 2008). A Levy walk consists of two movement patterns: an intensive foraging mode when the predator has located a patch of prey and remains in an isolated position, and an extensive foraging mode where the predator is within a region of potential prey and is searching for a patch of prey (Shlesinger et al. 1987, Sims et al. 2008), herein referred to as "foraging" and "casting" respectively. This specialized, random-walk strategy is utilized by a diverse range of organisms that feed on prey that is heterogeneously distributed ("patchy") or sparse (Viswanathan et al. 2002, Humphries & Sims 2014). Previously, leatherback telemetry studies have not addressed the occurrence of casting behavior within behavioral models, and have differed in their ability to distinguish between foraging and migration because of measurements in the "gray area" between distinct behavioral shifts. As obligate gelatinous zooplankton consumers, they rely on the ingestion of large quantities of this low caloric prey to meet their metabolic needs. Therefore, highly successful leatherback foraging grounds are associated with large medusa species that are commonly found in mass aggregations, thus providing an ample supply of food and low energy cost for prey search (Houghton et al. 2006).

Productive foraging regions have been identified from the tropics to temperate waters around the globe (James et al. 2005, Benson et al. 2007, Benson et al. 2011, Heaslip et al. 2012, Eckert et al. 2012). Although leatherbacks have adaptations that allow them to travel and reside in temperate waters (reviewed by Eckert et al. 2012), there is a trade-off between the energy expense needed to survive the environmental conditions and the energy gained from the consumption of the available prey. Foraging typically occurs along physical oceanic boundaries (i.e. convergences, discontinuities, and gradients) that aggregate prey in the open ocean and coastal habitats (Graham et al. 2001, Eckert 2006, Hays et al. 2006, Benson et al. 2011). Typical parameters that regulate the abundance of jellyfish include salinity, temperature, nutrients, distance from shore, and water movements (Purcell 2012, Lucas et al. 2014, Aleksa et al. in press). The investigation of leatherback distributions and their association with oceanographic properties that aggregate prey is possible with the use of satellite tags.

The use of satellite telemetry has transformed our ability to address ecological questions about many marine vertebrates that are difficult to study because of their long migrations and extended time away from easily accessible environments (Gillespie 2001, Hussey et al. 2015). Telemetry studies allow researchers to track migration patterns, identify high-use areas, and investigate how organisms react and respond to environmental and anthropogenic interactions (Hussey et al. 2015). Satellite telemetry also allows for analysis of dive behavior and characteristics, water temperature, and other oceanographic features (James et al. 2005, Fossette et al. 2010b, Roquet et al. 2014, Lander et al. 2015, Wallace et al. 2015). Coupling these data with behavioral models allows for the distinction between reproductive, foraging, and migration behaviors.

Differentiation between behavioral modes has been observed by several analyses and results are consistent amongst leatherback studies. Leatherback migration, compared to area restricted search (ARS) behavior, is characterized by a nearly straight trajectory of faster swimming speed (mean 2.2 vs. 1.6 km h^{-1}), with fewer dives that have a deeper maximum depth (mean 81.5 vs. 45.2 m; max 792.3 vs. 359.2 m) and a longer duration (mean=16.2 vs. 8.7 mins; max 71.7 vs. 40.4 mins; values derived from the Eckert et al. 2012 review). Because ARS behavior can represent reproduction or foraging, parameters such as time of year, location, and visual observation of nesting can be used to differentiate between these behaviors (Eckert 2006, Hays et al. 2006, Jonsen et al. 2007, Fossette et al. 2010a, Benson et al. 2011, Bailey et al. 2012, Wallace et al. 2015).

Little is known about the leatherbacks that utilize the GoM. Genetic analysis from GoM bycatch samples showed that the largest proportion of leatherbacks caught were from the Trinidad/French Guiana nesting stock (~ 54%), followed by Costa Rican (~43%), St. Croix (~2%), and Brazilian (~1%) nesting populations (Stewart et al. 2016). Satellite telemetry from the Costa Rica/Panama rookery has shown leatherbacks utilizing the Gulf of Mexico (GoM) during post-nesting periods (Evans et al. 2007, Evans et al. 2012). Consistently, the GoM has been the greatest contributor to leatherback bycatch interactions for the U.S. Atlantic Coast, including 2013 when the GoM fisheries were responsible for 144 out of 362 longline interactions (Garrison & Stokes 2014). These data provide evidence that the GoM is a high-use area; however, no studies have been published to date that quantify the leatherbacks' basic ecological information within the GoM, including, but not limited to, stock assessment, spatio-temporal movements and patterns, residence times, and habitat usage. This study utilized satellite telemetry data to run a switching state-space model (SSSM) and analyze dive characteristics to examine movement patterns and behavioral modes of leatherback turtles travelling to, from, and within the GoM, as a means to answer if foraging is the main behavior expressed in the GoM, is the space use distributed non-uniformly, and if movements are associated with ocean circulation and frontal features? It is hypothesized that leatherbacks within the

GoM are foraging and reside within the region throughout multiple seasons. Investigating and quantifying these parameters will provide a better understanding of how leatherbacks are utilizing this environment and can help with future management and protection of the species.

2.2 Methods

2.2.1 Data Collection

To address the movement of leatherbacks in the GoM, two sets of satellite telemetry data were utilized: 1) a nesting beach tagging operation in Panama and 2) an in-water deployment in the northern GoM. The beach tagging was part of the Sea Turtle Conservancy's (STC) effort named "Sea Turtle Tracking: Caribbean Leatherback Tracking and Conservation Project". Satellite transmitters were affixed to 10 nesting leatherbacks at Chiriqui Beach and Soropta Beach, Panama from 2004 to 2015. During operation, curved carapace length (CCL) was measured and a monel tag was applied to each rear flipper. SirTrack KiwiSat 101 Argos satellite transmitters (n=3 of the 10 tags) were attached using a custom-fit harness made from polyvinyl tubing and nylon webbing connected with two elastic rings, each with an integrated corrodible link to facilitate release of the harness (Eckert & Eckert 1986). SirTrack KiwiSat 202 Argos satellite transmitters (n=3) and Wildlife Computer SPOT5 (n=1) and SPOT-317A (n=3) Argos satellite transmitters were attached directly through the dorsal ridge of the carapace using wires or cable ties with an integrated corrodible link to facilitate release of the transmitter (Dodge et al. 2014). The nesting beach project was facilitated under the Cooperative

Agreement for the Conservation of Sea Turtles of the Caribbean Coast of Costa Rica, Nicaragua and Panama, cooperative agreement number F14AP00361.

The in-water tagging took place off the coast of Destin, Florida during September of 2015, and was the first in-water tagging of leatherbacks in the GoM. Captures were made aboard the NOAA vessel R/V *Hildebrand* via the direct capture methodology utilizing a hoop net to capture free-swimming leatherbacks. A breakaway hoop net fitted with breakaway stays to attach the net was pursed over the turtle. Turtles were quickly brought to the stern of the vessel and lifted from the water in a lift basket for satellite tag attachment. Turtles were taken out of the net, quickly examined and secured so that their limbs were held close to their body to prevent injuries to the turtle and crew. Once on board, turtles were measured, visually sexed, satellite tagged, and flipper and PIT tagged following procedures described in the SEFSC Sea Turtle Research Techniques Manual (NMFS 2008). Data-Collecting GPS Argos Satellite tags (Wildlife Computers MK-10AF) equipped with FASTLOC to provide GPS positions were deployed. Tags were attached via tether to the caudal peduncle (NMFS 2008). Turtles were immediately released following completion of sampling procedures and transmitter attachment. All efforts were made to assure that turtles, once landed, were in good physical condition before being tagged and returned to the sea. The SEFSC had a NMFS Section 10a1a permit to conduct this study (NMFS permit 16733).

For the spatial analysis, the GoM study area was defined by the coastline of enclosed basin and latitudes above 21.8°N in the Caribbean Sea (line across the Yucatán Channel). The east boundary of the Gulf between Florida and Cuba was set at 80.4°W. To remove movement associated with nesting or reproductive behaviors, all telemetry data below 15°N was omitted from analysis. This extension beyond the GoM boundary was included in the study to assess the behavior expressed while entering and exiting the GoM.

2.2.2 Movement and Behavioral Analysis

A Bayesian switching state-space model (SSSM) was applied to the satellite telemetry data (Jonsen et al. 2005, Jonsen et al. 2007). The SSSM is a two-step time series model that first uses the measurement equation (Eq. 2.1) to correct for Argos location errors and interpolates the data into equal time steps to determine the animal's most likely position.

$$Y_{t,i} = (1-j_i)x_{t-1} + j_i x_t + \mathcal{E}_t \qquad \text{(Eq. 2.1)}$$

where Y is the observed position at a specific time interval (t) associated with the proportion of time interval when the ith observation was made (j) of the two-dimensional Argos position vector (x), adjusted by the Argos error value ($\mathcal{E}$; Jonsen et al. 2007). The second step determines the animal's behavioral mode based on a correlated random walk, using the transition equation (Eq. 2.2; Jonsen et al. 2005, Jonsen et al. 2007).

$$d_t \sim N_2[\gamma_{bt}T(\theta_{bt})d_{t-1}, \Sigma] \qquad \text{(Eq. 2.2)}$$

where d represents the difference between positions, N_2 is the bivariate Gaussian distribution of the covariance matrix Σ (variance in the longitude and latitude), γ is the autocorrelation of direction and speed and b_t denotes the behavioral mode. $T(\theta)$ is the transition matrix specifying the mean turning angle (θ) required to move from d_{t-1} to d_t. The provided behavioral value (b_t) for each location allows for the distinction between behavioral modes: migration and area restricted search (ARS).

The models were run with R software (v 3.2.4 revised; R Core Team 2016) using the bsam package (v 0.43.1; Jonsen 2016) and JAGS software (v 4.2.0; Sourceforge). A switching difference correlated random walk (DCRWS) model and the Markov Chain Monte Carlo (MCMC) method (2 chains with 12 hour time steps) were used, with an initial burn-in phase of 30,000 iterations to eliminate the effects of the initial conditions. A collection phase of 10,000 Markov Chain iterations where every tenth value was retained for analysis to remove the effects of autocorrelation (Bailey et al. 2008, Benson et al. 2011). Telemetry tracks with 20 days or more of consecutive positioning gaps were separated into independent tracks to reduce positioning error (Bailey et al. 2008). The Gelman and Rubin's convergence diagnostic (Gelman and Rubin 1992) was run using the R package "coda", to test for convergence between the two chains (convergence represented by a value close to 1) which ensures a stable parameter estimation. Three of the eighteen turtle tracks had not converged after the initial burn-in phase, so increments of 10,000 steps were applied until convergence was achieved. For all three cases, 60,000 burn-in steps were appropriate. Initial analysis separated the behavioral modes based on the probability of transit, where values with a probability greater than 0.5 were considered transit (Benson et al. 2011). A secondary analysis divided the behavioral modes based on the visual inspection of the SSSM data distribution and the separation of modes represented by troughs in the data.

Kernel density estimation (KDE) was applied to define clusters of observations which represent frequently used areas for the behavioral modes identified within the GoM. The KDE was performed using the Spatial Analyst Tools in ArcGIS (v 10.3; Esri). The max kernel density was used to scale each individual behavior mode, with a program derived cell area of approximately 89 km^2. A colored contoured density map, in increments of 12.5 % of the total density, was used to visually represent the high use areas for each mode.

Dive behavior analysis was only applied to the leatherbacks tagged from the in-water tagging operation, as tags deployed from the nesting beaches were not equipped with the instrumentation to record dive information. Dive behavior was divided based on the three behavioral modes using the SSSM temporal resolution (12 hr). Dive parameters analyzed consisted of maximum dive depth, dive duration, and surface duration between dives. Dive behavior was averaged by individual turtles for each behavioral mode.

2.2.3 Physical Oceanographic Properties Analysis

Leatherback locations were analyzed for association with sea surface height anomalies, ocean currents, divergence or convergence, and temperature and salinity fronts. Association analyses were performed for the entire GoM data as well as individually for any determined high-use foraging regions. Sea surface height data were gathered from E.U. Copernicus Marine and Environment Monitoring Service (CMEMS; marine.copernicus.eu; delayed time, global, allsat). Ocean current data, as well as mean daily temperature and salinity values, were accessed through the Hybrid Coordinate Ocean Model (HYCOM) database (hycom.org).

MATLAB (v R2016a) was utilized for extracting and processing data for the sea surface height analysis, as well as the ocean current and divergence/convergence associations. Turtle associations with sea surface height were investigated using weekly sea surface height anomalies (SSHa) fields. The anomalies were categorized into five levels (sea surface high, sea surface low, sea surface high boundary, sea surface low boundary, or the mean height as common water) based on Gulf-wide SSHa percentiles and water velocities (Domingues et al. 2016). Turtle positions were categorized based on their spatial overlap with SSHa features. Ocean current association was analyzed by calculating the turtle velocity from the change in latitude, longitude, and time between consecutive satellite SSSM locations. Turtle association with the currents was measured by level of effort exerted by the turtle, which was quantified by dividing the ocean current corrected turtle speed by the turtle speed 'over ground' in both the latitudinal and longitudinal directions. An effort of 1 represents a 100% independent movement relative to ocean currents (i.e. no aid or hindrance by the currents). An effort below 1 signifies the turtle exerted less energy than needed (i.e. help from the current) and an effort value above 1 means the turtle exerted more energy than needed to reach its destination (i.e. hindered by the currents). Swimming efforts between the behavioral modes were compared using a Kruskal-Wallis test and pairwise comparison to determine if leatherbacks were utilizing ocean currents differently amongst the behavioral modes. GoM divergence was derived from the HYCOM model velocities using the 2D MATLAB divergence function (in MATLAB). A divergence value was assigned for each turtle point based its spatial overlap within the divergence surface plot. Positive values signified divergence whereas negative values represented a convergence within the resulting continuous value range.

The analysis between leatherbacks and temperature and salinity fronts was performed in ArcGIS (v 10.3, Esri). Surface temperature and salinity fronts were detected individually from the daily HYCOM data by the Cayula-Cornillon edge detection algorithm from the ArcGIS (v 10.3, Esri) Marine Geo Ecology Tool (Roberts et al. 2010).

Distance between turtle position and front edge was measured in kilometers using the geodesic method of the ArcMap “near” tool, and the position relative to the warm or cold side in the temperature front analysis and fresh or saline side of the salinity front analysis was recorded visually. To confirm the presence of a relationship between oceanographic properties and the leatherback observations, a spatially random point was generated for every turtle observation and the same analyses were run on the random position dataset. The results of the observed data and the random data were compared using a Kruskal-Wallis test to determine if the relationship in the observed data was different from the random position dataset. A Bernoulli Trial was used to compare actual frontal position preferences to a sequence of random trials. The summation of the trial outputs was used to calculate quantiles and determine the 95% confidence interval to justify a behavioral association.

2.3 Results

The beach and in-water tagging efforts resulted in satellite telemetry data for sixteen leatherback that utilized the GoM from 2005 to 2015. Active telemetry data ranged from 30 to 413 days, while tracking within the GoM basin lasted between 12 to 316 days. The average curved carapace length (CCL) of the turtles tagged was 147.9 ± 8.0 cm. Leatherbacks tagged at nesting beaches were reproductive females; however, the in-water tagging operation identified two turtles as possible males from tail length, two females, and two with unknown gender. Turtle movements covered a large area of the GoM from the coast to the deep open ocean (Fig. 2.1). Clusters occurred in the northern Gulf from Louisiana to Florida and along the shelf break of the states Tabasco and Campeche in Campeche Bay, Mexico. Leatherbacks made a direct movement when migrating to and from Caribbean nesting beaches by traveling through the Yucatán Channel (n=12; Fig. 2.1).

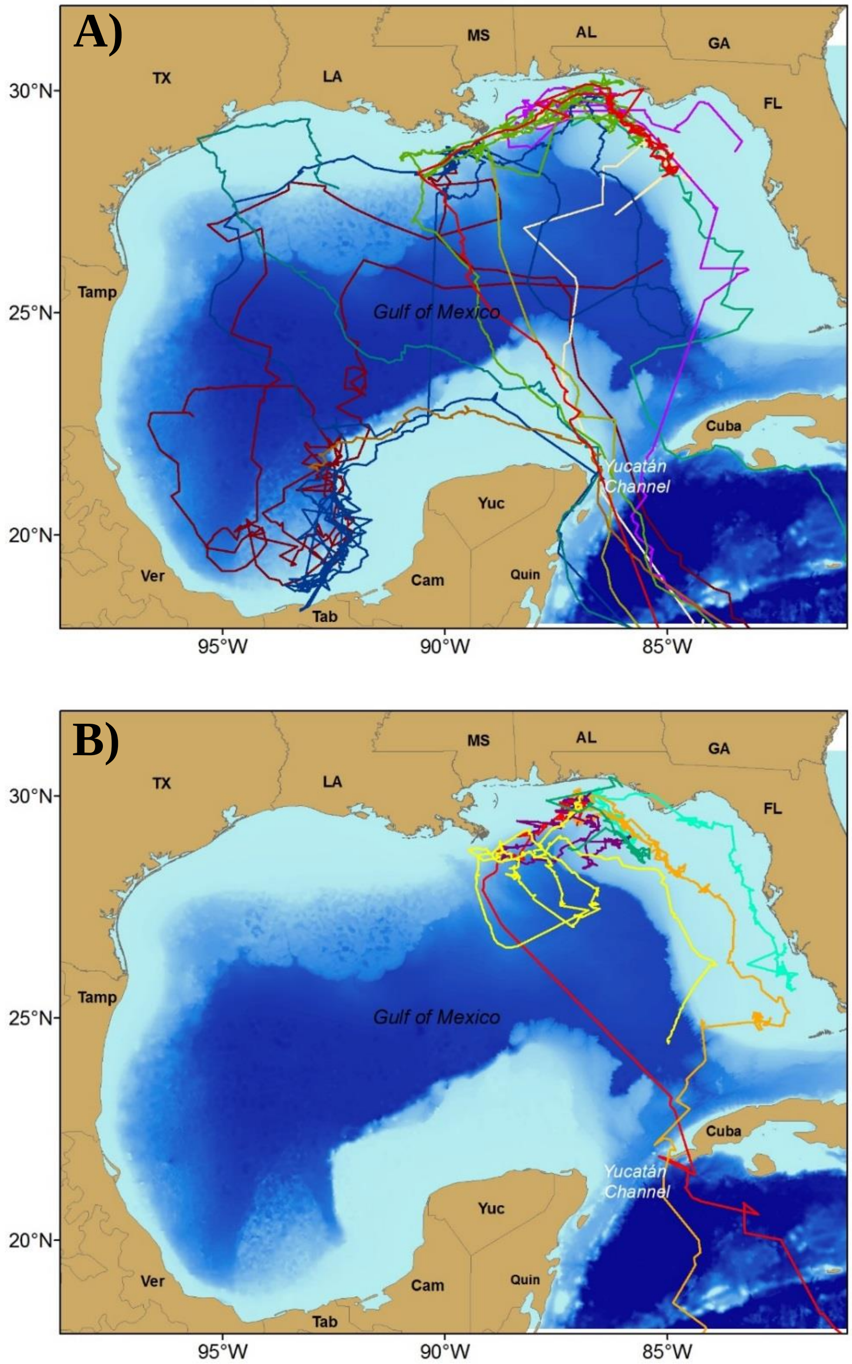


Figure 2.1 Leatherback telemetry data

Telemetry data from the **A)** Panama nesting beaches (n=10) and **B)** northeastern GoM in-water (n=6) deployments.

2.3.2 Behavioral Distribution

The SSSM revealed the expression of both migration and ARS behaviors within the GoM (Fig. 2.2A & B). The mean turning angle (θ) for ARS behavior was 193°± 2 suggesting frequent turns and reversals in direction, while during migration it was essentially a straight forward heading of 0.6°± 0.3 (Fig. 2.2A). The autocorrelation between speed and distance was greater in the migration behavior revealing the greater likelihood to swim fast when maintaining the same direction (Fig. 2.2B). The average (± se) swimming speed also differed between the behavioral modes, with an average speed of 0.21 ± 0.00 m s^{-1} during ARS behavior and an average speed of 0.58 ± 0.01 m s^{-1} during migration (Fig. 2.2C). ARS behavior was displayed on average 59% of the time while in the GoM (Table 2.1). However, if the mean was calculated only after the first mode switch from migration to ARS for leatherbacks tagged on the nesting beaches (i.e., removing the initial migration period into to the Gulf) then foraging represents 77% of the behavior expressed in the GoM. ARS behavior in this study is presumed to be detection of foraging because it occurred in the GoM after migration from nesting locations and without contact with the shoreline, which is observed in nesting behavior.

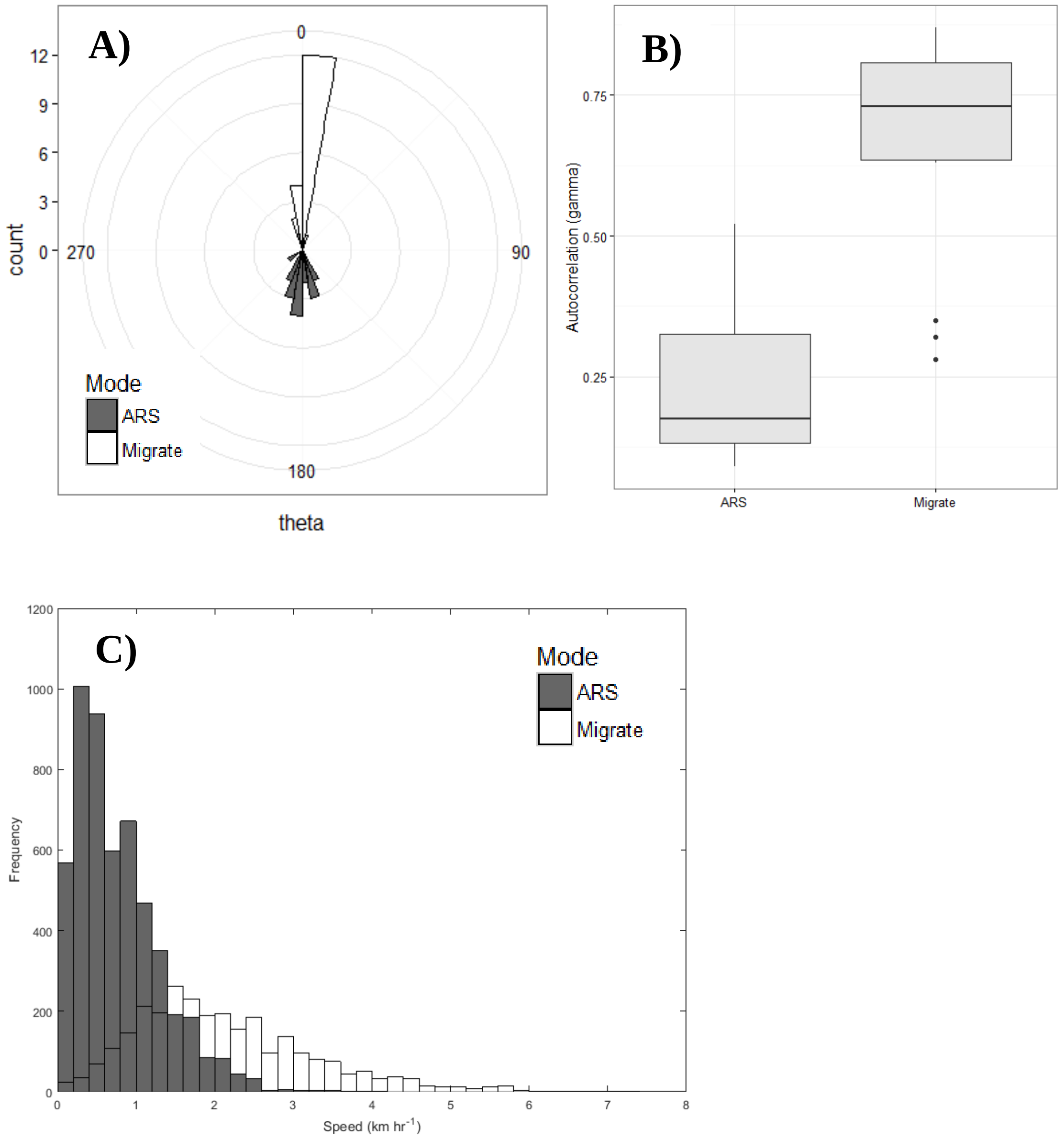


Figure 2.2 Switching state-space model outputs

Movement parameters of area restricted search (ARS; black) and migration (white) modes based on the switching state-space model positioning. **A)** Mean turning angle (theta) in degrees, **B)** Mean autocorrelation in speed and direction (gamma), and **C)** Histogram of speed values in km hr^{-1}.

Table 2.1 Behavior expressed by individual leatherback turtles

Turtle ID	# of Days Tracked	Migration (%)	Casting (%)	Foraging (%)
T1	64	19	28	54
T2	290	30	23	47
T3	72	22	78	0
T4	108	15	85	0
T5	316	35	51	14
T6	12	100	0	0
T7	38	100	0	0
T8	18	100	0	0
T9	176	17	33	50
T10	97	0	94	6
TA	29	29	71	0
TB	75	42	24	33
TC	42	0	100	0
TD	108	36	33	30
TE	97	42	13	45
TF	41	0	99	1

Percentage of behavior expressed by each track and number of days track was active (T1-T10 are nesting beach tags, TA-TF are in-water tags).

Kernel density estimation (KDE) highlighted two high-use areas and a third moderately used area in the GoM for foraging behavior (Fig. 2.3A). The northeast region of the GoM along the coastline of the Florida panhandle (Panhandle) and Campeche Bay, Mexico along the western shelf edge of the Yucatán Peninsula (Campeche) were isolated as the two high-use foraging areas in the GoM. The moderately-used area was located on the southwestern shelf of the Florida coast and was only occupied during 2005 by a single leatherback and by two leatherbacks in 2015. The highest kernel density for the foraging behavior reached 2.1 obs/km^2. Foraging locations also showed a strong temporal pattern with a high residence of leatherbacks in the Panhandle region during the fall and high occurrence in the Campeche during the winter and spring months (Fig. 2.4). The high-use transit areas identified by the KDE overlap with the foraging areas and expand to a wider region, particularly the central and eastern Gulf and to the Yucatán Channel (Fig. 2.3B). Peak density for a transit behavior kernel cell was 0.5 obs/km^2. The nesting females began entering the GoM basin in late June.

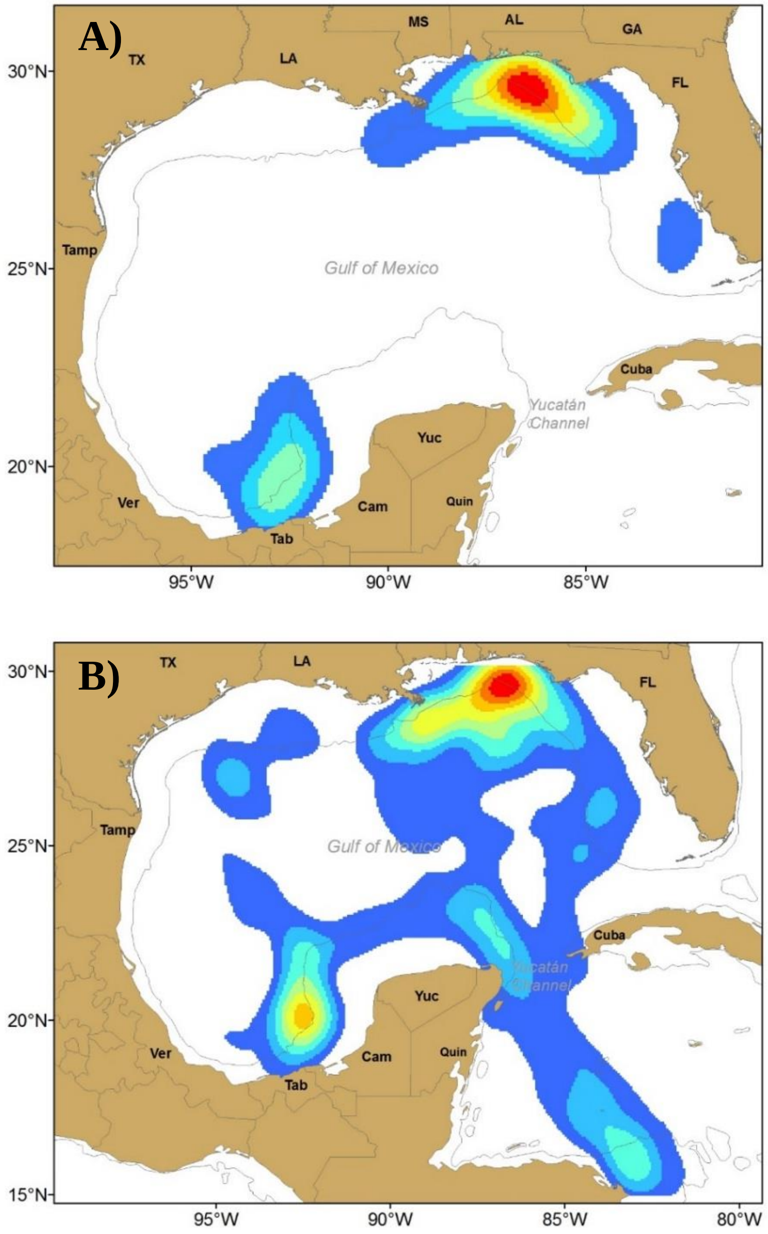


Figure 2.3 Kernel density estimation for two behavioral modes

Kernel density estimation for **A)** area restricted search (ARS) and **B)** migration behaviors isolated by the switching state-space model. Gray line represents the 200m isobath.

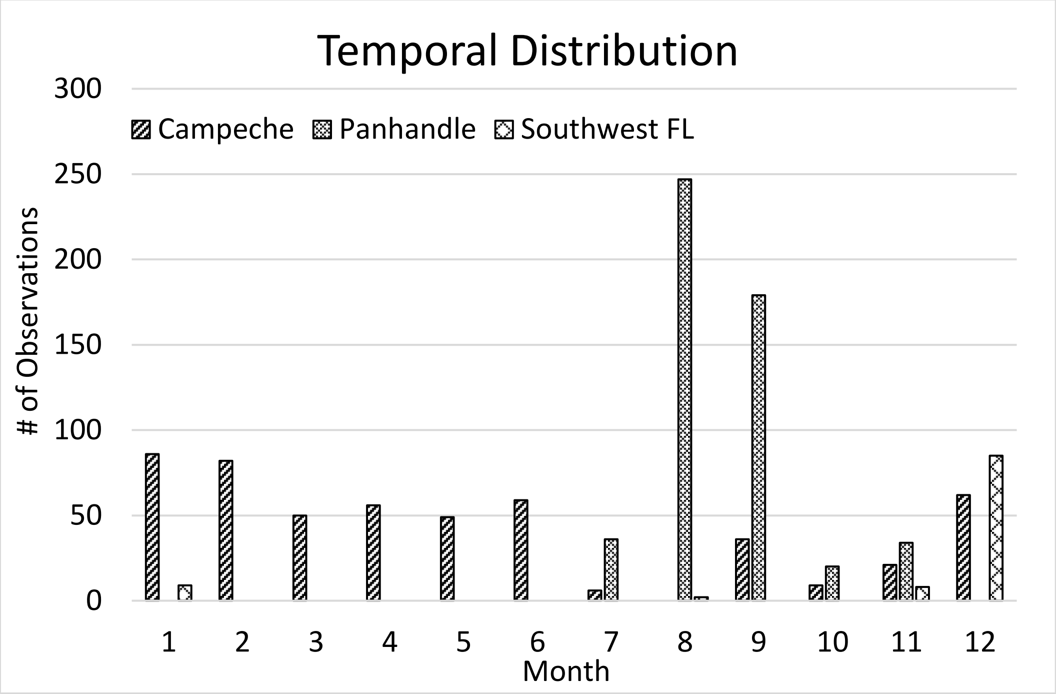


Figure 2.4 Monthly distribution of leatherback foraging observations

Monthly temporal distribution of leatherback observations for the foraging areas identified in the Gulf of Mexico.

A histogram of the behavioral mode (b_t) produced by the SSSM elucidated three peaks, one during the transit mode (b_t =1.0) and two in the ARS mode (b_t =1.65 and 2.0; Fig 2.5). Isolating behavioral modes based on the histogram distribution led to a three-behavior mode classification consisting of an initial migration mode for values less than 1.35, an intermediate foraging mode from 1.35 to 1.75 (casting), and an intensive foraging mode for values greater than 1.75 (Fig. 2.5). Separate KDE maps created for the three behavioral modes (Fig. 2.6) illustrate the strong spatial overlap between the foraging and casting behaviors (Fig. 2.6A & B) and a spatially separate migration behavior (Fig. 2.6C).

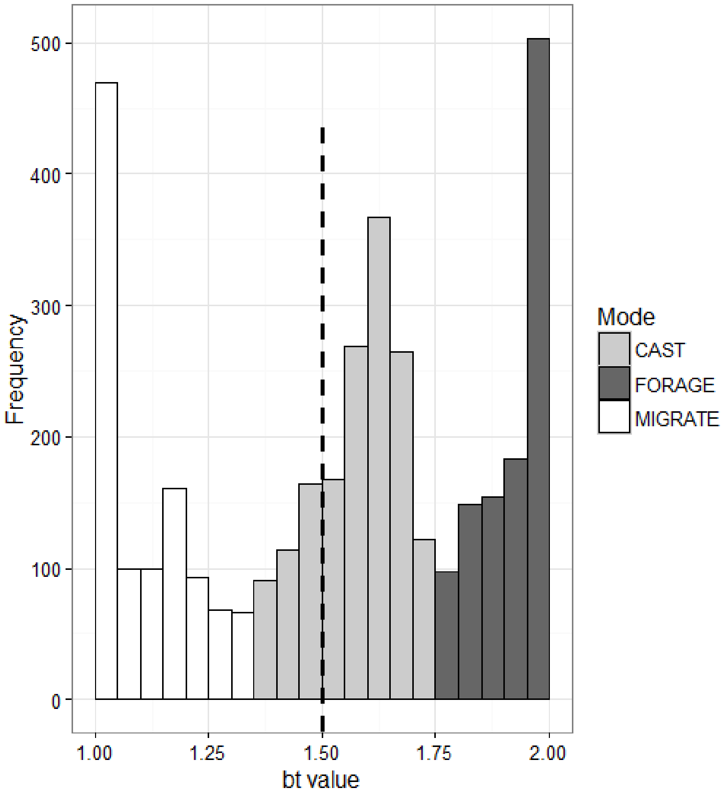


Figure 2.5 Histogram of switching state-space model behavioral (b_t) values

Histogram of switching state-space model behavioral (b_t) values for total track data. Shades of gray depicts mode separation based on the three behavior modes (migration, casting, and foraging), while the vertical dashed line represents the initial separation into two modes.

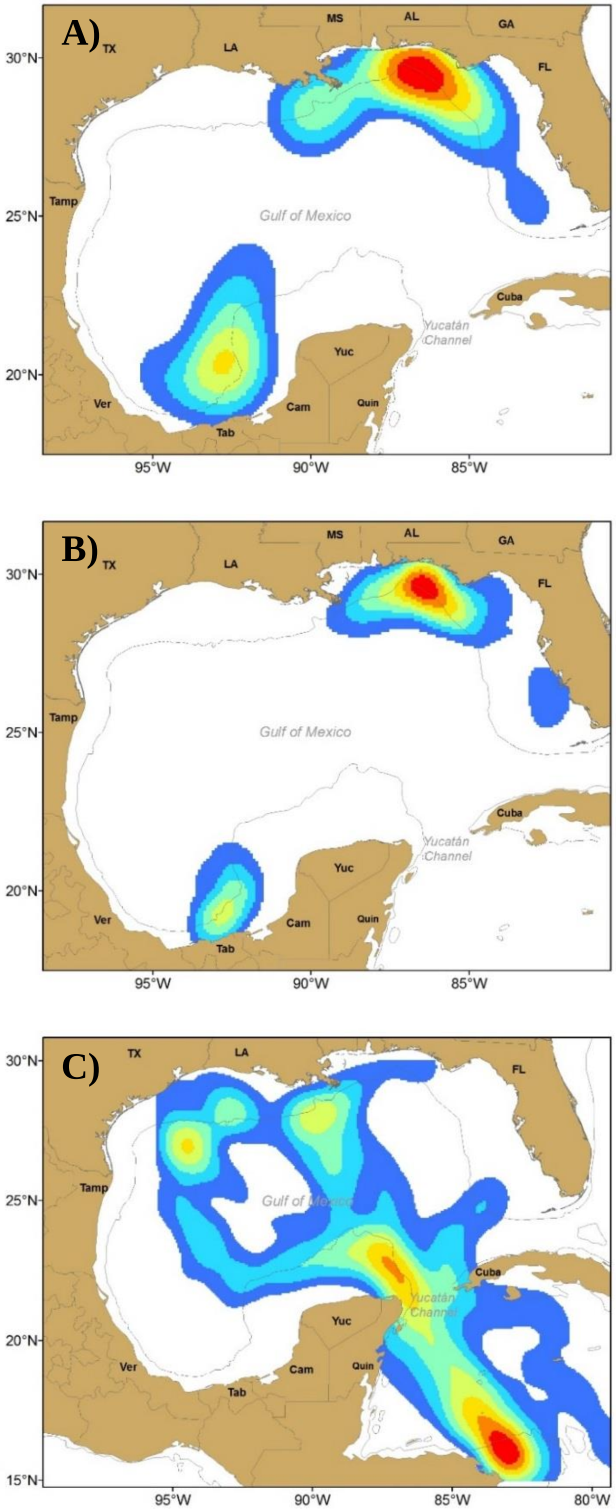


Figure 2.6 Kernel density estimation for three behavioral modes

Kernel density estimation for **A)** foraging, **B)** casting, and **C)** migration behaviors isolated by the switching state-space model behavior (b_t) values.

2.3.3 Dive Behavior

Diving behaviors, measured as dive depth, duration, and surface intervals, were unique amongst the six individual turtles equipped with depth recording tags (Fig. 2.7). The shallowest average foraging and casting dives were recorded by Turtle D. Turtle E displayed the most similar foraging and casting dives which were approximately 30 meters in depth with a 10 minute duration. This turtle also displayed the longest surface intervals and the greatest percentage of "V-shaped" dives. Turtle F was not tracked during any casting or migration behavior. The two turtles that were tracked while migrating south (C and E) had extremely different surface intervals during migration dives, with Turtle C only surfacing for an average of ~ 1.5 minutes and Turtle E remaining at the surface for typically 7 minutes or longer (Fig. 2.7C). Turtle B expressed migration dive behavior but was not tracked out of the GoM.

While differences were apparent between each individual turtle, some consistent patterns were observed amongst the dive behaviors expressed. The deepest dives corresponded with the longest dive durations; however, the surface intervals did not follow this trend or any apparent trend between the three behavioral modes (Fig. 2.7). The dive shape most commonly used in all behavioral modes was "U-shaped" rather than "V-shaped". No regular difference was observed between the dives associated with the foraging and casting behaviors (Fig. 2.7). The dive behavior expressed by turtles C and E during migrations back to Caribbean nesting locations was different from those associated with foraging and casting behaviors. This dive behavior consisted of deep

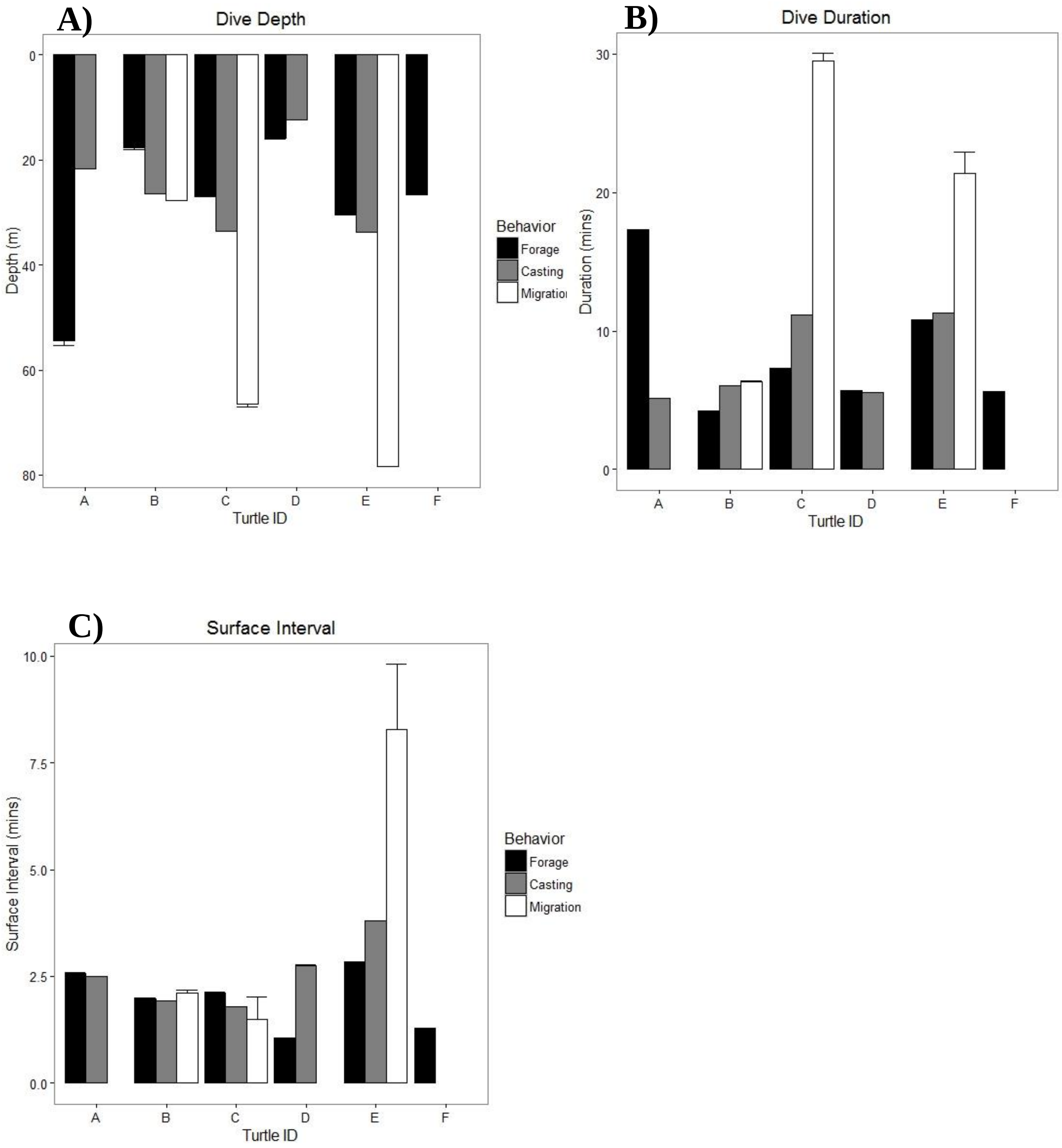


Figure 2.7 Leatherback dive behavior characteristics

Dive behavior characteristics (mean + se): **A)** maximum dive depth, **B)** dive duration, and **C)** surface duration between dives.

dives of long durations (Fig. 2.7). The average depths of the migration dives were twice the depths of the other two modes (Fig. 2.7A).

2.3.4 Impact of Physical Properties on Leatherback Movement

Leatherback movements were often associated with sea surface lows within the GoM. Approximately 46% of the observations recorded in the GoM were overlapped with a sea surface low feature. Isolating observations by behavioral modes revealed that ~63% of foraging behavior and ~60% of casting behavior was associated with sea surface lows (Fig. 2.8). Migration behavior overlapped ~60% with the common water (SSHa ~0). However, migration was the only mode found to be associated with sea surface highs (~9%; Fig. 2.8).

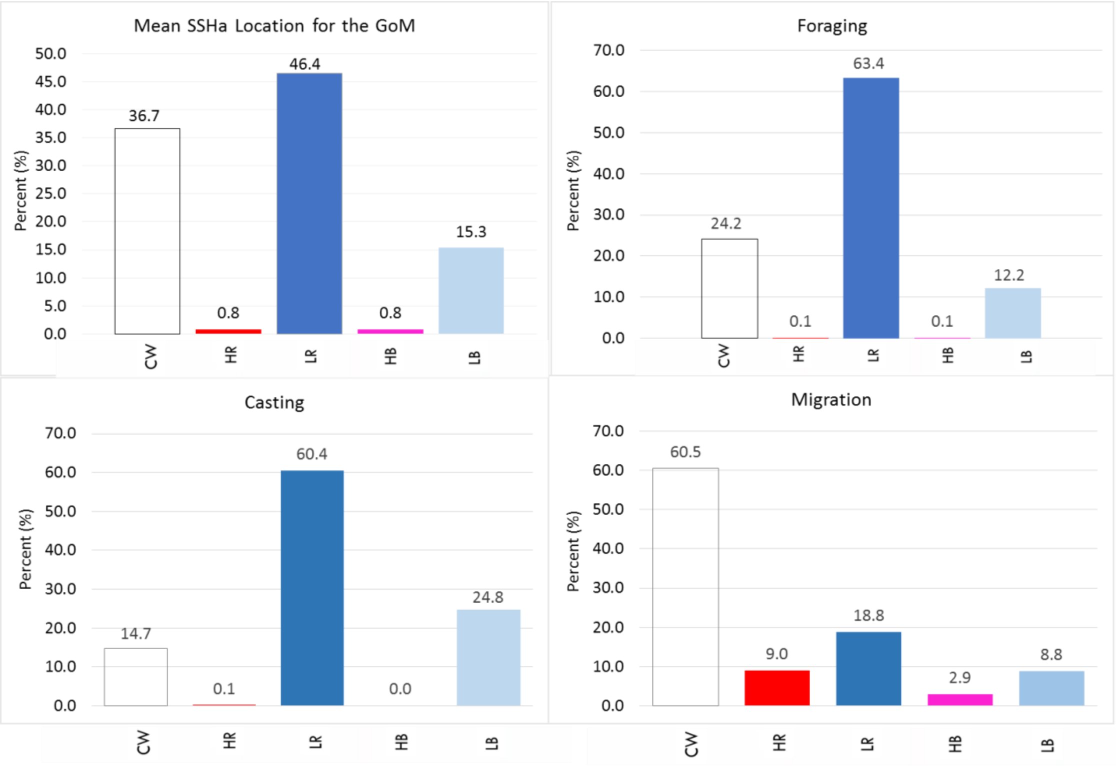


Figure 2.8 Percent of overlap between leatherback observations and sea surface height anomaly

Percent of overlap between leatherback observations and sea surface height anomaly features in the Gulf of Mexico. (CW=common water, HR=sea surface high, LR=sea surface low, HB=sea surface high boundary, LB=sea surface low boundary).

Analysis of turtle effort revealed similar swimming efforts during foraging and casting behaviors, but significantly less effort exerted during periods of migration (Kruskal-Wallis, $p<0.05$; Fig. 2.9). The time series of an individual turtle's effort showed an extreme saw-toothed pattern during foraging and casting behaviors, likely due to the oscillating swimming direction seen by the average 193° turn angle. The effort during migration periods had a higher occurrence of efforts below 1, indicating some current-aided swimming behavior. This relationship was also apparent spatially as all but one turtle entering the GoM basin swam on the west side of the Yucatán Channel, the location of the strongest northward current, and the two turtles that were observed leaving the GoM swam on the east side of the Channel.

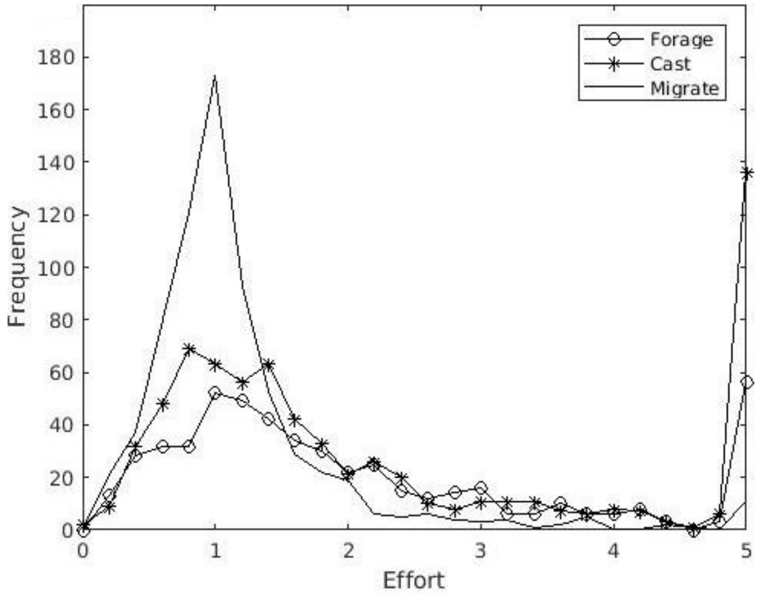


Figure 2.9 Histogram of leatherback swimming efforts

Histogram of leatherback swimming efforts during migration, casting, and foraging in the Gulf of Mexico. (A value of 1 is equivalent to no influence from currents, <1 = aided swimming, >1 = hindered swimming).

Divergence or convergence associations showed a Gulf-wide average for foraging behavior was related to convergence and casting behavior occurred at divergent structures (Table 2.2). Between the two high-use foraging regions, the Panhandle had an average convergent association for both foraging and casting, whereas the Campeche high-use area was associated with divergence (Table 2.2). Migration behavior was associated with divergence Gulf-wide. However, the extreme variability of these results and the lack of significant difference from the randomly distributed points, provides evidence that the results are inclusive for the resolution of the turtle observation data (12 hr).

Table 2.2 Divergence, temperature, and salinity associations with leatherbacks

	Gulf-wide	Panhandle	Campeche
FORAGING			
Divergence	$-3.24e^{-7}$	$-5.94e^{-7}$ ($3.30e^{-7}$)	$1.27e^{-7}$ ($2.97e^{-7}$)
Temperature (°C)	27.1 (0.1)	27.8 (0.1)	25.8 (0.1)
Salinity	35.3 (0.1)	34.7 (0.1)	36.3 (0.0)
CASTING			
Divergence	$4.50\ e^{-7}$	$-9.18e^{-9}$ ($2.00e^{-9}$)	$1.62e^{-6}$ ($3.68e^{-7}$)
Temperature (°C)	27.4 (0.1)	27.6 (0.1)	27.0 (0.1)
Salinity	34.9 (0.0)	34.4 (0.0)	34.7 (0.1)
TRANSIT			
Divergence	1.71e-6	-	-

Physical oceanographic properties associated with leatherback observations in the Gulf of Mexico for foraging, casting, and migration behaviors for the whole Gulf, and the Panhandle and Campeche high-use areas. (positive divergence values = divergence, negative=convergence)

Leatherbacks occupied a sea surface temperature range of 20.8°C to 31.5°C, with 95 % of the observations occurring between 23.6°C and 30.9°C. The temperature ranges differed between the Panhandle (subtropical) and Campeche (tropical) foraging regions (Table 2.2). The average temperature for Panhandle foraging and casting behaviors were 27.8 ± 0.1°C and 27.6 ± 0.1 °C, respectively. In the Campeche foraging area, the foraging temperature was 25.8 ± 0.1 °C and the casting temperature was 27.0 ± 0.1 °C. The span of salinity associated with the leatherbacks in the GoM ranged from 26.8 to 36.7; however 95% of the observations were between 32.4 and 36.5. Again the Panhandle region was more precise between the foraging and casting behaviors with an average salinity of 34.7 ± 0.1 °C and 34.4 ± 0.0 °C, respectively. The Campeche region showed foraging occurred at a higher salinity (36.3 ± 0.0 °C) than casting (34.7 ± 0.1 °C).

Table 2.3 Distance between fronts and leatherback observations

	Gulf-wide	Panhandle	Campeche
Foraging			
Temperature Front	17.87 (0.57)	16.14 (0.63)	20.77 (1.06)
Salinity Front	14.83 (0.37)*	15.37 (0.57)	14.21 (0.47)
Casting			
Temperature Front	21.94 (0.68)	18.82 (0.51)	29.64 (1.93)
Salinity Front	18.29 (0.62)	15.35 (0.36)	25.55 (1.92)
Random Samples			
Temperature Front	18.39 (0.40)	17.70 (0.50)	19.39 (0.67)
Salinity Front	16.62 (0.37)	15.58 (0.45)	18.10 (0.63)

Mean (se) distance (km) from nearest front (temperature or salinity) for the whole Gulf, and the Panhandle and Campeche high-use areas. * denoted significant difference between leatherback observations and random samples.

The distance measurement between the average daily fronts (temperature and salinity) and the turtle positions revealed that salinity fronts had more impact on leatherback movement. Leatherbacks were located closer to salinity fronts than temperature fronts during both foraging and casting behaviors (Table 2.3). However, the only front association that was significantly different from the random points was the Gulf-wide mean salinity front distance (Kruskal-Wallis, $p<0.05$). Visual analysis of frontal positioning preference (i.e. warm vs. cold or salty vs. fresh) exposed an association with salinity fronts only. Associations were found for foraging and casting in the Campeche and West FL areas, as well as casting in the mid-Gulf region. No association was identified for the Panhandle high-use area. Differential preference occurred between the salinity gradient amongst the two behaviors and within different regions (Table 2.4).

Table 2.4 Leatherback frontal gradient positioning preference

Location	Front Preference by Behavioral Mode	
	Forage	**Cast**
Panhandle	-	-
Campeche	Fresh	Saline
West FL	Saline	Fresh
Mid-Gulf (Casting only)	-	Saline

Salinity front position preference for leatherbacks in the Gulf of Mexico relative to the gradient of the nearest front.

Deployment of satellite telemetry introduced two levels of bias into the data. First, the deployment on nesting beaches only accounts for the movements of adult female leatherbacks and is a common bias in sea turtle investigations due to the accessibility and ease of operation at nesting beaches. The second bias is the deployment of the in-water tags in the northeast GoM. This location was chosen because of the reported aerial sighting of leatherbacks in the region (unpublished NOAA data). However, the six in-water Panhandle tracks may have led to the apparent higher density observed in the KDE compared to Campeche. Therefore, both high-use foraging areas were treated with the same level of importance in this study.

2.4 Discussion

The SSSM analysis of the satellite telemetry data demonstrated a distinctive shift in behavior within the GoM consistent with a transition from migration to foraging. While migrating, leatherbacks traveled at faster rates and in a relatively constant direction compared to the ARS behavior. The ARS behavior observed in the GoM occurred after migration from nesting beaches and after the mating/nesting season, therefore it is assumed to be a representation of foraging behavior. The turning angle (θ) and autocorrelation (γ) parameters were similar to values reported elsewhere for leatherback sea turtles (Jonsen et al. 2007, Bailey et al. 2008, Benson et al. 2011). Subsequent inspection of the SSSM b_t values revealed two peaks within the ARS mode which were interpreted as casting and foraging behaviors. Identification of 3 behaviors deviates from studies (Jonsen et al. 2005, Jonsen et al. 2007, Bailey et al. 2008, Benson et al. 2011), which consider 2 modes. The addition of casting addresses the uncertain behavior expressed between migration and foraging modes, which has been not been detected in other studies (Jonsen et al. 2005, Jonsen et al. 2007, Breed et al. 2009).

2.4.1 Spatial Distribution

The division of the ARS mode into two behaviors revealed a better classification of movement within the high-use areas in the GoM. Whereas the initial analysis expressed a strong overlap between the ARS and migration modes, the second analysis reassigned the behaviors to include casting, and the overlap between the migration and foraging high-use areas was greatly reduced. The spatial overlap between the casting and foraging behaviors highlights the importance of the Panhandle and Campeche high-use areas for energy consumption in the GoM (Fig. 2.6A & B).

Distinctive migration patterns were also observed for leatherbacks utilizing the GoM. Turtles in this study traveling to and from Caribbean nesting beaches swam through the Yucatán Channel. This differs from other Caribbean tagged leatherbacks heading to alternate foraging sites in the Atlantic Ocean, as they swam east through the

Greater Antilles (STC 2015; conserveturtles.org). None of the leatherbacks tracked into the GoM exited eastward through the Straits of Florida to reach a different foraging location. Furthermore, leatherback tracks returning to the Caribbean from the northwest Atlantic foraging locations do not enter the GoM (Michael James, pers. comm.). This behavior suggests that the GoM is a distinct leatherback foraging destination.

Specific locations identified in this study as foraging high-use areas agree with the environmental conditions needed to supply leatherbacks with a sustainable food source. Both regions are adjacent to robust riverine outflows from the two largest river systems (the Mississippi and Usumacinta-Grijalva rivers) that drain into the GoM (David & Kjerfve 1998). These high-use areas are also located over submarine canyons, Desoto Canyon (Panhandle) and Campeche Canyon (Campeche) and exist where the continental shelf edge (200m isobath) intrudes closer to the shore. With a close-proximity nutrient input and dynamic physical processes (e.g. upwelling, upcanyon flow, shelf edge fronts, eddies; Merino 1997, Salas-de-León et al. 1998, Morey et al. 2003, Zavala-Hidalgo et al. 2003, Salas-de-León et al. 2004) the Panhandle and Campeche high-use areas maintain highly productive waters (primary production > 0.3 and 0.04 gC m^{-2} d^{-1}, respectively; Lohrenz et al. 1997, Soto & Escobar-Briones 1995). Likewise, high biomass of zooplankton aggregates in locations of physical and bathymetric discontinuities, such as haloclines, pycnoclines, canyons, and shelf breaks (Genin 2004, Salas-de-León et al. 2011, Monreal- Gómez et al. 2013, Greer et al. 2015), making these regions optimal for sustaining the gelatinous zooplankton consumed by leatherbacks. The Panhandle high-use area overlaps with a high abundance of jellyfish (cnidarian medusozoans) during the fall season (Aleksa et al. in press) which coincides with the leatherback period of use for this region. The northern sector of a year-round Desoto Canyon fishing closure overlaps with the highest density of foraging behavior in the Panhandle (Garrison & Stokes 2014). The estuaries and mangrove forest off Tabasco and Campeche, Mexico are recognized as some of the most productive nursery areas in the GoM, which supports many species of offshore fishes and shrimp (Yåñez-Arancibia et al. 1988, Barbier & Strand 1998). Furthermore, a fishery for the human consumption of cannonball jellyfish (*Stomolophus meleagris*) was recently located in Campeche Bay (Mónica Reza, pers. comm.). This research provides further evidence to the importance of this region to leatherback turtles and the continuing need to monitor the species and safeguard these ecosystems.

2.4.2 Dive Behavior

Spatial movements provide some understanding to the discrepancy in the average dive behaviors amongst the individual turtles. The large separation in the dive depth and duration between the foraging and casting dives seen for Turtle A possibly occurred because all the foraging dives took place in one location and within a short time window (within one 12 hour time step) for only a total of 16 dives, while the casting behavior spanned 30 days and included 3460 dives. Therefore, an isolated intensive foraging opportunity was most likely acted upon and caused the deviation in the results for this turtle. The migration behavior displayed by Turtle B occurred towards the end of the tag activity when the track was headed south. This could have been the beginning of a return trip to a nesting location but the tag became inactive, so possibly only the shift between foraging and migration was captured. Turtle D displayed the shallowest dive depths of all the turtles in all behavioral modes, which is most likely because this turtle stayed on the western Florida continental shelf during the time when its tag was active. Turtle F only had dive data for its foraging behavior mode; however, casting behavior was identified by the SSSM for the last three days the tag was active, but no corresponding dive data were transmitted.

The analyzed dive behavior showed a measurable difference in behavior that supports the classifications used in the spatial analysis. The casting and foraging behaviors had similar characteristics and the extensive migrations were distinctly different (Turtles C and E). These data were consistent with previous studies, reporting that foraging leatherbacks, presumably searching the water column for prey, perform shorter, shallower dives when compared to migration when dive depth could be influenced by thermoregulation and predator avoidance (Eckert et al. 2012). The expected relationship between maximum dive depth and dive duration (deeper dives = longer duration) was observed, but no specific trend was detected between the surface intervals and the dives, which was similarly reported by Wallace *et al.* (2015).

2.4.3 Influence of Physical Properties on Distribution

Sea surface height anomalies (SSHa) are usually associated with oceanographic features that can concentrate or disperse ocean productivity (i.e. eddies, currents, upwelling/downwelling; Morey et al. 2003, Wang et al. 2003, Zavala-Hidalgo et al. 2003). Leatherbacks have been observed navigating around and within SSHa during migration and foraging movements (Luschi et al. 2006, Fossette et al. 2010a). These associations are also displayed by other large marine vertebrates that target patchy prey, like the gray seal and blue whale (Etnoyer et al. 2006, Breed et al. 2009). Sea surface lows are generally representative of colder, nutrient rich waters, whereas sea surface highs represent warm, low nutrient waters (Bakun 2006). The relationship seen here between leatherback foraging and casting observations and sea surface low regions correspond with the regions of high productivity that enable the presence of jellyfish aggregations. Transit patterns of the observed leatherbacks also followed the expected rotation of the associated sea surface highs and lows, providing more evidence that these features influence leatherback movement. Migration behavior in the GoM was largely associated with common water and represented links between sea surface low foraging spots. The association with sea surface highs occurred with the Loop Current in the Yucatán Channel and anticyclonic eddies that had pinched off from the Loop Current. During these times the swimming direction of the turtle coincided with the direction of current rotation, such that the turtle was utilizing the feature to reduce swimming effort and promote transit velocity.

Satellite telemetry data have shown that leatherback migration and foraging movements are influenced by ocean currents (Luschi et al. 2003, Gasper et al. 2006, Shillinger et al. 2008, Fossette et al. 2010b). Similar to the results found here, migration swimming effort can be greatly reduced (up to 50%) by the association with prevailing ocean currents (Luschi et al. 2003, Gasper et al. 2006). Luschi et al. (2006) also reported the influence of eddies on the rotational swimming pattern of foraging turtles. Studies have shown minor directional changes in apparent migration patterns (i.e. swimming further offshore, or slightly more north) to encounter concurrent prevailing currents (Luschi et al. 2003, Gasper et al. 2006). Leatherback migration patterns, for both hatchlings and adults, were observed to be similar to ocean drifter paths in certain locations (Fossette et al. 2010b). This correspondence suggests the association with ocean circulation, but because the paths did differ, turtles may only be using them when it is advantageous for transit and it is a behavioral choice as opposed to a passive association.

The distance from temperature or salinity fronts did not produce significant differences from the randomly generated samples in most cases. It has been shown that animals can detect and follow gradients on such a fine scale that models and edge detection algorithms do not identify them (Etnoyer et al. 2006). The aggregation of jellyfish can also occur along gradients much finer than mesoscale structures (Graham et al. 2001, McClatchie et al. 2012, Greer et al. 2015) which are missed by the horizontal and vertical gradients of the available oceanographic data. Therefore, based on the spatial and temporal resolution of the turtle positioning data and the ocean model, a valid relationship may not have been detected. At this point the data is inconclusive for an association with temperature fronts and only a tenuous relationship may be expressed with salinity fronts in the GoM. Although distinct distances to specific fronts may not be conclusive, regions that contain the presence of many fronts, like areas with mixing fluvial and oceanic water masses and near the shelf break as seen in the high-use foraging areas identified in the GoM, may provide successful foraging opportunities due to the high probability of aggregated prey.

The temperature and salinity ranges occupied by the leatherbacks did elucidate some behavioral patterns. The 7°C temperature range that accounts for 95% of the leatherback observations only occupied 28% of the total GoM temperature range observed in the random sample analysis (10.3-34.9 °C). This total surface temperature range represents the GoM basin year round. Temporal analysis showed that the leatherback observations in the winter months occurred in the warmer tropical areas of

Campeche and Southwest FL. Although the mean temperatures associated with the Campeche high-use area are slightly lower than the Panhandle, the turtles are utilizing these regions in different season and may be exploiting a more constant environment. This may also be an effect of the production and physical aggregation of the jellyfish. Currently, leatherbacks in the GoM are known to prey on jellyfish species that are more abundant in warmer temperatures; however, jellyfish data is lacking in winter and spring months. For example, the lion's mane jellyfish (*Cyanea capillata*) is regularly found in the northern GoM during the winter (reviewed by Seguro-Puertas et al. 2009) and is a common prey item of leatherbacks in other regions (James et al. 2005). Furthermore, bycatch records do show the presence of leatherbacks in the northern GoM during winter months (Stewart et al. 2016), but those observations are absent in the current satellite telemetry data. Currently, data are also lacking on the abundant jellyfish that are occurring in the Campeche high-use area in winter, with the exception of *Aurelia* spp.

A stronger association was found between leatherback observations and salinity within the GoM. The salinity range utilized by 95% of the leatherback observations only makes up 11% of the randomly sampled total GoM salinity range (5.4-40.7). The slightly larger variation in foraging and casting mean associated salinity in the Campeche high-use area is most likely due to the higher impact of freshwater directly to the foraging area compared to the Panhandle which is offset from massive freshwater influx and more influenced by oceanic waters. This oceanic water influence may also account for the reduced link between frontal positioning preferences in the Panhandle area. The differential use of the "fresh" vs. "salty" side of the fronts in different regions may be a reflection of the leatherbacks maintaining residence in a narrow range of salinity, which is potentially indicative of the conditions that produce the greatest abundance of prey. Salinity has been recognized as a driving force on the distribution and abundance of jellyfish (Decker et al. 2007, Lucas et al. 2014, Greer et al. 2015, Aleksa et al. in press), which would cascade up the food chain to influence the distribution of jellyfish predators.

2.4.4 Advantages of foraging in the Gulf of Mexico

Foraging within tropical and subtropical regions has the potential to reduce the energy demand on reproductive leatherbacks. Telemetry data has elucidated the use of both tropical and temperate foraging locations for the nesting population of the southwest Pacific Ocean (Benson et al. 2011). It was hypothesized that establishing a tropical foraging site may allow for a shorter interval between reproductive activity because less energy is required for the migrations (Benson et al. 2011). Wallace et al. (2006) calculated that ~80% of a female leatherback's reproductive energy cost is used for the round-trip migration between nesting and foraging locations. Therefore, Caribbean nesting leatherbacks that utilized the GoM (< 5000 km round-trip) for foraging, instead of a temperate site where the migration can reach an excess of 10,000 km (James et al. 2005), may have a reduction in their energetic need. Reducing the interval between reproductive events was also shown to increase the proportion of energy spent on reproduction verses metabolic functions (Wallace et al. 2006), again supporting the notion that a shorter migration distance could lead to a reduced time interval, which indicates a smaller energetic requirement. Lastly, foraging in a warmer climate removes the higher energy demand associated with processing cold prey items (Davenport 1998) and maintaining a core body temperature much warmer than the surrounding water (Davenport 1998, Southwood et al. 2005, Bostrom & Jones 2007), so leatherbacks utilizing the GoM may have a lower energy demand and a reduced energy expense from a shorter migration and reproductive interval compared to individuals that foraging in temperate waters.

2.4.5 Anthropogenic Impacts of Foraging in the Gulf of Mexico

Foraging closer to nesting beaches has energetic and reproductive advantages, yet there are also costs associated with the threat of anthropogenic interactions within the GoM. Leatherback foraging areas are known to occur within highly productive waters that also sustain large fisheries (Hays et al. 2003, Lewison et al. 2004, Houghton et al. 2006, Benson et al. 2007, Benson et al. 2011, Heaslip et al. 2012), and the nutrient-rich GoM is no exception with this productive marine ecosystem being exploited by large scale fishing, energy, and industrial trades. The GoM fisheries provide more shellfish, shrimp, and finfish annually than the combined efforts along the entire east coast of the United States (GMP 2014). The extensive longline effort for tuna, swordfish, and sharks represents the largest threat to the leatherbacks in the GoM, causing entanglement and drowning (Garrison & Stokes 2014). Locations of reported U.S. leatherback-fishery interactions coincide with this study’s identified Panhandle foraging area and extend into the identified migration regions (Garrison & Stokes 2014, Stewart et al. 2016). Currently no data are available to compare the fishing effort with the leatherback movements in the high-use Campeche area. Continued monitoring and investigation is needed to provide the necessary information for proper management of the species.

To further understand leatherback space use, residence time, post-nesting intervals, and foraging dynamics in the GoM, additional telemetry studies are needed. In-water tagging of leatherbacks within the Campeche Bay foraging area would further help determine space use and diving behavior within this region as well as further differentiate behavior between these two high-use foraging areas. Lastly, in order to fully comprehend the foraging of leatherbacks in the GoM more studies need to be done on the jellyfish, especially in Campeche Bay where data are extremely sparse. This continued research will improve our understanding of the subpopulations of leatherbacks utilizing this area, how to reduce interactions of leatherbacks with anthropogenic threats, and allow for better management and conservation of the species in the Gulf of Mexico.

CHAPTER III – Descriptive Density Models of Scyphozoan Jellyfish in the northern Gulf of Mexico

3.1 Introduction

Jellyfish (Cnidarian medusozoans) have existed in the world's oceans for approximately 500 million years (Cartwright et al. 2007), but only in the last couple decades have they been studied for their ecology and importance to the structure and health of an ecosystem. As planktonic organisms, most horizontal movements are controlled by the flow of ocean currents. However, jellyfish are motile organisms that have the ability to perform directional movements with muscular contractions allowing them to migrate throughout the water column in search of prey (Hays et al. 2008, Hays et al. 2012). Jellyfish are primarily carnivorous, feeding on a diverse range of prey from protists to fish larvae, which enables them to live in a variety of environments (Richardson et al. 2009). Previous experimental and observational work has shown that the occurrence and distribution of jellyfish can be affected by water temperature, salinity, dissolved oxygen, as well as ocean currents, fronts or other discontinuities such as thermoclines and pycnoclines (Decker et al. 2007, Purcell 2012, McClatchie et al. 2012, Lucas et al. 2014, Luo et al. 2014, Greer et al. 2015). Biological factors, such as primary production and zooplankton biomass (as food abundance), are also important for jellyfish development, growth, and reproduction (Purcell 2012, Lucas et al. 2014). Addressing the coupling of oceanographic features with the density distribution of jellyfish species is necessary to describe their population dynamics and investigate favorable and detrimental interactions within the environment.

The use of biological parameters as descriptors of jellyfish distributions can be difficult to quantify because of trophic interactions. Most studies that address ecological interactions with jellyfish use remotely sensed surface chlorophyll *a* concentrations as a proxy for the presence of jellyfish (Hays et al. 2006, Fossette et al. 2010b, Bailey et al. 2012); however, the surface signal of chlorophyll *a* may not always be valid. For example, trophic interactions with zooplankton may suppress the chlorophyll *a* signal in the location of the jellyfish, or a phytoplankton bloom may not overlap in time and space with zooplankton (Mackas and Boyd 1979, Lucas et al. 2012). Although no proxy is ideal, satellite derived chlorophyll *a* concentrations only measure surface concentrations, when it has been shown that phytoplankton blooms can occur subsurface out of the range of satellite instrumentation (Gould and Wiesenburg 1990, Richardson et al. 2000, Perry et al. 2008). Although remote sensing-based observations are wide spread and easily accessible, they have limitations; therefore, a more comprehensive environmental approach that combines satellite and *in situ* data should produce a better representation of jellyfish distribution patterns.

Jellyfish data are limited and inconsistent in most regions of the world (Brotz et al. 2012). The study and quantification of jellyfish is difficult because of their fragile bodies and high water content (Hamner et al. 1975, Remsen et al. 2004, Doyle et al. 2007). A small number of regions have time series data on jellyfish populations (Condon et al. 2013) where larger ecological questions are being addressed (Uye and Ueta 2004, Milisenda et al. 2014, Decker et al. 2014, Quiñones et al. 2015, Robinson et al. 2015). The need for continued monitoring and investigations on jellyfish is crucial to managing the health of the ocean’s ecosystems (Richardson et al. 2009, Purcell 2011, Brodeur et al. 2016).

Biophysical models that incorporate multiple parameters can provide a better prediction to the location and density of jellyfish where observational data are lacking. Several biophysical models have been developed to address the movement and abundance of jellyfish in terms of regime shifts and climate oscillations (Brodeur et al. 2008, Decker 2010). Decker et al. (2007) produced a jellyfish predictive model for the Atlantic sea nettle (*Chrysaora quinquecirrha*) based on temperature and salinity in Chesapeake Bay that is available on NOAA’s National Weather Service, Ocean Prediction Center website, and was later included in the Chesapeake Bay Ecological Prediction System (CBEPS) which forecasts physical, biogeochemical and organismal data (Brown et al. 2013). To date, a jellyfish biophysical model has not been developed for the Gulf of Mexico (GoM), possibly due to its large extent and dynamic ecosystems (Robbins et al. 2009, Salmeron-Garcia et al. 2011). An understanding of the environment is essential to producing an effective biophysical model.

A distinct environmental shift occurs in the northern Gulf of Mexico (nGoM) around Mobile Bay, AL and the submarine Desoto Canyon. In this area, the continental shelf shortens and the reach of the Mississippi River plume is lessened (Morey et al. 2003). From this point westward, the coastline contains many estuaries, marshes, and barrier islands and is dominated by riverine input. The consistent input of freshwater leads to a dynamic state of mixing water masses (Morey et al. 2003, Zavala-Hidalgo et al. 2003). Here the waters are turbid from the high amount of suspended particulate matter deposited from the Mississippi River system (Huh et al. 2001). The nutrient input from the Mississippi River supports high productivity and its reach changes seasonally based on the prevailing winds and currents (Morey et al. 2003). Salmeron-Garcia et al. (2011) showed distinct differences in the chlorophyll *a* concentrations between regions dominated by Mississippi River discharge and eastern region in the nGoM in space and time. East of the Mobile Bay/Desoto Canyon divide, herein referred to as the eastern nGoM, the shelf is large and shallow, and is influenced by the prevailing winds and the Loop Current circulation (Robbins et al. 2009). The nutrient levels are more oligotrophic compared to the western region. Seasonal changes that occur in the physical environment (e.g. temperature, salinity) also have an impact on the occurrence and distribution of jellyfish species. In the nGoM, the prevalent large medusae are *Chrysaora quinquecirrha* (sea nettle; herein referred to as *Chrysaora*) in the summer months and *Aurelia* spp. (moon jellyfish; herein referred to as *Aurelia*) in the fall (Graham 2001, Robinson and Graham 2013).

In efforts to expand the ecological knowledge of jellyfish in the productive waters of the nGoM, this study assessed density data for two jellyfish (*Chrysaora* and *Aurelia*) during the summer and fall seasons in order to determine the environmental parameters that can be used to model their distribution patterns within the nGoM. This investigation used multiple oceanographic datasets to determine how their changes affect jellyfish densities, and to compare the descriptive power of satellite measurements versus *in situ* measurements. Knowledge of jellyfish densities could assist in the management of some of the many anthropogenic interactions, both economically negative effects caused by jellyfish and detrimental effects on species that benefit from the presence of jellyfish, which occur in the nGoM.

3.2 Methods

3.2.1 Data

Jellyfish data were assembled for two scyphozoan medusa, *Chrysaora* and *Aurelia,* collected during the groundfish survey cruises of the Southeast Area Monitoring and Assessment Program (SEAMAP) from 2003 to 2013 (Stunz et al. 1985). Data for the west coast of Florida began in 2008. Individual trawl specimen counts were converted to density measurements using the water column trawl depth and volume filtered to determine jellyfish density (ind m^{-2}). The oceanographic *in situ* data collected concurrently with the groundfish trawls were also obtained from the SEAMAP database. Remote sensing data were gathered from NASA's Ocean Color WEB (oceancolor.gsfc.nasa.gov; MODIS-Aqua, L3, 4km resolution, 8day), the Physical Oceanography Distributed Active Archive Center (PO.DAAC; podaac.jpl.nasa.gov; OSCAR, L4, 1 degree), and E.U. Copernicus Marine and Environment Monitoring Service (CMEMS; marine.copernicus.eu; delayed time, global, allsat). The Open-source Project for a Network Data Access Protocol (OPeNDAP) software framework (http://www.opendap.org) was used to acquire the data from the satellite databases mentioned. Due to the varying resolution scale of the satellite data obtained, the spatiotemporal satellite grid that contained the specific time and coordinates of the jellyfish collection was used.

Data were further processed to correct for autocorrelation and skewness. A variance inflation factor (VIF) analysis was used to test for collinearity and eliminate any redundant variables. The only variables found to be correlated were the *in situ* environmental parameters measured at different depths (e.g. surface temp., mid-depth temp., max-depth temp.) but they were retained in the pool of variables to be used independent of each other to discern if different sections of the water column were more descriptive to the distribution of jellyfish and to help evaluate the comparison between the remote sensing and *in situ* models. To correct for the extreme skewness of certain data (Sharipo-Wilks and Kolmogorov-Smirnov tests), log transformations (log(n+1)) were applied to the environmental parameters: chlorophyll *a* concentrations, light attenuation, normalized fluorescent line height (standard measurement to discern living organisms from detritus; Gower and Borstad, 1981) and distance from shore, as well as the response variable, jellyfish density. The jellyfish density exhibited extreme skewness and a high amount of variance, so the log transformation was applied to reduce the skewness. Not transforming the density also gave nonsensical adjusted R^2 values. The complete list of oceanographic variables and their abbreviations are given in Table 3.1.

All data was sorted by month into two time windows, summer (June and July) and fall (October and November), due to the timing of the SEAMAP cruises. Using ArcGIS (v 10.3; Esri), the jellyfish combined densities (herein referred to as the observed data) were mapped to a 25 x 25 km fishnet grid, and all oceanographic variables were averaged to within the grid cells. This grid size was chosen to correct for the inconsistent catch effort across the northern Gulf, yet still retain detailed local distributions. Jellyfish species data were included as a binary presence/absence variable for each grid cell. Two Gulf-wide seasonal models (summer and fall) were constructed that incorporated the entire continental United States coastline in the GoM. The data were then separated into the west region and east region at longitude 87.9°W, roughly Mobile Bay, AL, to account for the environmental shift across the nGoM. This separation led to the development of four distinct regional models: summer west (SumW), summer east (SumE), fall west (FallW), and fall east (FallE).

Table 3.1 Oceanographic Variables for Jellyfish Biophysical Model

Variable Name	Abbreviation	Units
Remote Sensing Variables		
Chlorophyll *a* Concentration	chlor_a	mg m^{-3}
Sea Surface Temperature	sst	°C
Colored Dissolved Organic Matter	cdom	m^{-1}
Diffuse Attenuation Coefficient (@490 nm)	Kd	m^{-1}
Photosynthetically Available Radiation	par	E m^{-2} day^{-1}
Normalized Fluorescence Line Height	nflh	mW cm^{-2} um^{-1} sr^{-1}
Sea Level Height Anomaly (positive, negative)	sla_pos, sla_neg	cm
Surface Current Velocities (zonal, meridional)	zonal, meridional	cm s^{-1}
Surface Speed	surfspeed	cm s^{-1}
Eddy Kinetic Energy (positive, negative)	eke_pos, eke_neg	cm^2 s^{-2}
Distance from Shore	shoredist	m
Sea Surface Temperature Horizontal Gradient	gsst	°C per degrees (North/West)
***In situ* Variables**		
Water Temperature (surface, mid, max depth and vertical gradient)	TEMPSURF, TEMPMID, TEMPMAX, VGTEMP	°C
Salinity (surface, mid, max depth and vertical gradient)	SALSURF, SALMID, SALMAX, VGSAL	ppt
Oxygen (surface, mid, max depth and vertical gradient)	OXYSURF, OXYMID, OXYMAX, VGOXY	ppm
Chlorophyll *a* (surface, mid, max depth and vertical gradient)	CHLSURF, CHLMID, CHLMAX, VGCHL	mg m^{-3}
Turbidity (surface, mid, max depth and vertical gradient)	TURBSURF, TURBMID, TURBMAX, VGTURB	Percentage (%)
Maximum Water Depth	DEPTHMAX	m

Description of all variables used in the generalized additive models (GAMs), separated by collection method: remote sensing and *in situ*.

3.2.2 Model Development

The following model development steps were completed independently for each of the 6 models described above and implemented in R software (v 3.2.4 revised; R Core Team 2016). The oceanographic variables were pre-screened for predictive power by calculating the Information Value (IV; Larsen 2015; multithreaded.stitchfix.com) utilizing the R package ‘Information’ (Larsen 2016). Briefly, the IV tests the univariate strength of the variable by calculating the weighted sum of all the weight of evidence (log-odds + log-density ratio) for each predictive variable. A negative IV result eliminated the variable from the analysis. The remaining predictive oceanographic variables were divided based on the collection method, remotely sensed (RS) or *in situ* (IS) and a third method which included both the RS and IS descriptive variables to produce an all-parameter method (AP). The use of different methods (RS, IS, AP) were chosen to determine if there was a difference in the functionality of data sources and their potential for broader use. For example, if the RS methods produced similar results to the IS and AP methods then a RS model could be used more frequently and possibly on a wider area because of the availability of the data. The use of exclusively *in situ* variables could help determine the importance of below sea surface variables, which has been shown to be descriptive in jellyfish models, particularly in regions where stratification occurs (Liu et al. 2010).

A generalized additive model (GAM; Hastie and Tibshirani 1990) was applied to describe the relationship between the oceanographic variables and the log density of jellyfish by using the ‘mgcv’ R package (Wood 2011). A GAM analysis is a nonparametric regression where cross-validation is included in the model selection and the functional relationships are determined by the data via smoothing. The restricted maximum likelihood (REML) optimizing method was used along with a thin plate regression spline and a Tweedie distribution. Forward selection was used to retain any descriptive variables that improved model performance (increased the deviance explained, or decreased the REML value). Descriptive variables were determined for each genera of jellyfish using a variable coefficient model (Hastie and Tibshirani 1990), which is commonly used in ecological studies to account for heterogeneity in species abundance (Zuur et al. 2009). Variable interactions (f(x,y)) were tested to further optimize the model fit and, finally the best fit GAM was chosen by the lowest Akaike Information Criterion (AIC) value. A RS, IS, and AP GAM was constructed for each model.

Each model was run for a total of 500 iterations each time using a randomly selected 80% of the data to train the model, which described the remaining 20%. The selection of 500 iterations was based on the time to stability and an adequate predicted output for each grid cell. Any model density output greater than 50 log ind m^{-2} was flagged as an infinity value and removed from the analysis. The resulting density predictions, deviance explained (DE), r-squared values (R^2), estimated degrees of freedom (EDF), and residual sum of squares (RSS) were averaged and reported for each method to express the fit of each descriptive model. The overall average density and standard error of each model was calculated to compare the magnitude of the density provided by the models to the magnitude of the observed data. The descriptive models were mapped using the average predicted GAM log density from the 500 iterations. The jellyfish log density color scale was segmented in 0.25 ind m^{-2} intervals with the initial segment between 0 and 0.0001, representing a value less than 1 jellyfish. Missing grid cells represent a location where data was missing and no density was calculated.

3.3 Results

The general trend from the observed data show a higher average density of jellyfish in the fall (0.58 ± 0.04 log ind m^{-2}) compared to the summer (0.16 ± 0.01 log ind m^{-2}) (Fig. 3.1). In both seasons, the abundance was greater closer to the shoreline and most dense patches appear adjacent to fresh water inputs (Fig. 3.1). The regional division applied to the nGoM shows a difference in jellyfish density between the west and east region. The average regional densities for the summer were 0.26 ± 0.02 log ind m^{-2} for the west and 0.03 ± 0.01 log ind m^{-2} for the east, and the fall regional densities were 0.52 ± 0.04 log ind m^{-2} for the west and 0.67 ± 0.07 log ind m^{-2} for the east. In summer, the presence of *Chrysaora* (n= 127) was concentrated in the western region of the nGoM (Fig. 3.2A). The total presence of *Aurelia* (n=136) in the summer was lower compared to *Chrysaora* in the west, but was more abundant in the east (Fig. 3.2A). Less abundant in the fall season, *Chrysaora* (n= 93) were distributed throughout the nGoM but were clustered along the shoreline. *Aurelia* presence was dominant over the entire nGoM shelf during the fall (n=268; Fig. 3.2B). The overall highly variable densities reported reflect the patchy distribution of jellyfish.

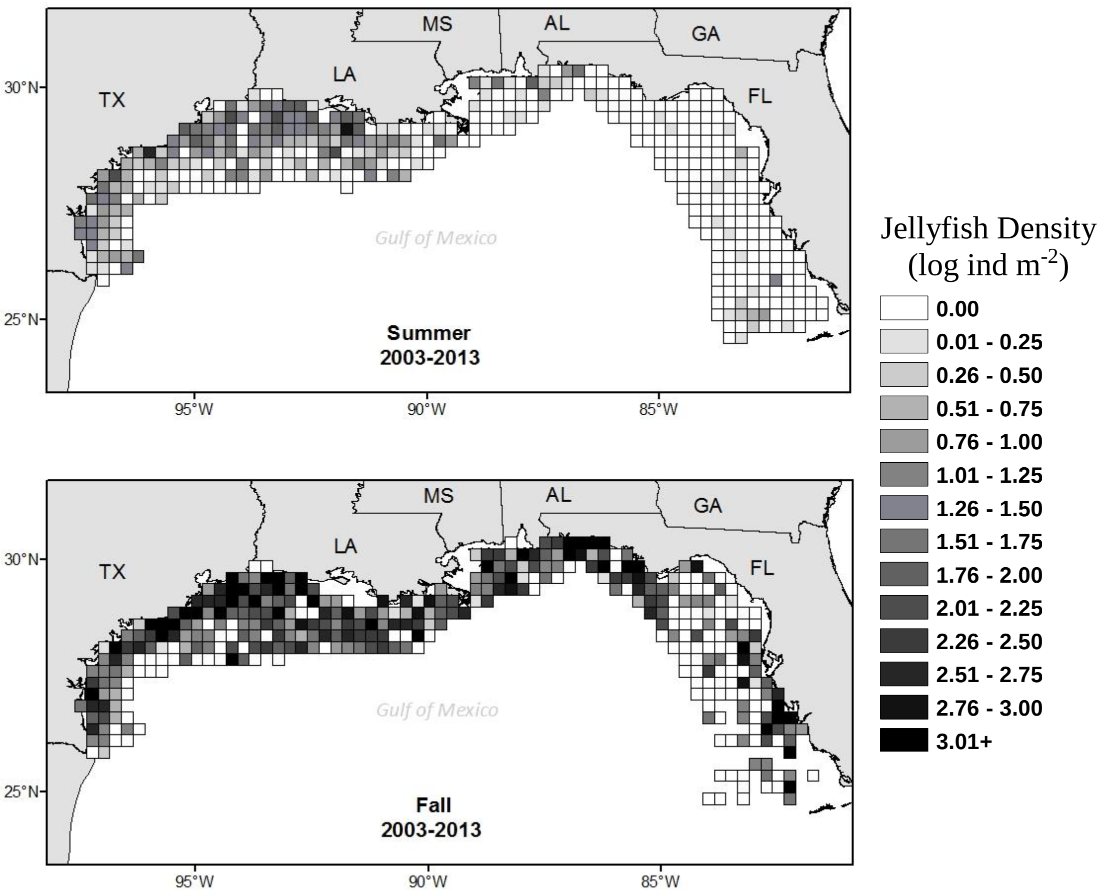


Figure 3.1 Jellyfish densities for summer and fall

Combined jellyfish densities (*Chrysaora* and *Aurelia*) from the SEAMAP survey database (averaged in 25 x 25 km grid) for **A)** summer and **B)** fall in the northern Gulf of Mexico.

Gulf-wide seasonal models had a lower descriptive fit than the regional models (Table A.3 in Appendix A). These models were unable to predict any zero density grid cells and underestimated the high density grid cells seen in the observed data. The summer gulf-wide model produced a nearly homogeneous distribution east of Louisiana (Fig. A.1), and the fall used variables that were descriptive in the western half of the nGoM and left a large amount of missing grid cells in the eastern half (Fig. A.2). These results support the notion that the high abundance of jellyfish in the west was driving the descriptive power of the models. This abundance difference seen in the observed density between the east and the west regions supports the application of regional models verses a Gulf-wide model. Therefore, because the Gulf-wide seasonal models produce results that were less descriptive than the regional models, they were excluded from the subsequent analysis.

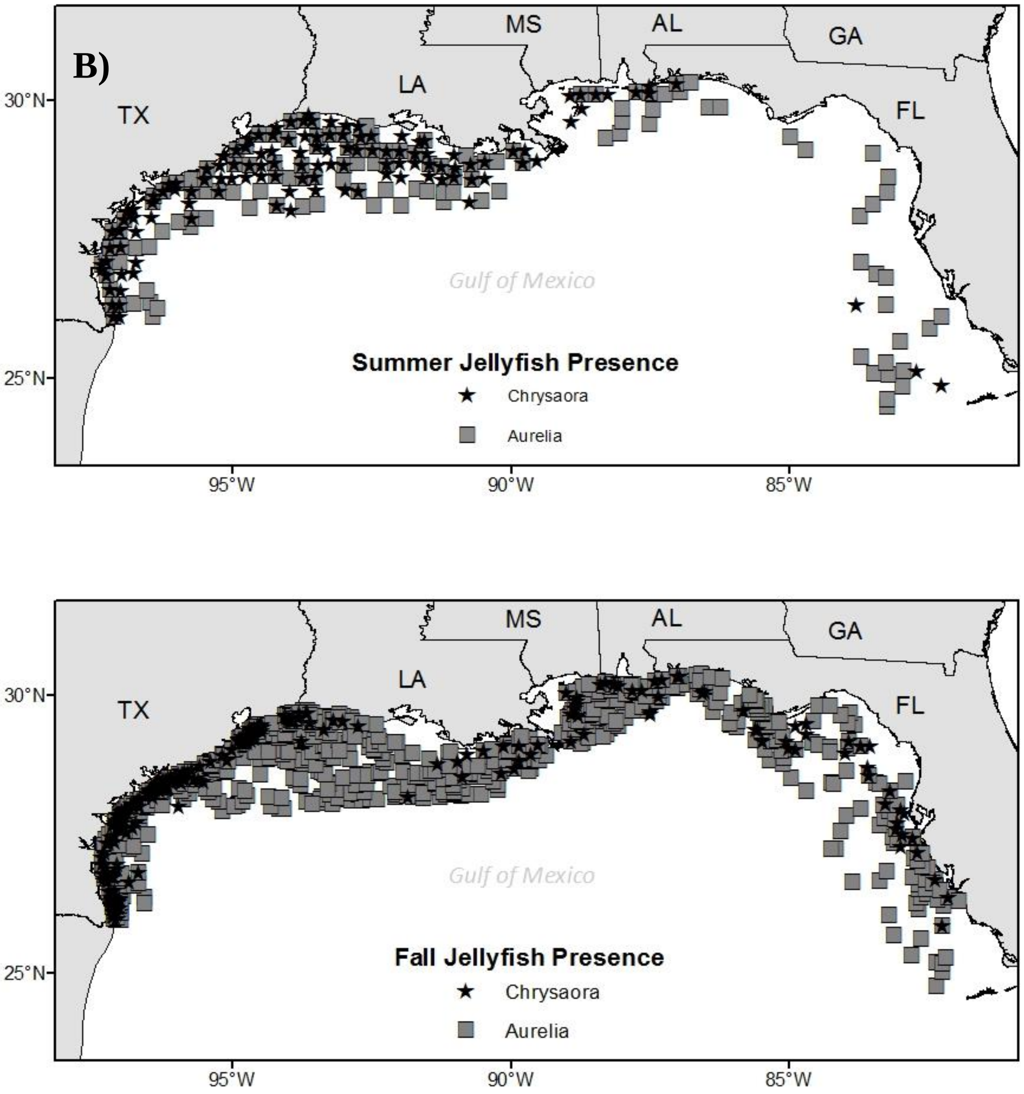


Figure 3.2 Presence data for *Chrysaora* spp. and *Aurelia* spp.

Location of sampling presence for *Chrysaora* and *Aurelia* jellyfish from 2003-2013 during the **A)** summer and **B)** fall.

3.3.2 Descriptive Variables

No single variable was found to be descriptive in every regional model; however, relationships with certain oceanographic features were apparent. A measurement of salinity was included in every model, and chlorophyll *a* concentration, surface currents, temperature and distance from the shoreline were components in 3 of the 4 models (Table 3.2). Even though the specific variable changed (i.e. mid-depth salinity vs. vertical salinity gradient), the continuous presence of a feature was taken to show its importance to the distribution and abundance of jellyfish in the nGoM. All *in situ* variables found to be descriptive were measurements taken at depth (mid or max), with the exception of surface turbidity in the SumW model. Between the two jellyfish genera, distance to shore was exclusively used and chlorophyll *a* concentrations were dominant when describing *Aurelia* distributions. More variables were also required to describe the distribution of *Aurelia* compared to *Chrysaora* (Table 3.2).

Table 3.2 Descriptive Variables for Regional Jellyfish Biophysical Models

		Aurelia	*Chrysaora*
Summer West			
	RS	chlor_a, zonal*	eke_pos, chlor_a
	IS	TEMPMAX, CHLMAX, SALMID	TEMPMAX, TURBSURF*
	AP	chlor_a, zonal*, TEMPMAX, CHLMAX, SALMID	eke_pos, chlor_a, TEMPMAX, TURBSURF*
Summer East			
	RS	zonal, shoredist, cdom,	zonal, cdom
	IS	CHLMAX, SALMAX, DEPTHMAX	DEPTHMAX
	AP	zonal, shoredist, cdom, CHLMAX, SALMAX	cdom, DEPTHMAX
Fall West			
	RS	chlor_a, cdom, shoredist, sla_pos	par
	IS	DEPTHMAX, CHLMID, SALMAX, OXYMID	VGOXY, TEMPMAX
	AP	(chlor_a, CHLMID), cdom, shoredist, sla_pos, DEPTHMAX	TEMPMAX
Fall East			
	RS	sst, shoredist, (zonal, eke_pos)	(zonal, eke_pos)
	IS	VGSAL, TEMPMID	VGSAL
	AP	sst, shoredist, TEMPMID	(zonal, eke_pos), VGSAL

Variables selected by the GAMs to describe the density distribution of jellyfish, separated by region, method (remote sensing, *in situ*, and all-parameter), and genera of jellyfish. () indicates interaction used between variables. * indicates smoother not factored by a genera of jellyfish. Variables defined in Table 3.1.

Dynamic relationships were observed between the jellyfish density and the descriptive oceanographic variables (Fig. 3.3). Jellyfish density increased with salinity, and steeper vertical salinity gradient. Zonal surface currents associated a higher density of jellyfish with westward currents. In the eastern region, distance from shore had a negative trend with the density of *Aurelia*; however, the west had no apparent trend across the shelf. In the SumE model, the DEPTHMAX variable followed the same trend as the distance from shore for *Aurelia*, but had a hump-shaped trend for *Chrysaora* with a peak in density around 50m deep. Temperature had a positive effect on *Chrysaora* densities, suggesting their density increases with higher temperatures. The reverse occurred with temperature and the density of *Aurelia*. Chlorophyll *a* concentrations had a varying affect in the different regions as well as whether remotely sensed or measured *in situ*. Other relationships revealed included a positive trend with eke_pos for both species, and the positive trend for *Aurelia* with sla_pos, suggesting mesoscale eddies are important for aggregated jellyfish in the nGoM (Fig. 3.3).

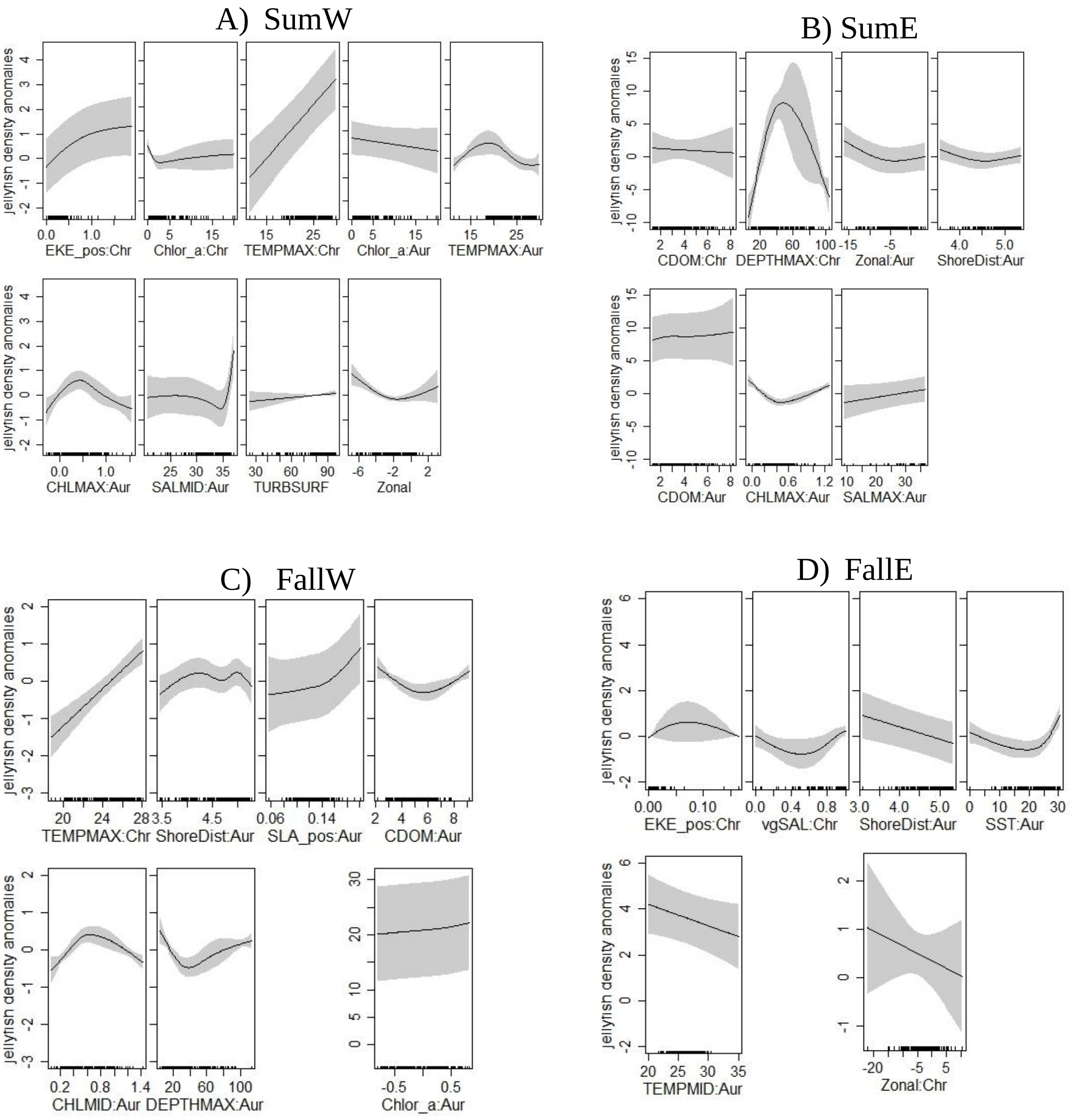


Figure 3.3 GAM descriptive variable relationships

Relationship between the changes in jellyfish log density and the descriptive variables used in the all-parameter (AP) regional models. Grey area indicates the 95% confidence intervals. Variables defined in Table 3.1 and :Chr/:Aur represents which genera the variable was applied to (Chr =*Chrysaora*, Aur =*Aurelia*).

3.3.3 Model Fitness

The AP method provided the best fit for each model, shown in the output values of average DE and adjusted R^2 (Table 3.3). The AP method used more independent variables than the RS and IS methods (ranged from 6-9), and therefore had a higher average EDF. In the fall, the AP method resulted in the lowest RSS which expresses a better precision between the observed and predicted jellyfish densities. The higher RSS observed in the summer models, especially the SumE, was most likely due to the limited number of non-zero data grid cells, which caused some iterations to be trained with or describe only all zero grid cells. The IS method described the jellyfish densities slightly better in 4 of the 6 models and was within 1% DE of the RS method in the remaining 2 models (Table 3.3). However, no distinct trend was observed in the differences of the fit between regional or seasonal IS and RS methods. All models underestimated the observed extreme high densities and slightly overestimated the density of jellyfish in true zero density grid cells (Fig. 3.4 & 3.5).

Table 3.3 GAM results for the regional Gulf of Mexico models

		DE	R^2	EDF	RSS
Summer West					
	RS	60.4 (0.12)	0.54 (0.002)	8.6 (0.04)	3.4 (0.12)
	IS	65.6 (0.11)	0.59 (0.001)	10.7 (0.03)	2.4 (0.18)
	AP	73.2 (0.12)	0.75 (0.002)	13.8 (0.07)	6.1 (0.96)
Summer East					
	RS	92.7 (0.08)	0.79 (0.004)	6.7 (0.07)	3.5 (1.3)
	IS	91.8 (0.07)	0.71 (0.004)	6.5 (0.05)	5.3 (2.6)
	AP	96.6 (0.06)	0.94 (0.002)	9.5 (0.09)	18.0 (5.8)
Fall West					
	RS	82.3 (0.11)	0.58 (0.002)	10.4 (0.04)	7.9 (0.15)
	IS	82.4 (0.13)	0.54 (0.002)	12.1 (0.05)	7.6 (0.19)
	AP	82.4 (0.09)	0.67 (0.003)	18.5 (0.08)	6.7 (0.19)
Fall East					
	RS	70.3 (0.14)	0.63 (0.002)	5.2 (0.03)	12.9 (0.20)
	IS	72.2 (0.13)	0.63 (0.001)	6.0 (0.03)	13.8 (0.22)
	AP	76.8 (0.13)	0.75 (0.001)	7.2 (0.03)	10.6 (0.19)

GAM output results (mean (standard error)) for deviance explained (DE), adjusted r-squared (R^2), estimated degrees of freedom (EDF) and residual sum of squares (RSS) from 500 iterations of remote sensing (RS), *in situ* (IS) and all-parameter (AP) methods.

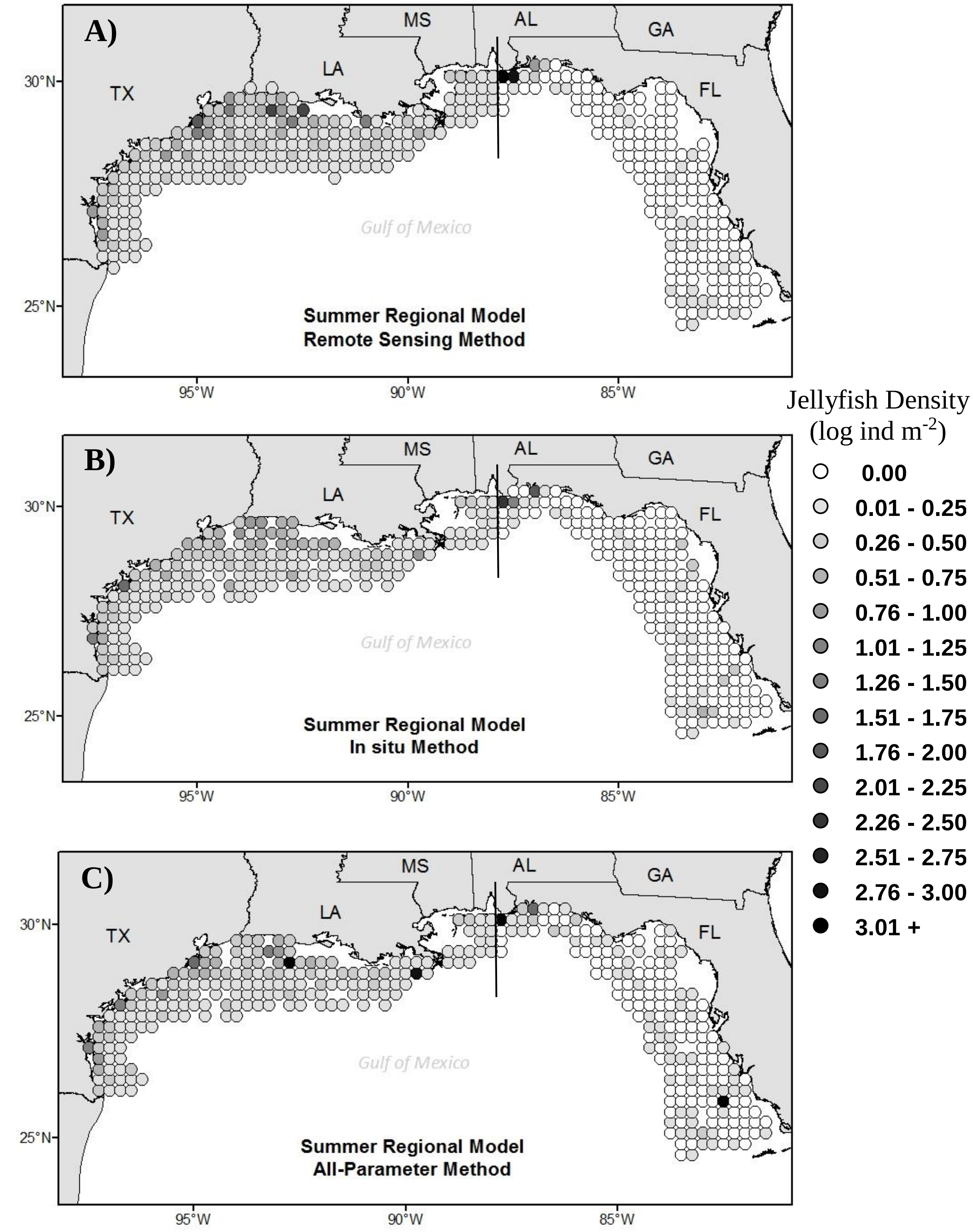


Figure 3.4 Summer regional jellyfish density GAM results

Summer regional jellyfish density GAM results for the **A)** remote sensing (RS), **B)** in situ (IS) and **C)** all-parameter (AP) methods. Each figure contains both the west and east models, separation shown by the vertical black line.

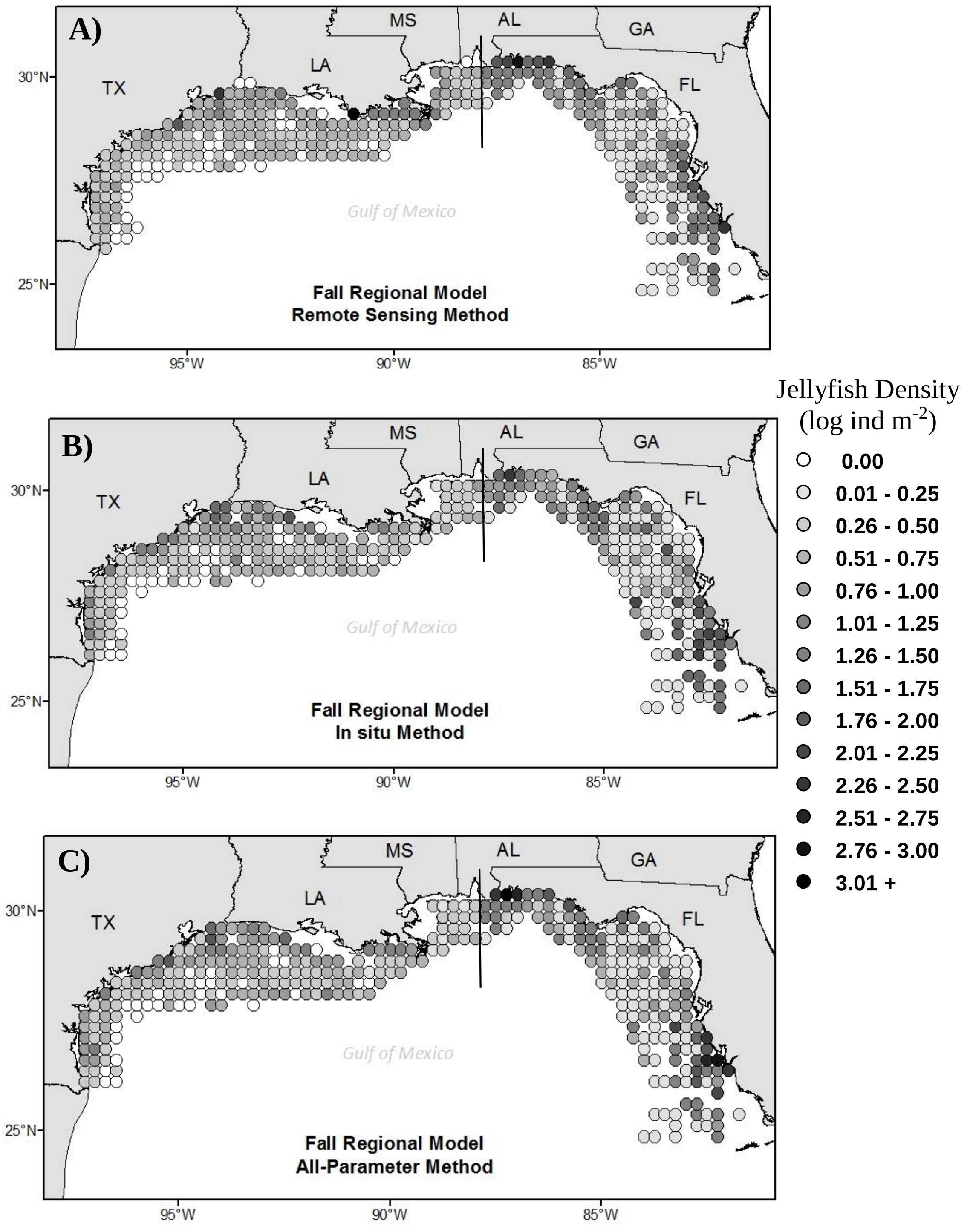


Figure 3.5 Fall regional jellyfish density GAM results

Fall regional jellyfish density GAM results for the **A)** remote sensing (RS), **B)** in situ (IS) and **C)** all-parameter (AP) methods. Each figure contains both the west and east models, separation shown by the vertical black line.

The regional models produced well-fit descriptions of the observed data based on the DE (73-96% for the AP method) and adjusted R^2 (0.67-0.94 for the AP method) (Table 3.3). The east models performed well in replicating the extreme variation of densities and describing the hotspots of high jellyfish density. The west models were adequate in describing zero density grid cells, but were unable to match the magnitude of high density areas (Fig. 3.4 & 3.5). With a more evenly distributed density, the models had significantly different variances (F-test, $p<0.05$) than the observed data, except in the SumW RS and AP models. Overall, the models produced significantly similar medians of density (Kruskal-Wallis test, $p<0.05$), but lower total density for the regions, with the exception of SumE where a greater density was described due to the overestimation of the zero grid cells. Although models underestimated the magnitude of the observed high densities, they were able to describe the similar distribution trends within the regions (Fig. 3.6).

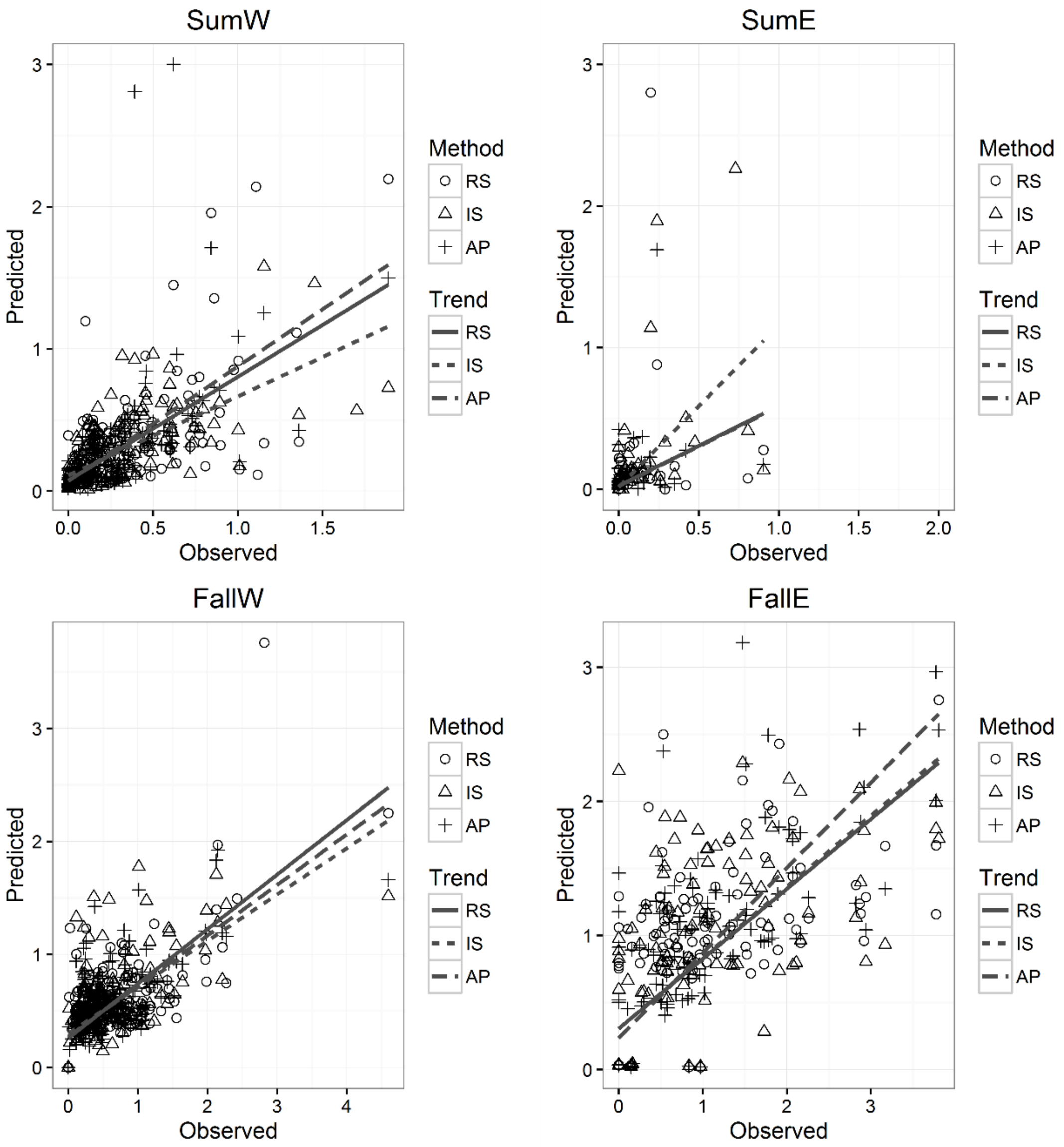


Figure 3.6 Predicted vs. observed jellyfish densities

Predicted vs. observed jellyfish densities (log ind m^{-2}) for the three methods (remote sensing, *in situ*, and all-parameter) used to describe the regional models.

The use of the consistent density scale, described in the methods, to visualize the data, restricts the visualization of the trends in the model outputs because of their lower densities. Therefore, as an example, the model output densities for the Fall AP method were scaled to the minimum and maximum densities reported, making the distribution trends visually apparent (Fig. 3.7).

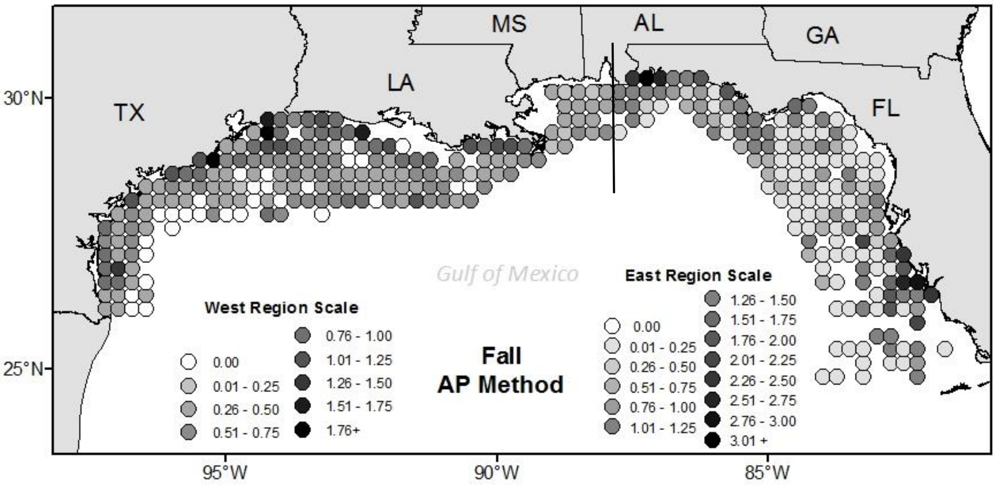


Figure 3.7 Scaled fall regional model

Fall regional map for the all-parameter (AP) method with each region (west/east; separated by vertical black line) scaled to the highest predicted jellyfish density (log ind m^{-2}).

3.4 Discussion

The regional models determined that the most descriptive factors for describing the distribution of jellyfish in the nGoM were salinity, surface currents, temperature, chlorophyll *a* concentration, and distance from shore. Similar variables were used to describe the two jellyfish genera within each region (Table 3.2). The models were able to reproduce the distribution trends seen in the observed data, specifically the locations of high density and the general increase of density closer to shore. The predicted density values were lower than the observed data, which lead to differences the amount of variance.

3.4.1 Effects of Oceanographic Features

The influence of salinity, surface currents, temperature, chlorophyll *a* concentration, and distance from shore are consistent with current knowledge of jellyfish distribution drivers. Both salinity and temperature impact jellyfish density and distribution by regulating asexual reproduction, growth rates, and predator-prey interactions (Bamstedt et al. 1999, Purcell 2005, Lucas et al. 2014). Salinity and temperature were the only two predictive measurements used in the Chesapeake Bay jellyfish model (Decker et al. 2007), and temperature has been included in distribution models produced for the Bering Sea (Brodeur et al. 2008, Liu et al. 2010). Similar to the findings in these reports, salinity had a positive relationship with jellyfish in this study. The relationship with temperature was different between the two genera in the nGoM. An increase in temperature was associated with a greater density of *Chrysaora*, which supports their prevalence in the warmer summer season. Conversely, *Aurelia* were more abundant as temperatures decreased, which follows the cooling trend from summer to fall when *Aurelia* were dominant across the nGoM.

The presence of chlorophyll *a* was found to be descriptive of the density and distribution of jellyfish in the nGoM. The chlorophyll variables were more descriptive for *Aurelia* than *Chrysaora* (Table 3.2), and varied depending on season and region. The descriptive power of chlorophyll *a* found here is not in agreement with the analysis of global cnidarian biomass predictors, nor was chlorophyll *a* concentrations included in the Bering Sea or Chesapeake Bay biophysical model (Decker et al. 2007, Brodeur et al. 2008, Lucas et al. 2014). However, the resolution of data used in the global model was 5° grid cells which could wash out the fine scale patchy distribution of chlorophyll *a* (Lucas et al. 2014). Although chlorophyll *a* was neglected in the Bering Sea model, zooplankton biomass was included which has a closer trophic relationship to large jellyfish, and was determined to be predictive in the summer model (Brodeur et al. 2008). Several studies have shown the connection between chlorophyll *a* and zooplankton biomass throughout the water column (Grimes and Finucane 1991, Genin 2004, Greer and Woodson 2016), as well as the overlap between gelatinous zooplankton and chlorophyll *a* (Graham et al. 1992, Benson et al. 2007, Greer et al. 2015). Although chlorophyll *a* concentrations were found to be descriptive variables in our model for the nGoM, the varying relationship between chlorophyll and jellyfish makes using the presence of chlorophyll as a proxy for the presence of jellyfish troublesome. A better alternative would be the combination of chlorophyll with additional parameters like salinity and temperature to signal the possible presence of jellyfish.

Distance from shore was only descriptive for *Aurelia*. The majority of the *Chrysaora* biomass was collected close to the shoreline (Fig. 3.2), so the lack of variation in the observed distance to shore may have reduced its descriptive power for *Chrysaora*. Coastal, hard substrate is the typical habitat for the polyp stage of development in these scyphozoan jellyfish; therefore, higher densities of medusae are often observed near the source of new biomass (Lucas et al. 2012, Lucas et al. 2014). Further evidence to explain the differing jellyfish distributions observed between the seasons is the variation in the surface currents. Northerly (coastal) currents in the summer and the southerly currents in the fall (Morey et al. 2003), could lead to the greater density observed across the continental shelf by *Aurelia* in the fall.

The use of drifters amongst similar east and west regions of the nGoM showed high transport and retention time in the west (Morey et al. 2003). The higher density of jellyfish observed with westward currents is consistent with the prevailing westward flow across the Louisiana and Texas shelves (Zavala-Hidalgo et al. 2003) and the seasonal southwestern flow of the GoM in the fall (Morey et al. 2003). Large aggregations of jellyfish can be the result of advection and convergent currents (Graham et al. 2001), and longer residence time of a slow moving water mass that contains jellyfish would lead to a higher local density (Graham et al. 1992). Such entrainment and advection was modeled in the GoM when a large density of the invasive *Phyllorhiza punctata* was present in the nGoM in 2000 (Johnson et al. 2005). Furthermore, the formation of mesoscale eddies and subsequent interactions are a factor in both the western and eastern nGoM regions (Wang et al. 2003, Morey et al. 2003). Eddy circulations can entrain jellyfish and contribute to higher measured densities, which is seen in the presence of positive eddy kinetic energy (eke_pos) as a descriptive variable in the SumW and FallE models. The descriptive power of sla_pos in the FallW model also supports the presence of convergent mesoscale features that can aggregate jellyfish. Since these driving surface currents differ between the two spatial regions, their establishment as a descriptive variable was only observed when the nGoM was divided in the regional models, and may be an essential factor in describing the distribution of jellyfish in the dynamic nGoM waters.

3.4.2 Model Performance

Using oceanographic measurements to describe jellyfish density in the nGoM is complex due to the dynamic environmental conditions. To reconcile some of the complexity, a spatial divide applied east of Mobile Bay, AL (87.9°W) to separate the two overarching ecosystems on the shelf of the nGoM: the eutrophic, river dominated west and the oligotrophic, oceanic east. A similar division of environments has also been applied to effectively address the oceanographic variables affecting jellyfish in the Bering Sea (Brodeur et al. 2008) and fishes in coastal Italy (Bonanno et al. 2016). Furthermore, a similar study investigated the influences of environmental factors on the distribution of shrimp in the nGoM with the development of Gulf-wide GAMs and had a median of DE equal to 33.6% (Drexler and Ainsworth 2013), which are lower than our results for the Gulf-wide model. These investigations show that a universal model for a large area with different underlying abiotic conditions will not obtain the same level of precision as isolating the different environmental regimes. Therefore, understanding the basic environmental conditions and drivers and how they affect jellyfish is key to producing an effective model.

The RS and IS methods produced comparable results amongst the models (Table 3.3). The IS method revealed the importance of the mid and max-depth water column measurements, as they were found to be descriptive variables in all models. Although similar, the slight advantage seen in the fit of most IS models could be explained by the fact that the IS measurements were taken at the time and location of the jellyfish collection. Therefore, they may be more relevant to the jellyfish distribution in the ever changing waters of the nGoM than the satellite measurements, which may not capture the same trends due to the lower temporal and spatial resolution of the data. Nevertheless, the remote sensing or *in situ* data only can provide guidance to jellyfish distributions and density, but if both datasets are available the AP methods are the most descriptive.

The descriptive models produced in this study have multiple applications for further research. These models help to detail the jellyfish distribution in the nGoM and could be used to investigate how changes in environmental conditions would affect jellyfish populations. Seasonally persistent jellyfish aggregations could be recognized with these models for large areas where public and industrial interactions may occur and should be monitored. Density data at this resolution could be used in predator-prey analyses to elucidate distribution overlaps. The output descriptions from this model could also be used to investigate the suggested association between persistent mesoscale eddies and jellyfish density. Conversely, at the resolution presented (25 x 25 km), this model would not be appropriate for sub-grid scale navigational avoidance or forecasting of jellyfish. At this time it is not feasible to construct a predictive model of sufficient time or spatial resolution to be used in ecological management models for higher trophic levels.

Knowledge was gained on the nGoM oceanographic parameters that contribute to the density and distribution of jellyfish in the summer and fall, but continued work would be advantageous. Future improvements to the model could include a finer resolution of the spatial grid as well as the satellite data to alleviate some of the averaging in the distribution and could allow for the evaluation of smaller regions of the coastline. The addition of other oceanographic variables like zooplankton biomass and mixed layer depth, which were excluded from this analysis due to lack of data across the study area, could provide a better fitting model. Lastly, with the collection of more data, models could be developed independently for specific jellyfish species or fit to include more species to investigate if certain oceanographic variables differently affect co-occurring jellyfish or jellyfish that are temporally separated.

CHAPTER IV – Body Composition and Energy Density of the Pink Meanie (*Drymonema larsoni*) in the northern Gulf of Mexico with Implications to Leatherback Sea Turtle Foraging

4.1 Introduction

Knowledge of body composition and energy density is important when addressing ecological interactions such as food web dynamics and the transfer of energy. An organism's water content and percentage of inorganic ash is inversely proportional to its nutritional value and energy content (Doyle et al. 2007). Foraging success has been shown to be optimized by targeting prey that is the most nutritionally advantageous (DeMott 1989, Duffy and Paul 1992, DeMott 1995, Plath and Boersma 2001). Gelatinous zooplankton characteristically have high water and low carbon content (Lucas et al. 2011, Kiørboe 2013), yet have been shown to play a dynamic role as predators, prey, competitors for resources, and as protection or shelter for smaller organisms in many ecosystems (Broduer et al. 2008, Pauly et al. 2009, D'ambra et al. 2015, Hays et al. 2012, Milisenda et al. 2014, Robinson et al. 2015). Despite their trophic interactions and importance to the diet of leatherback turtles, data are lacking on the caloric composition of many jellyfish species.

The Gulf of Mexico (GoM) has approximately 117 species of Medusozoans (herein referred to as jellyfish), 16 of which are scyphomedusae (Segura-Puertas et al. 2009). In northern GoM, the most seasonally-abundant, large medusae are *Aurelia* spp. and *Chrysaora quinquecirrha.* However, over the last two decades, sightings of the genus *Drymonema* have increased in the northern GoM. Among the scyphozoans that inhabit the GoM, *Drymonema* sp. appears to be the largest jellyfish and have a greater body mass and denser tissue, specifically in the oral arms and gonads, which are nutrient rich (Doyle et al. 2007). *Drymonema* spp. are rarely occurring, and therefore can often be misidentified or mistaken for more common species such as *Cyanea* spp. Because of its elusive nature, very little is known about the ecology of this family.

Only a few taxonomic and ecological studies of *Drymonema* spp. have been conducted worldwide. Bayha and Dawson (2010) define the scyphozoan family, Drymonematidea, which includes three species: the Mediterranean based *Drymonema dalmatinum*, *Drymonema gorgo* from South America, and a new species, *Drymonema larsoni*, from North America. Prior to the late 1980's, only sporadic observational data had been recorded. Since then, a few ecological studies have been conducted when large densities were observed, addressing their diet and occurrences (Larson 1987, Williams et al. 2001, Bayha et al. 2012, Malej et al. 2014). Similar to other scyphozoans, the production of *Drymonema* medusae are presumably influenced by oceanographic parameters like temperature and salinity. However, due to their seemingly erratic pattern of abundance, *Drymonema* spp. production may also be a biological response to a high availability of prey (Bayha and Dawson 2010). In the Mediterranean, observations of *D. dalmatinum* were predicted on a cycle of approximately 30 years (Stiasny 1940), which differs from cycles of other jellyfish that are known to be primarily driven by abiotic factors only (~12 year cycle; Stiasny 1940, Kogovšek et al. 2010). Irregular observations in the western Atlantic Ocean (reviewed by Bayha and Dawson 2010), presented similar challenges to determining the distribution, abundance, and ecological impacts of these large medusae.

Drymonema larsoni ("pink meanies") are found in the western Atlantic Ocean along the coast of the U.S., Bermuda, the Caribbean Sea, and the GoM (Bayha and Dawson 2010). They have been measured to have bell diameters up to 111 cm and have been observed to be as large as 200 cm (Williams et al. 2001). *Drymonema* spp. feed almost exclusively on species of *Aurelia* (Larson 1987, Williams et al. 2001, Bayha et al. 2012). Isotopic analysis showed that approximately 85% of the *D. larsoni* diet in the northern GoM was *Aurelia* spp. (D'ambra 2012). *D. larsoni* has also been found with an average of 2.7 *Aurelia* medusae captured with a determined digestion time between 2-3 hours (Bayha et al. 2012). To jellyfish predators the difference in size and potential nutrition could be an important advantage if *D. larsoni* is available and selectively preyed upon. Furthermore, a diet containing *D. larsoni* provides the opportunity for jellyfish predators, like the leatherback, to possibly consume multiple species at one time if *Aurelia* spp. are captured in oral arms or digestive tissue of *Drymonema* spp.

The ecological influences of *D. larsoni* are unknown, so investigation on the temporal distribution and body composition would help elucidate predator-prey interactions and nutritional value. In 2015, leatherback sea turtles were observed to be selectively feeding on *D. larsoni* in the northern GoM (Aleksa et al. in prep). This observation could have a large impact on the energy intake and population dynamics of these turtles. Here, a comprehensive record of *D. larsoni* sightings was gathered for the northern GoM and compared to the biomass of *Aurelia* spp., to investigate if a temporal association is present between high abundance of *Aurelia* spp. and the presence of *D. larsoni* in the GoM. Samples of *D. larsoni* were also collected and processed to calculate body composition, water content, ash percentage, and energy density, to address if a difference in energy density explain help explain selective predation? These data will provide necessary information on the occurrence and nutritional value of a possible ecologically impactful species of jellyfish and their potential role in the diet of leatherback sea turtles.

4.2 Methods

4.2.1 Occurrence of *Drymonema larsoni*

Multiple datasets were utilized to gather information on *D. larsoni* and *Aurelia* spp. in the northern GoM. Data for *D. larsoni* sightings were collected from the Southeast Assessment and Monitoring (SEAMAP) groundfish trawl and plankton survey data (Stunz et al. 1985), Fisheries Oceanography of Coastal Alabama (FOCAL) data (Carassou et al. 2012), jellywatch.org, and literature (Bayha and Dawson 2010, Bayha et al. 2012). Currently no distribution or concentration data exist for *D. larsoni* in the GoM; therefore, the results of this search only represents years when a medusa was observed or collected, which may be an underestimate of actual occurrences. *Aurelia* spp. biomass was gathered from the SEAMAP groundfish trawl data following the methods of Robinson and Graham (2013).

4.2.2 Analysis of Body Composition and Energy Density

The analysis of body composition and energy density was performed on a total of 14 *D. larsoni* specimens which were collected using snorkel gear and a large dip net for from two northern GoM sites during 2016. A single juvenile specimen was collected in September near Horn Island, MS. In October, 13 additional jellyfish were gathered from 2 locations on the coast of Panama City, FL. The first location was the beach approximately 20 meters from shore in water less than 2 meters deep and the second was a large boat basin. Specimens were stored separately in large plastic bags and kept on ice for approximately 12 hours before dissection.

A consistent dissection protocol was followed for each collected specimen. First, the bell diameter and total wet weight was measured, followed by the dissection of organism into oral arms, gonads, and bell sections. A sample of the gonadal tissue was preserved in 80% buffered formalin for gender identification under a compound microscope. Fresh dissected tissue sections were weighed (wet weight), and 5% of each tissue sample by weight (1% for extremely large specimen) was placed in glass jars and freeze dried (Labconco, FreeZone® Freeze Dry System: model 7753020) for 24 hours. The dry weight of the samples were recorded and then combusted at 550 °C for 8 hours (Thermo Scientific, Thermolyne Furnace Benchtop Muffle: Type F48000). The percent water content, revised ash weight, and proximate composition energy density (gross energy density (kJ g Wet Mass^{-1}) = 1.21-0.0132 (revised ash %)) of the tissues and whole animal were calculated using the methods of Doyle et al. (2007). Based on the relationship between percent ash and energy density, a revised ash % that is over 91.7 % calculates a negative energy density. An ANOVA was used to test for significant differences in the mean energy content among tissue types, followed by Tukey’s HSD tests for pairwise comparisons.

4.3 Results

4.3.1 Occurrence

Presence of *D. larsoni* was positively associated with a high biomass of *Aurelia* spp. suggesting a link between predator and prey. Based on published literature, marine databases, as well as citizen science, the first confirmed observation of *D. larsoni* was recorded in 2000 and mid-September has been the earliest recorded sighting date. The first two sighting years (2000 and 2002) occurred during the end of an abundant period of *Aurelia* spp. (Fig. 4.1). Consecutive years of low biomass for *Aurelia* spp. followed from 2003 to 2007, during which no sightings of *D. larsoni* were reported. In 2008, *Aurelia* spp. were back to a similar biomass as 2000 and sightings of *D. larsoni* reappeared. *D. larsoni* occurrences have been consistent in the northern GoM since 2008, corresponding with high abundances of *Aurelia* spp. (Fig. 4.1).

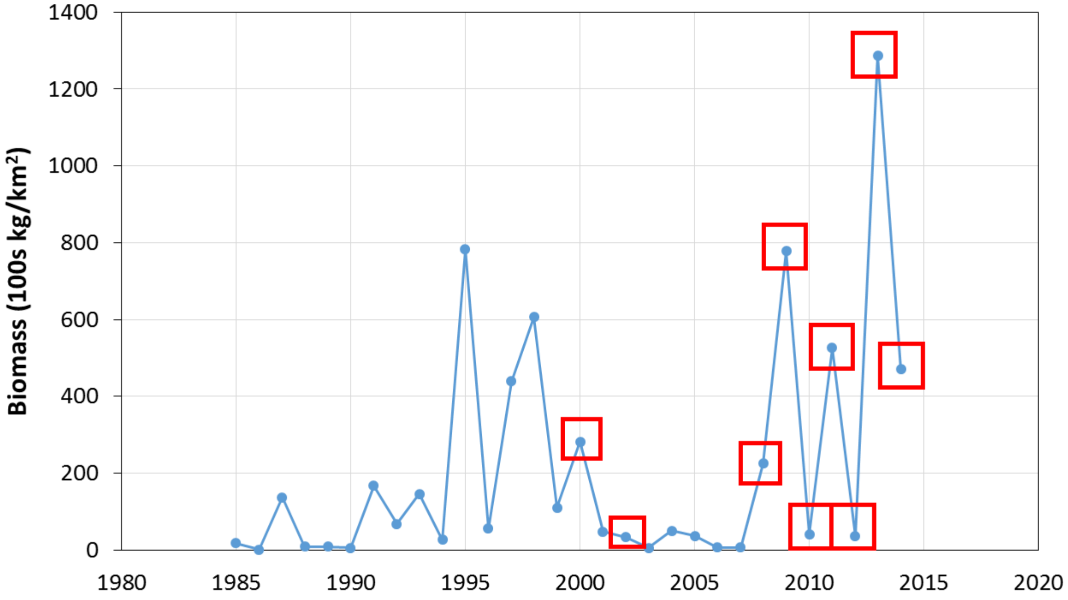


Figure 4.1 Temporal overlap between *Drymonema larsoni* and *Aurelia* spp.

Temporal overlap between sightings of *Drymonema larsoni* (presence denoted with a red box) and biomass of *Aurelia* spp. (blue line) in the northern Gulf of Mexico.

4.3.2 Body Composition and Growth

The 14 *D. larsoni* samples collected had bell diameters ranging from 18 to 45 cm and total wet weights (TWW) between 0.9 and 22.8 kg. The specimen collected were identified as 8 males, 5 females, and one immature juvenile (Fig. 4.2). Investigation of the gonadal tissue showed all females appeared to have already released their eggs.

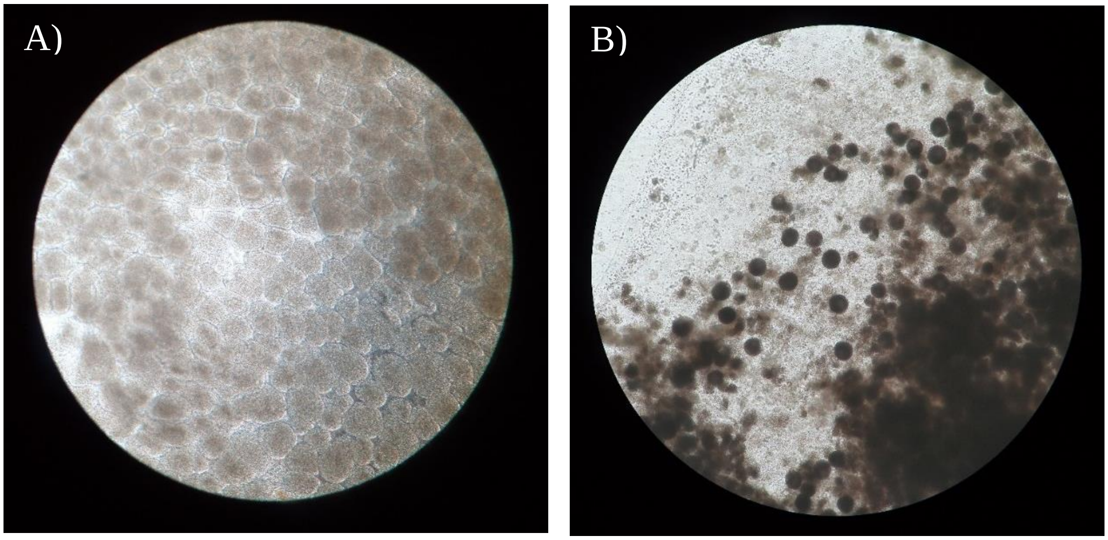


Figure 4.2 Images of *Drymonema larsoni* gonadal tissue

Microscopic images of *Drymonema larsoni* A) male and B) female gonadal tissue.

Based on the wet and dry weights, the three tissue types each represent approximately one third of the total animal (Table 4.1). Mean water content for the whole organism was calculated to be 96.1% ± 0.7%, with no significant difference between the tissue types (Tukey's HSD; $p < 0.05$; Table 4.2). The length-weight relationship for *D. larsoni* was $W = 0.1 L ^\wedge 3.12$ ($r^2 = 0.81$), where wet weight (W) is measured in grams and length (L) is measured in cm (Fig. 4.3).

Table 4.1 *Drymonema larsoni* wet and dry mass measurements

ID	Sex	Bell Diameter (cm)	Wet Mass (g)				Dry Mass (g)			
			B	OA	G	W	B	OA	G	W
1	-	18	236	638	68	941	0.3	1.7	0.1	2.1
2	F	30	1000	237	218	1455	2.4	0.5	0.4	3.3
3	F	32	1200	1157	199	2556	1.9	2.1	0.4	4.4
4	M	38	2500	1800	900	5200	4.5	3.7	1.8	10.0
5	M	45	2500	2500	2100	7100	1.0	0.6	0.5	2.1
6	M	25	800	900	238	1938	1.4	1.6	0.4	3.5
7	F	34	1300	1600	1600	4500	2.3	3.2	3.8	9.3
8	M	31.5	1700	1900	1700	5300	3.0	3.4	3.4	9.8
9	M	45	4500	5100	6000	15600	1.6	1.8	2.4	5.7
10	F	35	1800	1000	1000	3800	3.4	1.8	2.4	7.6
11	M	38	2200	2100	2700	7000	0.5	0.5	0.9	2.0
12	M	32	1400	1800	2700	5900	3.6	6.3	1.2	11.1
13	F	31	1200	1200	1000	3400	2.3	2.6	3.1	7.9
14	M	34	1400	1500	1100	4000	2.7	3.3	2.7	8.7
Mean (SD)			1695 (988)	1674 (1115)	1537 (1500)	4907 (3497)	2.2 (1.2)	2.4 (1.5)	1.7 (1.2)	6.2 (3.2)

Drymonema larsoni sex, bell diameter (cm), wet and dry mass (grams) for individual tissue sections (B= bell, OA=oral arms, G=gonads) and the whole organism (W).

Table 4.2 *Drymonema larsoni* dry mass and water content

ID	Dry Mass (% WM)				Water Content (% WM)			
	B	OA	G	W	B	OA	G	W
1	0.1	5.4	0.1	3.9	99.9	94.6	99.9	96.1
2	4.6	4.1	3.9	4.4	95.4	95.9	96.1	95.6
3	3.1	3.7	3.8	3.4	96.9	96.3	96.2	96.6
4	3.6	4.1	3.9	3.8	96.4	95.9	96.1	96.2
5	2.5	2.4	2.5	2.5	97.5	97.6	97.5	97.5
6	3.5	3.6	3.7	3.6	96.5	96.4	96.3	96.4
7	3.6	4.0	4.7	4.1	96.4	96.0	95.3	95.9
8	3.5	3.5	4.0	3.7	96.5	96.5	96.0	96.3
9	3.4	3.5	3.9	3.6	96.6	96.5	96.1	96.4
10	3.8	3.6	4.6	4.0	96.2	96.4	95.4	96.0
11	2.3	2.6	3.3	2.8	97.7	97.4	96.7	97.2
12	5.0	6.9	4.7	5.5	95.0	93.1	95.3	94.5
13	3.8	4.3	6.2	4.7	96.2	95.7	93.8	95.3
14	3.8	4.4	5.0	4.3	96.2	95.6	95.0	95.7
Mean (SD)	3.3 (1.1)	4.0(1.0)	3.9(1.3)	3.9(0.7)	96.7(1.1)	96.0(1.0)	96.1(1.3)	96.1(0.7)

Drymonema larsoni dry mass and water content as a percentage of wet mass for individual tissue sections (B= bell, OA=oral arms, G=gonads) and the whole organism (W).

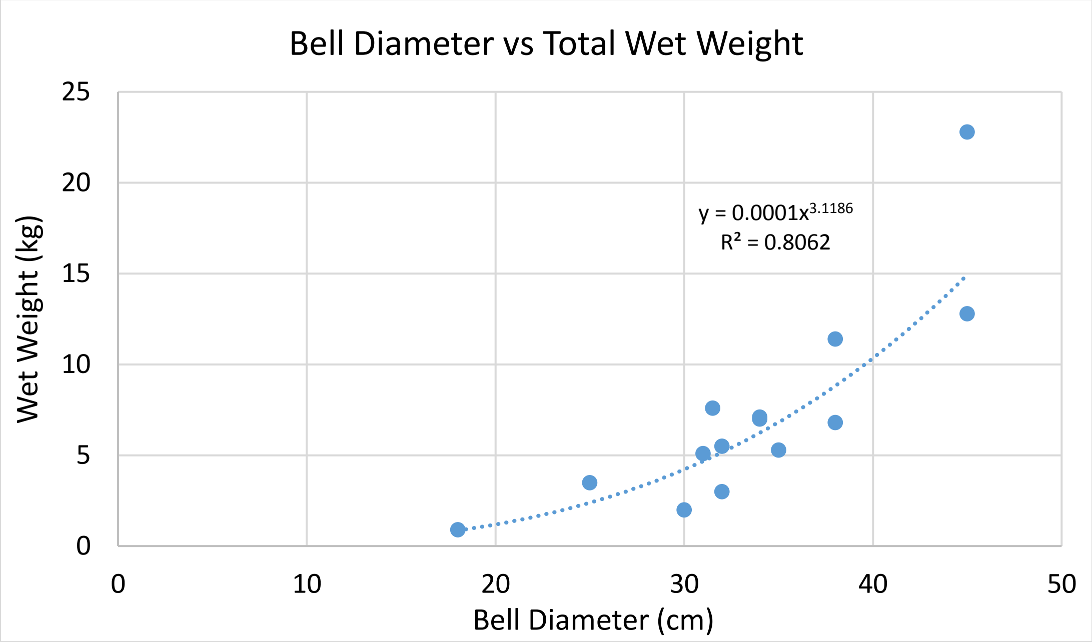


Figure 4.3 Weight-Length relationship of *Drymonema larsoni*

Weight-Length relationship of *Drymonema larsoni* in the north Gulf of Mexico.

4.3.3 Energy Density

Significant differences were observed in the ash content between the three tissue types. Mature jellyfish had less ash in the gonad tissue than in the bell and oral arms (Tukey's HSD, $p < 0.01$; Table 4.3). The oral arms contained slightly less ash than the bell (Tukey's HSD, $p=0.06$). For the juvenile, there was a difference in the ash content between all three tissue types, with the gonads having the most as followed by the bell, and oral arms containing the least amount of ash (Table 4.3).

Table 4.3 *Drymonema larsoni* revised ash percentage and energy density

ID	Bell Dia.	Revised Ash % (% DM)				Energy Density (kJ g^{-1} WM)			
		B	OA	G	W	B	OA	G	W
1	18	56.5	17.3	80.7	27.9	0.46	0.98	0.14	0.83
2	30	50.1	27.7	80.7	51.0	0.55	0.84	0.14	0.39
3	32	86.0	73.4	47.3	77.2	0.08	0.24	0.59	0.16
4	38	81.2	65.5	58.7	71.8	0.14	0.35	0.44	0.20
5	45	85.6	81.5	67.0	78.7	0.08	0.13	0.33	0.10
6	25	86.6	79.2	47.3	78.3	0.07	0.16	0.59	0.10
7	34	92.5	77.6	70.4	79.4	-0.01	0.19	0.28	0.11
8	31.5	72.5	75.3	66.9	71.7	0.25	0.22	0.33	0.18
9	45	91.1	72.2	64.9	74.9	0.01	0.26	0.35	0.15
10	35	77.2	60.6	52.9	66.4	0.19	0.41	0.51	0.24
11	38	93.4	102.7	74.9	89.1	-0.02	-0.15	0.22	0.05
12	32	79.7	51.1	60.7	62.3	0.16	0.54	0.41	0.42
13	31	76.0	64.6	63.6	68.3	0.21	0.36	0.37	0.21
14	34	74.3	72.7	53.0	67.9	0.23	0.25	0.51	0.18
Mean		80.5	69.5	62.2	72.1	0.15	0.29	0.39	0.19
(SD)		(11)	(17)	(10)	(9)	(0.16)	(0.22)	(0.13)	(0.10)

Drymonema larsoni revised ash percentage (as a percentage of dry mass) and energy density (kJ g-1 WM) for individual tissue sections (B= bell, OA=oral arms, G=gonads) and the whole organism (W). Mean was calculated for mature medusae (ID 2-14) only.

The energy density analysis of *D. larsoni* revealed differences among tissue types and changes in energy distribution as the animal grows. The mean energy density of whole mature jellyfish was 0.19 (0.10) kJ g WM^{-1} and 4.71 (1.87) kJ g DM^{-1}. The mature gonads had the significantly highest energy density, followed by the oral arms, and the bell (Tukey's HSD, $p<0.05$; Table 4.3). The juvenile had an energy density of 0.82 kJ g WM^{-1}, with more energy in the orals arms than the bell or gonads (Table 4.3). The comparison of energy density to bell diameter revealed that the energy decreased in both the bell and oral arms as the jellyfish grew in size (Table 4.3). Conversely, the gonadal tissue had an increasing trend as the bell diameter increased (Table 4.3). Because of the strong relationship between the bell diameter and the total wet weight, the same tissue energy trends were observed when comparing energy density and total wet weights.

4.4 Discussion

The presence of *Drymonema larsoni* in the northern GoM appeared to be related with the biomass of *Aurelia* spp. Abundance of *Aurelia* spp. has shown a clear link to climatological patterns, which cause natural cycles of high and low densities (Robinson and Graham 2013). *D. larsoni* was only observed when the average biomass of *Aurelia* spp. was greater than 30,000 kg km^{-2} in consecutive years (Fig. 4.1). The lag between initial observations of *Aurelia* spp. (summer) and *D. larsoni* (fall) in the northern GoM, and the corresponding absence of *D. larsoni* when *Aurelia* spp. abundance is extremely low, supports the notion that biological cues may be required for the production of *D. larsoni* medusae. The synchronous appearance of *Drymonema* spp. with periods of high abundance of *Aurelia* spp. has also been documented in the Caribbean and Mediterranean Seas (Williams et al. 2001, Malej et al. 2014).

Results for body composition and energy density of *D. larsoni* were consistent with findings from other scyphozoan medusae. Recorded water content of jellyfish have all been approximately 96% (Doyle et al. 2007, Palomares and Pauly 2009), including *D.*

larsoni studied here, and the dry mass (as % wet weight) of *D. larsoni* matches the average found for the Order Semaeostomeae (3.84 %; Lucas et al. 2011). The division of body mass based on tissue sections are consistent with the findings reported for 3 large Atlantic scyphozoans, with the bell having the largest proportion of mass followed by the oral arms and then gonads (Doyle et al. 2007). The length-weight relationship for *D. larsoni* was also consistent with the other scyphozoan medusa (reviewed by Palomares and Pauly 2009). The % ash and energy density calculated for *D. larsoni* were the most similar to the results for *Cyanea capillata* (revised % ash = 76.8(2.0), energy density = 0.18(0.05) kJ g WM^{-1}; Doyle et al. 2007). These two species have similar body composition and energy density because of their similar morphologies. The juvenile specimen (DL#1) had the highest energy density. For this specimen, 70% of the body was oral arms which had the highest energy density of any tissue sampled (0.98 kJ g WM^{-1}). The findings from Doyle et al. (2007) also showed a higher energy density in the orals arms of medusae with smaller bell diameters. Presumably the consumption of juvenile *D. larsoni* could be advantageous to predators if encountered in dense aggregations because of the reduced handling time of the smaller organism and the high energy density.

As jellyfish predators, leatherback turtles have been shown to selectively target prey species with the densest tissue within a foraging location (Houghton et al. 2006, Dodge et al. 2011, Heaslip et al. 2012). During September of 2015, leatherback turtles were observed to be spatially associated and feeding on *D. larsoni*. In fact, all observations of leatherback foraging were of *D. larsoni,* even when the turtles were in the presence of both *Aurelia* spp. and *D. larsoni*. This observation of foraging was the first time leatherbacks have been recorded to feed on *Drymonema* spp. and the first record of leatherback prey selection in the Gulf of Mexico (Aleksa et al. in prep). *D. larsoni* and *Aurelia* spp. have a similar percentage of dry mass and water content (Lucas 1994, Uye and Shimauchi 2005). With an energy density of 4.71 kJ g DM^{-1}, *D. larsoni* has the potential to have twice as much energy as *Aurelia* spp. (2.3-3.6 kJ g DM^{-1}; Arai 1997). Furthermore, if the abundance of *D. larsoni* is comparable to the density of *C. capillata* in established northern Atlantic leatherback foraging areas (Heaslip et al. 2012), the GoM could provide the same nutritional support.

Variability in the samples collected could be a result of the level of post-mating degrowth or senescence among specimen. The collection of *D. larsoni* from the coastal waters of FL occurred during a large aggregation event. The presence of both sexes and state of the females (spent) within the aggregation indicate recent mating behavior. Therefore, advection could have shifted the mass aggregation near the shoreline or reduced function due to senescence made them more susceptible to surface currents and tides. The level of degrowth in samples for both the males and females could lead to deviation in body composition and energy. For example, DL #2 was identified as a female by the presence of eggs in the gonadal tissue; however, the small weight and body composition was more similar to the juvenile sample than the mature jellyfish, suggesting a further stage of senescence. The lack of difference in energy density between the sexes could be the result of post-mating body conditions, but it is unresolved if a difference would have been present between egg-bearing females and sexually mature males.

Further investigation is needed to address the distribution and abundance of *D. larsoni* in the northern GoM. Analysis of carbon and nitrogen content, as well as, the organic composition of protein, lipids, and carbohydrates would aid in our understanding of the nutrient and energy transfer between predators and prey. With the potential to be the largest and most energetically valuable jellyfish in the GoM, *D. larsoni* could play a major role in the diets other jellyfish predators.

CHAPTER V – General Summary and Conclusions

Leatherbacks have been known to exist in the waters of the GoM for decades, but no quantitative investigations have been conducted until the last several years. Because of the growing number of fishery interactions and the unstable populations of leatherbacks around the globe, research on the GoM leatherbacks started with bycatch records and observations (Garrison and Stokes 2014, Stewart et al. 2016). Successful tagging operations from nesting sites started to elucidate some movement patterns (Evans et al. 2007). A genetic study from fishery interactions also provided some spatial distribution information and nesting stock identification (Stewart et al. 2016). Challenges to studying these marine turtles include their distance from shore and large habitat range. Biological surveys conducted within the GoM have reported sightings of leatherbacks, yet these data are unpublished. This research was the first attempt to quantify leatherback movement and behavior within the GoM and couple these movements with oceanographic processes that drive distributions of prey. The investigation of the potential prey field resulted in the development of a biophysical model for large medusae in this region, as well as an analysis of the occurrence and energy density of an observed preferred prey item, *Drymonema larsoni*.

Leatherback satellite telemetry data, from nesting turtles in Panama and in-water turtles captured off the coast of Florida, provided new information on foraging behavior in the GoM. Leatherbacks aggregated in two foraging high-use areas. The Panhandle foraging region, extending from Louisiana to the Florida shelf was utilized during fall months. The Campeche foraging area was occupied during the winter months, and observations were concentrated in Campeche Bay along the western edge of the Yucatán shelf. The Panhandle foraging area overlapped with spatial bycatch records (Garrison and Stokes 2014, Stewart et al. 2016) suggesting the use of this area makes the turtles susceptible to fishery interactions. Foraging behavior was positively correlated to the presence of salinity fronts and sea surface lows. With observations occurring year round, the GoM should be considered a foraging destination and managed habitat for leatherback turtles.

Spatiotemporal analysis of scyphozoan jellyfish in the northern GoM supported the theory of leatherback foraging behavior. A large density of scyphozoans were observed in the Florida panhandle region during the fall months, which overlaps with observations of leatherback foraging. Oceanographic parameters found to be descriptive of jellyfish distributions were salinity, ocean currents, temperature, chlorophyll a concentrations, and distance from shore. These findings coincide with oceanographic features identified in previous research to have an effect on the distribution and density in other regions and for many jellyfish types (Purcell 2012, Lucas et al. 2014, Greer et al. 2015). The leading descriptive variables in the GoM (salinity and ocean currents) correspond with the factors driving the locations of the leatherback foraging observations. The consistent presence of prey within the identified high-use areas provides evidence that the GoM could sustain a foraging population of leatherback turtles. Furthermore, the number of leatherback turtles in the GoM is not likely to be substantial enough to impact the abundance of jellyfish. However, with selective foraging, more ecological information is needed about the abundance and aggregations of *D. larsoni*, as some pressure may be applied to the biomass in specific locations.

The observed selective foraging on *D. larsoni* by leatherbacks in the northern GoM may provide a high levels of energy intake compared to the consumption of other jellyfish species in the GoM. Mean whole organism energy density of *D. larsoni* was 0.19 kJ g WM^{-1}. This is similar to the energy found in *Cyanea capillata* (0.18 kJ g WM^{-1}; Doyle et al. 2007), the selected prey in the successful foraging region of the Atlantic northwest (Heaslip et al. 2012). The consistent presence of *D. larsoni* over the past decade (2008-2016) linked with the high abundance of *Aurelia* spp. may provide a comparable food supply to leatherbacks foraging in more well-studied areas.

Although the GoM is an active foraging location for leatherback turtles throughout the year, data are still lacking on the distribution of many species of jellyfish and the selective foraging potential of leatherbacks. The high-use foraging areas are located adjacent to fluvial inputs, which supply nutrients that support high levels of primary, secondary, and jellyfish production. In the northeast GoM, the spatiotemporal overlap between jellyfish density and leatherback foraging behavior is apparent. However, large densities of jellyfish occur in the northwest, which was only crossed by one tagged turtle that maintained migration behavior through the area. One possible explanation for the lack of foraging in the northwestern GoM may be the absence of larger medusa in this region. To date, no observations of *D. larsoni* have been recorded west of the Mississippi River delta. The observed connection between *Aurelia* spp. and *D. larsoni* leads to the theory that their spatial distribution would be similar, as long as the conditions are favorable for the production of both species. Because little is known about *D. larsoni*, the heavy sedimentation and turbidity of the western GoM may not be advantageous to the production of medusae, but more research is needed on the polyp stage of *D. larsoni*. As visual predators, leatherbacks may also prefer the clearer, deeper waters east of the Mississippi River plume. Furthermore, the western GoM has an extensive continental shelf, which may be less appealing to the typical oceanic leatherbacks than the shorter shelf intersected by a deep water canyon in the Panhandle foraging region. Less is known about the prey field in the tropical foraging area in the GoM. The high-use foraging area in Campeche Bay currently does not have quantitative data on the density of jellyfish. This region is known to have *Aurelia* spp. and supported a fishery for *Stomolophus meleagris* (cannonball jellyfish). However, the depletion of the *S. meleagris* from the region led to the current closure of the fishery. Quantitative studies need to be conducted on identifying the species of jellyfish at occur in the Campeche high-use area.

5.1 Suggestions for Future Research

Efforts to continue tagging and tracking both in-water and nesting leatherbacks are needed to address the space use of leatherbacks in the GoM. Nesting beach tagging in the Caribbean has been well established for over a decade and should continue to be a priority to gather information about distribution as well as mating and nesting cycles. In-water tagging operations are also critical to addressing leatherback foraging destinations and migratory routes back to mating and nesting locations. In-water tagging, unlike nesting beaches, can provide information on males and sub-adults, which is lacking in many regions. Specifically within the GoM, in-water tagging needs to occur in both high-use foraging areas. In the Campeche foraging area, no in-water tagging has been completed, so less is known about the number of turtles utilizing this area and migratory patterns out of the foraging grounds. Continued tagging in the Panhandle region will provide more in about the movement patterns in the north Gulf and resident times. For example, bycatch data show leatherbacks in the Panhandle foraging during winter months, which has not been seen in the satellite track data. Overall, monitoring the movement and behavior will help establish a management plan for the protection of leatherbacks in the GoM.

Continued research on *D. larsoni* is vital to confirming the potential foraging success of leatherbacks in the GoM. Research on spatiotemporal distribution and abundance is needed to assess the overlap with leatherback movements. Biochemical research to determine the amount of carbon as well as the percentage of organic compounds (protein, lipid, carbohydrate) would further our ability investigate the nutrient and energy transfer between jellyfish and their predators. As these large jellyfish also serve as shelter and a potential source of nutrition for young fishes (D'Ambra et al. 2015), including economically important species like Menhaden, more knowledge about the life cycle, abundance, and distribution will benefit more than leatherback turtles alone.

The link to climatologic cycles and the predator-prey interaction between *Aurelia* spp. and *D. larsoni* poses a concern during periods of low *Aurelia* spp. abundance. Advancing the quantitative measurements of these jellyfish in the GoM could help to answer if during these times low abundance is there ample food to support the population of foraging leatherbacks, and if there is another species that is present during this time. Expanding the study of jellyfish to Campeche Bay would allow us to investigate if the same pattern occurs in the tropical Campeche foraging area or can the turtles adjust their behavior and move from the Panhandle high-use area to the Campeche high-use area sooner. Two leatherbacks were tracked in the GoM during the last *Aurelia* spp. low abundance period, and both turtles initially migrated to the Panhandle foraging area. The one tagged in 2005 stayed in the area for about one month before the tag stopped transmitting, and the other, tagged in the 2006, quickly left the Panhandle region, migrated west and then south to the Campeche foraging region where it remained throughout the following winter and spring. Broader monitoring of difference species of jellyfish and the continued tracking of leatherback movements may lead to insights on foraging behavior during these periods.

Advances in sampling techniques can address some weaknesses with current methods and improve our knowledge of leatherback foraging. Currently, stable isotope analysis is used as a non-invasive way to investigate prey items; however, the information is of prey indigested typically 2-3 month prior for skin samples of leatherback turtles (Seminoff et al. 2009). When the turtles are sampled, it is extremely rare that the location of the turtle is known for the last 4 months to establish where foraging took place, making isotope analysis difficult to apply to real-time behavioral data. Stable isotopes also can vary from year to year based on the baseline carbon and nitrogen levels. Advancements in DNA sequencing has made the identification of prey items from a fecal swab possible. The use of DNA sequencing and a fecal sample analysis, allows for discovery of the prey consumed in a specific location and currently being consumed. This real-time data could help identify selective foraging habits and energy intake.

Continued advancements in oceanographic technology is needed to gain a better understanding of the cues and features utilized by leatherbacks to search for and detect prey. Marine animals can detect minute changes in the environment and respond rapidly. Currently, the resolution of oceanographic data and models, as well as algorithms used to analyze them, are too broad to account for all behavioral nuisances. This includes better monitoring equipment for physical oceanographic features, such as temperature, salinity, and oxygen, on the attached satellite tags, finer scale oceanographic satellite sampling, and more precise modeling techniques for oceanographic processes and animal behavior. If the data resolution between animal-based sampling (i.e. positioning data, dive behavior) and satellite data match, then more advanced behavioral models can be used to conserve critical habitat for threatened species.

The coupling of leatherback behavioral data, prey selection and distribution, and oceanographic data would provide the baseline for forecasting potential threats and adaptive management of leatherback turtles. The identification of behavioral patterns can be recorded and monitored along with the available prey and ocean state to predict movement patterns and space use. This would allow for seasonal changes in the management of the species by adjusting fishery closures or protected areas. This active approach to conservation may provide better protection to species and be less economically detrimental than long term closures or moratoriums.

APPENDIX A – Supplementary material for Chapter 3

Table A.1 Gulf-wide GAM descriptive variables

Summer Gulf-wide		*Aurelia*	*Chrysaora*
	RS	cdom, shoredist	cdom, kd
	IS	VGTEMP, TEMPMAX	TEMPMAX, SALMAX
	AP	cdom, VGTEMP, TEMPMAX	TEMPMAX, SALMAX
Fall Gulf-wide			
	RS	chlor_a, cdom, shoredist, meridional	par, shoredist
	IS	CHLMID, TEMPMAX, VGSAL, SALSURF	TEMPMAX
	AP	cdom, shoredist, CHLMID, TEMPMAX, VGSAL, SALSURF	par, shoredist

Table A.1: Variables selected by the GAMs to describe the density distribution of jellyfish, separated by season, method (remote sensing, in situ, and all-parameter), and genera of jellyfish. Variables defined in Table 3.1.

Table A.2 GAM outputs for Gulf-wide Models

		DE	R^2	EDF	RSS
Summer					
	RS	60.4 (0.08)	0.30 (0.002)	7.01 (0.03)	6.50 (1.19)
	IS	65.5 (0.10)	0.49 (0.002)	7.51 (0.04)	4.74 (0.10)
	AP	67.2 (0.09)	0.44 (0.002)	10.03 (0.06)	4.71 (0.10)
Fall					
	RS	59.6 (0.12)	0.46 (0.001)	11.60 (0.06)	26.82 (0.50)
	IS	54.0 (0.13)	0.45 (0.002)	9.78 (0.03)	21.30 (0.33)
	AP	62.5 (0.13)	0.63 (0.002)	15.66 (0.05)	14.88 (0.22)

Table A.2: GAM Gulf-wide results (mean (standard error)) for deviance explained (DE), r-squared (R^2), estimated degrees of freedom (EDF) and residual sum of squares (RSS) from 500 iterations of remote sensing (RS), *in situ* (IS) and all-parameter (AP) methods.

Table A.3 Regional GAM REML and R^2 values for each model run

	RS			IS			AP		
	variable	-REML	R^2	variable	-REML	R^2	variable	-REML	R^2
SumW	zonal	143.4	0.080	TURBSURF	103.05	0.036	TURBSURF	103.05	0.036
	eke_pos:Chr	87.02	0.488	TEMPMAX:Chr	53.33	0.473	zonal	99.48	0.109
	chlor_a:Chr	64.12	0.566	TEMPMAX:Aur	27.31	0.504	eke_pos:Chr	39.64	0.673
	chlor_a:Aur	41.87	0.53	CHLMAX:Aur	22.78	0.530	chlor_a:Chr	33.45	0.608
				SALMID:Aur	19.11	0.589	TEMPMAX:Chr	29.67	0.655
							chlor_a:Aur	8.55	0.645
							TEMPMAX:Aur	3.64	0.697
							CHLMAX:Aur	0.74	0.722
							SALMID:Aur	-1.17	0.753
SumE	zonal:Chr	67.43	0.101	DEPTHMAX:Chr	67.34	0.081	cdom:Chr	59.04	0.090
	cdom:Chr	58.66	0.169	CHLMAX:Aur	7.98	0.495	DEPTHMAX:Chr	58.55	0.132
	zonal:Aur	6.67	0.686	SALMAX:Aur	7.19	0.555	zonal:Aur	4.58	0.691
	shoredist:Aur	6.40	0.746	DEPTHMAX:Aur	2.69	0.682	shoredist:Aur	4.08	0.777
	cdom:Aur	5.74	0.735				cdom:Aur	3.40	0.756
							CHLMAX:Aur	-2.23	0.957
							SALMAX:Aur	-2.59	0.944
FallW	par:Chr	194.39	0.026	VGOXY:Chr	195.56	0.011	TEMPMAX:Chr	193.66	0.034
	chlor_a:Aur	84.32	0.306	TEMPMAX:Chr	193.66	0.034	CHLMID,Chlor_a:Aur	72.84	0.399
	cdom:Aur	78.76	0.362	CHLMID:Aur	77.15	0.245	DEPTHMAX:Aur	58.30	0.452
	shoredist:Aur	76.32	0.381	DEPTHMAX:Aur	61.20	0.416	cdom:Aur	56.73	0.500
	sla_pos:Aur	68.38	0.583	OXYMID:Aur	61.63	0.419	shoredist:Aur	54.32	0.500
				SALMAX:Aur	55.31	0.54	sla_pos:Aur	50.24	0.695

Table A.3 *Cont.*

	RS			IS			AP		
	variable	-REML	R^2	variable	-REML	R^2	variable	-REML	R^2
FallE	(zonal,eke_pos):Chr	208.7	0.056	VGSAL:Chr	206.57	0.095	zonal:Chr	208.66	0.045
	sst:Aur	141.61	0.484	VGSAL:Aur	133.51	0.573	eke_pos:Chr	208.66	0.045
	shoredist:Aur	135.22	0.567	TEMPMID:Aur	132.76	0.625	VGSAL:Chr	206.45	0.113
	(zonal,eke_pos):Aur	133.32	0.632				sst:Aur	137.40	0.518
							shoredist:Aur	131.78	0.605
							TEMPMID:Aur	123.41	0.747

GAM forward selection fitness values (REML and R^2) for the remote sensing (RS), in situ (IS) and all-parameter (AP) methods of the regional models. Variables defined in Table 3.1 and :Chr/:Aur represents which genera the variable was applied to (Chr =*Chrysaora*, Aur =*Aurelia*).

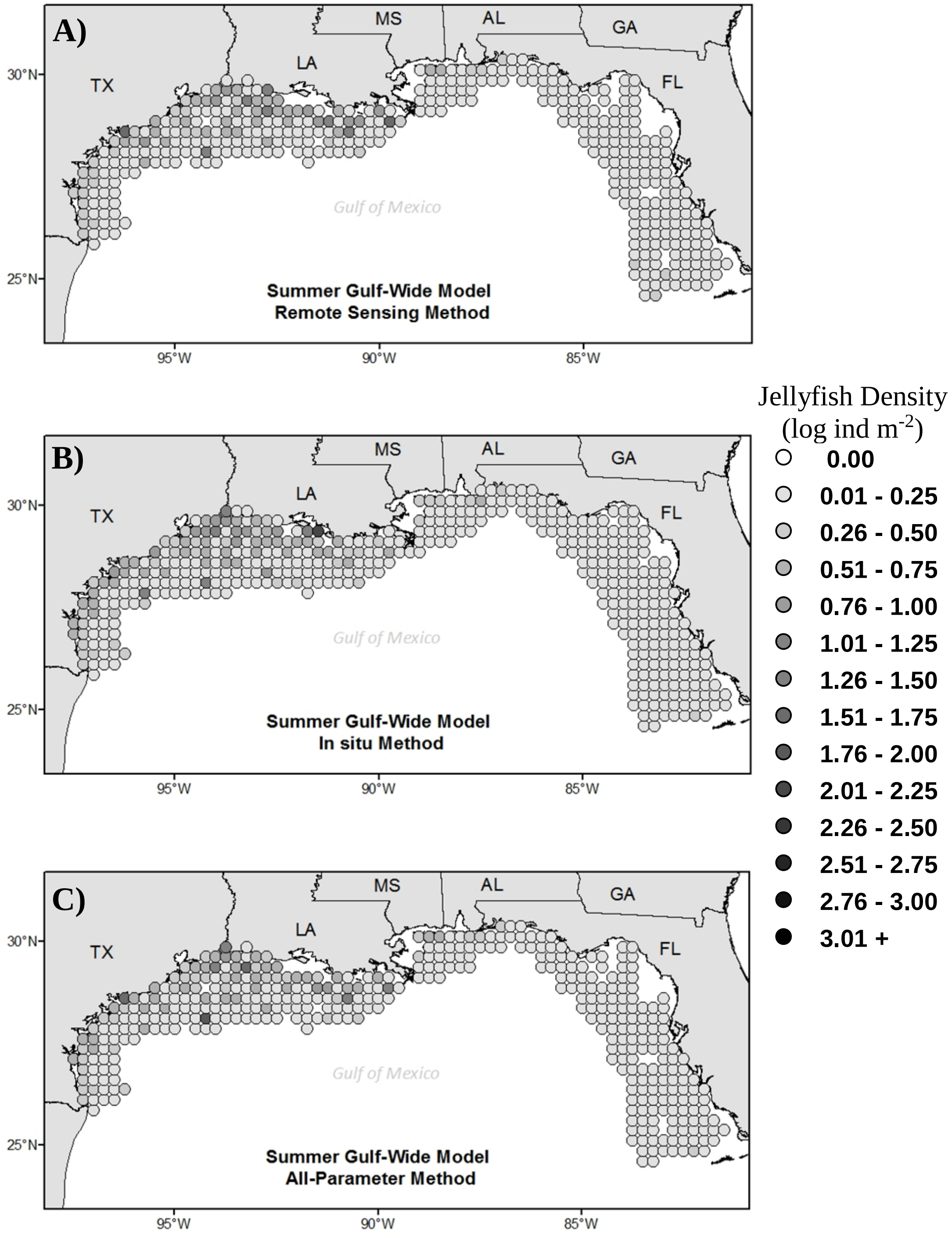


Figure A.1 Summer Gulf-wide jellyfish density GAM results

Summer Gulf-wide jellyfish density GAM results for the **A)** remote sensing (RS), **B)** in situ (IS) and **C)** all-parameter (AP) methods.

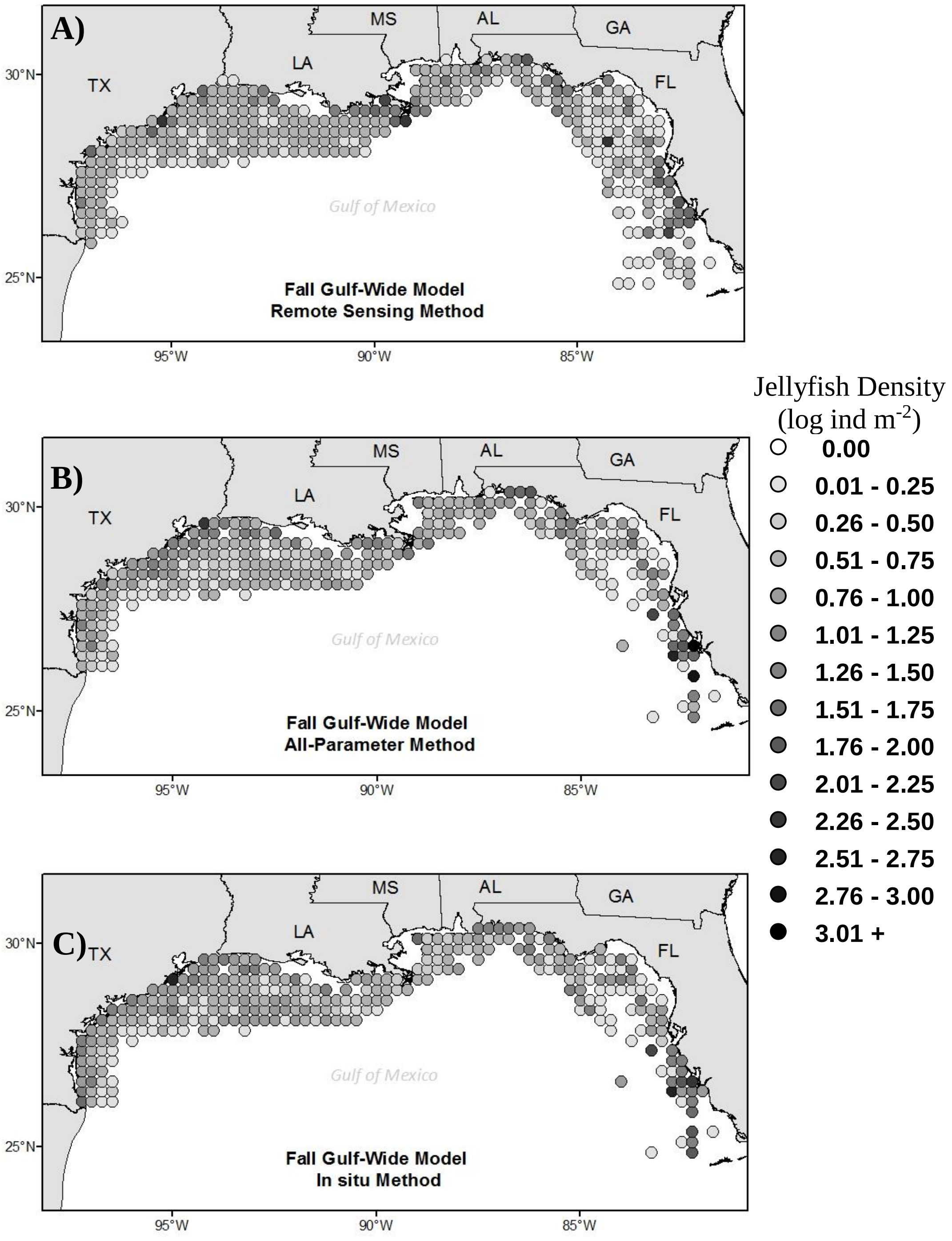
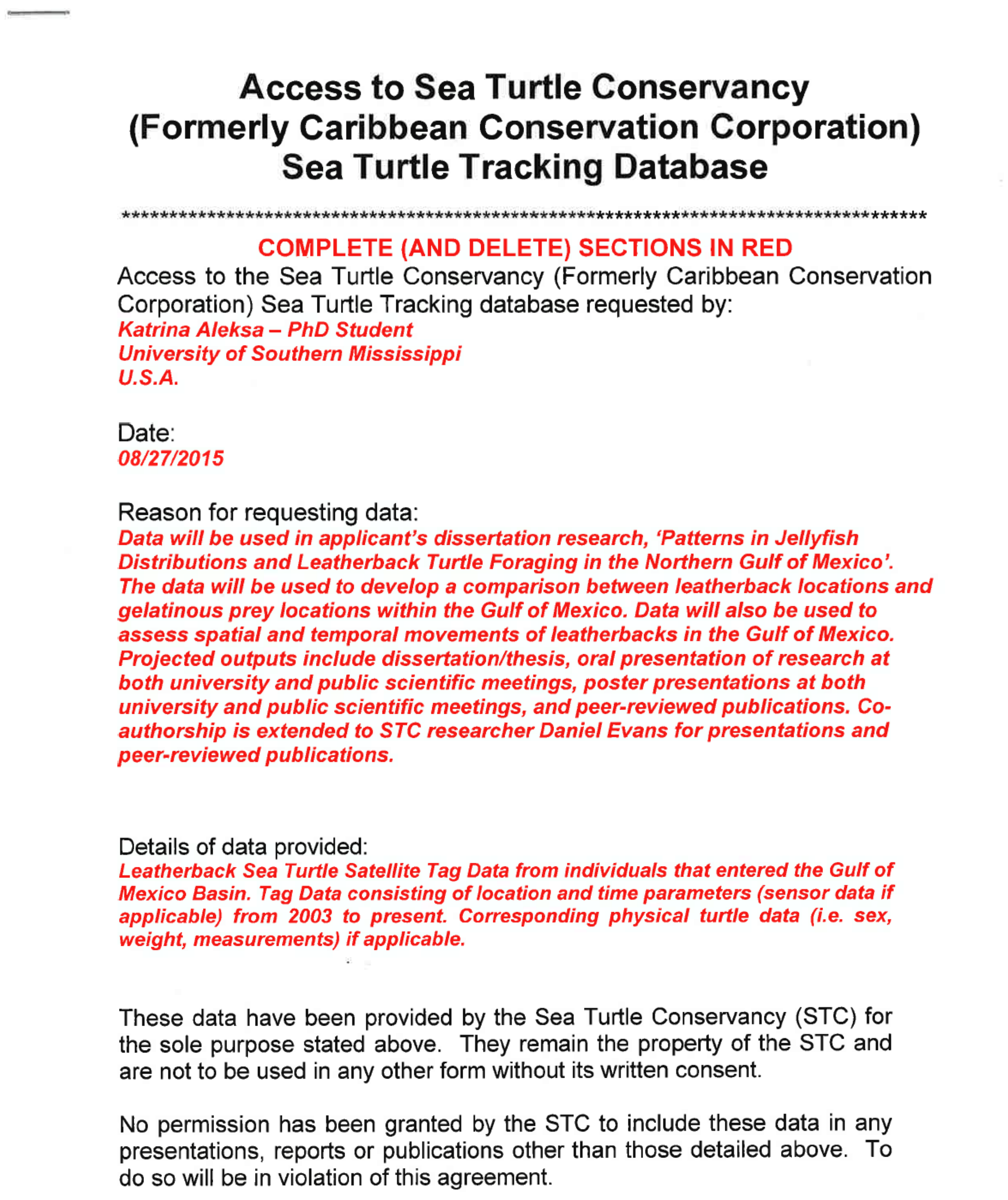


Figure A.2 Fall Gulf-wide jellyfish density GAM results

Fall Gulf-wide jellyfish density GAM results for the **A)** remote sensing (RS), **B)** in situ (IS) and **C)** all-parameter (AP) methods.

APPENDIX B – STC Data Usage Approval Letter



Access to Sea Turtle Conservancy (Formerly Caribbean Conservation Corporation) Sea Turtle Tracking Database

* * *

COMPLETE (AND DELETE) SECTIONS IN RED

Access to the Sea Turtle Conservancy (Formerly Caribbean Conservation Corporation) Sea Turtle Tracking database requested by:

Katrina Aleksa – PhD Student
University of Southern Mississippi
U.S.A.

Date:
08/27/2015

Reason for requesting data:
Data will be used in applicant's dissertation research, 'Patterns in Jellyfish Distributions and Leatherback Turtle Foraging in the Northern Gulf of Mexico'. The data will be used to develop a comparison between leatherback locations and gelatinous prey locations within the Gulf of Mexico. Data will also be used to assess spatial and temporal movements of leatherbacks in the Gulf of Mexico. Projected outputs include dissertation/thesis, oral presentation of research at both university and public scientific meetings, poster presentations at both university and public scientific meetings, and peer-reviewed publications. Co-authorship is extended to STC researcher Daniel Evans for presentations and peer-reviewed publications.

Details of data provided:
Leatherback Sea Turtle Satellite Tag Data from individuals that entered the Gulf of Mexico Basin. Tag Data consisting of location and time parameters (sensor data if applicable) from 2003 to present. Corresponding physical turtle data (i.e. sex, weight, measurements) if applicable.

These data have been provided by the Sea Turtle Conservancy (STC) for the sole purpose stated above. They remain the property of the STC and are not to be used in any other form without its written consent.

No permission has been granted by the STC to include these data in any presentations, reports or publications other than those detailed above. To do so will be in violation of this agreement.

REFERENCES

Aleksa KT, Nero RW, Wiggert JD, Graham WM (in press) Descriptive Density Models of Scyphozoan Jellyfish in the northern Gulf of Mexico. Mar Ecol Prog Ser. doi.org/10.3354/meps12327.

Aleksa KT, Sasso C, Benson S, Forney K, Stacy B, Chiaverano L (in prep) Observations of Leatherback Turtle Distribution and Foraging in the Northern Gulf of Mexico off Florida. Mar Turt Newsl.

Arai MN (1997) A Functional Biology of Scyphozoa. Chapman & Hall, London.

Bailey H, Fossette S, Bograd SJ, Shillinger GL, Swithenbank AM, Georges J, Gaspar P, Stromberg KHP, Paladino FV, Spotila JR, Block BA, and Hays GC (2012) Movement Patterns for a Critically Endangered Species, the Leatherback Turtle (*Dermochelys coriacea*), Linked to Foraging Success and Population Status. PLOS one. 7(5): 1-8. e36401.

Bailey H, Shillinger G, Palacios D, Bograd S, Spotila J, Paladino F, Block B (2008) Identifying and comparing phases of movement by leatherback turtles using state-space models. J Exp Mar Biol Ecol 356:128-135.

Bakun A (2006) Fronts and eddies as key structures in the habitat of marine fish larvae: Opportunity, adaptive response and competitive advantage. Scientia Marina 70:105-122.

Bamstedt U, Lane J, Martinussen MB (1999) Bioenergetics of ephyra larvae of the scyphozoan jellyfish *Aurelia aurita* in relation to temperature and salinity. Mar. Biol. 135: 89–98.

Barbier EB and Strand I (1998) Valuing mangrove-fishery linkages–A case study of campeche, mexico. Environ Resour Econ 12:151-166.

Bayha KM and Dawson MN (2010) New family of allomorphic jellyfishes, Drymonematidae (scyphozoa, discomedusae), emphasizes evolution in the functional morphology and trophic ecology of gelatinous zooplankton. Biol Bull 219:249-267.

Bayha KM, Graham WM, Higgins III JE, Fletcher HA (2012) Predation potential of the jellyfish *Drymonema larsoni* Bayha & Dawson (scyphozoa: Drymonematidae) on the moon jellyfish *Aurelia* sp. in the northern Gulf of Mexico. Hydrobiologia 690:189-197.

Benson SR, Eguchi T, Foley DG, Forney KA, Bailey H, Hitipeuw C, Samber BP, Tapilatu RF, Rei V, Ramohia P (2011) Large-scale movements and high-use areas of western pacific leatherback turtles, dermochelys coriacea. Ecosphere 2:1-27

Benson SR, Forney KA, Harvey JT, Carretta JV, Dutton PH (2007) Abundance, distribution, and habitat of leatherback turtles (Dermochelys coriacea) off California, 1990- 2003. Fish. Bull. 105: 337–347.

Bjorndal KA (1997) Foraging ecology and nutrition of sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles vol 1. CRC Press. p 199-231.

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed G, Harrison A (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86-90.

Bonanno A, Barra M, Basilone G, Genovese S, Rumolo P, Goncharov S, Popov S, Buongiorno Nardelli B, Iudicone D, Procaccini G, Aronica S, Patti B, Giacalone G, Ferreri R, Fontana I, Tranchida G, Mangano S, Pulizzi M, Gargano A, Di Maria A, Mazzola S (2016) Environmental processes driving anchovy and sardine distribution in a highly variable environment: the role of the coastal structure and riverine input. Fish. Oceanogr. 25: 471–490.

Bostrom BL and Jones DR (2007) Exercise warms adult leatherback turtles. Comp Biochem Physiol A Mol Integr Physiol 147: 323-331.

Breed GA, Jonsen ID, Myers RA, Bowen WD, Leonard ML (2009) Sex-specific, seasonal foraging tactics of adult grey seals (halichoerus grypus) revealed by state–space analysis. Ecology 90: 3209-3221.

Brodeur RD, Decker MB, Ciannelli L, Purcell JE, Bond NA, Stabeno PJ, Acuna E, Hunt GL (2008) Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. Prog. Oceanogr. 77: 103–111.

Brodeur RD, Link JS, Smith BE, Ford MD, Kobayashi D, Jones TT (2016) Ecological and Economic Consequences of Ignoring Jellyfish: A Plea for Increased Monitoring of Ecosystems. Fisheries 41(11): 622-629.

Brotz L, Cheung WWL, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in Large Marine Ecosystems. Hyrdobiologia 690: 3-20.

Brown CW, Hood RR, Long W, Jacobs J, Ramers DL, Wazniak C, Wiggert JD, Wood R, Xu J (2013), Ecological Forecasting in Chesapeake Bay: Using a Mechanistic-Empirical Modeling Approach, J. Mar. Sys. 10.1016/j.jmarsys.2012.12.007: 113-125.

Carassou L, Hernandez FJ, Powers SP, Graham WM (2012) Cross-shore, seasonal, and depth-related structure of ichthyoplankton assemblages in coastal Alabama. Trans Am Fish Soc 141:1137-1150.

Cartwright P, Halgedahl SL, Hendricks JR, Jarrard RD, Marques AC, Collins AG, Lieberman BS (2007) Exceptionally Preserved Jellyfishes from the Middle Cambrian. PLOS one 2(10): e1121.

Condon RH, Duarte CM, Pitt KA, Robinson KL, Lucas CH, Sutherland KR, Mianzan HW, Bogeberg M, Purcell JE, Decker MB, Uye S, Madin LP, Brodeur RD, Haddock SHD, Malej A, Parry GD, Eriksen E, Quinones J, Acha M, Harvey M, Arthur JM, Graham WM (2013) Recurrent jellyfish blooms are a consequence of global oscillations. PNAS 110(3): 1000-1005.

Croll DA, Tershy BR, Hewitt RP, Demer DA, Fiedler PC, Smith SE, Armstrong W, Popp JM, Kiekhefer T, Lopez VR (1998) An integrated approach to the foraging ecology of marine birds and mammals. Deep Sea Research Part II: Topical Studies in Oceanography 45:1353-1371.

D'Ambra I (2012) Application of stable isotopes in the analysis of trophic interactions between gelatinous zooplankton and fish. PhD Dissertation. University of South Alabama, Mobile, AL.

D'Ambra I, Graham WM, Carmichael RH, Hernandez FJ (2015) Fish rely on scyphozoan hosts as a primary food source: Evidence from stable isotope analysis. Mar Biol 162:247-252.

Davenport J (1998) Sustaining endothermy on a diet of cold jelly: Energetics of the leatherback turtle dermochelys coriacea. Bull-Brit Herp Soc :4-8.

David LT and Kjerfve B (1998) Tides and currents in a two-inlet coastal lagoon: Laguna de Terminos, Mexico. Cont Shelf Res 18:1057-1079.

Decker MB (2010) Modeling Climate Effects on Interdecadal Variation in Southeastern Bering Sea Jellyfish Populations. North Pacific Research Board Final Report 606, 63 p.

Decker MB, Brown CW, Hood RR, Purcell JE, Gross TF, Matanoski JC, Bannon RO, Setzler-Hamilton EM (2007) Predicting the Distribution of the scyphomedusa *Chrysaora quinquecirrha* in Chesapeake Bay. Mar. Ecol. Prog. Ser. 329: 99-113.

Decker MB, Cieciel K, Zavolokin A, Lauth R, Brodeur RD, Coyle KO (2014) Population Fluctuations of Jellyfish in the Bering Sea and Their Ecological Role in This Productive Shelf Ecosystem, in: Pitt, K.A., Lucas, C.H. (Eds.), Jellyfish Blooms. Springer Netherlands, Dordrecht, pp. 153–183.

DeMott WR (1995) Food selection by calanoid copepods in response to between-lake variation in food abundance. Freshwat Biol 33:171-180.

DeMott WR (1989) Optimal foraging theory as a predictor of chemically mediated food selection by suspension-feeding copepods. Limnol Oceanogr 34:140-154.

Dodge KL, Galuardi B, Miller TJ, Lutcavage ME (2014) Leatherback turtle movements, dive behavior, and habitat characteristics in ecoregions of the northwest Atlantic Ocean. PLoS One 9:e91726.

Dodge KL, Logan JM, Lutcavage ME (2011) Foraging ecology of leatherback sea turtles in the western north Atlantic determined through multi-tissue stable isotope analyses. Mar Biol 158:2813-2824.

Domingues R, Goni G, Bringas F, Muhling B, Lindo-Atichati D, Walter J (2016) Variability of preferred environmental conditions for Atlantic bluefin tuna (*Thunnus thynnus*) larvae in the Gulf of Mexico during 1993-2011. Fish. Oceanogr. 25, 320–336.

Doyle TK, Houghton JDR, McDevitt R, Davenport J, Hays GC (2007) The energy density of jellyfish: Estimates from bomb-calorimetry and proximate-composition. J. Exper. Mar. Biol. Ecol. 343: 239-252.

Drexler M, Ainsworth CH (2013) Generalized Additive Models Used to Predict Species Abundance in the Gulf of Mexico: An Ecosystem Modeling Tool. PLOS one. 8(5):e64458.

Duffy J and Paul aV (1992) Prey nutritional quality and the effectiveness of chemical defenses against tropical reef fishes. Oecologia 90:333-339.

Eckert KL, Wallace BP, Frazier JG, Eckert SA, Pritchard PC (2012) Synopsis of the biological data on the leatherback sea turtle (dermochelys coriacea). In: MacPherson SL (ed). Biological Technical Publications.

Eckert S and Eckert K (1986) Harnessing leatherbacks. Mar Turtle Newsl 37:1-3.

Eckert SA (2006) High-use oceanic areas for Atlantic leatherback sea turtles (*Dermochelys coriacea)* as identified using satellite telemetered location and dive information. Mar Biol 149:1257-1267.

Eckert KL, Wallace BP, Frazier JG, Eckert SA, Pritchard PC (2012) Synopsis of the biological data on the leatherback sea turtle (*Dermochelys coriacea*). In: MacPherson SL (ed). Biological Technical Publications.

Endres CS and Lohmann KJ (2012) Perception of dimethyl sulfide (DMS) by loggerhead sea turtles: A possible mechanism for locating high-productivity oceanic regions for foraging. J Exp Biol 215:3535-3538.

Etnoyer P, Canny D, Mate BR, Morgan LE, Ortega-Ortiz JG, Nichols WJ (2006) Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California peninsula, Mexico. Deep Sea Research Part II: Topical Studies in Oceanography 53:340-358.

Evans D, Harrison E, Ordoñez C (2012) Tracking “Dawn” into the Horizon oil spill. Pages 12–13 *in* TT Jones and BP Wallace, compilers. Proceedings of the Thirty-first Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NOAA NMFS-SEFSC-631: 322 p. San Diego, California, USA.

Evans D, Ordonez C, Troëng S, Drews C (2007) Satellite tracking of leatherback turtles form Caribbean Central America reveals unexpected foraging grounds. Pages 70–71 *in* AF Rees, M Frick, A Panagopoulou, and K Williams, compilers. Proceedings of the Twenty-seventh Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-569. International Sea Turtle Society, Myrtle Beach, South Carolina, USA.

Felder DL, Camp DK, Tunnell Jr. JW (2009) An Introduction to Gulf of Mexico Biodiversity Assessment. In: Gulf of Mexico origins, waters, and biota: biodiversity. Felder DL, Camp DK (eds). Texas A&M University Press, College Station,TX.

Fossette S, Hobson VJ, Girard C, Calmettes B, Gaspar P, Georges J, Hays GC (2010a) Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. J Mar Syst 81:225-234.

Fossette S, Girard C, López-Mendilaharsu M, Miller P, Domingo A, Evans D, Kelle L, Plot V, Prosdocimi L, Verhage S, Gasper P, Georges J-Y, Hansson L-A (2010b) Atlantic Leatherback Migratory Paths and Temporary Residence Areas. PLoS ONE 5(11): e13908.

Garrison LP, Stokes L (2014) Estimated bycatch of marine mammals and sea turtles in the US Atlantic pelagic longline fleet during 2013. In: US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center.

Gaspar P, Georges JY, Fossette S, Lenoble A, Ferraroli S, Le Maho Y (2006) Marine animal behaviour: Neglecting ocean currents can lead us up the wrong track. Proc Biol Sci 273:2697-2702.

Gelman A and Rubin DB (1992) Inference from iterative simulation using multiple sequences. Stat Sci :457-472.

Genin A (2004) Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Mar. Syst. 50: 3–20.

Gillespie TW (2001) Remote sensing of animals. Prog Phys Geogr 25:355-362.

Gould RW, Wiesenburg DA (1990) Single-species dominance in a subsurface phytoplankton concentration at a Mediterranean Sea front. DTIC Document.

Gower JFR, Borstad G (1981) Use of the In Vivo Fluorescence Line at 685 nm for Remote Sensing Surveys of Surface Chlorophyll a. In: Oceanography from Space. Volume 13. Springer US, New York, New York.

Graham WM, Field JG, Potts, DC (1992) Persistent "upwelling shadows" and their influence on zooplankton distributions. Mar. Biol. 114: 561–570.

Graham WM (2001) Numerical increases and distributional shifts of *Chrysaora quinquecirrha* (Desor) and *Aurelia aurita* (Linne) (Cnidaria: Scyphozoa) in the northern Gulf of Mexico. Hydrobiologia 451: 97-111.

Graham WM, Pagès F, Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451: 199–212.

Greer AT, Cowen RK, Guigand CM, Hare JA (2015) Fine-scale planktonic habitat partitioning at a shelf-slope front revealed by a high-resolution imaging system. J. Mar. Syst. 142: 111–125.

Greer AT, Woodson CB (2016) Application of a predator–prey overlap metric to determine the impact of sub-grid scale feeding dynamics on ecosystem productivity. ICES J. Mar. Sci. J. Cons. 73: 1051–1061.

Grimes CB, Finucane JH (1991) Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. Mar. Ecol. Prog. Ser. 75: 109–119.

Hamner WM, Madin LP, Alldredge AL, Gilmer RW, Hamner PP (1975) Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. Limnol. Oceanogr. 20: 907–917.

Hastie T, Tibshirani R (1990) Generalized Additive Models. Chapman and Hall/CRC, Boca Raton, FL USA.

Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, Pade NG, Sims DW (2012) High activity and Levy searches: jellyfish can search the water column like fish. Proc. R. Soc. B Biol. Sci. 279: 465–473.

Hays GC, Broderick AC, Godley BJ, Luschi P, Nichols WJ (2003) Satellite telemetry suggests high levels of fishing-induced mortality in marine turtles. Mar Ecol Prog Ser 262:305-309.

Hays GC, Doyle TK, Houghton JDR, Lilley MKS, Metcalfe JD, Righton D (2008) Diving behaviour of jellyfish equipped with electronic tags. J. Plankton Res. 30: 325–331.

Hays GC, Hobson VJ, Metcalfe JD, Righton D, Sims DW (2006) Flexible Foraging Movements of Leatherback Turtles across the North Atlantic Ocean. Ecology. 87(10): 2647-2656.

Heaslip SG, Iverson SJ, Bowen WD, James MC (2012) Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): Video evidence from animal-borne cameras. PloS One 7:e33259.

Houghton JD, Doyle TK, Wilson MW, Davenport J, Hays GC (2006) Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. Ecology 87:1967-1972.

Humphries NE and Sims DW (2014) Optimal foraging strategies: Lévy walks balance searching and patch exploitation under a very broad range of conditions. J Theor Biol 358:179-193.

Huh OK, Walker ND, Moeller C (2001) Sedimentation along the eastern chenier plain coast: down drift impact of a delta complex shift. J. Coast. Res. 72–81.

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, and others (2015) ECOLOGY. aquatic animal telemetry: A panoramic window into the underwater world. Science 348:1255642.

James MC, Myers RA, Ottensmeyer CA (2005) Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. Proc Biol Sci 272:1547-1555.

Johnson DR, Perry HM, Graham WM (2005) Using nowcast model currents to explore transport of non-indigenous jellyfish into the Gulf of Mexico. Mar. Ecol. Prog. Ser. 305: 139–146.

Jones TT, Bostrom BL, Hastings MD, Van Houtan KS, Pauly D, Jones DR (2012) Resource requirements of the pacific leatherback turtle population. PloS One 7:e45447.

Jones TT and Seminoff J (2013) Feeding biology: Advances from field-based observations, physiological studies, and molecular techniques. In: Wyneken J, Musick JA, Lohmann KJ (eds) The Biology of Sea Turtles vol 3. CRC Press. p 211-247.

Jonsen ID, Myers RA, James MC (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Mar Ecol Prog Ser 337:255-264.

Jonsen ID, Flemming JM, Myers RA (2005) Robust state–space modeling of animal movement data. Ecology 86:2874-2880.

Kiørboe T (2013) Zooplankton body composition. Limnol Oceanogr 58:1843-1850.

Kogovšek T, Bogunović B, Malej A (2010) Jellyfish in the northern Adriatic: A 200 year story. Rapp.PV.Réun.-Comm. Int. Explor. Sci. Mer Mediterr 39.

Lander ME, Lindstrom T, Rutishauser M, Franzheim A, Holland M (2015) Development and field testing a satellite-linked fluorometer for marine vertebrates. Anim Biotelem 3:40.

Larsen K (2016) Information: Data Exploration with Information Theory (Weight-of-Evidence and Information Value). R package version 0.0.8. https://CRAN.R-project.org/package=Information.

Larson RJ (1987) First report of the little-known scyphomedusa *Drymonema dalmatinum* in the Caribbean Sea, with notes on its biology. Bull Mar Sci 40:437-441.

Lewison RL, Freeman SA, Crowder LB (2004) Quantifying the effects of fisheries on threatened species: The impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecol Lett 7:221-231.

Liu H, Ciannelli L, Decker MB, Ladd C, Chan K-S (2010) Nonparametric Threshold Model of Zero-Inflated Spatio-Temporal Data with Application to Shifts in Jellyfish Distribution. J. Agric. Biol. Environ. Stat. 16: 185–201.

Lohmann K, Hester J, Lohmann C (1999) Long-distance navigation in sea turtles. Ethol Ecol Evol 11:1-23.

Lohmann KJ, Putman NF, Lohmann CM (2008) Geomagnetic imprinting: A unifying hypothesis of long-distance natal homing in salmon and sea turtles. Proc Natl Acad Sci USA 105:19096-19101.

Lohrenz SE, Fahnenstiel GL, Redalje DG, Lang GA, Chen X, Dagg MJ (1997) Variations in primary production of northern Gulf of Mexico continental shelf waters linked to nutrient inputs from the mississippi river. Mar Ecol Prog Ser :45-54.

Lucas CH (1994) Biochemical composition of *Aurelia aurita* in relation to age and sexual maturity. J Exp Mar Biol Ecol 183:179-192.

Lucas CH, Graham WM, Widmer C (2012) Jellyfish Life Histories: Role of Polyps in Forming and Maintaining Scyphomedusa Populations, in: Advances in Marine Biology. Elsevier, pp. 133–196.

Lucas CH, Jones DOB, Hollyhead CJ, Condon RH, Duarte CM, Graham WM, Robinson KL, Pitt KA, Schildhauer M, Regetz J (2014) Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers: Global gelatinous biomass. Glob. Ecol. Biogeogr. 23: 701–714.

Lucas CH, Pitt KA, Purcell JE, Lebrato M, Condon RH (2011) What's in a jellyfish? Proximate and elemental composition and biometric relationships for use in biogeochemical studies. ESA Ecology 92:1704.

Luo J, Grassian B, Tang D, Irisson J, Greer A, Guigand C, McClatchie S, Cowen R (2014) Environmental drivers of the fine-scale distribution of a gelatinous zooplankton community across a mesoscale front. Mar. Ecol. Prog. Ser. 510: 129–149.

Luschi P, Lutjeharms J, Lambardi P, Mencacci R, Hughes G, Hays G (2006) A review of migratory behaviour of sea turtles off southeastern Africa. S Afr J Sci 102:51-58.

Luschi P, Sale A, Mencacci R, Hughes GR, Lutjeharms JR, Papi F (2003) Current transport of leatherback sea turtles (*Dermochelys coriacea*) in the ocean. Proc Biol Sci 270 Suppl 2:S129-32.

Lyons KG, Brigham C, Traut B, Schwartz MW (2005) Rare species and ecosystem functioning. Conserv Biol 19:1019-1024.

Mackas DL, Boyd CM (1979) Spectral Analysis of Zooplankton Spatial Heterogeneity. Science 204: 62–64.

MacKenzie DI, Nichols J, Sutton N, Kawanishi K, Bailey LL (2005) Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101-1113.

Malej A, Vodopivec M, Lucic D, Onofri I, Pestoric B (2014) The lesser-known medusa *Drymonema dalmatinum* haeckel 1880 (scyphozoa, discomedusae) in the Adriatic sea In: Anonymous Annales: Series Historia Naturalis. Scientific and Research Center of the Republic of Slovenia.

McClatchie S, Cowen R, Nieto K, Greer A, Luo JY, Guigand C, Demer D, Griffith D, Rudnick D (2012) Resolution of fine biological structure including small narcomedusae across a front in the Southern California Bight: Fine biological structure across a front. J. Geophys. Res. Oceans 117: doi:10.1029/2011JC007565

Merino M (1997) Upwelling on the yucatan shelf: Hydrographic evidence. J Mar Syst 13:101-121.

Milisenda G, Rosa S, Fuentes VL, Boero F, Guglielmo L, Purcell JE, Piraino S (2014) Jellyfish as Prey: Frequency of Predation and Selective Foraging of *Boops boops* (Vertebrata, Actinopterygii) on the Mauve Stinger *Pelagia noctiluca* (Cnidaria, Scyphozoa). PLOS one. 9(4): e94600.

Monreal Gómez MA, Salas de León, David Alberto, Flores Coto C, Flores Hernández F, Salas Monreal D, Riverón Enzástiga ML (2013) Tidal effects on ichthyoplankton aggregation and dispersion in the southern gulf of mexico. Braz J Oceanogr 61:231-241.

Morey SL, Martin PJ, O'Brien JJ, Wallcraft AA, Zavala-Hidalgo, J (2003) Export pathways for river discharged fresh water in the northern Gulf of Mexico. J. Geophys. Res. 108: doi:10.1029/2002JC001674

National Marine Fisheries Service Southeast Fisheries Science Center. (2008). Sea Turtle Research Techniques Manual. NOAA Tech. Memo., NMFS-SEFCS-579, 92 pp.

Palomares M and Pauly D (2009) The growth of jellyfishes. Hydrobiologia 616:11-21.

Pauly D, Graham W, Libralato S, Morissette L, Palomares MD (2009) Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia 616:67-85.

Perry MJ, Sackmann BS, Eriksen CC, Lee CM (2008) Seaglider observations of blooms and subsurface chlorophyll maxima off the Washington coast. Limnol. Oceanogr. 53: 2169–2179.

Plath K and Boersma M (2001) Mineral limitation of zooplankton: Stoichiometric constraints and optimal foraging. Ecology 82:1260-1269.

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. J. Mar. Biol. Assoc. U. K. 85: 461–476.

Purcell JE (2011) Jellyfish and Ctenophore Blooms Coincide with Human Proliferations and Environmental Perturbations. Annu. Rev. Mar. Sci. 4:1.1-1.27.

Purcell JE (2012) Jellyfish and Ctenophore Blooms Coincide with Human Proliferations and Environmental Perturbations. Annu. Rev. Mar. Sci. 4: 209–235.

Quiñones J, Mianzan H, Purca S, Robinson KL, Adams GD, Marcelo Acha E (2015) Climate-driven population size fluctuations of jellyfish (Chrysaora plocamia) off Peru. Mar. Biol. 162: doi:10.1007/s00227-015-2751-4

Remsen A, Hopkins TL, Samson S (2004) What you see is not what you catch: a comparison of concurrently collected net, Optical Plankton Counter, and Shadowed Image Particle Profiling Evaluation Recorder data from the northeast Gulf of Mexico. Deep-Sea Res I. 51:129-151.

Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol. Evol. 24: 312–322.

Richardson K, Visser AW, Pedersen FB (2000) Subsurface phytoplankton blooms fuel pelagic production in the North Sea. J. Plankton Res. 22: 1663–1671.

Robbins LL, Coble PG, Clayton TD, Cai W-J (2009) Ocean Carbon and Biogeochemistry Scoping Workshop on Terrestrial and Coastal Carbon Fluxes in the Gulf of Mexico, St. Petersburg, FL, May 6-8, 2008: U.S. Geological Survey Open-File Report 2009-1070, 46 p.

Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN (2010) Marine geospatial ecology tools: An integrated framework for ecological geoprocessing with ArcGIS, python, R, MATLAB, and C. Environmental Modelling & Software 25:1197-1207.

Robinson KL, Graham WM (2013) Long-term change in the abundances of northern Gulf of Mexico scyphomedusae *Chrysaora* sp. and *Aurelia* spp. with links to climate variability. Limnol. Oceanogr. 58: 235–253.

Robinson KL, Ruzicka JJ, Hernandez FJ, Graham WM, Decker MB, Brodeur RD, Sutor M (2015) Evaluating energy flows through jellyfish and gulf menhaden (*Brevoortia patronus*) and the effects of fishing on the northern Gulf of Mexico ecosystem. ICES J. Mar. Sci. J. Cons. 72: 2301–2312.

Roquet F, Williams G, Hindell MA, Harcourt R, McMahon C, Guinet C, Charrassin JB, Reverdin G, Boehme L, Lovell P, and others (2014) A southern Indian Ocean database of hydrographic profiles obtained with instrumented elephant seals. Sci Data 1:140028.

Salas-De-Leon DA, Monreal-Gomez MA, Sanvicente-Añorve L, Flores-Coto C (1998) Influence de la circulation à long terme sur la répartition des organismes zooplanctoniques dans la baie de Campeche, Mexique. Oceanol Acta 21:87-93.

Salas-de-León DA, Carbajal N, Monreal-Gómez MA, Gil-Zurita A (2011) Vorticity and mixing induced by the barotropic M 2 tidal current and zooplankton biomass distribution in the Gulf of California. J Sea Res 66:143-153.

Salas-de-León DA, Monreal-Gómez MA, Signoret M, Aldeco J (2004) Anticyclonic-cyclonic eddies and their impact on near-surface chlorophyll stocks and oxygen supersaturation over the Campeche Canyon, Gulf of Mexico. J Geophys Res Oceans 109.

Salmerón-García O, Zavala-Hidalgo J, Mateos-Jasso A, Romero-Centeno R (2011) Regionalization of the Gulf of Mexico from space-time chlorophyll-a concentration variability. Ocean Dyn. 61: 439–448.

Segura-Puertas L, Celis L, Chiaverano L (2009) Medusozoans (Cnidaria: Cubozoa, Scyphozoa, Hydrozoa) of the Gulf of Mexico. In: Gulf of Mexico origins, waters, and biota: biodiversity. Felder DL, Camp DK (eds). Texas A&M University Press, College Station,TX.

Seminoff JA, Jones TT, Eguchi T, Hastings M, Jones DR (2009) Stable carbon and nitrogen isotope discrimination in soft tissues of the leatherback turtle (*Dermochelys coriacea*): Insights for trophic studies of marine turtles. J Exp Mar Biol Ecol 381:33-41.

Shillinger GL, Palacios DM, Bailey H, Bograd SJ, Swithenbank AM, Gaspar P, Wallace BP, Spotila JR, Paladino FV, Piedra R (2008) Persistent leatherback turtle migrations present opportunities for conservation. PLoS Biology 6:e171.

Shlesinger M, West B, Klafter J (1987) Lévy dynamics of enhanced diffusion: Application to turbulence. Phys Rev Lett 58:1100.

Sims DW, Southall EJ, Humphries NE, Hays GC, Bradshaw CJ, Pitchford JW, James A, Ahmed MZ, Brierley AS, Hindell MA (2008) Scaling laws of marine predator search behaviour. Nature 451:1098-1102.

Soto LA and Escobar-Briones E (1995) Coupling mechanisms related to benthic production in the SW Gulf of Mexico. Biol Ecol Shal Coast Wat :233-242.

Southwood AL, Andrews RD, Paladino FV, Jones DR (2005) Effects of diving and swimming behavior on body temperatures of pacific leatherback turtles in tropical seas. Physiol Biochem Zool 78:285-297.

Stiasny G (1940) Über *Drymonema dalmatinum* haeckel. Zool. Jb. Abt. Anat 66:437-461.

Stewart KR, LaCasella EL, Roden SE, Jensen MP, Stokes LW, Epperly SP, Dutton PH (2016) Nesting population origins of leatherback turtles caught as bycatch in the US pelagic longline fishery. Ecosphere 7.

Stunz WE, Bryan CE, Savastano K, Waller RS, Thompson PA (1985) SEAMAP environmental and biological atlas of the Gulf of Mexico, 1982. Gulf States Fisheries Commission Report: 145pp.

Uye S and Shimauchi H (2005) Population biomass, feeding, respiration and growth rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the inland sea of japan. J Plankton Res 27:237-248.

Uye S, Ueta U (2004) Recent increase of jellyfish populations and their nuisance to fisheries in the Inland Sea of Japan. Bull. Japanese Soc. Fish. Oceanogr. 68: 9-19.

Viswanathan G, Bartumeus F, Buldyrev SV, Catalan J, Fulco U, Havlin S, Da Luz M, Lyra M, Raposo E, Stanley HE (2002) Lévy flight random searches in biological phenomena. Physica A: Stat. Mech. 314:208-213.

Wallace BP, Kilham SS, Paladino FV, Spotila JR (2006) Energy budget calculations indicate resource limitation in eastern Pacific leatherback turtles. Mar Ecol Prog Ser 318:263-270.

Wallace BP, Kot CY, DiMatteo AD, Lee T, Crowder LB, Lewison RL (2013) Impacts of fisheries bycatch on marine turtle populations worldwide: Toward conservation and research priorities. Ecosphere 4:1-49.

Wallace BP, Zolkewitz M, James MC (2015) Fine-scale foraging ecology of leatherback turtles. Front Eco Evol 3:15.

Wang D-P, Oey L-Y, Ezer T, Hamilton P (2003) Near-surface currents in DeSoto Canyon (1997-99): Comparison of current meters, satellite observation, and model simulation. J. Phys. Oceanogr. 33: 313–326.

Williams E, Bunkley-Williams L, Lilyestrom C, Larson R, Engstrom N, Ortiz-Corps E, Timber J (2001) A population explosion of the rare tropical/subtropical purple sea mane, *Drymonema dalmatinum*, around Puerto Rico in the summer and fall of 1999. Caribb J Sci 37:127-130.

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73(1): 3-36.

Yåñez-Arancibia A, Lara-Dominguez A, Rojas-Galaviz J, Sånchez-Gil P, Day J, Madden C (1988) Seasonal biomass and diversity of estuarine fishes coupled with tropical habitat heterogeneity (southern Gulf of Mexico). J Fish Biol 33:191-200.

Zavala-Hidalgo J, Morey SL, O'Brien JJ (2003) Seasonal circulation on the western shelf of the Gulf of Mexico using a high-resolution numerical model. J. Geophys. Res. 108: doi:10.1029/2003JC001879

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith, GM (2009) Mixed effects models and extensions in ecology with R. Springer Science+Business Media, New York, New York.