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Role of an Upwelled Coastal Area in Northeastern Colombia in the Distribution, Population Dynamics and Genetic Diversity of the Migratory Habitat-Shifting Chelonia Mydas

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UNIVERSITY OF MIAMI

ROLE OF AN UPWELLED COASTAL AREA IN NORTHEASTERN COLOMBIA IN THE DISTRIBUTION, POPULATION DYNAMICS AND GENETIC DIVERSITY OF THE MIGRATORY, HABITAT-SHIFTING *CHELONIA MYDAS*

By

Catalina Vasquez Carrillo

A DISSERTATION

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of the University of Miami
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Role of an Upwelled Coastal Area In Northeastern Colombia in the Distribution, Population Dynamics and Genetic Diversity of the Migratory, Habitat-Shifting *Chelonia mydas* (December 2017)

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The Caribbean is generally an oligotrophic sea; however, in the southern portion between Venezuela and Colombia, a yearly, moderate, coastal upwelling fuels a very productive marine ecosystem, the Southern Caribbean Upwelling System. Extensive submerged aquatic vegetation (SAV) ecosystems are found in the Colombian side of the system, by La Guajira peninsula. SAV ecosystems constitute key habitat for multiple marine fauna species, specially at juvenile/larval stages. La Guajira's SAV unique, upwelled ecosystems are hypothesized as important foraging and developmental habitat for the endangered migratory sea turtle *Chelonia mydas*.

The complex habitat-shifting behavior and very long-lasting juvenile stage traits of the species limit its populations' growth. This lengthy juvenile stage its spent primarily at the Developmental Habitat (DH). The identification of quality DHs for the species, and the acknowledgement of their relative contribution to the overall dynamics of the *C. mydas* populations, is important for its ecology and conservation. This work aimed to quality the extent and diversity of SAV communities, known food items of the species, in the upwelled coastal waters of La Guajira, Colombia, a likely DH for the species. Also, this work looked at the quality of this DH from external indicators of the individuals aggregating in these

waters, including distributional and body condition indicators. Additionally, this work aimed to estimate the connectivity patterns of this DH to nesting populations of the species in the Atlantic basin.

Extensive and highly diverse SAV ecosystems dominated by macroalgae taxa were found in the studied area. Preferred food items by the species, were macroalgae species such as the red *Gracilaria sp.* Red algae were very common taxa in the area, even driving differences in species richness among sites. The study area was occupied by an aggregation of mostly immature turtles ranging from 16.2 cm to 87 cm in carapace straight length. The body condition of immature sea turtles in La Guajira was good and slightly better than other populations in the Caribbean. Thus, it is proposed that la Guajira is a quality habitat for *C. mydas* in the Atlantic.

Finally, the genetic diversity of the turtle aggregation was high and slightly more so than other foraging or developmental areas in the Atlantic. This could be due to the origin populations of immature turtles from from three distinct demographically-connected groups of the species. Observed contributions may be explained by the opposite-direction, rapid currents that reach the study area. However, regional differences within the area existed that cannot be explained only by the influence of currents. A model system, the Central Caribbean was proposed to explore the role of habitat quality in explaining patterns of demographic connectivity of the Atlantic *C. mydas* within regions, using a migratory network theoretical framework.

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CC	Central Caribbean
DH	Developmental Habitat
FG	Foraging Ground
SAV	Submerged Aquatic Vegetation

CHAPTER 1

Role of Coastal Upwelled Ecosystems as Habitat for Marine Migratory Species

1.1. Dissertation Theoretical Framework

1.1.1. Coastal ecosystems and spatially-structured species habitat

Species occupy areas where the resources and environmental conditions they need to survive, grow and reproduce are met (Hall et al., 1997). These areas are considered the species habitat. In the ocean, areas where resources for the production and accumulation of biomass such as sunlight or nutrients, are not randomly distributed (Bakun, 1996). To cope with the limitation of finding areas where resources for biological production accumulate, marine animal species have evolved complex life histories and dispersal behaviors (*e.g.* long migrations) that allow them to find these areas and inhabit them, at least temporally (Werner, 1988).

Migratory marine species in particular, tend to have multiple life stages (*e.g.* egg, larvae, adult) and disperse out to different areas (habitat) as they go through these different stages of their life cycle (a behavior called ontogenetic habitat shifting) (Werner, 1988; Ludwig & Rowe, 1990). This complex behavior hinders the identification and/or delineation of the species habitat. However, habitat studies for these species can be directed towards areas known to harbor the resources or conditions that are more likely to produce the occupancy of a given species.

Some of the most important areas providing habitat for marine species, at least for one of multiple life stages, are found near coasts (Carter, 2013; Dahlgren et al., 2006

Heck et al., 2003). In coastal, shallow areas, some of the most productive, diverse ecosystems such as coral reefs, mangrove forests and seagrass meadows, occur (Roberts et al., 2002; Nagelkerken et al., 2000). Coastal ecosystems have a privileged location in the land-ocean interface, which allow them to obtain nutrients, for instance from river discharges, land-runoff or coastal upwelling (Cloern et al., 2014). Nutrients, in addition to sunlight availability at shallow coastal waters, allow the conspicuous primary production and biomass accumulation characteristic of coastal ecosystems (Sigman & Hain, 2012). Some of the most productive, diverse fisheries of the world occur near coastal areas (Pauly & Christensen, 1995). Their high structural complexity and physical heterogeneity allows for complex species-species and species-habitat interactions, such as observed in coral reefs and/or seagrass meadows (Graham & Nash, 2013).

Coastal seagrass and other submerged aquatic vegetation (SAV) ecosystems (*e.g.* benthic macroalgae) are key nursery habitats for marine species (Nero & Sealey, 2006; Heck et al., 2003) (Figure 1.1). The structural complexity, biomass and diversity of these ecosystems, allow large numbers of individuals at least during one life stage, typically larval/juvenile stages. SAV beds provide habitat for multiple populations of species of invertebrates as well as vertebrates, including populations of endangered species such as manatees or sea turtles (Cullen-Unsworth & Unsworth, 2013).

Seagrass meadows as well as other nearshore marine ecosystems that sustain marine populations are being degraded and lost at a rapid pace with global environmental change (Mann, 2009; Waycott et al., 2009; Duarte et al., 2008). Causes of their degradation are the conversion of these environments to commercial uses including housing, tourism, aquaculture, fishing, and the resulting pollution, among others (Lotze et al., 2006; Orth et al., 2006). The degradation and loss of coastal ecosystems decreases marine species habitat, and due to the tight species-habitat relationship, has profound effects on the dynamics of marine populations (Duarte et al., 2008).

Population sizes usually correlate positively to the size and quality of their habitat (Griffen & Drake, 2008). When habitat is lost or degraded, populations of species become threatened by a series of events including, but not limited to, the reduction of population size and consequent genetic diversity loss, increased mortality (*e.g.* from disease) and decreased fecundity (Sodhi et al., 2009; Frankham, 2005). Small populations are known to be at higher risk of extinction because populations are more prone to inbreeding depression and chance reduction of genetic diversity (*i.e.* by random genetic drift) which in turn compromises the potential to adapt (Frankham, 2005). Natural communities are further degraded or irreversibly changed with the loss or drastic reduction in the abundance of keystone or critical species (Symstad et al., 1998). The continued positive feed-back between decline of populations and degradation/decline of critical habitats leads to extinction through a process called “The extinction vortex” (Murphy et al., 2017; Caughley, 1994). Therefore, in small populations such as those of threatened or endangered species, the identification and protection of critical habitat for each life stage, is necessary; especially for those stages with the most influence on population dynamics (growth, survival and reproductive rates).

1.1.2. *Chelonia mydas* ecology and life history traits

Chelonia mydas is a neritic, tropical and subtropical marine turtle that occupies multiple habitats and corridors throughout its life cycle (Lutz et al., 2003) (Figure 1.2). The species spends each life stage at a particular habitat type, a behavior called ontogenetic habitat-shifting. At each habitat, the species fulfills important life processes such as development and reproduction (Table 1.1).

The highly migratory and habitat-shifting behavior of *C. mydas* poses a challenge in the identification, characterization and delineation of habitat for the species. The species may move through multiple areas encompassing thousands of kilometers some of which under the jurisdiction of different countries. Also, some areas are only transitionary routes (corridors) whereas some others may be habitat in which the species finds the resources needed to complete a specific biological function of the life cycle such as reproduction or growth (Table 1.1). Therefore, the scale of habitat must be defined in studies according to the scope of each study.

C. mydas populations are fairly spatially structured (differentiated) and thus are quasi demographically-independent, thus the demographics of these populations would depend more on local recruitment (the number of births and death locally) than on immigration from other populations. Therefore, *C. mydas* habitat studies have been facilitated by focusing on understanding each population's habitat use during different life stages.

A population of *C. mydas* is defined for this dissertation as the group of individuals that are born, and then return to reproduce, in the same nesting habitat (sandy or rocky beach). Once *C. mydas* has nested on sandy beaches, it hatches and rapidly reaches the pelagic environment to avoid high predation risk of the neritic zone. It uses rapid currents and eddies to disperse out from nesting beaches, bypass the neritic zone, and reach the safer pelagic zone (Lutz et al., 2003). In the pelagic zone, *C. mydas* are entrained in frontal vegetation mats (pelagic habitat) for months to years until a larger body size is acquired and the likelihood of predation decreases (Carr, 1987). Once the right body size is reached, after one to four years of passive migration, *C. mydas* recruits into its developmental habitat (DH) for growth and development until reaching the adult stage (Meylan, et al., 2011). DHs are typically located in the neritic zone, in nearshore, coastal ecosystems such as seagrass meadows and nearby coral reefs (Valiela et al., 2001; Orth et al., 2006). *C. mydas* will stay at DHs until reaching maturity, and acquire the energy and body mass needed to then engage in long migrations for reproduction at breeding and nesting habitats nearby coastal areas, they were born (Lutz et al., 2003).

1.1.3. *C. mydas* habitat understanding gaps

The recruitment of juvenile *C. mydas* into DH after their pelagic migration seems to be a key feature of the species' life history. In order to move into its reproductive migration, *C. mydas* needs to reach a large body size and a level of energy. However, the body condition and growth rates of the species are highly influenced by the food resources nutritional value and the environmental conditions at the DH (Heithaus et al., 2007; Bjorndal, 1985). *C. mydas* recruits into DHs containing extensive beds of SAV species in meadow-like arrangements, and some form of reefs (Musick and Limpus 1997; Bass et al., 1998). During the juvenile stage, *C. mydas* allocates energy from food primarily to maximize growth and avoid predation. SAV, either seagrass or macroalgae or both, and also small animals, are common food items of *C. mydas* that provide the required nutrients and energy for growth of the species (Amorocho & Reina, 2007; McDermid, et al., 2007; Bjorndal, 1985). Nutrient-limited diets can delay growth, maturity attainment and the timing of reproductive migrations. Therefore, turtles can remain at juvenile and subadult stages for many years (up to 20 years), limiting the intrinsic growth rate of their populations (Lutz et al., 2003). Recruiting and taking residency into quality habitat with the resources and conditions for rapid growth (*i.e.* the developmental habitat) and energy accumulation can contribute to populations' positive growth.

Populations' growth is a goal for conservation of *C. mydas* in the Atlantic. The size of *C. mydas* populations was conspicuously reduced to the point of local extinctions, and nesting beach conservation programs took place throughout the basin (McClenachan et al., 2006). These programs have been successful yet populations have not recovered as expected. Part of the delay in recovery is due to the long-lasting juvenile stage which is spent at the DH. Therefore, studies have focused on identifying where those DHs for the species are found and how are they connected to each population of the species in the Atlantic basin (Meylan et al., 2011; Naro-Maciel et al., 2012; Eckert et al., 1999). Due to the tight species-habitat relationship and the key role of DHs for the growth and survival of *C. mydas*, their loss and degradation increases the chance of local extinction. Therefore, the identification, study and protection of DHs has become a conservation priority for the species (Eckert et al., 1999).

In the Atlantic, multiple foraging grounds and some DHs have been identified in coastal ecosystems of Bermuda, the southeast coast of US, Mexico, Panama, the coast of Brazil and Surinam, among others (Figure 1.3). However, studies of DHs are limited by the lack of knowledge on the distribution, extent, and quality, as well as other ecological characteristics of these habitats. Studies have focused on describing these habitats based on the target-species characteristics, for instance, the time of residency at an area or the ratio of juvenile to adult individuals (*e.g.* Meylan et al., 2011). However, studies will benefit from using oceanographic and/or environmental characteristics as predictors of occupancy by the species, to direct further studies. Also, little is known about the relative contribution to the overall population dynamics and maintenance, of a particular habitat with respect to others; an issue that relates to the differential quality of habitat among areas.

These habitat knowledge gaps remain in part, because in-water studies are difficult to perform. Sea turtles are highly mobile and hard to observe in the field. Additionally, recommended key ecological or oceanographic areas, such as current convergences or fronts, or boundary area between population connectivity groups, do not always have the logistical feasibilities for studies to be performed (Bolker et al., 2007).

1.1.4. The Southern Caribbean Upwelling System of La Guajira, Colombia

Some of the most productive and diverse coastal, marine ecosystems are located nearby areas where oceanic upwelling occurs (Bakun, 1996). Coastal upwelling causes deep, nutrient-rich waters to replace and nutrient-poor waters of the surface in the water column, thus, it causes these areas to become meso or eutrophic (have medium to high level of nutrient content). Wherever sunlight is available, the nutrient supply from upwelling, allows for primary production and then biomass accumulation (Sigman & Hain, 2012). As a result, coastal areas under this phenomenon tend to have high biomass of marine plants and animals, energy flows and complex food webs, etc. (Criales-Hernandez et al., 2006). Some of the most productive (high fish biomass) fisheries in the world occur near coasts where upwelling occurs such as those off the Peruvian coast.

The Greater Caribbean Sea is a generally oligotrophic sea (low in nutrients) Sullivan-Sealey & Bustamante, 1999). However, in the southern part, a yearly, seasonal, moderate, coastal upwelling occurs among the months of January to April, known as the Southern Caribbean Upwelling System (Rueda-Roa & Muller-Karger, 2013). Ranging from the northeast of Colombia to the easternmost of Venezuela, this system has several foci and contributes to the high biological productivity and extension of coastal marine ecosystems in the region (Andrade & Barton, 2005).

La Guajira peninsula in Colombia, is a dry, massive, rocky landmass, located on the western side of the Southern Caribbean upwelling system (Figure 1.3). As a result of the land extending into the deep ocean basin and the coastal upwelling, the peninsula is known to harbor the most productive marine ecosystems of Colombia (Invemar, 2012). This high productivity contributes to its well-known prolific, diverse fishery, as well as the most extensive SAV meadows of both seagrass and/or macroalgae of Colombia (Díaz, et al., 2003; Gómez-Lopez et al., 2014; Chasqui et al., 2013).

La Guajira's upwelling ecosystem complex flows of energy and matter sustains a high diversity of marine fauna (~900 sp) such as mollusks and small fish which in turn, provide quality forage for the growth of large/top consumer species including larger fish, seabirds and marine turtles (Criales-Hernández et al., 2006). In addition, the remoteness and harsh environmental conditions (*e.g.* high temperatures, drought) for human settlement in eastern La Guajira (also known as Upper Guajira), have prevented coastal and nearshore development, conversion and pollution; the most important drivers of habitat loss and degradation for coastal marine species worldwide.

Additionally, La Guajira is strategically located at the confluence of two major, rapid current systems that flow in opposite directions in the Caribbean Sea; the Caribbean Current which flows from east to west, and the Panama Gyre which flows from west to east in the Panama-Colombia basin (Figure 1.3) (Andrade, 2003). Hatchling turtles passively migrating on these rapid opposite direction ocean currents in the marine pelagic zone, may be able to recruit into La Guajira's nearshore, neritic areas once they have reached a minimum size (~18cm SCL).

1.2. Dissertation Hypotheses and Predictions

The high biological productivity and pristine state of submerged aquatic vegetation, known forage items for *C. mydas,* in addition to the location in respect to current systems of Upper La Guajira, may contribute the requirements and conditions for *C. mydas* occupancy and use as a developmental habitat to grow and mature. If La Guajira is a developmental habitat for *C. mydas*, several characteristics of the aggregation of turtles are expected when studying this area:

1) The area is occupied by juvenile and subadult *C. mydas* more than adults.
2) Juvenile *C. mydas* take long-term residency in the area and have higher growth rates or body conditions than other aggregations of the species in other less-productive areas such as feeding or transitory (corridor) areas.
3) Due to the random dispersal on current systems of hatchlings, and the privileged location of La Guajira in respect to strong, rapid, opposite direction currents, the aggregation of turtles in this area is expected to have a high diversity of populations of origin.
4) If the study area is a DH for the species where juvenile from multiple parental populations recruit and are able to survive to the adult stage and migrate back to

reproduce in their origin populations, this habitat may be contributing individuals to the local recruitment of multiple populations.

1.3. Dissertation Objectives

If La Guajira is a quality habitat for the development of *C. mydas* while stopping over from their long-distance migrations in the Atlantic, its characterization and study may contribute knowledge on the distribution and ecology of *C. mydas.* Furthermore, the management and conservation of this area may enhance the population survival, growth and genetic diversity of the species, key components for the long-term recovery of the species.

However, the geographic remoteness and harsh terrestrial environment, especially towards the east side of the Guajira's peninsula (*e.g.* arid with strong prevailing winds), combined with the peninsula's location at the political border between two nations, have limited any habitat ecological and oceanographic studies in the area. La Guajira remains "forgotten" from corresponding studies in the region.

Therefore, the general goal of the dissertation was to expand current understanding of the distribution and characteristics of habitat for the endangered, ontogenetic habitat shifter *C. mydas* in the Atlantic. Specifically, this work aimed to determine the quality and extent of La Guajira's marine nearshore SAV ecosystems food resources, a component of habitat favoring long term retention of the studied species. It also aimed to explore whether this area may constitute a developmental habitat for the species by looking at multiple, well-stablished population demographics indicators in the aggregation of turtles, such as the body condition, growth rate, genetic diversity and size distribution. Additionally, this work attempts to look at an important component of the nursing role of developmental habitats for marine turtles of High Guajira, which is its connectivity to parental populations of the species in the Atlantic.

1.4. Methodological Approach and Chapters Overview

A first step in determining the nursery habitat role and quality of eastern La Guajira for *C. mydas* was to characterize the food resources that shallow waters of this area have. Multiple SAV species (*e.g.* seaweeds and seagrasses meadows) are known food items for the macroherbivore *C. mydas* worldwide. In upwelled ecosystems, nutrients accumulate, and seaweeds are expected to proliferate. Thus, in chapter two of this dissertation, the extent, composition and species richness of seagrass and seaweed communities, along the northeast coast of La Guajira, were explored and quantified. The potential *C. mydas* forage species of eastern Guajira's SAV ecosystems were explored and their diversity and extent were used to predict occupancy by the species.

In the third chapter of this dissertation, the quality of La Guajira upwelled coastal ecosystems as habitat for juvenile stage *C. mydas* was assessed by looking at different population demographic indicators in the target species. This chapter attempted to verify the occupancy of the study area by *C. mydas*, by documenting what age classes and in what proportions. Additionally, it provided an overview of the body size and condition of the aggregation of turtles in the area as indicators of quality of the habitat.

One of the most important characteristics of a nursery habitat for marine species with complex life histories is its connectivity to parental populations (Gillanders et al., 2003). The connectivity of La Guajira's developmental habitats to parental populations of

C. mydas in the Atlantic was explored in Chapter four of this dissertation. With the use of genetic markers, the population genetic diversity and origin of the aggregation of juvenile and subadult *C. mydas* in the study area was explored. Additionally, the genetic diversity of this aggregation was compared to other habitats in the Atlantic. The role of major rapid currents in the Southern Caribbean in explaining genetic diversity patterns was also explored in this chapter.

Finally, in the last chapter (5) of this dissertation, the nursery role of SAV ecosystems such as La Guajira's as quality habitat for the development of immature *C. mydas* was discussed. Discussions are enlightened by the theoretical framework of migratory networks models. These models provide insight regarding the contributions of multiple habitats and transitions in a migratory path to the demographics of migratory species. This chapter proposes a model system in the Atlantic to explore the role of habitat quality in the differential per capita contributions to the local recruitment of populations of *C. mydas,* and how it can help to identify patterns of connectivity within regions (smaller scale), by accounting for the variation due to habitat quality in the system. The per capita contributions of certain habitats can be greater than others, as could be the case of developmental habitats for *C. mydas.* Thus, outcomes of the model can be contrasted and compared with observed contributions with mixed stock genetic models. The result of these comparisons can contribute to understand how changes at key habitats or stop over areas can impact the demographics and the population dynamics of the species. The limitations of the dissertation and the directions of future work were presented in this concluding chapter.

1.5. Figures and Tables

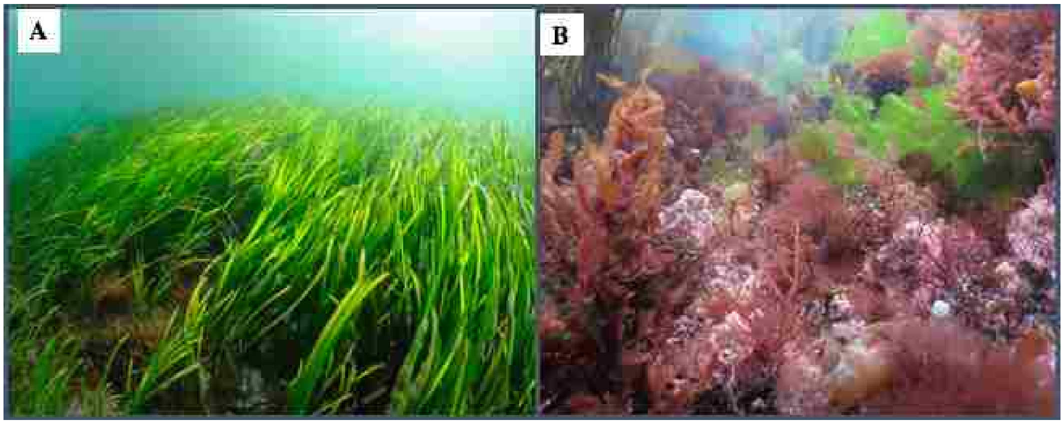

Figure 1.1. Coastal ecosystems of submerged aquatic vegetation. A) seagrass meadow and b) macroalgae bed. Images credit to Scottish Natural Heritage at https://www.flickr.com/photos/ and An Bollenessor at https://anbollenessor.com/tag/ seaweeds.

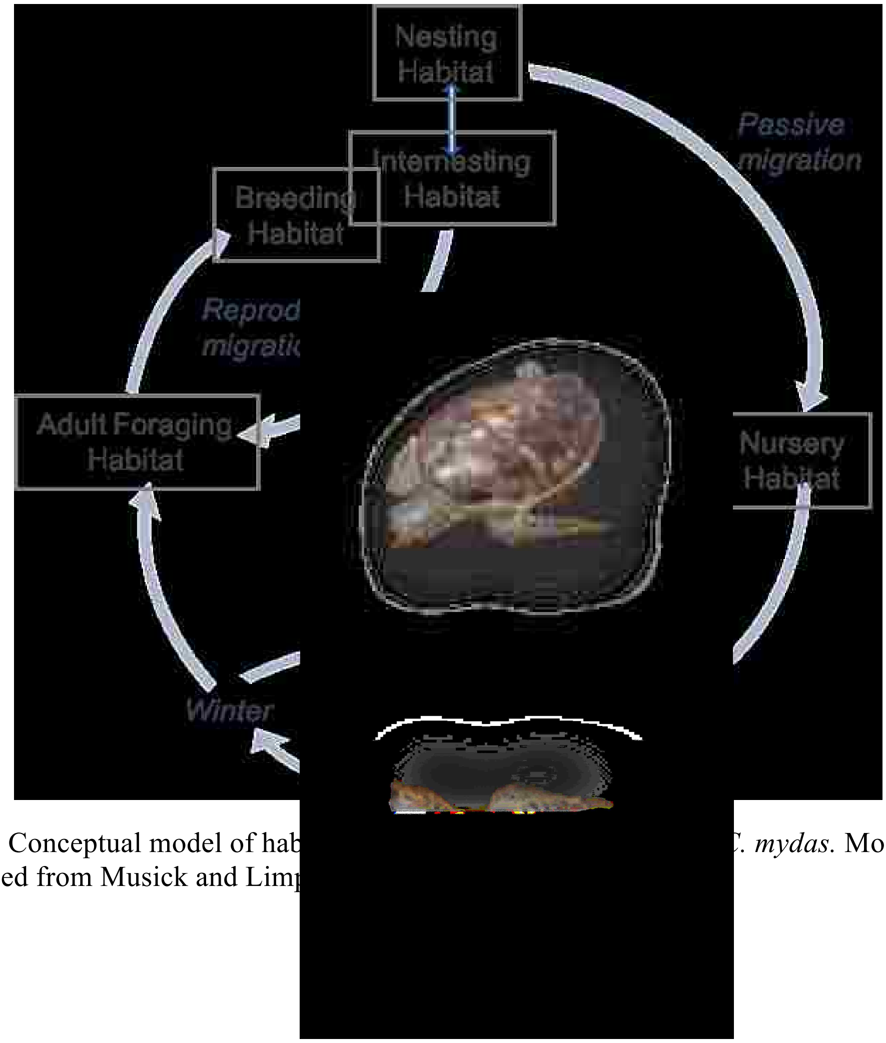

Figure 1.2. Conceptual model of hab *. mydas*. Model taken and modified from Musick and Limp

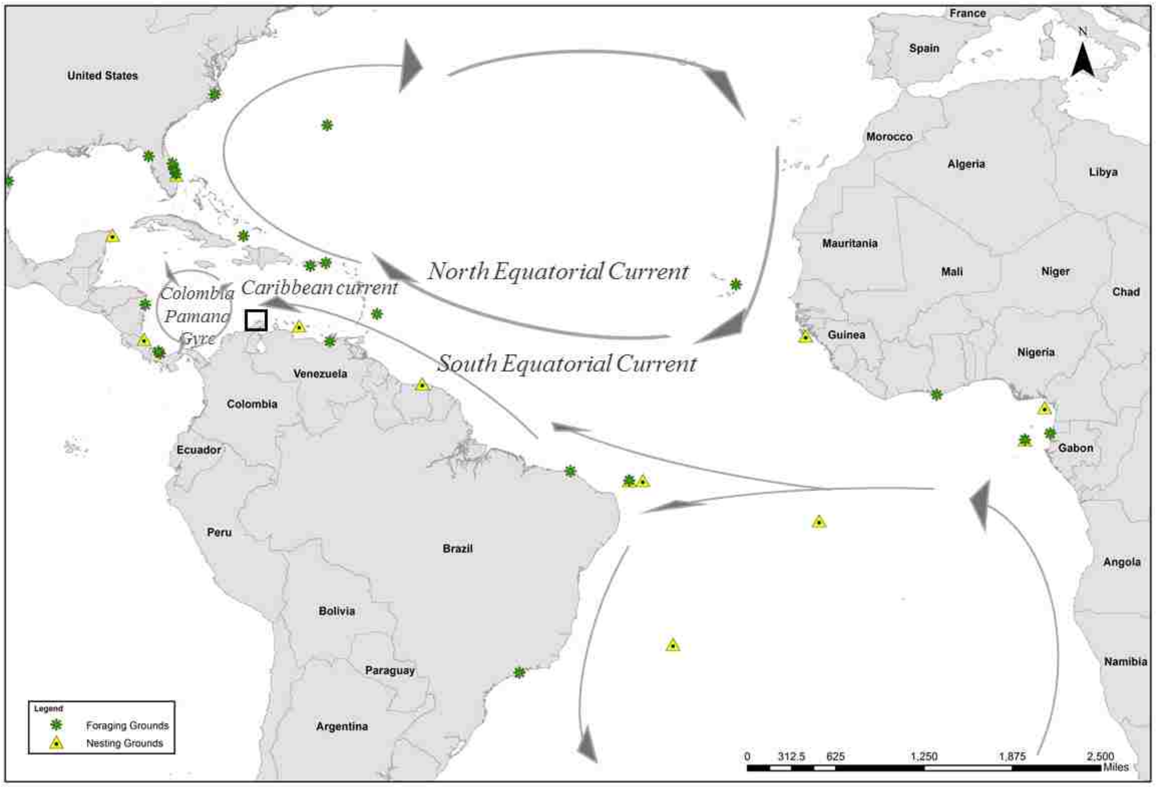

Figure 1.3. Map of the location of La Guajira peninsula of Colombia, a postulated habitat for juvenile *C. mydas,* and other nesting and foraging habitat for the same species in the Atlantic Ocean.

Table 1.1. Summary of habitat characteristics, feeding ecology and energy allocation of *C. mydas*, per life stage.

Life Stage	**Egg/Hatchling**	**Juvenile**	**Subadult**	**Adult**
Size	Egg -18 cm SCL	18 - 50 cm SCL	51 - 75 cm SCL	80 - 110 cm SCL
Habitat				
Water column	Pelagic oceanic	Demersal neritic	Demersal neritic	Pelagic and Demersal
Depth	O m	1-10m	5-20m	>20m
Associations	*Sargassum* mats	SAV beds Coral reefs	SAV beds Coral reefs	SAV beds Coral reefs
Energy Allocation	Predator avoidance	Growth (length and mass) Predator avoidance	Growth (mass)	Reproduction
Food items in order of consumption	Animal Fish eggs seaweeds	Seagrass and/or macroalgae Animal Mangrove roots	Seagrass and/or macroalgae Animal Mangrove roots	Seagrass and/or macroalgae
Nutritional need	Protein	Energy and Protein	Energy	Energy and Protein

CHAPTER 2

Diversity and Extent of Submerged Aquatic Vegetation in Upwelled La Guajira, Colombia

2.1. Theoretical Framework

Subtidal and intertidal Submerged Aquatic Vegetation (SAV) including seagrasses and seaweeds, form extensive, diverse and complex marine ecosystems (Hemminga & Duarte, 2000; Short, 2007; Waycott et al., 2009) (Figure 1.1). Seagrass meadows, for instance, are foci of primary productivity and accomplish key ecological roles in the land-ocean interface (Duarte & Chiscano, 1999; Orth et al., 2006). SAV communities protect the coast from erosion by stabilizing sediments as well as contribute to nutrient recycling through the production of organic carbon (Cullen-Unsworth & Unsworth, 2013). SAV communities also provide habitat to a large number of marine taxa (*e.g.* crustaceans, fishes, reptiles) specially during their larvae/juvenile stages (Nagelkerken et al., 2000). Thus, seagrass meadows are postulated as marine nursery habitats (Dahlgren et al., 2006).

Circumtropical, macroherbivore *Chelonia mydas* distributes in coastal areas partly or mostly composed of SAV (Burkholder et al., 2011; López-Mendilaharsu et al., 2003; López-Mendilaharsu et al., 2005). Both macroalgae and seagrass types of SAV are common diet items for juvenile, subadult and adult stages of *C. mydas*, although it can also include animal and terrestrial plant material (Amorocho & Reina, 2007; Bjorndal, 1985; Balazs, 1980). The preference of one food type over another varies geographically and correlates to the site-specific food availability and quality (Brand-Gardner et al., 1999, Read & Limpus, 2002). For instance, *C. mydas* in the Pacific islands of Japan, Galapagos and Hawaii, feed on benthic or drifting marine algae (Shimada et al., 2014; (Arthur & Balazs, 2008). In contrast, the species feeds almost exclusively on seagrasses in Nicaragua, Australia, India and Yemen, (Lutz et al., 2003).

Foraging on SAV species allows *C. mydas* to fulfill its nutritional needs to grow, migrate and reproduce (Bjorndal, 1985). Marine macroalgae contain the highest levels of essential minerals and the second highest level of protein of all food items evaluated in the stomachs of juvenile *C. mydas* from the Pacific coast of Colombia (Amorocho & Reina, 2007). *C. mydas* has been reported to feed on more than 50 species of algae throughout the ocean basins where it is distributed. A diverse, nutrient-rich diet, may contribute to faster individual growth rates and healthy body conditions. At the population level, it may contribute to positive population growth.

C. mydas populations have been reduced or extirpated along its distribution range and its considered an endangered or threatened species worldwide. A major cause of its endangered status has been the loss and degradation of coastal habitats such as nesting beaches and nearshore benthic ecosystems (McClenachan et al., 2006). The degradation of coastal ecosystems affects the quality of food resources and increases the likelihood of disease and malnutrition (Van Houtan et al., 2010). Coastal degradation reduces the diversity of SAV species to the point it can affect the feeding habits of *C. mydas* (dos Santos et al., 2010). *C. mydas* population’s growth rates are limited by the long-lasting juvenile stage (up to 20 years) (Lutz et al., 2003). Therefore, the identification, delineation and protection of coastal habitats with quality or abundant forage offer is a conservation/management goal for *C. mydas*.

La Guajira's coastal waters harbor the most extensive SAV pastures of Colombia (34.674 ha) (Gómez-Lopez, 2014; Andrade & Barton, 2005). The western side of the peninsula is composed of dense, monospecific or mixed seagrass pastures (14%), and sparse, seagrass pastures (22%) (Chasqui et al., 2013). Whereas on the eastern side, SAV meadows occur in unique, mixed beds of macroalgae (dominant) and seagrasses. On this same eastern side, coastal development and pollution are very low, and the nearshore SAV beds are maintained in a more "pristine" state.

The presence of significant numbers of *C. mydas* on nearshore waters of La Guajira (*e.g*. in the juvenile and subadult stages), and the abundance and pristine state of these ecosystems, suggest that the area could be a quality habitat able to sustain aggregations of the Atlantic *C. mydas*.

This work intended to characterize the geographic extent and species' diversity of SAV pastures in shallow, nearshore waters of northeastern La Guajira peninsula, in Colombia, a postulated developmental habitat for juvenile and subadult *C. mydas* in the Southern Caribbean. The characterization of forage resources in areas where juvenile turtles are known to aggregate, is a first step in the identification of quality habitats for this threatened species.

2.2. Materials and Methods

2.2.1. Study area

The study took place at the northeastern-most part of La Guajira peninsula, in the Uribia municipality (Figure 2.1). In this area, winds reach speeds of 10m/s, there is very low mean precipitation (mean 415mm/y) and high temperatures (mean 29°C) (Invemar, 2012). The waters have a mean temperature of 25.1-26.3 °C and have high primary biological productivity (chlorophyll concentrations of 0.21-1.4 mg/l) due to a seasonal coastal upwelling phenomenon. This study took place prior to the start of the "rainy season", after upwelling occurs, in the months of July and August (2016), for seven weeks. Sea turtles are typically observed in the water and by-caught on fishing gear during these months more than in others.

2.2.2. Submerged Aquatic Vegetation (SAV) Surveys

Surveys of SAV were carried out at the marine nearshore intertidal and/or subtidal zone on six different sites along the northeastern coast of Uribia, La Guajira (Figure 2.1). The study area was divided into two regions. One region at the north of the peninsula, included a shallow hypersaline lagoon (Bahia Hondita) and a protected ocean embayment at its mouth (sites Parei and Patswaroru). The second region, located on the eastern side of the peninsula, included six different shoreline type coastal sites, from Masichii beach to Jiwotpolu beach (Figure 2.1). Some sites were known to be dominated by nearshore SAV communities, and thus were included to determine the species composition of marine plants. Specifically, the region of Chimare was included because previous surveys had showed mixed macroalgae-seagrass beds present (Gómez-Lopez, 2014) (Figure 2.1).

Sea water temperature, salinity and turbidity were recorded at each site with a water quality sampling and monitoring meters (YSI). High water turbidity limited surveys of SAV benthic communities offshore and SCUBA support was not available to apply standard methodologies to obtain SAV species coverage and abundance (*e.g.* quadrants). Alternatively, SAV species were collected once, at each site, over forty-five minutes, by two surveyors who randomly sampled SAV specimens by hand, at varying depths from 0 (subtidal zone) to 4m depending on the coastal geomorphology, covering an area not larger than $10m^2$ at each site. At low relieve, rocky shores with some accessibility, SAV surveys were performed by sampling from rocks at 0-1m depth (Puerto Chimare). Accessible sandy beaches were sampled both in the subtidal and intertidal areas up to 2 m depth. High relief, low accessibility rocky shores were reached from a boat, and surveyors dived up to at 3-4m depth to the seafloor to collect samples (Patsualoru, Palei). After collection, SAV samples were held in seawater until laboratory sorting and identification to the lowest taxonomic level possible using dichotomous classification guides (Littler & Littler, 2000). A list of species occurrences was established for each survey site.

2.2.3 SAV Diversity and Extent Estimations

The species richness S, was calculated for each survey site and the total study area. Species diversity was also calculated for each site (alpha diversity), using the Shannon diversity index (H'), only from the species presence and without considering their abundances because, the high turbidity of the water impeded to obtain this information. All calculations were done using the Vegan package on R (R Development Core Team, 2008). The extent of SAV pastures was assessed by comparing species composition between sites. Correlation with coastal orientation (Azimuth) and wave energy (*e.g.* Low, Medium, High) were explored. The similarity in SAV species assemblages among sites grouped by coastal geomorphology (e.g., beaches, rocky or mangroves) was calculated using the Jaccard dissimilarity index (Somerfield et al., 2008). This index was also used in a non-metric multidimensional ordination (Shepard, 1962) of the samples (sites), performed to better understand patterns of diversity organization. The Jaccard dissimilarities between sites were also compared to geographic separation using the Mantel's test in Vegan package on R.

Additionally, during SAV surveys, local fishermen of La Guajira allowed the surveyors to observe their catch (bycatch included). When sea turtles were part of the bycatch they were often processed for consumption within hours of the catch (less than 8h). Opportunistic observations of five fresh gut content of *C. mydas* were examined for the species composition. SAV species were determined to the lowest taxonomic possible using biological keys (Littler & Littler, 2000).

2.3. Results

2.3.1 Diversity of Submerged Aquatic Vegetation of Northeastern La Guajira

A total of 116 species of SAV were observed in the surveyed area, the majority of which (113 species) were macroalgae and a few (3 species) were seagrasses (Plantae: Tracheophyta) (Table 2.1). However, according to the rarefaction analysis, the number of SAV species in the study area is expected to increase if sampling effort increases (Figure 2.2).

The rhodophytes embodied more than half of the species (57%) found in the coasts of northeastern Guajira, followed by the chlorophytes (27%) and the phaeophytes (16%) (Figure 2.3). The phaeophytes were represented only by two families, the common Dictyotaceae (12 sp) and Sargassaceae (6 sp). Instead, the most common species found in the surveyed area were rhodophytes, with eighteen families present, the most common of which were Rhodomelaceae (15 sp), Gracilariaceae (11 sp) and Corallinaceae (10 sp). The Chlorophytes were represented in the area by 10 families, the most abundant in number of species were the sea lettuces (Ulvaceae, 9) followed by the Cladophoraceae and the Caulerpaceae with six species each (Figure 2.3).

Many species of macroalgae observed in eastern Guajira during this survey study had not been reported before for La Guajira region of Colombia (n=22) (Table 2.1). These new reports for the region included six species of chlorophytes, three species of phaeophytes and thirteen species of rhodophytes. Furthermore, at total of twenty-eight species of macroalgae observed in this survey had not been reported in Colombia previously to this study. These new reports included five species chlorophytes, five species of phaeophytes and eighteen species of rhodophytes.

2.3.2. Extent of Submerged aquatic vegetation in eastern La Guajira

All surveyed sites in the study area had multiple macroalgae species and seagrasses except for Playa Jiwotpolu in which no seagrasses were observed (Table A.1). Bahia Hondita sites (the western region) differed in species composition from the eastern region (significance test). Bahia Hondita had SAV species that where not found on the eastern side such as *Codium sp*., *Ceramium sp., Dasya ocellata, Heterosiphonia gibbeseii* and *Halodule wrightii*, whereas several species present on the eastern side were not found on Bahia Hondia area (*e.g. Bryopsis hypnoides, Chaetomorpha linum, Lobophora variegate, Spatoglossum schroederi, Gracilaria cervicornis, Gracilaria mammillaris, Osmundaria obtusiloba, Sporolithon episporum*) (Table A1).

The composition of SAV species differed among surveyed areas (stat test, of the Jaccard dissimilarities and t-test among them but only for the 7 sites). This is because about half of the species (55sp) occurred only at one sampling site, instead only 10 species were shared or common species among sites (*e.i.* they were present at least in 4 of the 7 sites). Shared species include one *Caulerpa sp*., one *Chaetomorpha sp*., four *Gracilaria sp*., two *Hypnea sp*., one *Sargassum sp*. and one seagrass, *Thalassia testudinum*; from these, *T. testudinum* and *Gracilaria dominguensis*, were present in almost all sites. In fact, *Gracilaria* genus was the most common in number of species (10 species) and number of sites present, thus this group significantly contributed to the observed similarities in species diversity among sites (Figure 2.4).

The sites with the highest species richness and alpha diversity were the inlet, rocky shore of Puerto Chimare (49 sp.), followed by three sandy beaches located to the south named Puerto Santa Cruz (37 sp.), Neimao and Wannal beaches (29 sp. each) (Table 2.2). Bahia Hondita had a moderate species richness (26 sp.), although in this area, the sampling effort was larger than on the eastern side.

Species dissimilarity did not correspond with Euclidean distance (Mantel test, NS). That is, sites that were spatially closer were not more similar in species composition than sites farther apart. Sites from Puerto Chimare to Puerto Santa Cruz, had the highest species diversity and were also the most different. Instead, the extreme regions of Playa Jiwotpolu (southern tip of the survey area) and Masichii (northern tip of the survey area) had the lowest species diversities.

2.3.3 Forage offer for *C. mydas* in eastern La Guajira

Twenty-five genera, twenty-two of macroalgae and three of seagrasses, found in the eastern Guajira have been reported before as food items for sea turtles (Table 2.3). Within these genera, fifteen food items have been identified to the species level, twelve macroalgae and three seagrasses. Six of these SAV species, the Chlorophyte *Caulerpa racemosa*, at least 3 different species of *Gracilaria sp*, 1 species of *Hypnea sp*., and the seagrass *Thalassia testudinum*, were observed in the stomach contents of juvenile and subadult sea turtles coming from areas surveyed in this study. These areas were Puerto Santa Cruz, Playa Neimao and nearby areas (Table 2.4).

2.4. Discussion and Conclusions

A preliminary assessment of the coastal submerged aquatic vegetation diversity at eastern La Guajira peninsula, an under explored area of the Caribbean Sea, was performed in this study. This area had highly mixed, diverse, SAV meadows, as opposed to, monospecific, less diverse meadows observed to the eastern side within the same peninsula (*e.g.* Chasqui et al., 2013). A large list of intertidal and subtidal SAV species was compiled with more than twenty-five species never reported before for Colombia. This lack of previous information on the species diversity, reflects the difficulty of performing studies in the surveyed area, partly due to its remoteness and dessert-like weather conditions.

The high level of SAV species richness and diversity found here could be attributed to the great amount and type of nutrients made available through the coastal upwelling experienced in the area (Barth et al., 2007). This nutrient supply, which is unique in the Caribbean Sea, contributes to the production of biomass and diversification of vegetation forms in the marine environment (Waide et al., 1999).

Species-rich SAV meadows in eastern La Guajira are dominated by macroalgae and seem to extend widely along the coast, at least from eastern Masichii in Chimare, all the way to the Santa Cruz area. However, these SAV ecosystems are likely to be limited on their oceanic extent by the lack of light, due to the high turbidity of the water. Several species found here at very low depths, are typically found at higher depths, in other parts of the Caribbean Sea with more light availability (less turbidity) (Littler & Littler, 2000). Also, these meadows are limited by the extent of the continental platform which on the eastern side is smaller than on the western side of the Guajira peninsula (Invemar, 2012).

This difference, in addition to the different types of substrates among the two sides of the peninsula, help explain the observed differences in SAV meadows composition between western (reported here) and eastern sides of La Guajira peninsula. To the west of Bahia Hondita, where the platform is extensive and substrates are sandy, seagrass *Thalassia testudinum* dominates over macroalgae and forms conspicuous, monospecific pastures, and to a lesser degree mixed-species pastures with macroalgae (Chasqui et al., 2013). Instead, to the south of Bahia Hondita, from Masichii to Puerto Santa Cruz surveyed areas, substrates are finer (*e.g*. muddy sands and sandy muds) with embedded rocks and boulders, and SAV macroalgae were observed forming species-rich mixed pastures with patches of seagrasses along the intertidal and subtidal coastline at very low depths.

These diverse, macroalgae-dominated SAV meadows of eastern La Guajira, seem to be eaten by small juvenile and subadult *C. mydas*. Feeding on macroalgae species is a common behavior of the species in the Pacific and the Atlantic Oceans, even more so than feeding on seagrass (Amorocho & Reina, 2007; Arthur & Balazs, 2008; Seminoff et al., 2003). Eastern La Guajira displayed a diversity of macroalgae species known to be food for *C. mydas* worldwide. A large proportion (44%) of the macroalgae genera, and about a dozen species of macroalgae found in eastern La Guajira during this study, have been reported in the stomach contents of juvenile, subadult and/or adult *C. mydas*. Five of these reported species were found in the stomachs of juvenile and adult *C. mydas* in the study area during this study.

If *C. mydas* are feeding on the diverse forage offer that SAV ecosystems of La Guajira have, questions remain on the impact of this rich, diverse diet on the dynamics and demographics of the local sea turtle population. The extent and biomass of the SAV ecosystems in La Guajira could potentially sustain a large *C. mydas* population or populations. However, the density of sea turtles in these waters has not been estimated yet. Historical sea turtle fishing records suggest that large aggregations of *C. mydas* (45% subadults and juveniles) occur in this area (Rueda et al., 1992). These commercially exploited turtles, came from several sites surveyed in this study. Additionally, the consumption of a diverse, extensive SAV diet such as the one being offered at coastal eastern La Guajira, has the potential to contribute to faster growth rates, and/or good body conditions than in other less diverse, less extensive areas. Estimates of the body condition and the characteristics of the aggregation of *C. mydas* in eastern La Guajira will be provided in the following chapter of this document.

2.5. Figures and Tables

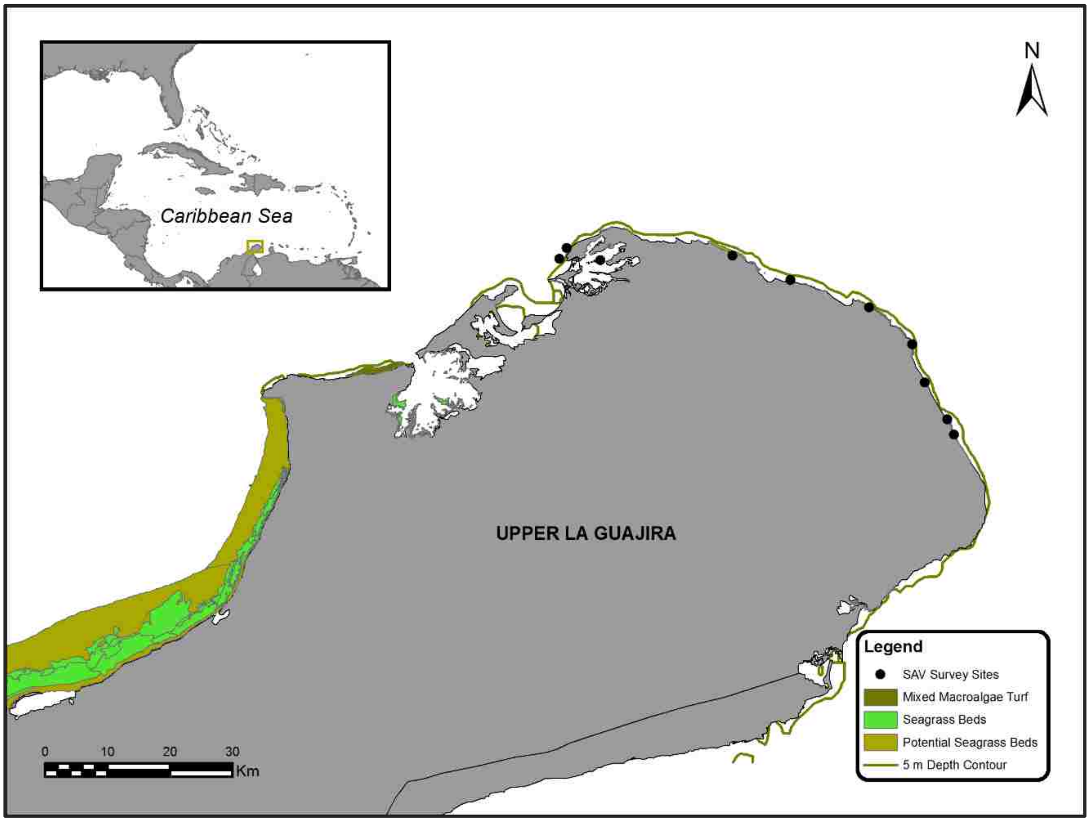

Figure 2.1. Location of the study area in upper La Guajira peninsula, in the Caribbean Sea. The map displays the distribution of SAV vegetation communities from Gomez-Lopez et al (2015), and the location of SAV survey sites in this study.

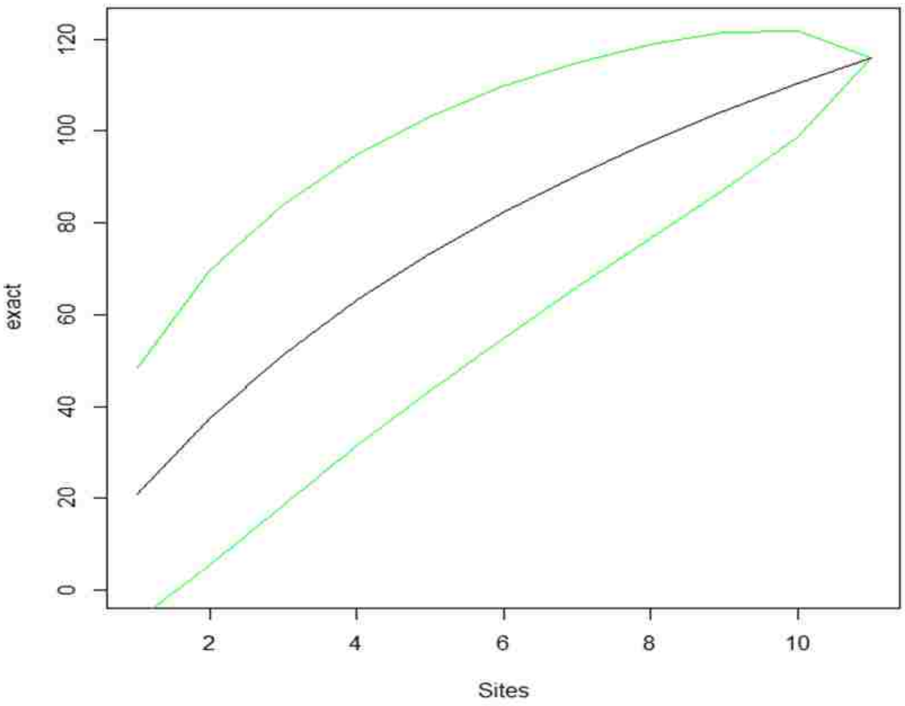

Figure 2.2. Rarefaction curve of the exact expected number of SAV species with the number of survey sites.

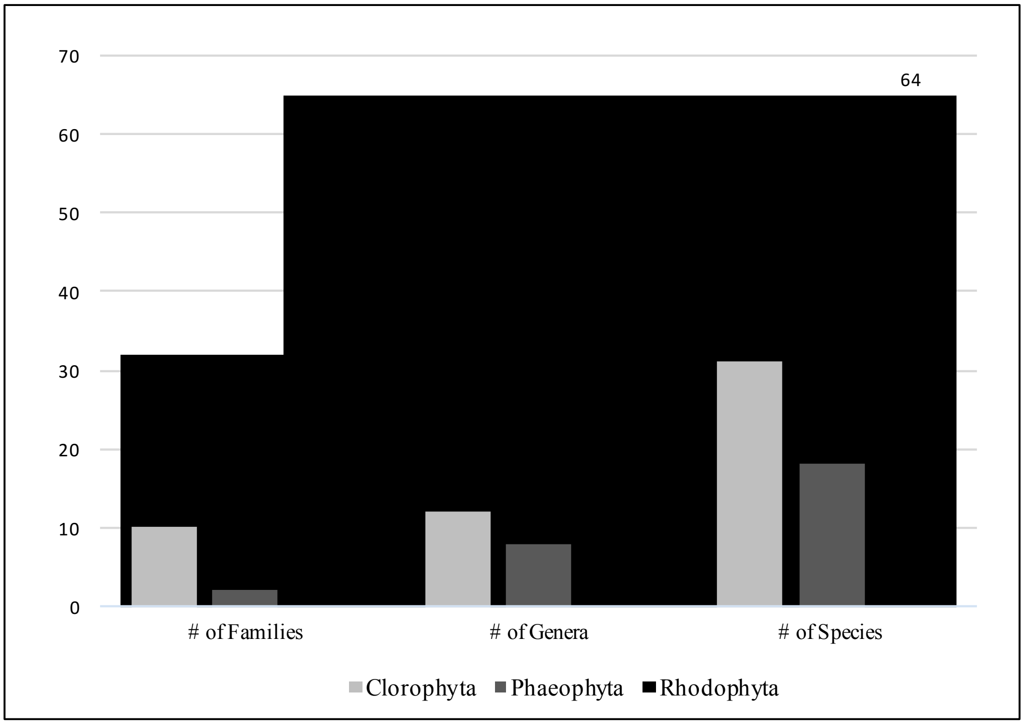

Figure 2.3. Number of species, genera and families of macroalgae main taxonomic groups found in Eastern La Guajira study area.

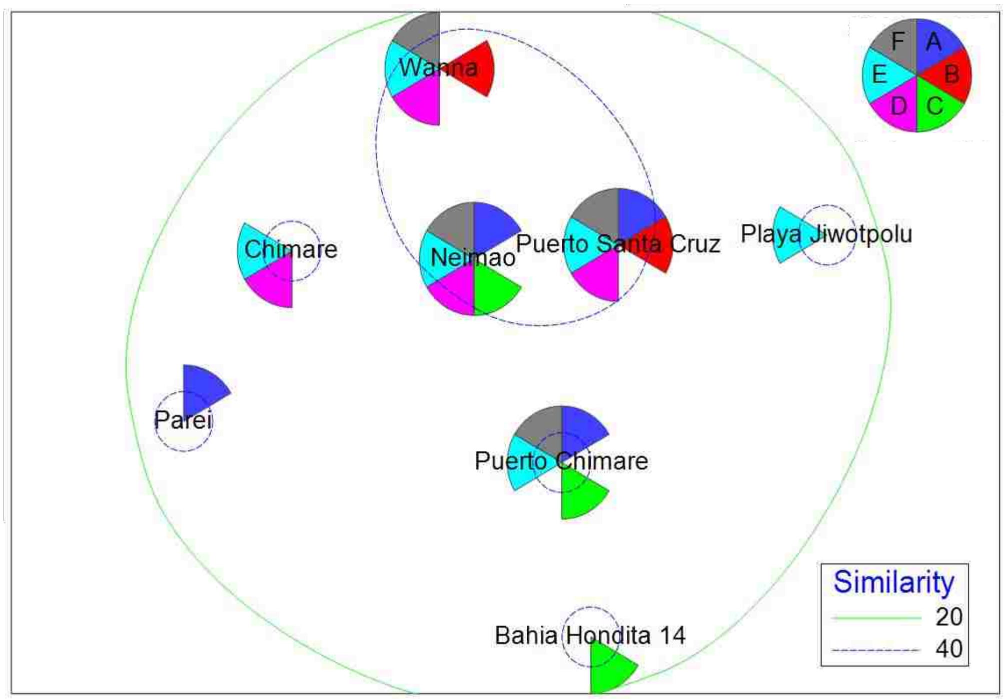

Figure 2.4. Multi-Dimensional scaling (MDS) for SAV surveying sites in La Guajira using the Bray-Curtis similarity based on the presence-absence of species of rhodophytes of the genus *Gracilaria*. Species area letter coded as follows: A. *Gracilaria caudata* B. *Gracilaria curtissae* C. *Gracilaria cylindrica* D. *Gracilaria damaecornis* E. *Gracilaria dominguensis* F. *Gracilaria mammillaris.*

Table 2.1. Taxonomic table of SAV species for the study area in eastern La Guajira, Colombia. Species names highlighted in gray and bolded are new reports for Colombia. Bolded species names are new reports for La Guajira region.

Chlorophyta

Class	Family	Genera	Species
Ulvophyceae	Anadyomenaceae	*Anadyomene*	***Anadyomene stellata***
	Boodleaceae	*Cladophoropsis*	*Cladophoropsis membranaceae*
	Bryopsidaceae	*Bryopsis*	*Bryopsis hypnoides*
			Bryopsis pennata
			Bryopsis plumosa
	Caulerpaceae	*Caulerpa*	*Caulerpa mexicana*
			Caulerpa prolifera
			Caulerpa racemosa
			Caulerpa racemosa var. lamourouxii
			Caulerpa sertularoides f. farlowii
			Caulerpa taxifolia
	Cladophoraceae	*Chaetomorpha*	***Chaetomorpha aerea***
			Chaetomorpha antennina
			Chaetomorpha linum
		Cladophora	***Cladophora catenata***
			Cladophora liniformis
			Cladophora prolifera
	Codiaceae	*Codium*	*Codium repens*
			Codium sp.
	Dichotomosiphonaceae	*Avrainvillea*	***Avrainvillea nigricans***
	Gayraliaceae	*Gayralia*	*Gayralia oxysperma*
	Halimedaceae	*Halimeda*	***Halimeda scabra***
	Udoteaceae	*Udotea*	*Udotea unistrarea*
	Ulvaceae	*Enteromorpha*	***Enteromorpha flexuosa***
			Enteromorpha flexuosa subsp. paradoxa
			Enteromorpha intestinalis
			Enteromorpha lingulata
			Enteromorpha prolifera

		Ulva	*Ulva fasciata*
			Ulva lactuca
			Verdigellas fimbriata

Phaeophyta

Class	Family	*Genera*	*Species*
Phaeophyceae	Dictyotaceae	*Dictyopteris*	*Dictyopteris jamaicensis*
			Dictyopteris jolyana
			Dictyopteris justii
			Dictyopteris plagiogramma
		Dictyota	*Dictyota caribaea*
			Dictyota cervicornis
			Dictyota crenulata
			Dictyota humifusa
		Lobophora	*Lobophora variegata*
		Padina	***Padina profunda***
		Spatoglossum	*Spatoglossum schroederi*
		Stypopodium	***Stypopodium zonale***
	Sargassaceae	*Sargassum*	*Sargassum filipendula*
			Sargassum platycarpum
			Sargassum polyceratium
			Sargassum pteropleuron
			Sargassum vulgare
		Turbinaria	***Turbinaria tricostata***

Rhodophyta

Class	Family	*Genera*	*Species*
Florideophyceae	Areschougiaceae	*Meristiella*	*Meristiella schrammii*
	Ceramiaceae	*Centroceras*	***Centroceras clavulatum***
		Ceramium	*Ceramium cruciatum*
			Ceramium sp.
	Champiaceae	*Champia*	*Champia parvula*
			Champia salicornioides
			Champia vieillardii
	Corallinaceae	*Amphiroa*	*Amphiroa rigida*
		Haliptilon	***Haliptilon cubense***

		Haliptilon subulatum
	Hydrolithon	*Hydrolithon boergesenii*
	Jania	***Jania pumila***
		Jania rubens
	Mesophyllum	***Mesophyllum mesomorphum***
	Neogoniolithon	*Neogoniolithon spectabile*
	Porolithon	***Porolithon pachydermum***
	Titanoderma	***Titanoderma pusttulatum***
Cystocloniaceae	*Hypnea*	*Hypnea musciformis*
		Hypnea spinella
		Hypnea valentiae
Dasyaceae	*Dasya*	*Dasya baillouviana*
		Dasya ocellata
		Dasya spinuligera
	Heterosiphonia	*Heterosiphonia gibbeseii*
Galaxauraceae	*Galaxaura*	*Galaxaura marginata*
	Tricleocarpa	*Tricleocarpa cylindrica*
	Wrangelia	***Wrangelia bicuspidata***
Gelidiellaceae	*Gelidiella*	*Gelidiella acerosa*
Gracilariaceae	*Gracilaria*	*Gracilaria blodgetti*
		Gracilaria caudata
		Gracilaria cervicornis
		Gracilaria cuneata
		Gracilaria curtissae
		Gracilaria cylindrica
		Gracilaria damaecornis
		Gracilaria domingensis
		Gracilaria mammillaris
		Gracilaria sp.
		Gracilaria tikvahiae
Halymeniaceae	*Cryptonemia*	*Cryptonemia seminervis*
Hymenocladiaceae	*Asteromenia*	***Asteromenia peltata***
Kallymeniaceae	*Kallymenia*	*Kallymenia sp.*
		Kallymenia cribogloea
Lomentariaceae	*Gelidiopsis*	***Gelidiopsis planicaulis***

	Peyssonneliaceae	*Peysonellia*	*Peysonellia sp.*
	Rhodomelaceae	*Acanthophora*	***Acanthophora muscoides***
			Acanthophora spicifera
		Bostrychia	***Bostrychia montagnei***
			Bostrychia tenella
		Bryothamnion	*Bryothamnion triquetrum*
		Chondria	***Chondria capillaris***
			Chondria cnicophylla
			Chondria floridana
		Laurencia	***Laurencia (Chondrophycus) iridescens***
			Laurencia gemmifera
			Laurencia intricata
			Laurencia obtusa
			Laurencia poiteaui
		Osmundaria	*Osmundaria obtusiloba*
		Wrightiella	***Wrightiella blodgettii***
	Rhodymeniaceae	*Rhodymenia*	***Rhodymenia divaricata***
		Solieria	*Solieria filiformis*
	Solieriaceae	*Agardhiella*	***Agardhiella ramosissima***
	Sporolithaceae	*Sporolithon*	***Sporolithon episporum***

Tracheophyta

Class	Family	*Genera*	*Species*
Liliopsida	Cymodoceaceae	*Halodule*	*Halodule wrightii*
		Syringodium	*Syringodium filiforme*
	Hydrocharitaceae	*Thalassia*	*Thalassia testudinum*

Table 2.2 Species richness and diversity indexes per survey site in northeastern La Guajira, Colombia.

Survey Site	***S***	**d**	**H'**
Parei	11	4.1703	2.3979
Patsuaroru	4	2.1640	1.3863
Bahia Hondita	26	7.6732	3.2581
Masichi	15	5.1698	2.7081
Neimao	29	8.3153	3.3673
Punta Negra	6	2.7906	1.7918
Wannal	29	8.3153	3.3673
Puerto Chimare	49	12.3336	3.8918
Puerto Santa Cruz	37	9.9698	3.6109
Playa Jiwotpolu	22	6.7938	3.0910

S= Species Richness; d= Margalef Index; H'= Shannon Index

Table 2.3. SAV species found in this study that have been reported as food items for *C. mydas* previously in the literature, and during this study.

Food item of *C. mydas*		**Reference(s)**
Group	Species	
Chlorophyta	*Caulerpa sp.*	Santos-Baca 2008; Balazs 1979; Read 2015
Chlorophyta	*Caulerpa mexicana*	Santos *et al* 2012
Chlorophyta	*Caulerpa prolifera*	Mortimer 1981
Chlorophyta	*Caulerpa racemosa*	<u>This study</u>
Chlorophyta	*Caulerpa taxifolia*	Santos-Baca 2008
Chlorophyta	*Chaetomorpha sp.*	Raymundo-González 2010
Chlorophyta	*Chaetomorpha aerea*	Ross 1985; Santos *et al* 2011
Chlorophyta	*Chaetomorpha antennina*	Seminoff *et al* 2002;
Chlorophyta	*Cladophora sp.*	Arthur and Balazs 2008; Makowski *et al* 2006; Amorocho and Reina 2007; Santos *et al* 2011
Chlorophyta	*Codium sp.*	Shimada *et al* 2014; Read 2015; Seminoff *et al* 2002; Santillan 2008; Balazs 1979
Chlorophyta	*Enteromorpha sp.*	Seminoff *et al* 2002; Makowski *et al*2006
Chlorophyta	*Ulva lactuca*	Seminoff *et al* 2002; Santillan 2008; Santos-Baca 2008; Carrión-Cortez, *et al* 2010; Awabdi *et al* 2013
Chlorophyta	*Ulva sp.*	Gonzalez-Carman *et al* 2014; Santos *et al* 2011; Guebert-Bartholo *et al* 2011; Nagaoka *et al* 2012; Read 2015
Phaeophyta	*Dictyopteris sp.*	Makowski *et al*2006
Phaeophyta	*Padina sp.*	Seminoff *et al* 2002; Santos-Baca 2008
Phaeophyta	*Rhodymenia sp.*	Gonzalez-Carman *et al* 2014
Phaeophyta	*Sargassum sp.*	Guebert-Bartholo *et al* 2011; Seminoff *et al* 2002; Garnett *et al* 1985
Phaeophyta	*Sargassum vulgare*	Awabdi *et al* 2013
Phaeophyta	*Turbinaria sp.*	Read 2015
Rhodophyta	*Acanthophora spicifera*	Makowski *et al* 2006
Rhodophyta	*Bostrychia sp.*	Nagaoka *et al* 2012
Rhodophyta	*Bryothamnion sp.*	Makowski *et al* 2006
Rhodophyta	*Caulerpa sp.*	Balazs 1979; Read 2015; Santillan 2008; Santos-Baca 2008
Rhodophyta	*Ceramium* sp.	Read 2015
Rhodophyta	*Gelidiella acerosa*	Awabdi *et al* 2013

Rhodophyta	*Gracilaria cylindrica*	Read and Limpus 2002
Rhodophyta	*Gracilaria mammillaris*	Makowski *et al* 2006; Santos *et al* 2011
Rhodophyta	*Gracilaria sp.*	This study; Santillan 2008.; Arthur *et al* 2009; Fuentes *et al* 2007; Guebert-Bartholo *et al* 2011
Rhodophyta	*Hypnea musciformes*	Russell and Balazs 2009; Santos *et al* 2011
Rhodophyta	*Hypnea sp.*	Arthur and Balazs 2008; Arthur *et al* 2009; Brand-Gardner 1999; Garnett et al 1985; Guebert-Bartholo 2011; Carrión-Cortez *et al* 2011; Fuentes et al 2007; This study
Rhodophyta	*Hypnea spinella*	Read and Limpus 2002
Rhodophyta	*Hypnea valentiae*	Read 2015
Rhodophyta	*Jania sp.*	Makowski et al 2006
Rhodophyta	*Laurencia sp.*	Santos et al 2011; Garnett *et al* 1985
Rhodophyta	*Osmundaria sp*	This study
Seagrass	*Halodule wrightii*	Mendonca 1983
Seagrass	*Syringodium filiforme*	Mendonca 1983; Mortimer 1981
Seagrass	*Thalassia testudinum*	Mortimer 1981; Bjorndal 1997

Table 2.4. *Chelonia mydas* stomach content and proportion of each food item tyep per wet sample.

Turtle	Location, Depth	Life Stage	SCL (cm)	Stomach Content		
				Type	Taxonomic Name	%WV
1	P. Santa Cruz, Shallow	Juvenile	27	Macroalgae	*Caulerpa sp.*	70%
				Macroalgae	Rhodophyta pos. *Osmundaria sp.*	10%
				Seagrass	*Thalassia testudinum*	20%
2	P. Santa Cruz, shallow	Juvenile	29.9	Macroalgae	*Gracilaria sp.*	93%
				Macroalgae	Undetermined	1%
				Seagrass	*Thalassia testudinum*	5%
				Animal	Undetermined	1%
3	P. Santa Cruz, Shallow	Juvenile	32.7	Seagrass	*Thalassia testudinum*	100%
4	P. Neimao, Shallow	Juvenile	40.5	Macroalgae	*Gracilaria sp.1*	20%
				Macroalgae	*Gracilaria sp.2*	10%
				Macroalgae	*Gracilaria sp.3*	10%
				Macroalgae	*Caulerpa racemosa*	45%
				Animal	Sponge	15%
5	Pushu Pushui, Deep	Adult	87	Macroalgae	*Hypnea sp.*	90%
				Macroalgae	*Hypoglossum hypoglosoides*	10%

SCL= Straight Carapace Length
%WV= Percentage of the food item volume in the total wet volume.

CHAPTER 3

Quality of Northeastern La Guajira as Habitat for *Chelonia mydas* inferred from Individual Distribution and Body Condition

3.1. Ecology of Habitat for *C. mydas*

Chelonia mydas is a highly migratory, stage-structured species, with four different life stages spent at geographically separated habitats (Musick & Limpus, 2003) (Table 1.2.). Habitat for the species is found all throughout coastal waters of the tropics and subtropics (Figure 1.2). In the Atlantic basin, *C. mydas* historically had large thriving populations, however, loss of habitat (primarily for nesting), caused their reduction, and even local extirpation (McClenachan et al., 2006). For the species to recover, populations will need to achieve positive population growth rates.

The intrinsic population growth rate of the Atlantic *C. mydas* is limited by the multi-year immature stages (juvenile and subadult) (Bjorndal & Bolten, 1988; Limpus & David, 1980). Juvenile *C. mydas* recruit into developmental habitats (DHs), which are shallow, neritic areas with beds of aquatic vegetation, after their long pelagic migration, away from nesting habitat (Meylan et al., 2011; Musick and Limpus, 2003). Juveniles will remain in DHs until maturation starts to occur (Meylan et al., 2011). For *C. mydas* to return to nesting habitats and reproduce, it needs to gain large body sizes and energy reserves to migrate long distances (*e.g.* migration takes 10-24% of the female's accumulated energy) (Bjorndal, 1985). The majority of body size growth occurs at the immature stages at developmental habitats, before the onset of maturity (Bjorndal et al., 2013). Growth rates start decreasing when larger body sizes are reached and stop at maturity. Thus, pre-maturity body growth rates are significantly, negatively correlated with age at sexual maturity in *C. mydas* (Bjorndal, et al., 2013). The faster the age at sexual maturity is reached, the sooner individuals will reproduce and thus populations could be replenished. Thus, individual growth rates at the DHs are relevant to the growth of populations in *C. mydas*.

Individual productivity (growth rates and reproductive output) in *C. mydas* is a response to the conditions and resources of the environment; most important resource being food resources (Bjorndal et al., 2017). Because the majority of somatic growth previous to reproduction occurs at DH, it is expected that the energy and nutrients required for reproductive migrations come from the diet at DHs (Table 1.1). Quality nutrition has been shown to directly impact the rate of somatic growth. Under nutrient-rich diets, *C. mydas* grows faster and thus reaches the age of maturity sooner (Limpus & David, 1980; Bjorndal & Bolten, 1988). Thus, it is expected that developmental habitats with quality food resources have a positive impact on vital rates such as the intrinsic population growth rate.

3.1.1. *C. mydas* food resources distribution

C. mydas is a macroherbivore that feeds mostly on benthic marine plants (e.*g*. seagrass, macroalgae), but also on small invertebrates (Vander Zanden et al., 2013; Amorocho & Reina, 2007; Bjorndal, 1985). Hind-gut fermentation releases the necessary nutrients and energy from a vegetation-based diet during the digestion process (Bjorndal, 1980). However, the nutrient value of marine plants varies with the condition of the plant, which in turn is dependent on the type and amount of nutrients as well as light available in their growing environment (Duarte & Chiscano, 1999).

Nutrients are made available to marine plants through several physical mechanisms, one being ocean upwelling. Upwelling is the upper movement of nutrient-rich, deep waters to the surface of the water column where primary producers use these nutrients and light to photosynthesize and proliferate (Figure 1.5) (Rueda-Roa & Muller-Karger, 2013). In some locations, upwelling can facilitate not only water column productivity, but also macroalgae biomass productivity. The abundance of these benthic marine provides habitat for benthic fauna and forage for macroherbivores such as *C. mydas*.

The coastal waters of La Guajira peninsula, Colombia, harbor extensive seagrass beds and diverse macroalgae beds, unique to the coastal systems of the Caribbean, partly due to shallow coastal shelf, abundant sunlight and nutrient enrichment provided by seasonal coastal upwelling (Invemar, 2012; see Chapter 2). *C. mydas* of different sizes have often been observed feeding in this area (Ceballos, 2004; Rueda et al., 1992). Turtles forage on both macroalgae and seagrass (see Chapter 2). In the eastern part of La Guajira, there is limited human development along the coast or any other anthropogenic activity (*e.g.* mining, farming) causing changes or degradation of the nearshore marine plants communities. Thus, La Guajira waters have been proposed as high-quality habitat for the development of *C. mydas.*

3.1.2. Research Hypotheses and Goals

If La Guajira is a high-quality DH, as a result of unique diverse, nutrient-rich, food offer (SAV species), then immature sea turtles are expected to recruit in these waters to grow, and remain in the area for long periods of time. The response to a high-quality DH to *C. mydas* would be an improved body condition and fast growth rate due to the nutritional value of its diet.

This work aimed to assess the quality of northeastern la Guajira coastal SAV ecosystems as a DH for *C. mydas*, by measuring several distributional and somatic condition indicators of individual turtles aggregating in this area.

The assessment of habitat quality and characteristics is a necessary precursor for discerning the effects of habitat on population dynamics such as growth rates (Pulliam, 2000; Runge et al., 2006; Wiederholt et al., 2017). The quality of a habitat, understood as the per-capita contribution to the growth of populations from that given habitat can be measured in two ways (Johnson, 2007):

1) By assessing indicators in the habitat itself, or
2) Evaluating indicators in the species of interest using the habitat.

The somatic growth rate and condition of individual *C. mydas* correlates with the nutritional value of food (Bjorndal and Bolten 1988). *C. mydas* responds to physical variables of the environment such as temperature and salinity with modification of the feeding habits (Lutz et al., 2003). Non-lethal effects of predation, parasitism, diseases can be observed in the somatic condition of marine turtles; and these effects have been quantified using somatic condition indexes considering body length and weight relationships (Heithaus et al., 2007; Thomson et al., 2009). Thus, an assessment of the physical condition of the body of an aggregation of turtles at a given habitat can provide indication of the quality of the habitat for the species.

3.2. Materials and Methods

3.2.1 *C. mydas* aggregation surveys

La Guajira peninsula's productive waters sustain a large coastal artisanal fishery. On the northeastern side of the peninsula, the upper Guajira, the coastal human communities are from the Wayuu indigenous group. The Wayuu rely on fishing for subsistence and have historically fished a variety of marine and coastal species including sharks, rays, lobster, and several fin fish as well as sea turtles. In 1995, the laws in Colombia changed to protect all sea turtles from commercial fishing and their catch was banned nationwide (Corpoguajira, Res. No 2879) in order to agree with international protection measures globally (Morales-Betancourt, et al., 2015). However, sea turtles are often accidentally caught (as by-catch) in artisanal fishing nets (Rueda et al., 1992).

Fishing is done mostly using nylon or thread nets fixed near the bottom (*e.g*. rays and lobster nets) or near the surface (*e.g*. turtle and shark nets), in shallow areas, no deeper than 11m (6 fathoms). *C. mydas* needs to surface to breathe; also, it feeds mostly on benthic vegetation. Therefore, turtles move both vertically and horizontally in the water column overlapping with the majority of local fishing practices. Additionally, fishing activities overlap with the distribution of smaller, immature turtles, the target group of this study. Small or juvenile turtles tend to occupy shallower waters (~1-10m) whereas bigger subadult or adult turtles occupy deeper waters (~10-20m).

C. mydas bycaught by local fishermen, who had been previously consulted about this project, were surveyed for this study. Turtles that had been bycaught in nearshore coastal waters of four main fishing ports were included in this study (Figure 3.1). Turtles were physically inspected for external signs of body condition, measured and weighed following standard methods (Eckert et al., 1999). Fishermen provided information on the location, habitat and depth of their catch. In Bahia Hondita site, a group of local sea turtle conservation stewards contributed substantially to this study by providing *C. mydas* bycatch data they have been collecting for years (2014 to 2016), as part of their sea turtle conservation stewardship program. In the rest of the study area, surveys took place during summer of 2016.

3.2.2. Individual condition assessment

The somatic condition and life stage of by-catch turtles was assessed using the body length (Straight Carapace Length, SCL, in cm) and weight (in kilograms). Life stage was inferred directly from the body length, using the ranges provided in the literature for the closest Caribbean population of *C. mydas,* in Panama, in which individual′s maturity stage was determined using laparoscopy (Meylan et al., 2011) (Table 3.1). The proportion of individuals at each life stage was used to describe aggregations demographically (*e.g.* as adult or largely sub-adults and juveniles). Also, the length (SCL cm) and weight (kg) were used to calculate a body condition index, thought to reflect diet quality and energy reserves. The Fulton's Body Condition Index (BCI) (Froese, 2006) has been used globally to assess the health of turtle populations. Individual values of the index were averaged to obtain a population-level index for comparisons with other locations (Labrada-Martagón, et al., 2010).

Environmental constraints to sea turtle individuals' body condition have been previously identified (Labrada-Martagón, et al., 2010; Heithaus et al., 2007; Johnson 2007). Accounting for these constraints can increase understanding of habitat quality for a target species. *C. mydas* were visually inspected for several of these constraints including external parasites, external symptoms of environmental-transmitted diseases (*i.e.* Fibropapilloma), and signs of malnutrition (Figure 3.2). The environmental conditions of the water such as azimuth and wave energy differ among regions within the study area, thus, the region of Bahia Hondita was analyzed separately from the eastern La Guajira region (including Chimare, Puerto Estrella and Santa Cruz).

3.2.3. Assessment of habitat occupancy and residency time

To assess if immature *C. mydas* are taking residency in La Guajira coastal areas, the movement of an individual turtle was tracked with satellite telemetry. As part of the collaboration with the group of Bahia Hondita sea turtles' conservation stewards, a 42cm carapace length *C. mydas* bycaught by a local fisherman, was marked with a small Argos satellite telemetry tag SPOT 6 (dimensions 72 x 56 x 22 mm, Wildlife Computers®, 2015). The turtle was released from the same area where it was caught on August 2015

(Figure 3.3). The position of the turtle (named Iwa) was obtained from the Argos website (http://www.argos-system.org). Position data was edited to include only high-quality positions (scores A or B) with the software STAT (Coyne & Godley, 2005). After edition, position data were imported and analyzed spatially using the “hotspot analysis’ tool in ArcGIS (ESRI, 2015). The analysis identified the areas of more frequent use “hotspots”, considering the length of time of the turtle at a spot (X, Y location).

Worldwide studies attempting to understand the ecology of *C. mydas* have been marking individuals of the species with unique ID metal tags. In La Guajira, turtles have been tagged by the Humboldt Research Institute (http://www.humboldt.org.co/en). During local fishing activities, marked turtles have been recaptured. Information on the place and time of the animal first tagging and the animal recapture was used to estimate the time of residency.

3.3 Results

3.3.1. Size and stage distribution in upper La Guajira

Alive and dead *C. mydas* turtles (n= 54) from juvenile to adult life stages, were reported by fishermen and surveyed in this study (Table 3.1). The carapace length ranged from 16.2 cm to 87 cm SCL (Mean = 48.3, SD ±17) (Figure 3.3). Carapace width ranged from 19.7 cm to 68.2 cm SCL (Mean = 43.5±, SD 13.6). The weight of bycaught turtles ranged widely from 1.1 Kg (smallest juvenile) to 96.3 Kg (largest adult male) (Figure 3.3.). The majority of individuals were immature, 53.8% of which were juveniles and

46.2% were subadults (Table 3.1). The ratio of juvenile to subadult was 1.17:1. The size distribution and stage ratios did not differ among regions or among sites within the study area (data not shown).

3.3.2. Body condition and health status of immature *C. mydas*

The average somatic condition of the immature *C. mydas* of northeastern La Guajira was good (Fulton's Index=1.47, SD± 0.38, range 1.24 - 1.72) (Figure 3.5). The Body condition index was similar throughout size and stage classes and did not differ among regions within the study area (Figure 3.4). The value of the index followed within the range of values observed in other populations of the species, and it was higher than in other populations in the Caribbean region (Table 3.2).

The most common environmental constraint to a healthy body condition was external parasitism (mostly barnacles) followed by environmentally-borne diseases (*i.e.* Fibropapilloma) (Figure 3.6). The incidence of fibropapilloma significantly differed regionally, with all cases observed only in Bahia Hondita. The prevalence of fibropapilloma in the area was constant over three years.

3.3.3. Immature *C. mydas* habitat occupancy and time of residency

The satellite-tracked juvenile *C. mydas* traveled 29 km straight line from the releasing point in the north of Bahia Hondita to the last point of record, in Chimare (Figure 3.4). The juvenile turtle remained in La Guajira's nearshore waters for four months, 37 days of which it was satellite tracked, and two and half months more until it was bycaught by a fisherman who returned the unique ID metal tags the turtle had been marked with. During the first 10 days of tracking the turtle remained in or nearby Bahia Hondita, however, the turtle actively dispersed east and then southwards along the coastline of the peninsula, against the prevailing current direction. The majority of the tracking time, and until capture, the juvenile turtle remained in the same area at Chimare. This area was identified with a high probability (95%) as a hotspot or “preferred” site for the turtle (Figure 3.4).

Two immature turtles (the first one 52 cm and the second one 35.5 cm SCL) that had been marked with unique ID metal tags in Bahia Hondita previously to this study, were bycaught (recaptured) by fishermen of this same bay. The first individual was recaptured 3 years after first capture, and the second one was recapture 3 years and four months after first capture.

3.4. Discussion and Conclusions

The patterns of juvenile recapture and satellite tracking observed in this study suggest that at least some of the immature *C. mydas* of northeastern La Guajira remain at, or come back to this area for a period of at least three years. Also, juveniles spend significantly more time at certain sites within La Guajira than in others; and they actively swim against currents to reach these “preferred” sites. The DH hypothesis, based on observations of immature aggregations of the species in the Atlantic, suggest that immature *C. mydas* remain at these habitats and have specific sites to which they are faithful (Meylan et al., 2011). Although scarce, the information gathered in this study supports this hypothesis for at least some part of the immature turtle aggregation.

During the tracking period of the small juvenile *C. mydas*, the survey site of Chimare was identified as a hotspot. This area had the highest macroalgae species richness of all surveyed sites of this dissertation (see Chapter 2). It was also one of the areas where more bycaught *C. mydas* were reported by fishermen to this study.

The immature aggregation is distributed among the juvenile and subadult stages in almost equal proportions. This size structure differs from the structure observed in a previous study on the commercial use of sea turtles in middle La Guajira 25 years ago (Rueda et al., 1992). Differences could be due to environmental differences among middle and upper regions. However, it's likely that differences are due to sampling effort. The previous study was performed on turtles fished for commercial purposes, before sea turtle fishing was banned in Colombia, and the largest turtles targeted were adults. This study now includes the smaller size classes of turtles because of the subsistence fishing occurring in shallower depths, and this study included primarily smaller turtles caught as by-catch.

The Gulf of Venezuela which is considered one of the most important feeding areas in Venezuela for *C. mydas*, and is one of the only three areas hosting both adult and immature stages of the species in the Caribbean (Guada & Sole, 2000). Other important turtle habitats include Nicaragua and Florida. Regionally, there is a lack of information on the role of La Guajira as a DH for the species. In this work, the quality of eastern La

Guajira on the Colombian side of the Gulf was assessed by looking at the somatic condition of immature turtles as a response to the nutritional quality of the habitat.

The average body condition indices from La Guajira was “good” and higher than other Caribbean populations (*e.g.* Bjorndal et al., 2000). Turtles at La Guajira seem to be feeding on an extensive, diverse, algae and seagrass diet. Macroalgae species dominate in upper La Guajira areas surveyed in this dissertation. Red algaespecies are very common and species rich. Algae-based diets and red algae diet items preference, have been reported before for the species (Brand-Gardner et al., 1999). Sea turtles in the Baja California, Pacific Ocean preferred high nitrogen algae (even invasive) with lower fiber content over lower nitrogen, high fiber content algae (Brand-Gardner et al., 1999). Nitrogen is a limiting nutrient that *C. mydas* need to obtain from the diet to be able to produce biomass and develop. High fiber content plant food limit the access to nutrient nitrogen present in the food (Bjorndal, 1980). Macroalgae species have lower amounts of fiber than seagrass, and tend to have more nitrogen. Red macroalgae have the highest levels of Nitrogen among plant diet items of *C. mydas* and they seem to be preferred by *C. mydas* (Jones and Seminoff, 2013). Benthic macroalgae, especially red *Gracilaria sp.* were very diverse and common in SAV communities of northeastern La Guajira. The diversity of this high-nitrogen, low fiber, food items may provide a nutrient-rich diet to *C. mydas* to support growth and energy accumulation. Pacific populations of green sea turtle found in upwelling areas off Peru also showed higher body condition values compared to turtles from nutrient deprived area (Velez-Suazo et al., 2014).

Quality diets may contribute to faster attainment of the reproductive stage, which is likely to influence the timing of reproductive migrations due to storage reserves. Sea turtles that reach quicker the age of maturity may recruit faster to reproductive populations. However, the quality of food resources in not the only aspect of habitat quality that may contribute to *C. mydas* population′s local recruitment. Although food resources are a key component of species habitat and a driver of distribution and occupation of habitat, other aspects of habitat are important to be considered when assessing its quality or its contribution to the growth rates or survival of populations. For instance, energy gained from quality food may be spent in predation avoidance at an area with high predator abundance. In the case of DHs, their contribution to population growth also depends on its connectivity to parental populations at reproductive and nesting habitats, which individuals need to reach in order to reproduce. In the next chapter (4), the levels of connectivity of La Guajira habitats to different nesting rookeries in the Atlantic will be explored.

3.5. Figures and Tables

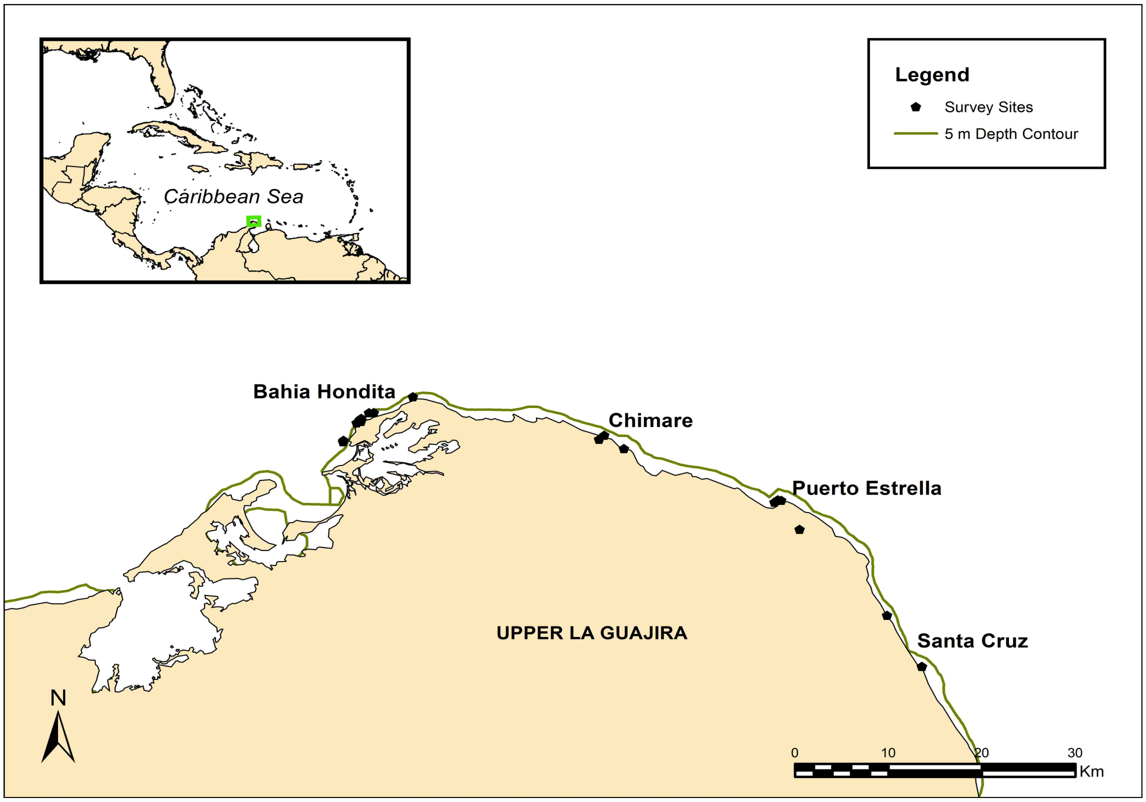

Figure 3.1. Study area map with surveying sites for bycaught *C. mydas* in northeastern of La Guajira, Colombia, in the southern Caribbean.

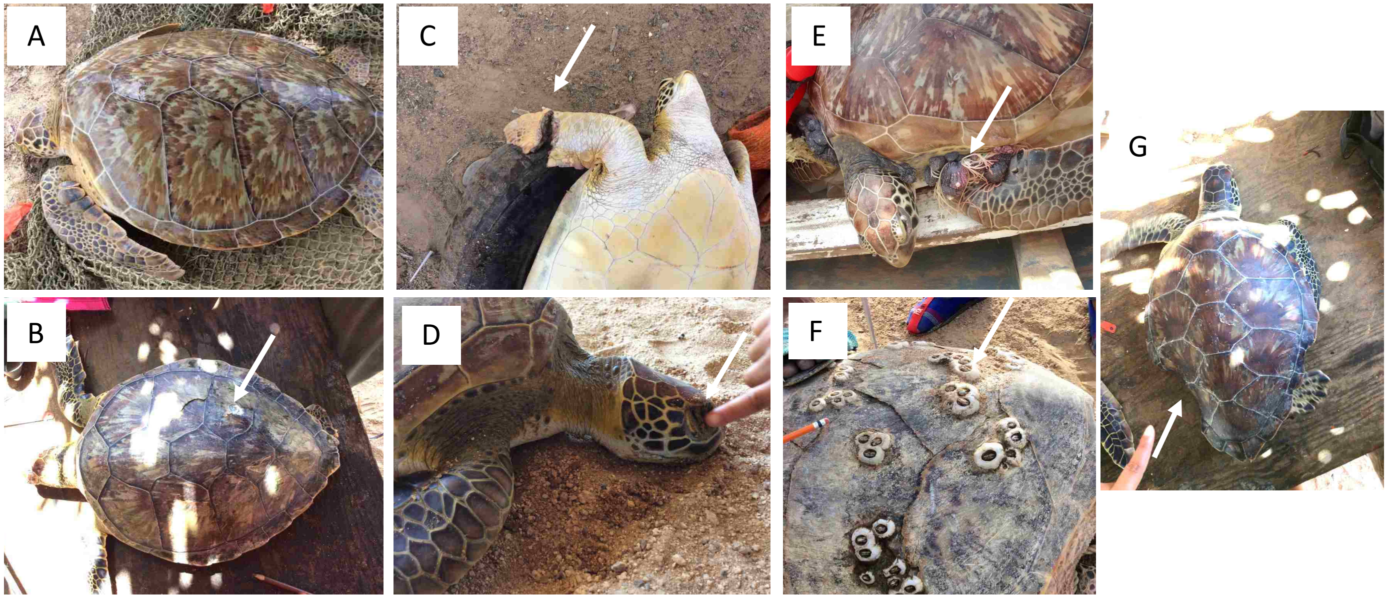

Figure 3.2. Examples of indicators of health status observed in *C. mydas* during this study. Indicators were classified in several categories: A) No indicators. B) Malnutrition (e.g. Carapace scutes lifted from decalcification). C) Injures or wounds (e.g. Cuts on body parts from fishing handling). D) Drowning (no eye reflection indicates death). E) Disease (e.g. Skin tumors from Fibropapilloma). F) External Carapace parasites (e.g. barnacles). G) Predation (e.g. Body parts missing).

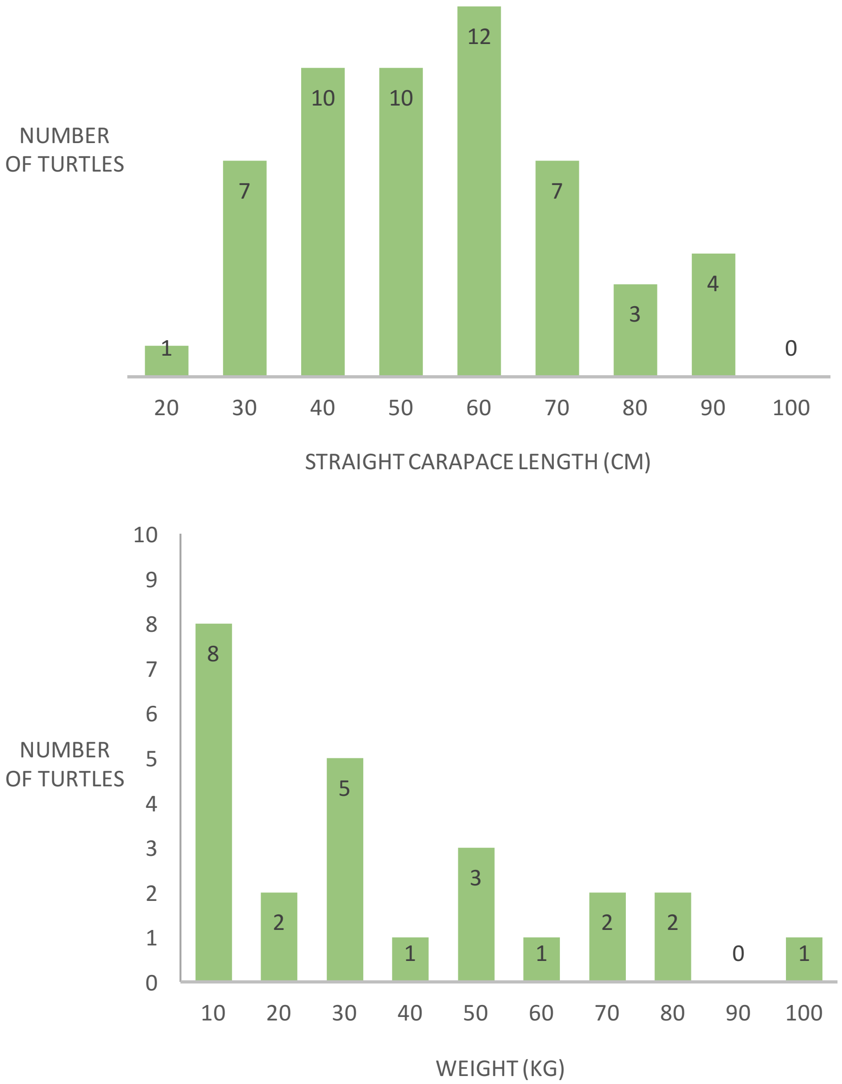

Figure 3.3. Size and weight distribution of the aggregation of *Chelonia mydas* in northeastern La Guajira.

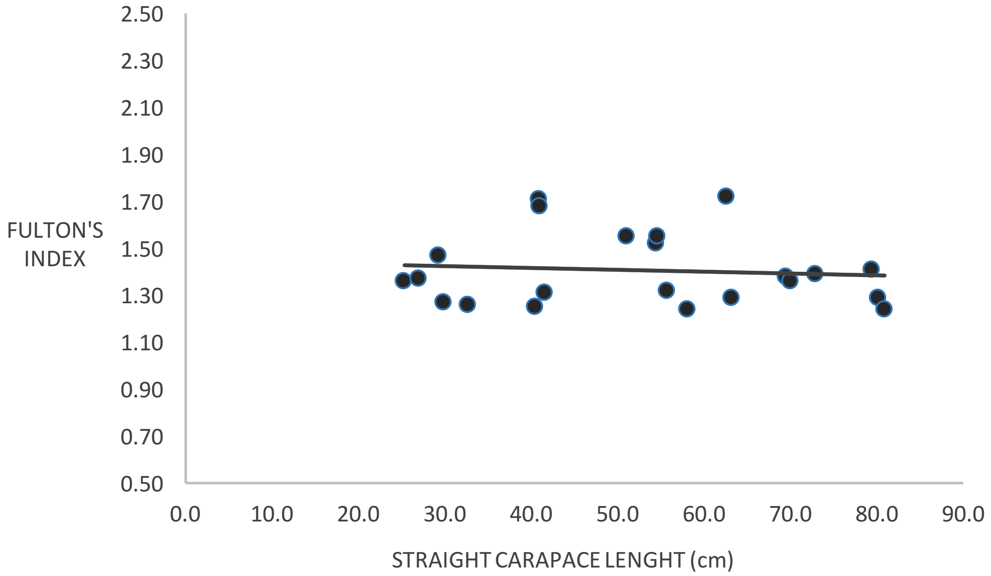

Figure 3.4. Relationship between the carapace length and weight and the body condition (Fulton's Index) of immature *Chelonia mydas* in northeastern La Guajira.

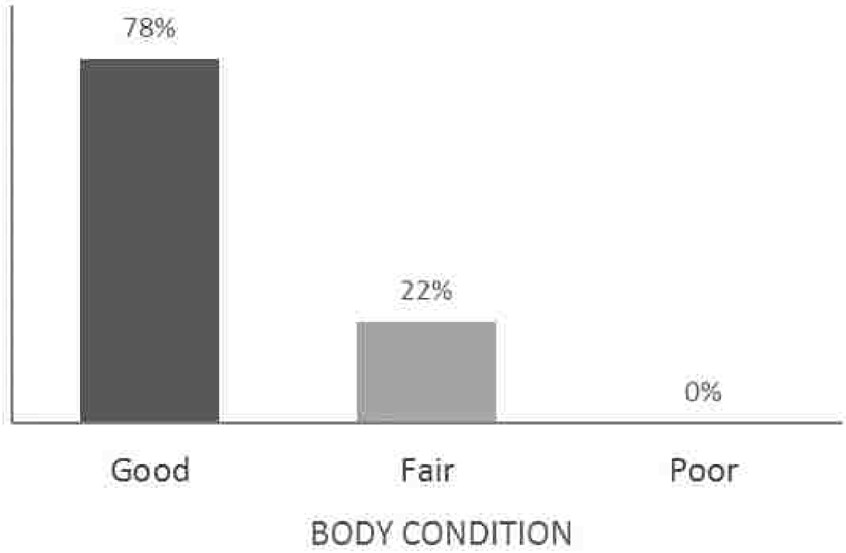

Figure 3.5. Body condition of immature *Chelonia mydas* surveyed in northeastern La Guajira obtained from Fulton's Body Condition Index and following Thompson et al. (2009) classification: Good > 1.30, Fair 1.20 - 1.29, Poor: < 1.10.

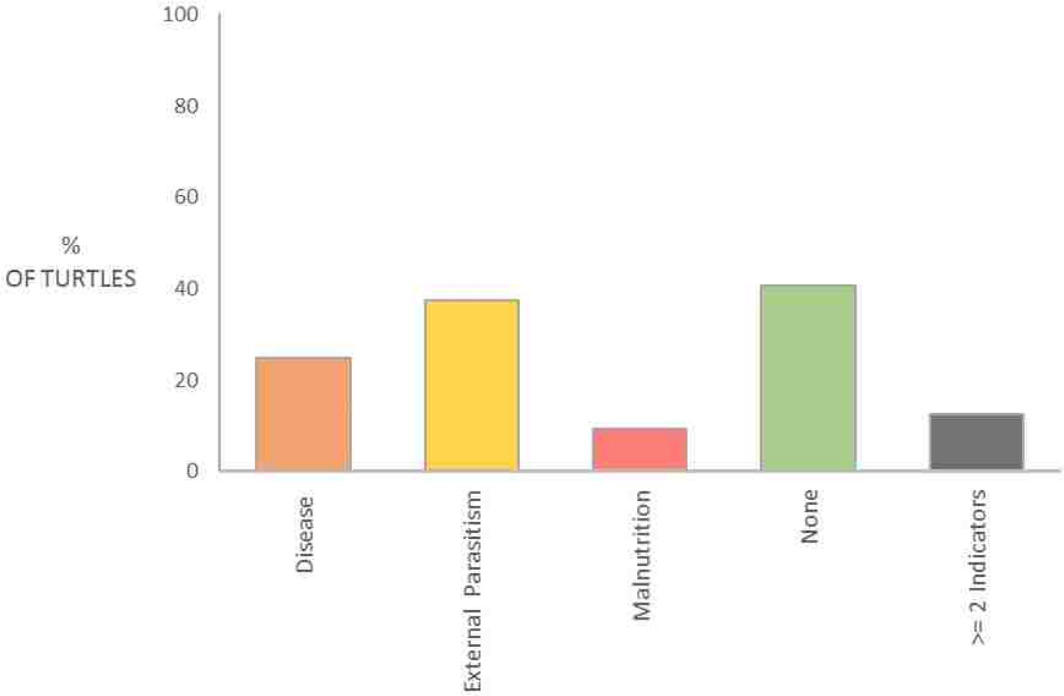

Figure 3.6. Proportion of surveyed turtles displaying each of the environmentally-driven visual indicators of body condition.

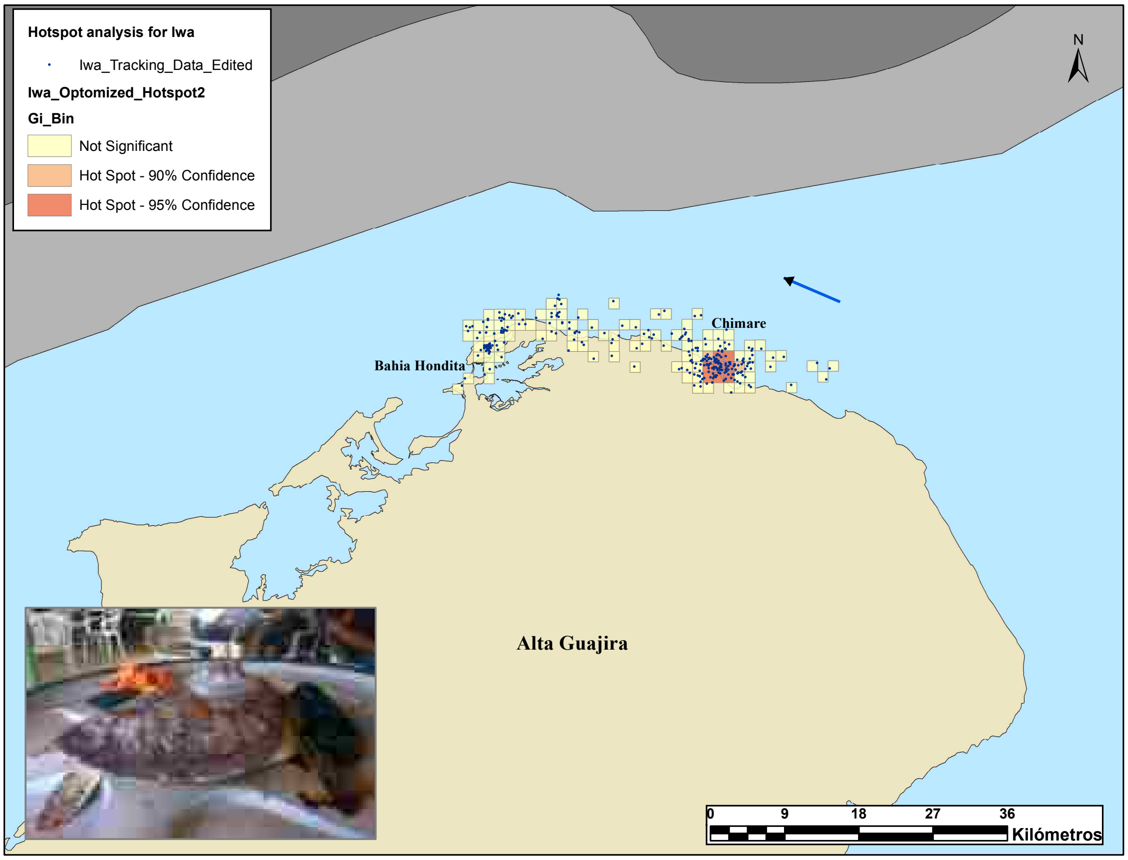

Figure 3.7. Satellite telemetry tracked movements of a juvenile *C. mydas* “Iwa” in Upper La Guajira coastal area in August 2015. Coloring squares display the frequency that areas were used by the turtle from a hotspot analysis in GIS. More frequently visited areas are displayed in red squares. The arrow displays the average direction of prevailing currents at the time of tracking.

Table 3.1. Life stage distribution of the *C. mydas* aggregation of northeastern La Guajira.

Life Stage	Sex	Size Range (SCL in cm)	Number of turtles
Hatchling		4 - 5 cm	0
Juvenile		< 50 cm	28
Subadult		50 - 80 cm	24
	Male	> 80 cm	2
Adults	Female	> 85 cm	0
		Total	54

Table 3.2. Body condition index of immature *C. mydas* from eastern La Guajira observed in this study, and other populations in the Pacific and Atlantic oceans.

C. mydas Population (Ocean Basin)	Fulton's Index (W/SCL^3)	SD	Range	Reference
Bahamas (Caribbean)	1.27			Bjorndal et al 2000
Gulf of Venezuela	1.11	± 0.03	0.29 – 2.34	Barrios-Garrido unp.
Mexico (Pacific)	1.42	± 0.02		Lopez-Castro et al 2010
Baja California (Pacific)	1.42	± 0.01	1.03 - 2.19	Seminoff et al 2003
La Guajira (Caribbean Upwelled)	1.47	± 0.38	1.24 - 2.61	This study
Peru (Pacific, Upwelled)	1.55			Velez-Zuazo et al 2014

W: Weight in Kg.
SCL^3: Cube of the Straight Carapace Length in cm.

Table 3.3. Number of turtles showing each of three environmentally-driven visual indicators of body condition for *C. mydas* in eastern La Guajira, and by region and survey site. The square highlights significant regional differences.

Survey Area	n	Fibropapiloma Incidence		Parasite Incidence		Malnutrition incidence	
		Counts	Percent	Counts	Percent	Counts	Percent
La Guajira	37	8	22%	12	32%	3	8%
Bahia Hondita	19	8	42%	6	32%	1	5%
Eastern Guajira	18	0	0%	6	33%	2	11%
Chimare	5	0	0%	4	80%	0	0%
Puerto Estrella	9	0	0%	0	0%	0	0%
Santa Cruz	4	0	0%	2	50%	2	50%

CHAPTER 4

The Role of Northeastern Colombia in the Demographic Connectivity and Genetic Diversity Patterns of the Atlantic Green Sea Turtle Populations

4.1. Research Background

The persistence of marine species over time may depend on their ability to maintain genetic diversity (Frankham, 2005; Lacy, 1997). Genetic diversity is found at different biological organization levels, within individuals, among individuals within populations, and/or among populations within the species (Hartl et al., 1997). Genetic differences among populations can result from genetic drift and from differential natural selection (resulting in local adaptation) (Clarke et al., 2010). Local adaptations allow distinct segments of the species to survive or reproduce at different areas or seasons. The maintenance of these local adaptations and their underlying genetic diversity, allows populations to survive and contributes to the overall species genetic diversity (Sanford & Kelly, 2011).

Marine populations are subject to differential environmental pressures temporally and spatially, including variation in the availability of resources and physical conditions such as temperature or salinity (Sanford & Kelly, 2011). In order to survive and reproduce, marine organisms are often obligated to disperse out from their local populations to cope with oceanographic variation. Some marine species have evolved complex life history strategies with distinct life stages that are spent at different and sometimes very distant habitats (*i.e.* ontogenetic habitat shifting), with the risk of losing unique local adaptations and their underlying genetic diversity (*e.g.* if interbreeding with other populations)

(Snover, 2008). Thus, in spite of physical/temporal separation, individuals need to remain connected to their own populations so that adaptive genetic differences can be maintained.

Prior to European arrival to the Tropical Western Atlantic (wider Caribbean), the green sea turtle *Chelonia mydas* was an abundant keystone species in a pan-tropical marine distribution, with high levels of genetic diversity (Jackson et al., 2001; McClenachan et al., 2006). This successful species had survived with large population sizes for hundreds of thousands of years. Part of its success relied on key local adaptation to nesting habitat close to favorable dispersal current systems to avoid predation (Putman et al., 2010; Wyneken & Salmon, 2002).

C. mydas nests at sandy beaches located near oceanographic points prompting quick dispersal of hatchlings to offshore environs where predation is lower (Wyneken & Salmon, 2002). Once hatchlings are entrained in high velocity currents and associated fronts and eddies, they are dispersed stochastically over long distances until acquiring a size at which they are more difficult to be preyed upon (~20cm) (Luschi et al., 2003; Putman & Naro-Maciel, 2013). Then, juvenile *C. mydas* recruit into foraging grounds (FG) or developmental habitats (DHs) in nearshore, shallow waters. These habitats offer the conditions that allow for growth and survival during the long juvenile stage (up to 20 years) (Meylan et al., 2011).

Due to the stochasticity of the dispersal in oceanic motions, juvenile turtles from a given population can have multiple foraging grounds or developmental grounds. Also, turtles from different genetic populations (nesting rookeries) can reach the same developmental habitat and thus the aggregation of turtles found at these habitats are genetically mixed and thus are called mixed stocks (Naro-Maciel et al, 2007; Bolker et al., 2007). If juvenile turtles survive at developmental habitats until reproductive stages, the now adult individuals actively disperse back to reproduce and recruit into parental populations for reproduction, often on the same area of born, a behavior called natal philopatry (Musick and Limpus, 2003). The demographic connectivity between nesting habitat and foraging/developmental habitats is important for the maintenance of local adaptations to key nesting areas, and the overall genetic diversity of the species given by the population-level differences.

In spite of the highly dispersive, successful life history of *C. mydas,* the species' dramatic declines in the number and size of nesting populations over the past 100 years, there has been loss of genetic diversity. Reductions of genetic diversity in turn increase the risk of extinction of populations through a process coined as the vortex effect (Gilpin and Soule, 1986).

Major threats to survival of *C. mydas* populations are concentrating in the neritic developmental habitat, such as in seagrass meadows (Valiela et al., 2001; Waycott et al., 2009). These threats are related to fishing bycatch and coastal habitats loss and degradation (Finkbeiner et al., 2011; Koch et al., 2006). If habitat degradation or increased mortality occurs at foraging or developmental grounds, where juvenile turtles from multiple genetic populations gather to grow until they start maturing, then species-wide genetic diversity reductions are expected.

There is a need to identify, study and conserve juvenile habitats that allow the survival and connectivity of individuals to their populations of origin worldwide, in order to direct conservation planning (Hamann et al., 2010). However, little is known about where these juvenile habitats are located and what is their particular contribution the demographics and overall genetic diversity maintenance of the species in the Atlantic basin (Eckert et al., 1999).

Patterns of demographic connectivity have started to be revealed with the use of molecular technologies such as genetic markers. Genetic markers are genes or other small nucleic acid sequences that when examined can indicate on the level of genetic diversity or any other characteristic of the genome of the species. Due to the natal philopatry behavior of female *C. mydas*, in which females will reproduce in the same area of born, populations of the species have a strong spatial structure. Thus, populations are differentiated and this differentiation is observable in the genome. Maternally-inherited genetic markers such as mitochondrial DNA (mtDNA) are commonly used to study patterns of demographic connectivity between a parental population at a nesting rookery and its developmental habitat(s).

Using mtDNA markers it has been shown that Parental populations at nesting rookeries and their feeding/developmental habitats in the Atlantic basin follow a close-to-home pattern, at a regional scale (Figure 4.1) (Bolker et al., 2007). Thus, individual from a parental population at a given region (*i.e.* Western Atlantic, Central Atlantic and Eastern Atlantic, Figure 4.1) will end up foraging or/and developing at FGs/DHs closer to their parental populations than more far apart. Instead, within a region, FGs/DHs will contain individuals from nesting rookeries either close or far apart, without a clear pattern (Bolker et al., 2007).

One of the most important factors explaining the large scale observed patterns of demographic connectivity for populations the Atlantic *C. mydas* and their feeding grounds are ocean currents (Putman & Naro-Maciel, 2013; Naro-Maciel et al., 2012). Major rapid currents can cause hatchlings of the species to be carried far away from the nesting beaches of birth (for thousands of km). However, observed connectivity patterns may change when additional areas are studied. Specifically, when areas at boundary locations among connectivity groups or at strategic points relative to strong currents and current divergences, are studied. These areas can harbor higher levels of genetic diversity than average (Bolker et al., 2007).

This study aimed to establish the level of genetic diversity and the demographic connections of two feeding grounds for *C. mydas* in the Northeastern region of Colombia. The region is located at the confluence of two major, rapid, opposite-direction sea surface currents, the Caribbean Current and the Panamá Counter-Current (Andrade, 2003) (Figure 4.1). These currents may favor the arrival of juvenile turtles after their pelagic migration from at least two of the population connectivity groups of the species in the Atlantic, the western and the central connectivity groups (Figure 4.1).

If *C. mydas* from different genetic populations in the Atlantic are recruiting into Northeast Colombia, which also harbors extensive and diverse foraging resources in the area of La Guajira for this turtle (see Chapter 2), its conservation may contribute to maintenance of multiple nesting populations of the species in the Atlantic basin.

4.2. Methods

4.2.1. Study Area

The study area included two marine nearshore coastal areas in Northeast Colombia, Southern Caribbean (Figure 4.1). The Upper La Guajira area, located in the northeastern coast of La Guajira peninsula, next to the Gulf of Venezuela, and the Santa Marta area, located between the Ciénaga Grande de Santa Marta swamp and Don Diego beach in the Magdalena department. Both La Guajira and Santa Marta areas are foci of the Southern Caribbean Upwelling System (Figure 4.1) (Rueda-Roa & Muller-Karger, 2013). However, the two areas differ in the amount and type of submerged aquatic vegetation, the food items for *C. mydas.* La Guajira area has a larger, more diverse and unspoiled SAV communities than Santa Marta, and thus seems to harbor a large aggregation of *C. mydas*. Instead, at Santa Marta coastal SAV communities sea turtles are less frequently observed.

The coastal upwelling occurring in northeastern Colombia, is a yearly, seasonal (January to May) coastal upwelling. Thus, the study included two seasons, the "upwelling" of dry season, and the non-upwelling or wet season (July to December) (Invemar, 2012).

4.2.2. Genetic Analyses

Although no direct catch of sea turtles is allowed in Colombia, artisanal fishery activities taking place in the study area, can result in the incidental catch of sea turtles, especially of *C. mydas*. For this project, local fishermen from both of the study areas in Colombia allowed access to their accidental catch that included sea turtles as *C. mydas,* during August 2014 to January 2017. In La Guajira area, surveyed sites included Bahia Hondita lagoon, Masichi, Jiwotpolu and Neimao beaches, as well as fishing ports Puerto Chimare, Puerto Estrella and Puerto Santa Cruz (see Chapter 2 for habitat descriptions) (Figure 4.1).

The body size (Straight and Curve Carapace Length, SCL and CCL) of bycaught *C. mydas* turtles, either dead or alive, was measured, in order to estimate the life stage of the turtle. For this estimation, a length to stage conversion from published estimates of size at maturity of other Caribbean *C. mydas* populations was used (Lutz et al., 2003; Meylan et al., 2011). Only neritic sea turtles that were juvenile or subadult were included in this study.

Bycaught turtles were sampled for a 3mm diameter tissue piece from the edge of the back-flipper, and the sample was stored on 70% Ethanol until genetic laboratory procedures were performed (IACUC Research protocol no.14-142 approved by the University of Miami). The natal-homing behavior, especially of females *C. mydas*, allows for a strong genetic differentiation among populations (nesting rockeries) that can be traced in maternally-inherited DNA such as mitochondrial DNA (Bowen et al., 1992) Individuals sampled were traced to their population of origin (the nesting beach of birth) using the mtDNA Control Region markers. The control region of extracted mtDNA was amplified by PCR using primers HL950 and LCM (~790bp) and sequenced in both directions using Sanger sequencing and following standard protocols for sea turtles (*e.g.* (Naro-Maciel et al., 2007). Forward and reverse sequences were aligned and manually inspected for errors using Geneious 6 software (Kearse et al., 2012).

4.2.3. Statistical Analyses

Both the haplotype diversity (*Hd*) and nucleotide diversity (π) indices (Nei, 1972) for a 781bp sequence of the mitochondria control region, were calculated as surrogates of the genetic diversity of Northeast Colombia, as well as for La Guajira and Santa Marta areas separately using the software DNAsp (Rozas & Rozas, 1999). Control region haplotypes were obtained by comparison to reference lists for the Atlantic Green Sea Turtle nesting rockeries (available at the Archie Carr Center) sequences published on Genebank using Blast algorithm (https://blast.ncbi.nlm.nih.gov).

In order to estimate the proportional contribution of each green sea turtle nesting rockery (source population) to the mixed aggregation in Northeast Colombia foraging grounds, a Bayesian Many-To-One Mixed Stock Analysis was performed (Bolker et al., 2007). First, the observed frequencies of each mtDNA haplotype on the mixed stock of NE Colombia (calculated) and each nesting rockery (from the literature) were input into the model (Naro-Maciel et al., 2012). The observed frequencies as well as the rockery population sizes, obtained from yearly census of the number of nesting females per year at nesting beaches of the species, are fitted into a Bayesian hierarchical model, similarly to other Bayesian assignment test, using a standard Markov Chain Monte Carlo algorithm (Bolker et al., 2007). Then, the estimated contributions of each rockery were obtained from the posterior probabilities, and their confidence intervals were calculated from 10000 Markov Chain iterations. This analysis was performed using the Mixstock package (Bolker et al., 2007) in the software environment R (2.14.1, R Core Team). Other traditional models were also applied to the data for comparisons, including Conditional and Unconditional Maximum Likelihood, using the same software tools.

The trajectories (Lat/Lon position in time) of 32 satellite tracked sea surface drifters released in the Atlantic basin, that passed nearby the study area were obtained from the National Oceanic and Atmospheric Administration (NOAA) Global Drifter Program (GDP) (http://www.aoml.noaa.gov/phod/dac/index.php). Given that hatchling and early juvenile sea turtles entrain and passively disperse with sea surface currents, they mirror the behavior of drifters. Therefore, the drifter trajectories were used to identify the likely oceanographic routes of pelagic migration for *C. mydas* in Colombia, and contrast them with the results obtained from the mixed stock analysis above. The most relevant trajectories were displayed on a basemap of the Atlantic basin using ArcGIS mapping tools (ESRI, 2010).

4.3. Results

4.3.1. Genetic diversity of *C. mydas* aggregation in Northeast Colombia

A total of forty-three bycaught green sea turtles, thirteen from the Santa Marta area and thirty from La Guajira area, that were either juvenile or subadult-staged turtles, were successfully sequenced for 781bp of the mtDNA Control Region (Table 4.1). The alignment identified 28 polymorphic sites that contributed to a high nucleotide diversity (Tables 4.1 and 4.3). A total of 12 parsimony informative sites defined 11 different haplotypes that had been previously described and annotated in Genbank for *C. mydas* (Tables 4.2). The haplotype diversity for the entire aggregation of turtles was high (*Hd* = 0.8), and greater than each of the two study regions separately. La Guajira's turtle aggregation nucleotide and haplotype diversities, although slightly larger, were similar to those of the Santa Marta's aggregation (Table 4.1).

Mitochondrial Control Region haplotypes differed in their frequency in the Northeast Colombia green sea turtle aggregation, with some being very common and some being rare (Figure 4.2). The most common haplotypes for the overall turtle aggregation in Northeast Colombia as well as for La Guajira aggregation only, were CM-A3 and CM-A5 (Figure 4.3). Instead, the most common haplotypes for Santa Marta aggregation, were CM-A5 and CM-A8 (Figure 4.3). Haplotype frequencies differed significantly among these two regions (Fisher's Exact Test, p= 0.0023).

Haplotypes CM-A3 and CM-A5 are very common in nesting rockeries of the Caribbean Sea (Figure 4.2). CM-A3 is very common on nesting rockeries of the western Caribbean including Tortuguero in Costa Rica and Mexico. CM-A5 is the most common haplotype of nesting rockeries on the Eastern Caribbean including Surinam, the U.S. Virgin Islands and the Aves Island in Venezuela. Instead, haplotype CM-A8 is more common in nesting rockeries outside of the Caribbean Sea, in the southern Atlantic nesting rockeries of Brazil and even off the west coast of Africa (e.*g.* Guinea Bissau).

The Northeastern Colombia CR haplotype frequencies did not differ significantly among dry and wet weather seasons (Figure 4.3, Fisher's Exact Test, p= 0.72589). During both seasons, the most common haplotypes were CM-A3 and CM-A5.

4.3.2. Populations of origin of the mixed sea turtle aggregation in Northeast Colombia

Several nesting rockeries in the Atlantic seem to be contributing individuals to the mixed stock of *C. mydas* in Northeastern Colombia from the mixed stock analysis results. The major contributor rockeries estimated with the foraging-ground centric Bayesian approach were Costa Rica and Mexico (20-26% each), followed by Aves Island and U.S. Virgin Islands (~11% each) (Figure 4.5). Other minor contributors were Bioko and Guinnea Bissau in Africa (~3-5 % each). Estimated contributions were very similar with the different analytic approaches including both Unconditional and Conditional Maximum Likelihood) and Bayesian mixed stock analysis (table 4.4).

Estimated contributions from nesting rockeries differed among regions within the study area ($X^{2,}$ p=0.0001). For la Guajira, the nesting rockeries contributing the most to the observed genetic composition were Costa Rica and Mexico with a~30% each, and Florida to a lesser extent (15%) (Figures 4.4 and 4.5). Whereas for Santa Marta region, the major contributing rockeries were Aves Island, Surinam and the U.S. Virgin Islands (~20% each) and Guinea Bissau to a lesser extent (Figure 4.4 and 4.5).

No important seasonal differences in the major or minor nesting rockeries contributions to the overall *C. mydas* aggregation of northeast Colombia were observed (Figure 4.5). The major contributions come from nesting rockeries in the western Caribbean, although, during the wet season there is an increase in the contribution from African rockeries such as that of Guinea Bissau.

4.4. Discussion and Conclusions

The immature *C. mydas* aggregation found in northeast Colombia displayed high levels of genetic diversity that are consistent with a mixed stock of individuals originating from multiple parental populations. The nucleotide and haplotype diversities for the mtDNA haplotypes were similar when not higher than the ones reported for other mixed stocks at foraging or developmental grounds in the Atlantic basin (Table 4.4).

Haplotypes found in the Colombian *C. mydas* aggregation have been reported in nesting rockeries (parental populations) far apart from each other and widely distributed in the Atlantic Ocean to the east (*e.g.* Guinnea Bissau), west (*e.g.* Costa Rica) and center (*e.g.* Aves Island). Although, the most common haplotypes originate from nesting rockeries in the western (*i.e.* Costa Rica or Mexico) and central Atlantic (*i.e.* Aves

Islands, Surinam or US Virgin Islands) regions. Similarly, the rockeries contributing the most to the observed composition of the *C. mydas* mixed stock in the Colombian Caribbean were Costa Rica, Mexico, Aves Island and the US Virgin Islands.

The major contributing nesting rockeries to the Colombia's mixed stock differed among the two sampling regions. La Guajira region's contributing nesting rockeries were similar to the overall aggregation, but for the Santa Marta region, the western Atlantic rockeries such as Costa Rica or Mexico did not contribute as significantly as the Central Atlantic rockeries such as Aves Islands or U.S. Virgin Islands. Also, the African rockeries (*e.g*. Guinnea Bissau) were more important contributors to Santa Marta region than to La Guajira.

C. mydas has three connectivity groups in the Atlantic basin, the eastern, central and western groups (Bolker et al., 2007). The *C. mydas* immature aggregation in northeastern Colombia is composed of individuals coming from all three of the population connectivity groups, although mostly from the Central and Western Atlantic groups. The convergence of individuals from at least two genetically differentiated groups at the studied area, may explain the high level of genetic diversity observed in this aggregation and when compared with other aggregations in the Atlantic (Table 4.4). This pattern may be due to the boundary location of northeastern Colombia in respect to the two most important contributing connectivity groups.

This pattern seems to be feasible when looking at large scale current systems passing by Colombia, such as the Caribbean current and the Colombia-Panama counter-current. These two currents flow in contrary directions (Figure 4.6). The Caribbean current is a branch of the South Equatorial Current that originates in the Eastern Atlantic, and flows east to west. Instead, the Colombia-Panama Gyre results from the reversing of the Caribbean current when it hits the continental shelf in Nicaragua and thus it flows west to east; during the wet season this current is capable of reaching up to La Guajira, Colombia (Invemar, 2012). These opposite-direction currents may favor the arrival of individuals from opposite locations in the Atlantic (*e.g.* Western vs. Eastern Atlantic) where different connectivity groups have been described.

Sea turtle hatchlings' passive dispersal in currents and other ocean motions, mirrors the one of ocean surface drifters. The trajectories of multiple ocean surface drifters placed at random locations in the Atlantic basin followed the direction and speed of the South Equatorial Current, Caribbean Current and the Colombia-Panama Gyre (Figure 4.6). Hatchlings from nesting beaches far apart from Colombia such as Guinea Bissau, or from opposite sides of the region, such as Costa Rica and Aves Island, could reach La Guajira's waters by entraining in the above-mentioned currents.

Oceanic currents in the Atlantic help explain the observed genetic composition of the overall immature aggregation of *C. mydas*, yet they do not shed light on the differences among La Guajira and Santa Marta regions within Northeastern Colombia. Sea turtles are passive dispersers in oceanic currents until they reach a body size of ~18 cm SCL. After that, they can actively swim, have positive buoyancy, and are able to recruit into shallow, neritic, developmental habitats (Meylan et al., 2011; Carr, 1987). However, these habitats are not continually distributed, but patchy. Furthermore, DHs met a set of conditions and requirements for the long-term survival and growth of *C. mydas* that other transiting areas such as foraging grounds do not. Thus, other ecological and/or oceanographic factors related to habitat quality may contribute to the observed regional differences in the genetic composition of Colombia's immature aggregations.

La Guajira harbors the most extensive and productive SAV beds of Colombia, (Gómez-Lopez, 2014). Historically, large numbers of immature sea turtles have been extracted from this area (Rueda et al., 1992) and thus is considered a habitat for the species (see Chapter 1). La Guajira's turtle aggregation was largely supplied by western connectivity group nesting rockeries, particularly Costa Rica, the largest nesting rockery for the species in the Atlantic. Thus, La Guajira could be an important developmental habitat for *C. mydas* and needs to be considered in the population connectivity pattern of the Atlantic *C. mydas*.

4.5. Tables and Figures

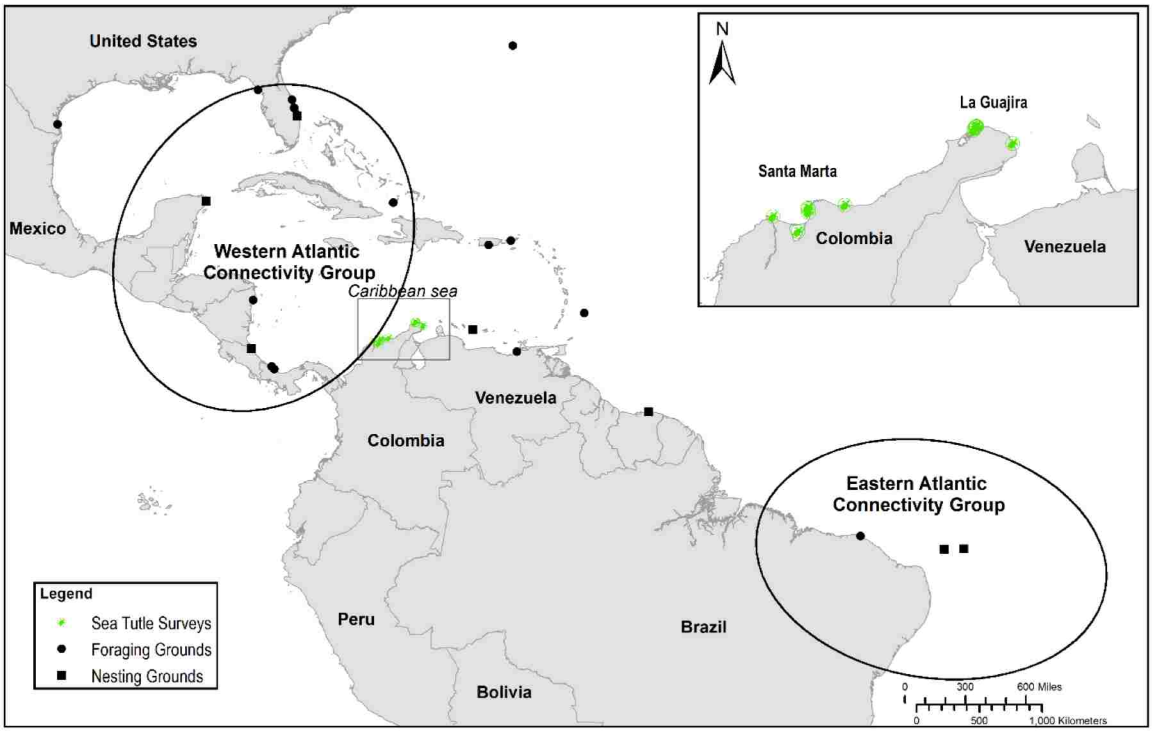

Figure 4.1. Location of the study area in Northeastern Colombia and the two sea turtle survey sites (square). The map displays the location of the two main population connectivity groups and the location (circles) of nesting rockeries and foraging grounds for the Atlantic *C. mydas* (from Putman & Naro-Maciel (2013).

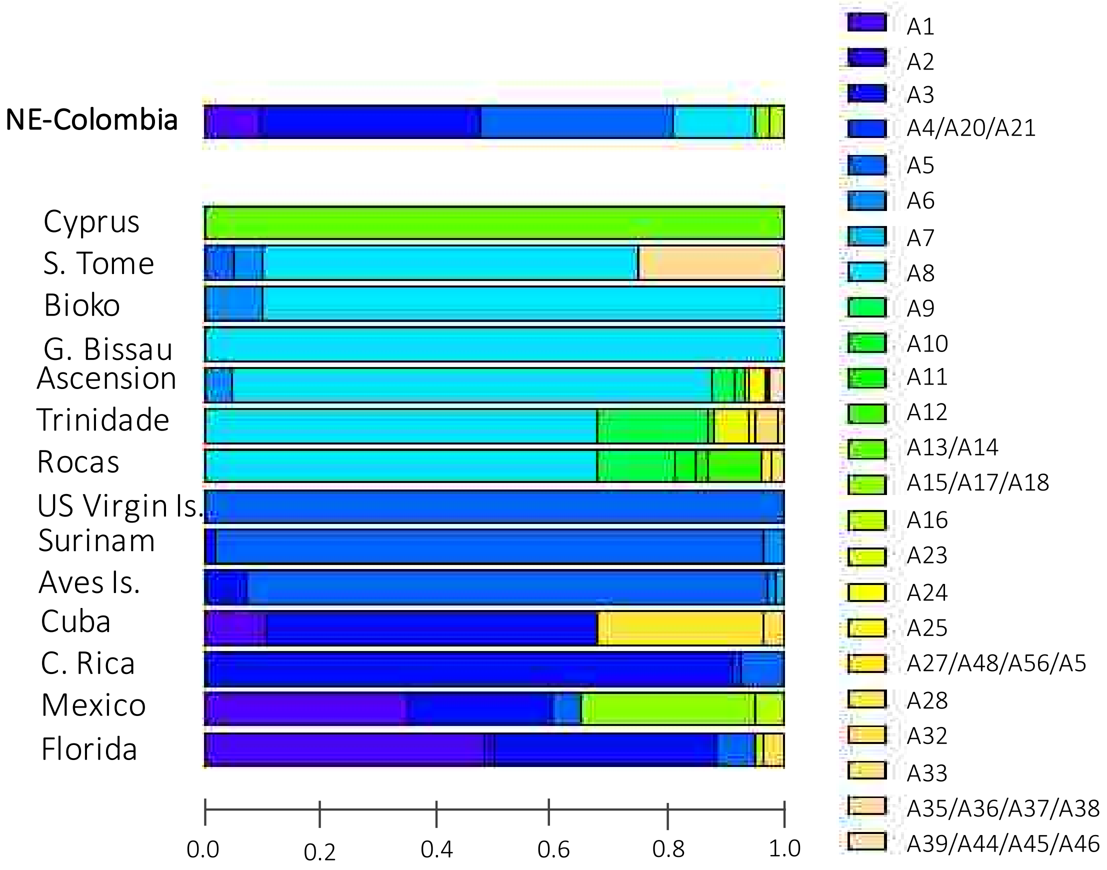

Figure 4.2. Mitochondria Control Region haplotype frequencies of the mix-stock aggregation in northeast Colombia and the likely populations of origin population (nesting rockeries) for the Atlantic *C. mydas*.

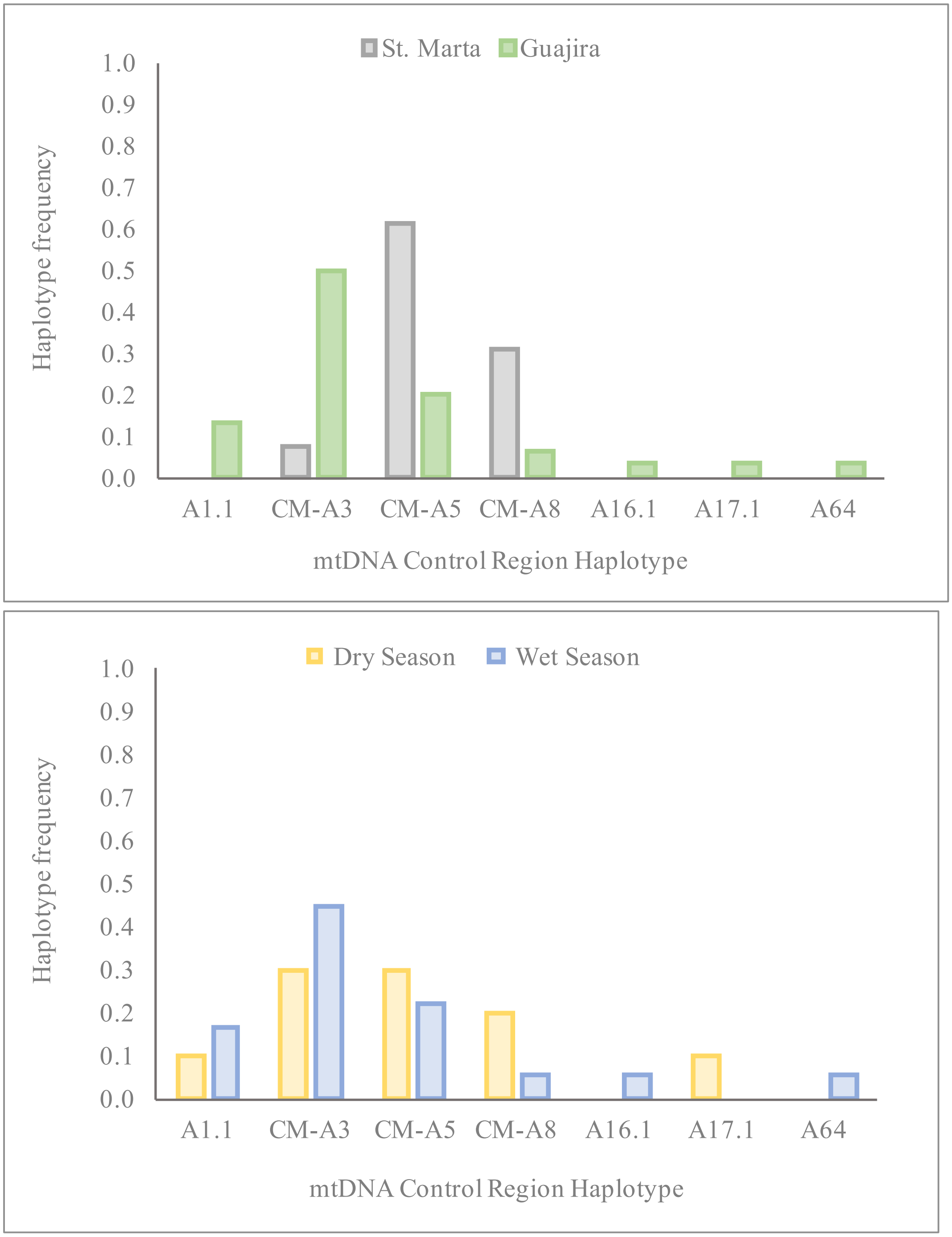

Figure 4.3. Variation in mtDNA Control Region haplotype frequencies for the *C. mydas* juvenile/subadult aggregation in Northeastern Colombia. Variation among regions on the top and variation among weather seasons on the bottom.

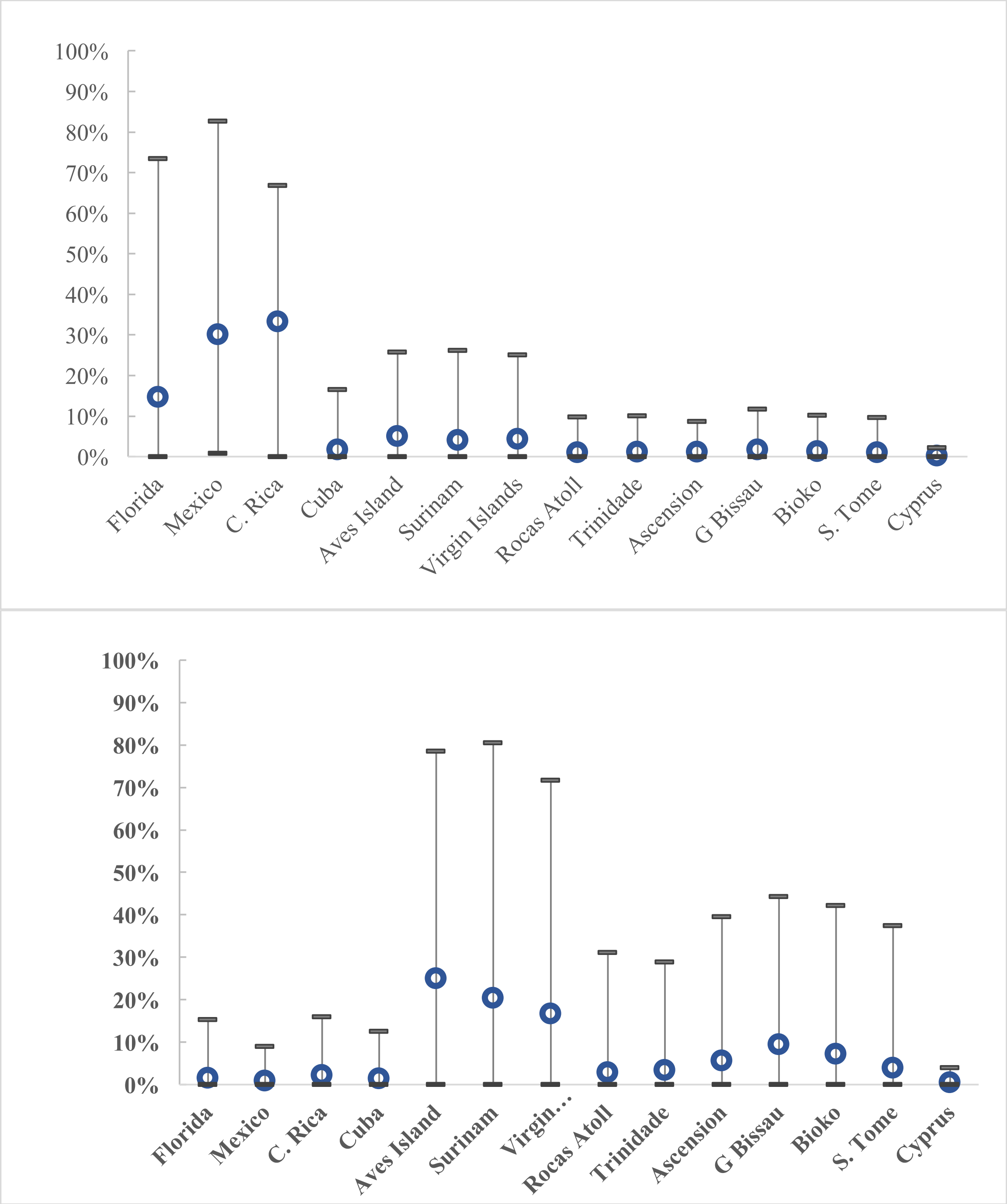

Figure 4.4. Inferred proportional contributions from each Atlantic nesting rookery of *C. mydas* to the mixed aggregations in upper La Guajira, Colombia (top) and Santa Marta (bottom), using a Bayesian Many-to-one mixed stock analysis.

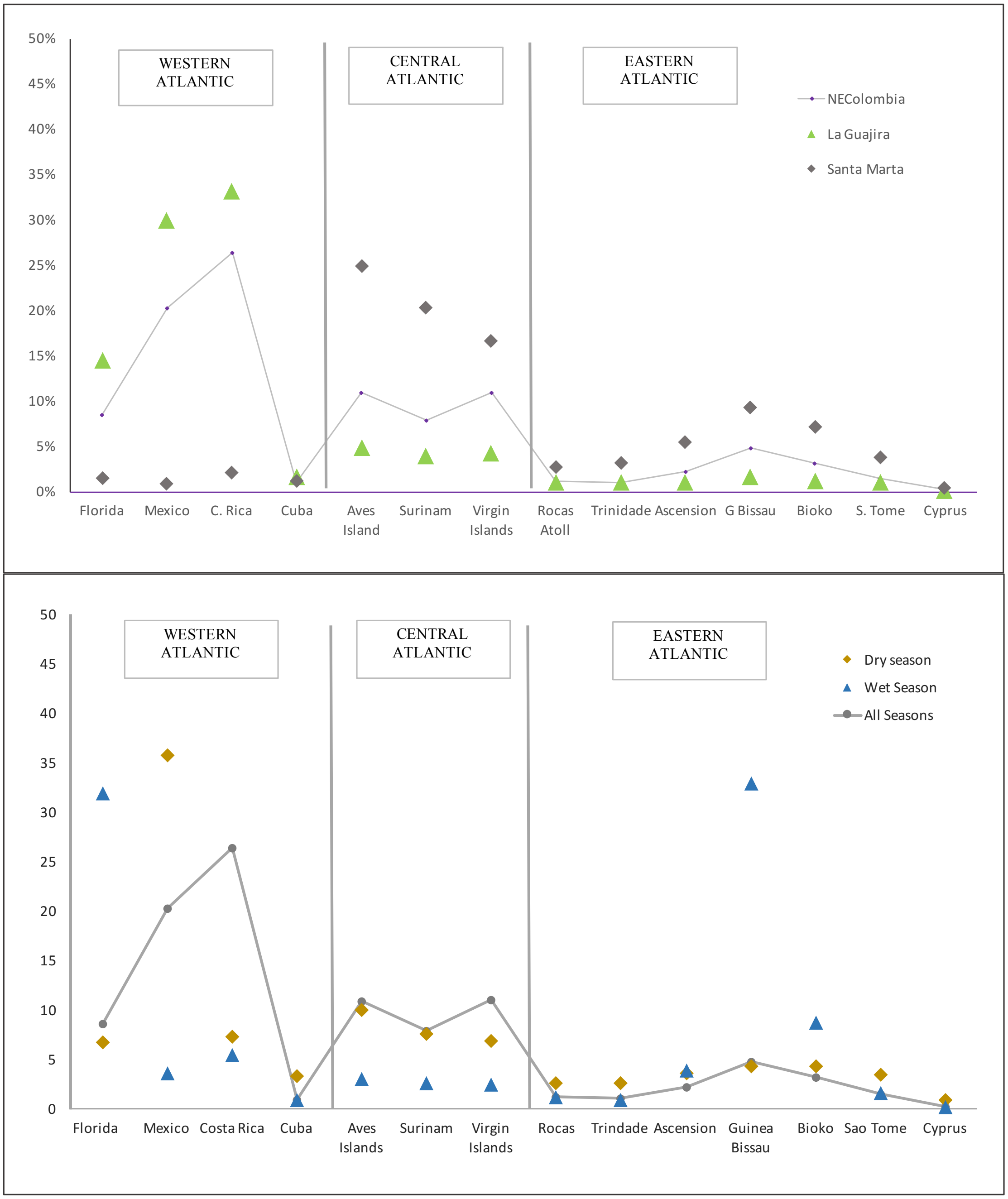

Figure 4.5. Comparison of the inferred contributions of nesting rockeries in the Atlantic to the mixed stock aggregations between different studied regions (above) and different seasons (below), using the many-to-one Bayesian Mixed Stock Analysis.

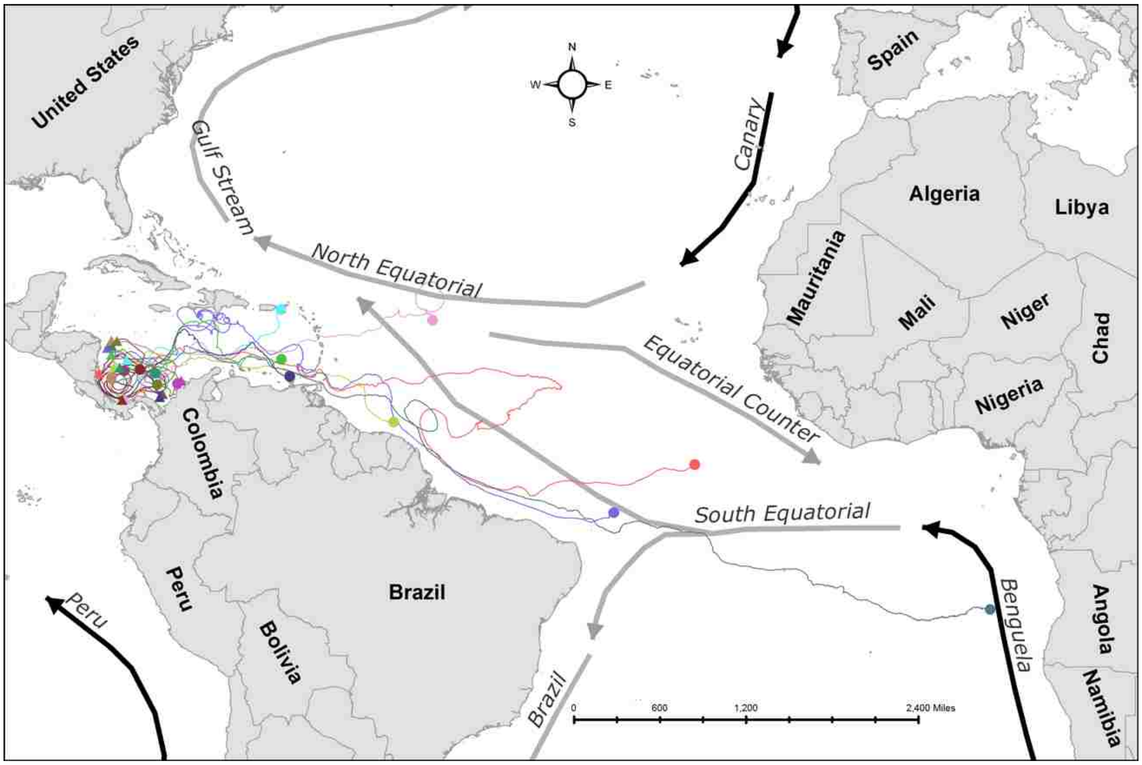

Figure 4.6. Trajectories of several selected ocean surface drifters in the Atlantic Ocean. The figures shows the feasibility of drifters released at different location in the Atlantic to pass by the study area in Northeastern Colombia.

Table 4.1. Genetic diversity at mtDNA control region for two green sea turtle aggregations in Northeastern Colombia.

Index	Overall Colombia	Santa Marta	La Guajira
Number of individuals	43	13	30
Number of mutations Eta	28	13	26
Number of haplotypes	11	5	9
Haplotype diversity Hd	0.80 ± 0.039	0.73 ± 0.096	0.75 ± 0.070
Nucleotide diversity π(JC)	0.008 ± 0.001	0.004± 0.002	0.007 ± 0.001

Table 4.2. List of mtDNA Control Region haplotypes found and assigned to juvenile and subadult *C. mydas* from the Northeastern Colombia.

Haplotype #	Haplotype Code	Sample Freq.	Turtle ID		
Hap 1	CM-A64	1	CM-GUA-14		
Hap 2	CM-A1.1	4	CM-GUA-02	CM-GUA-29	CM-GUA-30
Hap 3	CM-A5.2	11	CM-GUA-03	CM-GUA-28	CM-STM-08
			CM-GUA-LLA828	CM-GUA-12	CM-GUA-16
			CM-STM-01	CM-STM-03	CM-STM-06
			CM-GUA-37	CM-STM-09	CM-SM-14
Hap 4	CM-A3.1	15	CM-GUA-04	CM-GUA-13	CM-GUA-08
			CM-STM-12	CM-GUA-07	CM-GUA-20
			CM-GUA-EEB644	CM-GUA-EEB642	CM-GUA-EEB640
			CM-GUA-36	CM-GUA-21	CM-GUA-LLA826
			CM-GUA-09	CM-GUA-25	CM-GUA-32
Hap 5	CM-A16.1	1	CM-GUA-26		
Hap 6	CM-A8.1	6	CM-STM-07	CM-STM-10	CM-GUA-EEB646
			CM-GUA-11	CM-STM-04	CM-STM-05
Hap 7	CM-A3.1	1	CM-GUA-05		
Hap 8	CM-A5.2	1	CM-GUA-10		
Hap 9	A17.1	1	CM-GUA-34		
Hap 10	CM-A3.1	1	CM-STM-13		
Hap 11	CM-A5.2	1	CM-STM-02		
	Total	43			

Table 4.3. *Chelonia mydas* mtDNA Control Region haplotypes and the location and nucleotide of parsimony informative polymorphic sites.

	Position of polymorphic sites																											
									1	1	2	2	3	3	3	3	3	4	4	4	5	6	6	6	7	7	7	7
	1	2	4	5	6	6	7	9	1	3	1	4	0	0	2	6	6	4	6	8	8	0	3	4	0	3	7	8
Haplotype	8	5	6	9	0	8	4	0	8	1	7	6	0	2	3	2	6	9	1	3	4	0	7	0	2	8	3	0
Hap 1	T	T	G	T	G	C	C	T	G	A	T	T	C	T	A	C	C	A	G	A	C	C	T	A	A	A	A	A
Hap 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	T	G	G	.
Hap 3	.	.	.	.	.	.	.	.	A	.	.	C	T	C	G	.	T	C	.	G	.	T	C	G	T	G	G	.
Hap 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	G	G	.
Hap 5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	G	T	.	.	G	T	G	G	.
Hap 6	.	.	.	.	.	.	.	.	A	.	.	.	T	C	G	.	T	C	.	G	.	.	C	G	T	G	G	.
Hap 7	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	T	G	G	.
Hap 8	C	C	T	.	.	.	.	.	A	.	.	C	T	C	G	.	T	C	.	G	.	T	C	G	T	G	G	.
Hap 9	.	.	.	C	A	T	T	A	.	.	.	.	.	.	.	T	.	.	.	G	T	.	.	G	T	G	G	.
Hap 10	.	.	.	.	.	.	.	.	A	T	.	C	T	C	G	.	T	C	.	G	.	T	C	G	T	G	G	.
Hap 11	.	.	.	.	.	.	.	.	A	.	.	C	T	C	G	.	T	C	.	G	.	T	C	G	T	G	G	G

Table 4. 4. Comparison of estimated contributions from Atlantic *C. mydas* nesting rookeries to the juvenile aggregation in eastern La Guajira, Colombia, using multiple inference methods: Conditional Maximum Likelihood (CML); Unconditional Maximum Likelihood UML; and Bayesian Mixed Stock Analysis (MSA).

Nesting Rookery	CML	UML	MSA
Florida	14.7%	11.6%	14.6%
Mexico	18.2%	20.9%	30.0%
C. Rica	44.7%	44.6%	33.2%
Cuba	0.0%	0.0%	1.7%
Aves Island	0.0%	3.7%	4.9%
Surinam	0.0%	6.6%	4.1%
Virgin Island	15.5%	6.1%	4.3%
Rocas Atoll	0.0%	0.0%	1.0%
Trinidade	0.0%	0.0%	1.1%
Ascension	0.0%	0.0%	1.1%
G. Bissau	6.9%	6.5%	1.7%
Bioko	0.0%	0.0%	1.2%
S. Tome	0.0%	0.0%	1.0%
Cyprus	0.0%	0.0%	0.2%

Table 4.5. Mitochondrial Control Region genetic diversity estimates for mixed stock aggregations of *C. mydas* at different foraging grounds in the Atlantic Ocean.

Region	Mixed Stock	Haplotype Diversity (*Hd*)	Nucleotide Diveristy (π)	Reference
Eastern Atlantic	Cape Verde	0.588 ± 0.045	0.004 ± 0.003	
	Argentina	0.553 ± 0.051	0.002 ± 0.002	Prosdocimi et al. 2011
	Ubatuba	0.446 ± 0.056	0.002 ± 0.002	
	Almofala	0.717 ± 0.031	0.007 ± 0.004	Naro-Maciel et al 2012
	Arvoredo	0.557 ± 0.070	0.002 ± 0.002	Naro-Maciel et al 2012
	Rocas Atol (juv)	0.688 ± 0.036	0.005 ± 0.003	
	Espirito Santo	0.595 ± 0.031	0.003 ± 0.002	Naro-Maciel et al 2012
Western Altantic	Florida	0.626 ± 0.018	0.004 ± 0.002	Naro-Maciel et al 2012
	Bahamas	0.612 ± 0.021	0.006 ± 0.003	
	Barbados	0.773 ± 0.028	0.010 ± 0.005	
Central Atlantic	Santa Marta	0.73 ± 0.096	0.75 ± 0.070	This study
	La Guajira	0.75 ± 0.070	0.007 ± 0.001	This study

CHAPTER 5

Atlantic *C. mydas* Population Demography: Concluding Remarks, Knowledge Gaps, and a Proposed Model System for the Role of Developmental Habitat Quality

5.1. Population Demographics of the Atlantic *C. mydas*

The Atlantic *C. mydas* is a highly migratory species, with ontogenetic habitat shifts throughout its life history. The complexity of the species' life history, in response to marine environmental pressures, poses a challenge to understanding the demographics of its populations (Heppell et al., 2003). The demographics of migratory species with multiple movement corridors and habitats, requires a broad range of both temporal and spatial parameters in order to accurately describe population size, growth and reproductive vital rates. Habitat- and movement corridor- specific parameters are important to better model the vital rates of migratory populations as well as to predict changes in these rates from environmental stressors such as anthropogenic activities or climate change (Wiederholt et al., 2017).

C. mydas population's significant decline in the Atlantic, prompted the species to be listed as the endangered or threatened throughout the Tropical Atlantic basin. The greatest changes in abundance of populations occurred due to the rapid nesting beach habitat loss and adult harvesting which started in the 1800s (McClenachan et al., 2006). In order for the species to recover, populations need to achieve positive growth.

Population abundance (N) is a function of the number of births minus the number of deaths (local recruitment), and the number immigrant minus the number of emigrants (Net migration):

$$N_{t+1} = N_t + \underset{\text{Local recruitment}}{[\text{Births - Deaths}]} + \underset{\text{Net Migration}}{[\text{Immigrants - Emigrants}]} \quad \text{(eq.1)}$$

In demographically independent populations, local recruitment is the most important driver of changes in abundance (or ΔN), whereas for demographically dependent populations, net migration is equally or more important. Sea turtles such as *C. mydas* have a medium to high degree of demographic independence. Natal philopatry to key nesting areas (especially in females) drives population structure, though some migration among populations occurs at a regional scale (especially of males) (Lutz et al., 2003) (Figure 5.1). Therefore, a demographic unit (population) for *C. mydas* is a group of genetically similar turtles within the reproductive habitat (RH) (composed of the nesting habitat and its surrounding breeding habitats) and the developmental habitat (DHs) (can be several) of immature turtles. The RH and the DHs are geographically separated but demographically linked through dispersal for local recruitment (Figure 5.1).

Each component of *C. mydas* life cycle is spent at geographically separated habitat, and plays a key role in the demography of populations:

1) The Pelagic Dispersal Phase: From hatching to small juvenile stage (which recruits into the DH). This component is spent in the nursery habitat (drifting mats of sargassum in currents fronts and eddies).

2) The Growth and Survival Phase: From juvenile to subadult stage. Spent in the developmental habitat

3) The Reproductive Phase: From subadult to adult stage (which recruit into the reproductive habitats RH, near nesting sites of birth). This component is spent actively migrating to the RH and then at multiple inter-nesting and reproductive areas.

C. mydas spends many years (~20) in the growth and survival phase of their life cycle at DHs. After this phase it disperses out to recruit back to its natal population (Hendrickson, 1980; Lutz et al., 2002). However, recruitment to adult populations cannot occur unless turtles have the body size and energy resources to disperse long distances, reach maturity and reproduce. Thus, the time required for juveniles to grow to adults (the age at maturity) is a key parameter in the population dynamics of sea turtles. Also, the species has the highest survival rate during the adult stage, which can last for decades.

Age at maturity in *C. mydas* is significantly and inversely correlated with pre-maturity growth rates (determined by changes per unit time in length and mass) (Bjorndal et al., 2013). Pre-maturity growth rates in turn, are an integrative response to the environmental conditions of the habitat (Bjorndal et al., 2017). The majority of pre-maturity growth occurs at DHs. Thus, the local recruitment of a population of *C. mydas* is influenced by the growth and survival component, occurring within DHs. Slow growth and/or higher mortality at a developmental habitat would limit overall population growth. Thus, the identification, as well as the assessment of the DHs contribution to the growth of a given population, is important for management and conservation planning for *C. mydas*.

Identifying critical DHs to populations of *C. mydas* and incorporating them into conservation strategies is challenging for several reasons. First *C. mydas* is a highly migratory species that utilizes (occupies) multiple DHs and dispersal corridors across political borders. A given nesting population may be separated from its potential DHs both by distance and jurisdiction. If conservation actions take place for a reproductive population in a given country, their positive impact on the population's growth may be hindered by the extraction or increased mortality at a key DH of that population in a different country (Board & Council, 2010). Also, the multi-year and multi-area studies that are required to establish the demographic links between RH and DHs are both costly and difficult to implement across countries.

5.2. Patterns of Demographic Connectivity Between Reproductive and Developmental Habitats

In spite of multiple difficulties in measuring demographic connections of *C. mydas* populations to their DHs, important progress has been made with molecular technologies such as genetic markers. Due to the philopatric behavior, mostly in females, the species has a strong population structure (populations are demographically independent to some degree) (Figure 5.2). This structure is observable at the genetic level, and thus genetic markers can be used to trace individuals to their population of origin (Bass et al., 2006; Monzón-Argüello et al., 2010; Chapter 4). With the random dispersal of turtle hatchlings by currents and eddies, *C. mydas* juvenile recruitment into DHs occurs from multiple contributing nesting populations, and thus the aggregation of immature turtles at DHs are called "mixed stocks" (Figure 5.2). Using mtDNA markers from samples of juvenile *C. mydas* in multiple DHs throughout the Atlantic, it is possible to trace the populations that are using that habitat for development or growth (Bass et al., 2006; Bolker et al., 2007). From these genetic studies, it has been inferred that RH and

DHs are not randomly connected, but follow, at least, regional-scale patterns of demographic connectivity. In this pattern, parental populations are more connected to DHs that are located closer, rather than farther away, within a region (regions being: western, central and eastern Atlantic) (Bolker et al., 2007). These regional scale patterns can be explained by the influences from the direction and speed of major ocean surface currents as well as the size of the parental populations (number of nesting females/year) (Bass et al., 2006; Naro-Maciel et al., 2007).

5.2.1. Developmental Habitats of Northeastern Colombia: Insights from this dissertation

Although nesting rookery size and oceanographic physical factors such as surface currents contribute to the degree and type of demographic connectivity between parental populations and their DHs at a large regional scale, other factors, acting at smaller scales within regions (*e.g.* the western Atlantic), may explain the parental population's contributions observed at DHs with genetic markers, or conversely, the contributions of different DHs to a given parental population (Bass et al., 2006). Inferred patterns of demographic connectivity from genetic studies may change when more DHs are identified or when DHs at strategic or understudied location are studied like at boundary areas between connectivity groups (Bolker et al., 2007).

Throughout this dissertation research, the quality of coastal benthic communities as DH of *C. myda*s was investigated in the coastal upwelling system off La Guajira, Colombia. Its location at the boundary between two connectivity groups of the species to the east and west, as well as the influence of two major opposite-direction oceanic currents, may allow for arrival and long-term retention of juvenile *C. mydas.* The major research findings of this dissertation also indicate that:

1. The nutrient enriched, shallow coastal waters of north eastern La Guajira support highly diverse, pristine, submerged aquatic vegetation (SAV) communities with abundant macroalgae, especially Rhodophyta (calcareous and fleshy red algae). These SAV communities are extensive in the shallow near shore environment along the coastal peninsula, and are unique in the Western Atlantic. Red macroalgae are well known food items for the species and have higher levels of nitrogen, a limiting nutrient, than other common diet items for the species like seagrasses.

2. An aggregation of juvenile and subadult individuals of the species occupies the study area, has some preferred sites of occupation, and these sites seem to with the location of the diverse macroalgae communities. Immature *C. mydas* remains or seasonally returns to the area over a period of at least three years, feeding on the available vegetation, especially on red algae. Likely as a result of the consumption of diverse nutrient diet, and the influence of diet type on the growth rate of *C. mydas*, as well as the pristine state of the habitat forage offer, the average body condition of the immature aggregation was good and greater than that of other areas in the Caribbean.

3. The overall good body condition of the immature aggregation, in conjunction to extensive diverse forage offer are indicators of the good quality of La Guajira waters as habitat for the growth and survival of immature *C. mydas*. However, further work that addresses other aspects of the habitat quality are recommended, including its potential contribution to reproductive populations of the species.

4. The location of Northeastern Colombia in regard to two major, opposite-direction current flows, the Panama-Colombia Counter-current and the Caribbean Current, seems to allow the arrival of individuals from multiple nesting rockeries into its waters. The aggregation of *C. mydas* in these waters comes from several reproductive populations of the three connectivity groups in the Atlantic: Western, Central and to a lesser degree, Eastern Atlantic. These multiple connections may explain the slightly higher genetic diversity of this mixed stock immature aggregation, in comparison to other mixed aggregations in the Caribbean. Major connections were found with reproductive populations in Costa Rica, Aves Island and Surinam.

5. The connectivity to parental populations differed significantly among regions (La Guajira vs Santa Marta) within the study area of Northeast Colombia. For instance, Santa Marta is closer to Costa Rica than La Guajira, but based on the mixed stock analyses, Costa Rica is highly connected to La Guajira but not to Santa Marta. Therefore, questions arise concerning what other factors help explain observed differences in the populations of origin of juveniles found in these two areas. According to these findings, La Guajira is highly connected to the Costa Rica reproductive population, the largest population of *C. mydas* in the world, and could be an important contributor of recruiters for this reproductive population.

Ecological and/or oceanographic factors that occur at smaller scales than that of major ocean surface currents, or different connectivity corridors, can influence the composition of immature sea turtle aggregations at DHs. Within Colombia, La Guajira DH differs from Santa Marta DH mainly in habitat-based factors (*e.i.* size and food offer) (Invemar, 2012). Habitat is defined here as the sum of resources and conditions that produce the occupancy by sea turtles of an area. Whereas currents and the distance of a DH from a parental population can influence who arrives to a DH, habitat-based factors in the DH can influence who remains (survival) in and exits the very long juvenile-to-adult phase (growth and dispersal), to recruit back to reproductive populations (recruitment).

Many factors at DHs can influence the growth and dispersal to a reproductive population, and thus can determine the specific DH contribution (number of recruiters) to a population. Important factors include

a. Food: In the DH growth rates are maximized. Growth rates in *C. mydas* depend on the nutrition that comes from diet. Nutrient rich diets allow faster growth rates and better body condition (Bjorndal, 1985). The food items of *C. mydas* vary widely in their nutritional value marine plants such as seagrasses and macroalgae (see chapter 2) to small animals such as small crustaceans, mollusks, sponges and jellyfish). Nitrogen is a limiting nutrient and *C. myda*s selects nitrogen-rich or low- fiber (which impedes access to Nitrogen) plant items for their diets. The species is hindgut fermenting, thus depends on microbiota for plant material digestion (Bjorndal, 1980). Starvation can result in mortality of *C. mydas* or delays in the start of reproductive migrations because the energy provided from food is reserved in subadults for long-distance reproductive migrations to the reproductive habitats. The energetic state of first nester females comes from their DHs diet and thus it influences the reproductive output of the population.

b. Predators: The main predators of sea turtles are sharks and some large fish. The mortality rates are higher at smaller sizes/ages, but decreases with age (Lutz et al., 2002). Larger turtles have less of a chance to be predated. Habitats for *C. mydas* tend to be SAV beds along or near sites with physical structure such as reefs (coral worm) or near mangroves (roots) (Amorocho and Reina 2007). These structures may allow refuge from predation and provide resting sites. Absence of adequate physical structure for instance at open ocean DHs, increases the rate of mortality, thus the contribution recruiters of these areas may be lower that more protected or structured DHs.

c. Anthropogenic stressors: Fishing pressure and or vessel traffic, at DHs or at migratory routes between DHs and RHs can increase mortality and thus decrease the number of individuals that are able to recruit back to their populations (Finkbeiner et al., 2011; Gardner & Nichols, 2001). These stressors can also have non-lethal effects that influence the allocation of body energy in a turtle towards survival more than growth, therefore decreasing the growth rates (Heithaus et al., 2007). Delayed growth, also delays maturity attainment in *C. mydas* and thus decreases the contribution of a given habitat at a given time to its reproductive population.

d. Temperature: Temperature influences the rate of food ingestion, the metabolic rate of food digestion, the allocation of energy, and finally the growth of turtles. Also, temperature affects the rate of food production in coastal environments. The amount and availability of food, in turn influence *C. mydas* growth rates.

All of these habitat-based factors and many others, could be descriptors of the "habitat quality" of a given DH. Juvenile turtles are able to identify and/or actively swim towards areas of better quality habitat than others, as it has been suggested by satellite telemetry data and the minimum body size of recruitment at DHs (Meylan et al., 2011;

Putman et al., 2012; see Chapter 3). Thus, how can habitat-specific factors affect the dynamics of *C. mydas* populations? How does the habitat quality of DHs influence the contribution of these habitats to the dynamic of parental populations?

5.3. The Central Caribbean (CC): A Proposed Model System to Explore the Role of DH's Quality in the Dynamics of *C. mydas* populations

5.3.1. The Migratory Network Modeling Framework

The purpose of this chapter is to propose a theoretical modelling framework and a model system to star exploring the role of habitat quality in their differential contribution to the dynamics of populations of migratory species. If a population is spatially structured in several habitats separated by dispersal corridors, such as in the case of marine migratory species, the different habitats or corridors all habitats contribute differently to the dynamics of populations. Additionally, the specific contribution of a habitat/corridor, to a given population of individuals, that move among many reproductive and non-reproductive habitats and corridors, depends not only on the habitat itself but also on the other habitats and dispersal corridors contributions (Figure 5.3) (Wiederholt et al., 2017).

Discrete migratory network dynamics models (Wiederholt et al., 2017), can be to assess habitat- and corridor-specific contributions to the overall dynamics while considering the contributions of all other habitats in the network. These models build on source-sink metapopulation dynamics models but are adapted to migratory, spatially structured species.

In a migratory network, each node is a habitat and the nodes are linked by transitions (lines) (Figure 5.3). The per-capita contribution of each habitat or transition can be assessed from a set of probabilities related to the key vital rates of populations, survival, dispersal and reproductive rates. Survival probability is given by ***s***, the probability of reproduction is given by ***r*** and the probability of dispersal is given by ***p***. Each habitat (***o*** or ***d*** depending on the direction of the transition, *o* for origin and *d* for destiny) and transition (***i***), age (***a*** for adult or **j** for juveniles) is has its own ***s, r*** and ***p*** probabilities. The contribution of a given habitat will be given by

$$C^{o} = \sum_{i=1}^{n} \sum_{d=1}^{n} C^{oid} p_{oi} p_{id} \qquad \text{Eq. 2}$$

Similarly, the contributions of transitions and even pathways within the network can be estimated using Wiederholt's et al., (2017) equations. The vital rate-based framework of this model permits testing of different scenarios that perturb a habitat or a transition contribution and observe their effect on the vital rates of the population. Overall, it provides a framework to identify among the many likely routes, habitats and transitionary pathways a migratory species population can be occupying, which ones are in reality contributing to its demographics. This information is relevant for migratory species conservation and management schemes aimed to identify or protect habitats or marine corridors that contribute the most to population's growth, because these species are widely and transnationally distributed. Effective conservation will involve multiple habitats in different countries within the migratory network.

5.3.2. The Central Caribbean Proposed Model System

The migratory network framework can be used to explore the role of candidate factors such as DH quality, able to change the vital rates of populations, at the multiple habitats and migratory pathways of migratory *C. mydas* populations. DH quality may be an important factor determining the demographic contributions to reproductive populations of the Atlantic *C. mydas*, at the smaller scale of within a region.

An ideal system to test for the role of DH quality in the demographics of the Atlantic *C. mydas* populations using the migratory network framework is the Central Caribbean system (CC). The CC is a semi-enclosed sea encompassing several developmental habitats of *C. mydas* (including the two studied in this dissertation) for which the contributions from reproductive populations have been estimated using genetic analyses (Figure 5.4, Table 5.1 and 5.2). The CC encloses the largest reproductive population of the Atlantic *C. mydas*, in Tortuguero, Costa Rica. Two major ocean surface currents flow through this system in opposite directions, the Caribbean Current, and the Panama-Colombia counter-current, which allows to distinguish their influence in the observed contribution patterns (Andrade, 2003). Also, smaller scale oceanographic features such as eddies (ranging from tens to 700 Km Diameter, 20-30 cm/s speeds and 3-4 months lifetime) are very common in the area, originating in the Venezuela basin or entering the Caribbean trough the Antillean passages (St. Lucia Channel, the Annegada passage and north Trinidad) towards the Gulf of Mexico (Andrade & Barton, 2000).

The study system encompasses multiple ecological provinces and subdivisions. These subdivisions have been delineated based on physical oceanography (Chollett et al., 2012); marine fish and coral population connectivity; and coastal ecosystem types which are known habitats of *C. mydas* (*e.g.* seagrass beds, coral reefs, mangrove forests) (Figure 5.4). The diversity of subdivisions, differing in oceanographic and ecological characteristics, allows contrasting different regions in terms of habitat quality, for their expected contributions to the reproductive populations within the system. Differences in habitat quality adds another layer of explanatory power to the observed connectivity patterns between DHs and RHs at the within region scale (within the western Atlantic).

5.3.3. Parameters Estimation for Modeling

Vital rates (as probabilities), including survival, dispersal and reproductive rates, are the parameters of migratory network models that allow to estimate the habitat- and transition-specific contributions. Some of these parameters will be primarily obtained from the literature (Table 5.3). The rest of the parameters, such as the transition probabilities from one habitat to the next, can be estimated from currently available models for sea turtle species (explained below).

Reproductive Habitat Parameters

a. *The per-capita contribution of RHs*

The reproduction probability r is given by the size of the nesting rookeries in the Atlantic measured in terms of the number of nesting females per year, which is known from the literature (Table 5.2). The greater the size of the nesting rockery, the greater the probability that it will contribute $\boldsymbol{r}$. Non-breeding habitat will have a value of $\mathbf{r}=0$.

b. *Probability of adult dispersal*

The probability of adult dispersal $\boldsymbol{P}$ *is* assigned by the size and body condition of the individual as well as the distance between the two habitats involved in the transition. These distances are not only Euclidean geographic distances but, oceanographic distances, that can be obtained from a computational simulation using data-assimilated oceanographic Lagragian circulation models, as it has been suggested for marine population connectivity analyses (White et al., 2010) (Kool et al., 2011). These approaches account for the physical oceanographic variables influencing that are more likely to influence *C. mydas* dispersal. These include ocean temperature, salinity, currents and wind speeds. Bio-assimilated circulation models include the Connectivity Modeling System (CMS) (Paris et al., 2013).

The CMS model system allows the input and modification of biological characteristics of the dispersal organisms into the model. The dispersal trajectories of hatchling sea turtles between nesting rockeries (sources) and DH (destinations) will be simulated assuming a short-time, active, followed by a long-term passive, dispersal behavior. Particle (hatchling) releasing locations are known nesting rockeries (whose size will be taken into account to avoid bias on the individual contribution of each beach) (Table 5.1). Once a size threshold has been reached by the organism, active swimming behavior follows. The simulation of hatchling trajectories will be performed over several years to account for the inter-year variation in recruitment as well as the inter-year variation of nesting females observed in the species (Bjorndal & Bolten, 2008).

Developmental Habitats parameters

a. Juvenile and adult Survival probabilities

The probabilities that juvenile and adult turtles survive at a DH depends on the size of the aggregation at the habitat and the stage structure of the aggregation (proportion of juveniles:subabults:adults). Also, these probabilities depend on the age-specific predation rate, either natural and/or anthropogenic. Age specific predation rate will be obtained from the predator densities and the habitat physical structure, refuge sites availability and sea turtle density. Turtle densities have been estimated for several of the DHs and RHs within the CC system. Physical complexity in turn will be used as a proxy of habitat refuge availability. Physical structure will be given by the proportion of marine coastal communities known to provide 3D structure to coastal areas such as mangrove forests and coral reefs. The proportional area of these ecosystems within a habitat will be used as a proxy of habitat structure. The areas will be obtained using Geographic information biological databases such as the Ocean Biogeographic Information System OBIS (http://www.iobis.org).

Survival is also a function of age and age-specific size which in turn is a function of the quality, density and availability of forage, as well as the abundance and turtle density. Nutrition quality positively correlates to body condition and growth rates in *C. mydas*. *C. mydas* feeds on SAV such as seagrass and macroalgae, and the marine distribution of FGs and DH corresponds with the location of extensive SAV beds. Thus, extension (Area, Km^2) and the abundance (Biomass unit/ area) of these ecosystems could be used as proxy of habitat quality (Table 3.3). The area and abundance of forage, for which SAV communities are a proxy, will be obtained from the literature or biodiversity databases such as OBIS), using the satellite imagery analyses tools within ArcGIS (ESRI 2010).

b. Probability of dispersal

This probability is given by the maturity status of the individual, the age-specific growth rates, the body condition and the oceanographic distance between DH and RH. The higher the body size and the body condition the higher the probability of dispersal. These probabilities will be estimated similarly to adult dispersal probabilities using bio-assimilated ocean circulation model such as the CMS system.

5.3.4. Expected outcomes of the modeling exercise

The application of the migratory network framework to the CC model system will allow to obtain estimations of the per-capita contribution (number of individuals produced during the life cycle) of multiple DHs in the migratory pathway of the largest population of *C. mydas* in the Atlantic, and in proportion to the other habitats and corridors in the network. The estimated proportional per-capita DH contributions are a similar estimate to the nesting rookery contributions to mixed stocks aggregations of *C. mydas* at DHs, obtained from genetic markers frequency data. Thus, the estimated contributions with migratory network models could be compared to the "observed" ones from genetic markers in order to test the fit of the model to the data. Differences found between these two estimations could then be attributed to the source of variation that the network model accounts for besides size of nesting populations or currents, which is among habitats and/or corridors within regions. By accounting for variation among habitats, this model has the potential to reveal patterns of connectivity at smaller scales like within regions.

Differences among habitats are given in the model by differences in key vital rates parameters such as survival or growth. Growth and survival are vital rates for *C. mydas* populations. The majority of growth occurs during the long-lasting immature stage of the life cycle of *C. mydas* spent at the DH. Growth is highly influenced by the quality of habitat; as well as survival rates are. Both of these two are determinants of the production of DHs sea turtle recruiters into parental populations, thus influencing the local recruitment portion of the demography of Atlantic *C. mydas* populations.

The high natural variation in developmental habitat characteristics (or habitat quality) of the CC system may account for variation in the model. Accounting for this variation may permit to observe patterns of demographic connectivity between reproductive populations and DHs at a smaller scale, that had not been seen before. The identification of regional patterns of connectivity is important for a thorough understanding of the ecology of the migratory, Atlantic *C. mydas.*

Furthermore, the identification of key contributors (habitats or dispersal corridors) to the dynamics of its populations can allow for better planning of conservation measures at the regional level. *C. mydas* regional-level conservation or management measures that need to prioritize among the many habitats and corridors the species occupies during its migration, will benefit from targeting migratory corridors and/or stop over sites such as DHs that are key contributors to the local recruitment and thus to the growth of populations.

5.4. Figures and Tables

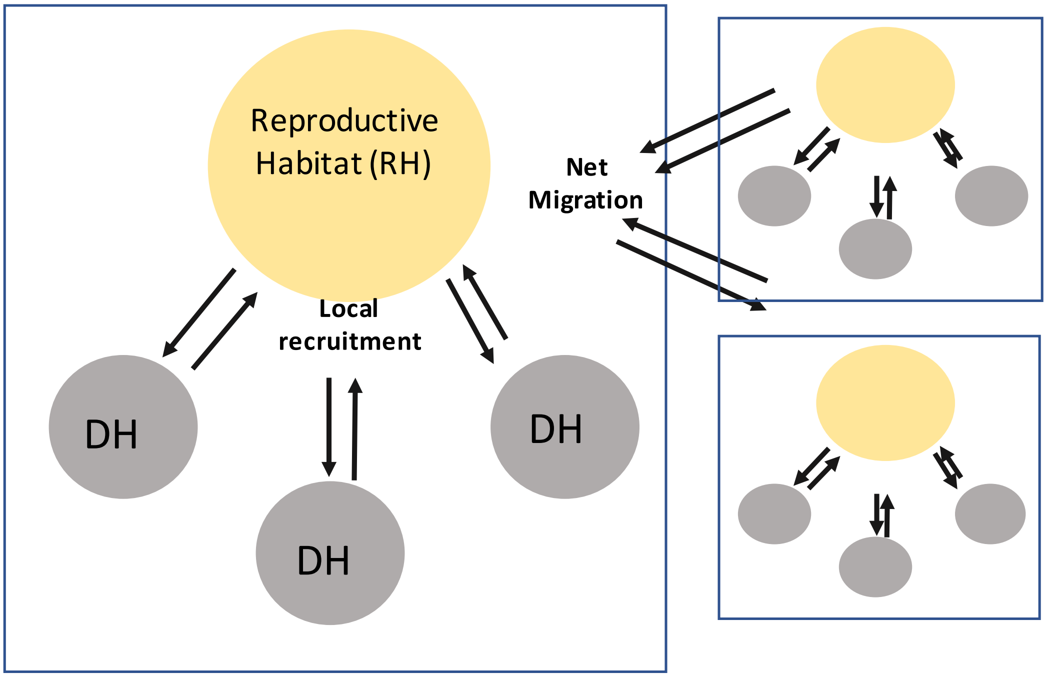

Figure 5.1. Conceptual model of a demographic unit for *C. mydas* (a population) represented by the squares.

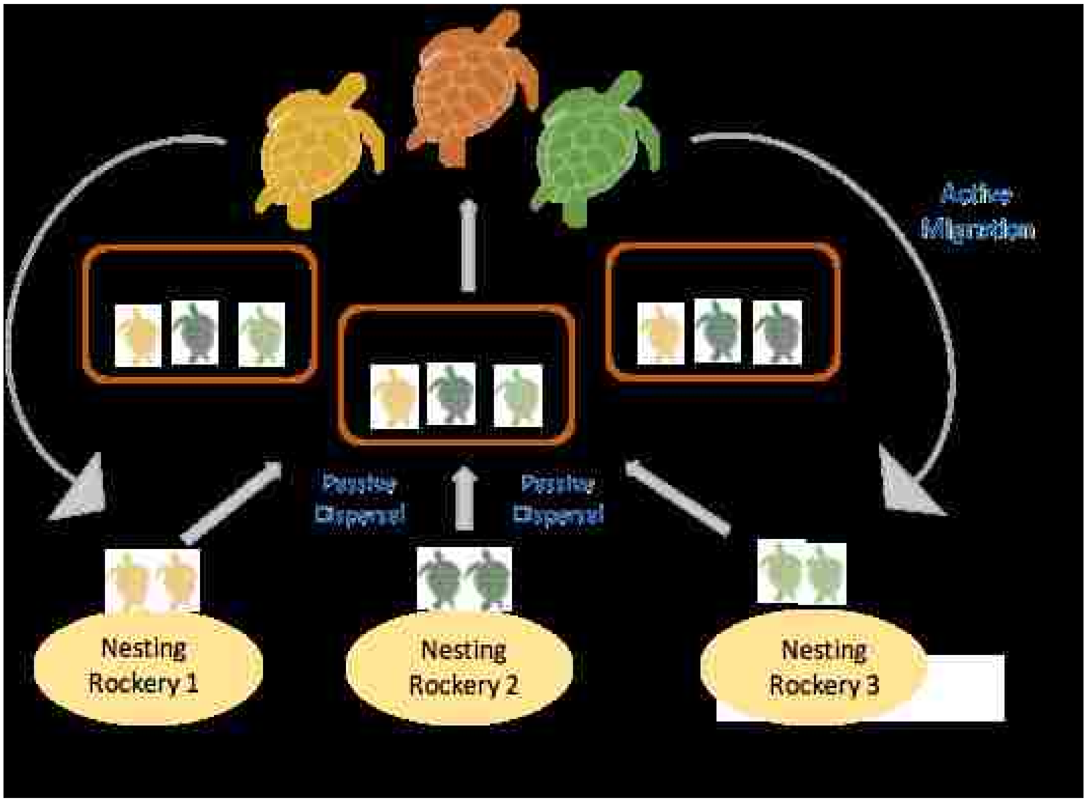

Figure 5.2. Theoretical genetic composition of mixed-origin aggregations of *C. mydas* at DHs and contributing parental populations at reproductive habitats often called nesting rookeries. The population(s) of origin of individuals a DHs can be known using genetic tags.

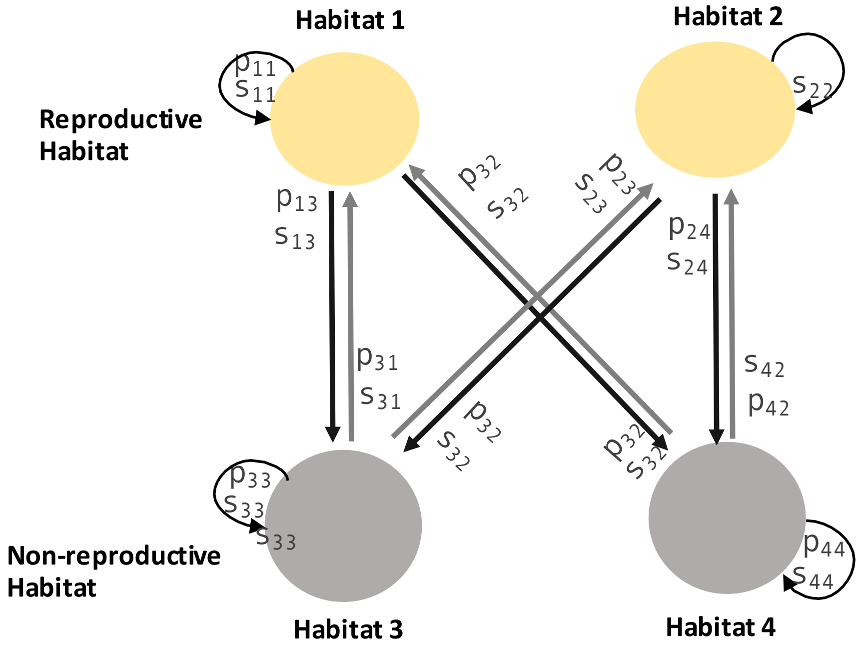

Figure 5.3. Conceptual model of a migratory network for a species with multiple reproductive and non-reproductive habitats. Vital rates parameters are used for estimation of the per-capita contributions of a given habitat (circles) or dispersal corridor (transitions represented by arrows) to the overall network or part of the network. Modified from Wiederholt et al., 2017.

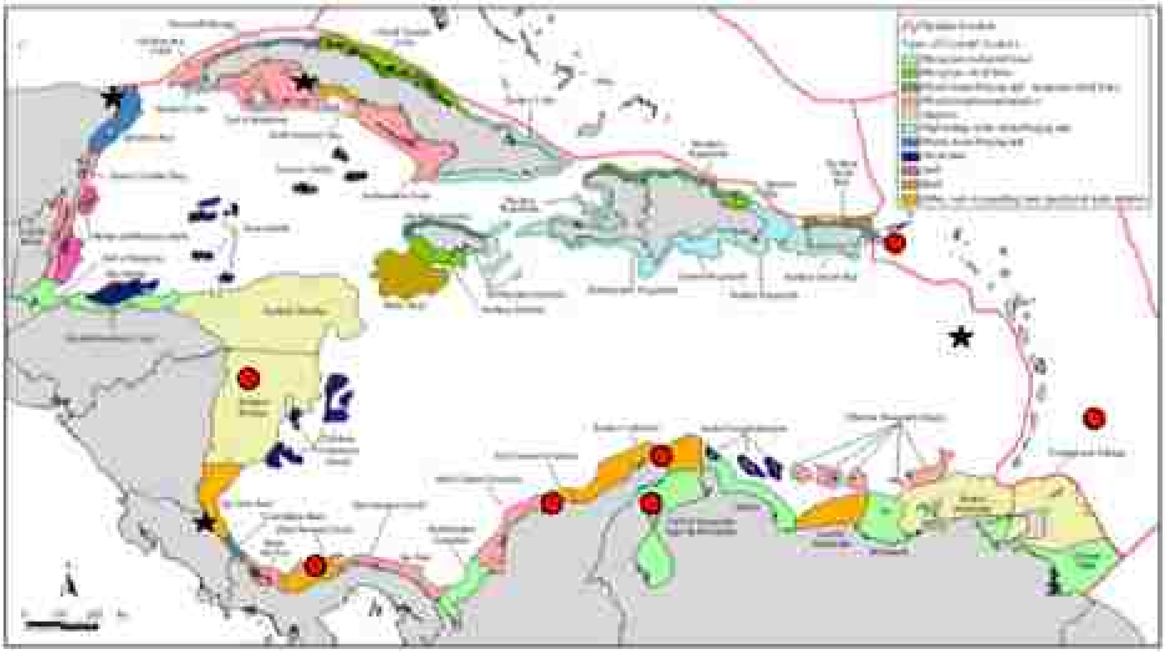

Figure 5.4. Map of the Central Caribbean (CC) study system including the main coastal ecosystems (Sullivan-Sealey and Bustamante, 1999) relevant for sea turtle habitat. Distribution of nesting rookeries (black stars) and Developmental Habitats (red circles).

[redacted]

Major Nesting Colonies of *C. mydas* in the Atlantic	**Number of Nesting Females per year**
[redacted]	[redacted]

Table 5.2. Developmental Habitats for *C. mydas* in the Caribbean and southern Atlantic.

Habitat	**Type**	**Reference**
Culebra, Puerto Rico	Developmental	Collazo et al., 1992
La Guajira, Colombia	Developmental?	This work
Santa Marta, Colombia	Transitory	This work
Secretary, Panama	Developmental?	Meylan et al 2011
Zapatilla, Panama	Developmental	Meylan et al 2011
Gulf of Venezuela	Developmental	Barrios-Garrido Pers. Com.
St. Croix, Virgin Islands, U.S.	Developmental	Ogden et al., 1983
Barbados	Foraging?	Luke et al., 2004
Miskito Cays	Foraging	

Table 5.3. Parameter for estimation of per capita contribution of multiple habitats or corrido dispersal corridors to the dynamics in *C. mydas* population.

Description	**Parameter**	**Value Range**	**Reference**
Reproductive Habitat (RH)			
Per-Capita RH Production	$r_{o,j}$	0-1	Lutz et al., 1997
Probability of Adult Survival	$s^{a}_{o,j}$	0.5-0.95	
Transition to DH			
Probability of Juvenile Survival	s^{j}_{oi}	0.1-0.5	Carr et al., 1978
Probability of Dispersal	p_{oi}	?	
Non-Reproductive Habitats (Dh)			
Probability of Juvenile Survival	$s^{j}_{j,o}$	0.5-0.9	
Probability of Adult Survival	$s^{a}_{i,o}$	0.7-0.9	
Transition to RH			
Probability of Juvenile Survival	$s^{j}_{id,oi}$	?	Heithaus et al., 2007
Probability of Adult Survival	$s^{a}_{id,oi}$	high	
Probability of Dispersal	$P_{id,oi}$	?	

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Appendix

[redacted]

	Parei	Patsuarora	Bahia Hondita	Masichi	Neimao	Punta Negra	Wannal	Puerto Chimare	Puerto Santa Cruz	Playa Jiwotpola
Anadyomene stellata	0	0	1	0	0	0	0	0	0	0
Avrainvillea nigricans	0	0	0	0	1	0	0	0	0	0
Bryopsis hypnoides	0	0	0	0	0	0	1	1	1	0
Bryopsis pennata	1	0	0	0	0	0	0	0	1	0
Bryopsis plumosa	0	0	0	0	0	0	0	0	1	0
Caulerpa mexicana	0	0	0	0	0	0	1	1	0	0
Caulerpa prolifera	0	0	0	0	1	0	1	1	1	0
Caulerpa racemosa	0	0	1	0	0	0	0	0	0	0
Caulerpa racemosa var. lamourouxii	0	0	0	0	0	0	1	0	0	0
Caulerpa sertularioides f. farlowii	0	0	0	0	0	0	1	0	1	0
Caulerpa taxifolia	0	0	1	0	0	0	0	0	0	0
Chaetomorpha aerea	0	0	1	0	0	0	0	0	0	1
Chaetomorpha antennina	0	0	0	0	0	0	0	1	0	0
Chaetomorpha linum	0	0	0	0	1	0	1	1	1	1
Cladophora catenata	0	0	0	0	0	0	0	1	1	0
Cladophora liniformis	0	0	0	0	0	0	0	0	1	0
Cladophora prolifera	0	0	0	0	1	0	0	1	0	0
Cladophoropsis membranaceae	0	0	0	0	0	0	0	1	0	0
Codium sp.	0	0	1	0	0	0	0	0	0	0
Codium repens	0	0	1	0	0	0	0	0	0	0
Enteromorpha flexuosa	0	0	0	0	0	0	0	0	0	1

Enteromorpha flexuosa subsp. paradoxa	0	0	0	0	1	0	0	0	0	0
Enteromorpha intestinalis	0	0	0	0	1	0	0	0	0	0
Enteromorpha lingulata	1	0	0	0	0	0	0	0	0	0
Enteromorpha prolifera	0	0	0	0	0	0	1	0	0	0
Halimeda scabra	1	1	0	0	0	0	0	0	0	0
Udotea unistratea	0	0	0	0	1	0	0	0	0	0
Ulva fasciata	0	0	0	0	0	0	1	1	0	0
Ulva lactuca	0	0	1	0	1	0	0	1	1	0
Ulva oxysperma	0	0	1	0	0	0	0	0	0	0
Verdigellas fimbriata	0	0	0	0	0	0	0	1	0	0
Dictyopteris jamaicensis	0	0	0	0	0	0	0	0	1	0
Dictyopteris jolyana	0	0	0	0	0	0	1	0	1	1
Dictyopteris justii	0	0	1	0	0	0	0	0	0	0
Dictyopteris plagiogramma	0	0	0	0	0	0	0	1	0	0
Dictyota caribaea	0	0	0	0	0	0	0	1	0	0
Dictyota cervicornis	0	0	1	0	0	0	0	1	0	0
Dictyota crenulata	0	0	0	0	0	0	0	1	0	0
Dictyota humifusa	0	0	0	0	0	0	0	1	0	0
Lobophora variegata	0	0	0	0	1	0	1	0	1	0
Padina profunda	0	0	0	0	0	0	0	0	1	0
Sargassum filipendula	0	0	0	0	0	0	1	0	0	0
Sargassum platycarpum	0	0	1	0	0	1	0	1	1	1
Sargassum polyceratium	0	0	0	0	0	0	1	0	0	0

Sargassum pteropleuron	0	0	0	0	0	0	0	0	1	1
Sargassum vulgare	0	0	0	0	0	0	0	1	0	1
Spatoglossum schroederi	0	0	0	0	1	0	1	0	1	0
Stypopodium zonale	0	0	1	0	0	0	0	0	0	1
Turbinaria tricostata	0	0	0	0	0	1	0	0	0	0
Acanthophora muscoides	0	0	0	0	0	0	0	0	0	1
Acanthophora spicifera	0	0	0	1	0	0	0	0	0	0
Agardhiella ramosissima	0	0	0	0	0	0	0	1	0	0
Amphiroa rigida	0	1	0	0	0	0	0	0	0	0
Asteromenia peltata	0	0	0	0	0	0	0	1	0	0
Bostrychia montagnei	0	0	0	0	0	0	0	1	0	0
Bostrychia tenella	0	0	0	0	0	0	1	0	0	0
Bryothamnion triquetrum	1	0	0	1	0	0	1	0	0	1
Centroceras clavulatum	0	0	0	0	0	0	0	1	1	0
Ceramium cruciatum	0	0	0	0	1	0	0	1	0	0
Ceramium sp.	0	0	1	0	0	0	0	0	0	0
Champia parvula	0	0	0	0	0	0	0	1	0	0
Champia salicornioides	0	0	0	0	0	0	0	1	0	0
Champia vieillardii	0	0	0	0	0	0	0	1	0	0
Chondria capillaris	0	0	0	0	1	0	0	0	1	0
Chondria cnicophylla	0	0	0	0	1	0	0	0	0	0
Chondria floridana	0	0	0	0	0	0	0	1	0	0
Cryptonemia seminervis	1	0	0	1	0	0	1	0	0	0

Dasya baillouviana	0	0	0	0	1	0	0	0	0	0
Dasya ocellata	0	0	1	0	0	0	0	0	0	0
Dasya spinuligera	0	0	0	0	0	0	0	1	0	0
Galaxaura marginata	0	0	0	0	0	0	0	1	0	0
Gelidiella acerosa	0	0	0	0	0	0	0	1	1	1
Gelidiopsis planicaulis	0	0	0	0	0	0	0	0	1	0
Gracilaria blodgettii	0	0	0	1	0	0	0	0	0	0
Gracilaria caudata	1	0	0	0	1	0	0	1	1	0
Gracilaria cervicornis	0	0	0	0	1	0	1	0	1	0
Gracilaria cuneata	0	0	0	0	0	0	0	0	0	1
Gracilaria curtissiae	0	0	0	0	0	0	1	0	1	0
Gracilaria cylindrica	0	0	1	0	1	0	0	1	0	0
Gracilaria damaecornis	0	0	0	1	1	0	1	0	1	0
Gracilaria domingensis	0	1	0	1	1	0	1	1	1	1
Gracilaria mammillaris	0	0	0	0	1	0	1	1	1	0
Gracilaria sp	0	0	1	0	0	0	0	0	0	1
Gracilaria tikvahiae	0	0	1	1	1	0	0	1	1	0
Haliptilon cubense	1	0	0	0	0	0	1	0	1	0
Haliptilon subulatum	0	0	0	0	0	0	0	0	1	1
Heterosiphonia gibbesii	0	0	1	0	0	0	0	0	0	0
Hydrolithon boergesenii	0	0	0	0	1	0	1	0	0	1
Hypnea musciformes	0	0	1	1	0	0	1	1	1	0
Hypnea spinella	1	0	1	1	1	0	0	1	1	1
Hypnea valentiae	0	0	0	0	0	0	0	1	0	0
Jania pumila	0	0	0	0	0	0	1	0	0	0

Jania rubens	0	0	0	0	0	0	0	1	0	0
Kallymenia sp.	0	0	0	0	0	0	0	0	0	1
Kallymenia cribogloea	1	0	0	0	0	0	0	1	0	0
Laurencia (Chondrophycus) iridescens	0	0	0	0	0	0	0	1	0	0
Laurencia gemmifera	0	0	0	1	0	0	0	1	0	0
Laurencia intricata	0	0	1	1	0	0	0	1	0	0
Laurencia obtusa	0	0	0	0	0	0	0	1	0	0
Laurencia poiteaui	0	0	1	0	0	0	0	0	1	1
Meristiella schrammii	0	0	0	0	0	0	0	1	0	0
Mesophyllum mesomorphum	0	0	0	0	0	1	1	0	0	0
Neogoniolithon spectabile	0	0	1	0	0	0	0	0	0	0
Osmundaria obtusiloba	0	0	0	0	0	0	1	1	0	1
Peyssonnelia sp.	0	0	0	0	0	0	0	0	0	1
Porolithon pachydermum	0	0	0	0	0	1	0	0	0	0
Rhodymenia divaricata	0	0	0	0	1	0	0	0	1	0
Solieria filiformis	0	0	0	1	1	0	0	0	0	0
Sporolithon episporum	0	0	0	0	0	1	1	0	1	0
Titanoderma pustulatum	0	0	0	0	0	1	0	0	1	1
Tricleocarpa cylindrica	0	0	0	1	0	0	0	1	0	0
Wrangelia bicuspidata	0	0	0	0	1	0	0	0	0	0
Wrightiella blodgettii	0	0	0	1	0	0	0	0	0	0
Halodule beaudettei (wrightii)	0	0	1	0	1	0	0	0	0	0
Syringodium filiforme	1	0	1	0	1	0	0	1	1	0
Thalassia testudinum	1	1	1	1	1	0	1	1	1	0

The single line divides species of macroalgae from the species of seagrass