UCLouvain

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Modelling the dispersal of juvenile leatherback turtles in the Caribbean Sea

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Academic year 2019–2020
Master [120] in Civil Engineering

Preface

After three years of a bachelor's degree in civil engineering and two years of specialization in construction at the Université catholique de Louvain, we decided, with my colleague and friend Jérôme Pirmez, to take up this thesis topic. It may seem surprising but we wanted to change from our usual field, and the will to go off the beaten track was there. The bioengineering sector interests us for one of its objectives, to make the world a better place by responding to tomorrow's environmental challenges. The NGO Upwell, following the recovery of turtle field data in 2016 and 2018, needed help in modelling turtles during their first months at sea, which is a period that is still very poorly known for turtles. Turtles are exceptional and exciting creatures that can teach us a lot about the sea world. They travel tens of thousands of kilometres each year covering all the oceans. Therefore, this emblematic species, one of the oldest on Earth, is a good indicator of the health and marine biodiversity of our oceans.

First of all, I would like to thank Jérôme Pirmez, who helped me with the analysis of Upwell's data. Unfortunately, he was unable to complete the entire thesis. I would also like to thank him for all these years spent together in good and bad times. A special thanks to Emmanuel Hanert, my supervisor, for the meetings on Friday, and for supporting me in the moments when I was uncertain, discussing the directions of my work, helping me to find new ideas, and finding the contacts I needed to go through with it. Thanks to him for guiding my work in a very human way, being constantly available to answer my questions and reread my writings. Thank you to Eric Deleersnijder for supporting the project. Thanks to Pierre Latteur and Sandra Soares Frazao for agreeing to be the readers of my thesis. Particular thanks to Thomas Dobbelaere, whom I harassed and who helped me in the modelling part. The coding of the simulations using the SLIM oceanographic model was an important part I needed help with. Thanks to Antoine Saint-Amand for his useful advices. Special thanks to Phillipe Gaspar also for his time. His passion for turtles is easily transmitted when he shares his experience. It really made me want to learn more about the intriguing subject of the hidden life of juvenile sea turtles.

"Try to leave this world a little better than you found it."
Sir Robert Baden- Powell

Harold Coens

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Abstract

The mysterious period of the turtles' life, between their first day at sea and when they come to lay eggs years later on the same beach, continues to elude research of this critical life stage when mortality rates are the highest. The conservation efforts on beaches need to expand to the pelagic (offshore) life stage to reduce the mortality rate. It has long been assumed that turtles drift passively with the current during this period. Recently, it has been discovered that one year old turtles have an active behaviour in the current. The ability of turtles to be active in ocean currents, especially at early life stages, can significantly influence their future dispersal. The NGO Upwell recovered data by acoustic monitoring during the first hours of leatherback hatchlings from Pacuaré in Costa Rica, an important leatherback nesting beach in the Caribbean Sea. I used the data of the SLIM oceanographic model, developed by UCLouvain, to obtain the dispersion of the turtles during their two first months of life in this region. Based on previous studies and Upwell's data, I made simulations with different behavioural hypothesis including active swimming. The objective was to make an accurate map of the probability of turtle presence. My study suggests that the dispersion of leatherbacks in this region of the Caribbean Sea is influenced by annual local current conditions and by the swimming behaviour of the turtles. During the first days, the turtles were located alongside the coasts of Costa Rica and Panama before heading offshore, in the gyre near Pacuaré and in the Gulf of Darién. They moved gradually north towards the Gulf of Mexico. No turtle went east of longitude -74. The model predicts that the active swimming component is essential to the survival of the species since it brings the risk of stranding down from up to 50% to 0.19%. These findings open up research prospects that could have an impact on the defence of this species.

Chapter 1

Introduction

1.1 The disappearance of turtles

Ecosystems changed more intensively during the second half of the 20th century than at any other time in human History (Reid et al. 2005). The most important changes have been the transformation of forests into cultivated lands and the loss of coral reef areas (Hoegh-Guldberg et al. 2019). Fished species have declined by 90% since industrial fishing began (Dan 2018). Industrial fishing covers more than 55% of the oceans, an area of 200 millions km^2 (Kroodsma et al. 2018). Every year, hundreds of thousands of turtles get trapped in fishing nets or longlines (Hance 2010).

The second cause of the disappearance of sea turtles is habitat degradation due to fishing equipment hitting the bottom and destroying certain food resources or dispersing pollutants. This lead to a degradation of the role of the habitats : feeding, breeding and resting (Lewison et al. 2004). The development of beaches due to human activity, e.g. hotels and roads, destroys nesting beaches (Claro and Doin 2016) and the artificial light disorient the newborns away from the sea (Freund 2017).

The third cause is climate change. First of all, the sex of marine turtles is temperature-dependent (Ewert et al. 1994). An increase in global temperatures will change the proportion of female and male turtles and lead to instability in marine turtle populations (Laloë et al. 2014). In addition, the melting of ice and rising ocean water levels may cause a majority of turtle nesting beaches to disappear. And finally, eight million tons of plastic end up in our oceans every year and each plastic ingested has a 22% chance of killing the turtle. In fact, sea turtles feed abundantly on jellyfish and often mistake plastic materials for jellyfish. (Freund 2017).

Fourth, predators, particularly active during the juvenile stage, also put pressure on turtle populations. When the turtle's eggs hatch, birds and crabs are on the alert for turtles trying to reach the water. Once at sea, the young turtles are also attacked by birds, killer whales and sharks (Kennedy 2019).

Above all, turtles have to survive a long time, 13 to 14 years on average (Zug and Parham 1996; Stewart et al. 2007; Jones et al. 2011), before expecting to have any offspring. Due to these 4 causes of premature death, only 1 juvenile turtle out of 1000 reach their sexual maturity, that's a ratio of 0,1% (Ridley 2017).

1.2 The importance of marine turtle protection

The seven marine turtles species all have different and complex life cycles. Protection measures vary from one species to the other. In fact, all species are considered threatened (Wallace et al. 2013) and for each, conservation programs are being carried out. The large majority of the efforts to date have focused on protecting the egg-laying beaches where the females lay their eggs (Luschi and Hays 2003). It consists in restricting human access, managing artificial lights near the beach and fighting predation and poaching. These measures, which have been in place for several years, have had positive effects (Rivas et al. 2016).

The first reason to protect marine turtles is the information and understanding gained on marine ecosystems. Indeed, we learn more about the turtles themselves but also about the health of the different marine ecosystems they encounter. Marine turtles are migrants and occupy different tropic levels depending on the species and life stages. They are also sensitive to chemical and biological pollution. For that reason, tracking turtles can be useful to evaluate health of particular regions or ecosystems (Lalire and Gaspar 2017).

Second reason, turtles are good regulators of ecosystems. For example, by eating jellyfish, leatherback turtles help other fish populations to survive. Indeed, jellyfish, which proliferate due to the fishing of their predators, consume little fishes and compete against bigger fish populations for food (Lynam et al. 2006). Therefore, we consider sea turtles as "umbrella" species. This means that due to the diversity of the habitats they occupy, and the important role they play in biodiversity, the protection of sea turtles could help to protect many other species sharing the same habitats (Weng et al. 2015).

Marine turtles are present in all oceans (except the Arctic Ocean) and have existed for more than 150 million years. They have been around the dinosaurs and have survived all climate crises. They are a "flagship" species, an emblematic species of our oceans, which helps to raise the world's awareness of the threats to marine ecosystems and, more widely, to raise awareness of the problem of ocean pollution. When protected, marine turtles can support both the conservation of our seas and the development of other marine species (Kinan-Kelly and Dalzell 2005).

1.3 Aim of the research

Sea turtles are the most vulnerable migratory group of marine species (Lascelles et al. 2014). The nesting beaches of the Caribbean Sea, which include Pacuare Nature Reserve, are not experiencing a recovery in their overall population (Troëng and Chaloupka 2007; Hays and Scott 2013). Indeed, a lot of intensive longline fishing takes place in the Caribbean Sea and especially along the Costa Rican coast (Stewart et al. 2016). Unfortunately, conservation efforts on beaches are not enough. To reduce the mortality rate of intensive fisheries, we need to expand the effort to the pelagic (offshore) life stage. Moreover, all researchers on the subject agree (Hamann et al. 2010; Hays and Scott 2013), habitat and movements during their lifetime are two of the main factors in managing a migratory marine species at risk of extinction. However, the turtle hatchlings are difficult to track because of their small bodies and rapid growth. After emerging from their nest, they disappear before reappearing more than 10 years later when they first come to lay their eggs on the same beach. During this period, it was thought that the movements of the juvenile turtles were dictated solely by ocean currents (Carr 1967; Carr and Barkau 1980; Bolten and Witherington 2003). However, recently, advances in the miniaturization of tracking technology have made it possible to track these small turtles and refute this hypothesis (Shillinger et al. 2012; Mansfield et al. 2012; Scott et al. 2014).

For a long time we have assumed a passive behaviour of turtles, and little by little, we have found evidence that indicates that even turtles as young as 1 year old have an active behaviour in the current (Putman and Mansfield 2015). Much remains to be discovered about the early stages of a newborn's life when mortality rates are the highest. The active swimming component could be present from birth and be motivated by habitats, food, temperature, magnetic field, waves or innate insinct. Hoover in 2016 and the NGO Upwell 2018 used acoustic nano-tags to track the turtles for distances of up to 10 km and for a maximum of 2 hours. I used the collected data set in this thesis. I undertook to model and analyse the behaviour and dispersion of juvenile leatherback turtles for two months from the beach of Pacuaré in Costa Rica and more widely in the Caribbean Sea. The primary objective is to model the behaviour of hatchlings from one of the world's most important egg-laying coast (Rivas et al. 2016), which has never been done even for adults, and to produce dispersal maps of the probability of presence of leatherbacks. My second objective is to hypothesize about the behaviour that turtles adopt during their very first days, and during the two months after, whether they adopt an active behaviour or not. This will make it possible to take a step further in this unknown and poorly documented period of the life of turtles. In order to, in the short term, avoid the capture of turtles by intensive fishing in this region of the Caribbean Sea and, in the long term, contribute to the conservation of this iconic species.

Chapter 2

Context

2.1 The leatherback turtle

2.1.1 Characteristics

The six other species of turtles belong to the Chelonidae family (Dutton and Bowen 1999), while the leatherback is the last representative of the family of Dermochélidae which has existed for 150 million years in our oceans (Hirayama 1998). This family is characterized by the absence of a rigid osseous carapace. Instead, the leatherback or luth turtle, whose scientific name is Demochelys coriacea, has a dense skin stretched over a bony skeleton. This bony skeleton is composed of hulls, with visible ridges that run from the head to the tail (Spotila and Tomillo 2015). In addition, the luth turtle is the largest adult turtle with 200 to 1000 kg, and measures 200 cm in length (Robinson and Paladino 2013). Regarding its age, it can live about 50 years. Leatherbacks come to the surface every 10 minutes to catch their breath. They can stay underwater for more than 80 minutes and go to depths of 1300 meters (Robinson and Paladino 2013; Spotila and Tomillo 2015; Lalire and Gaspar 2017). Furtermore, the leatherback turtle is able to maintain its core body temperature at 20°C while being in water under 7°C. This allows it to withstand cold latitudes which are unimaginable for other species of marine turtles (Jones et al. 2012).

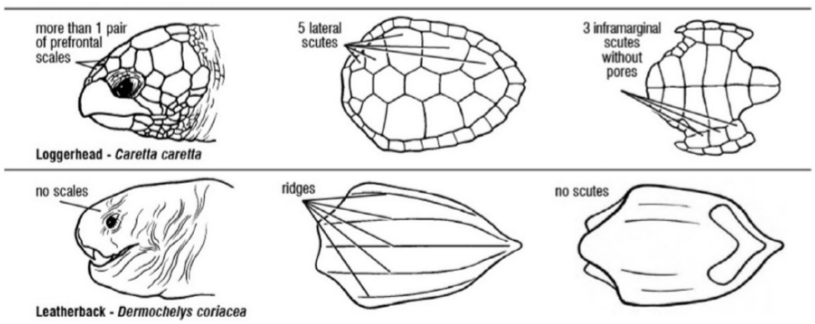

Figure 2.1: Specific characteristics of the leatherback turtle compared to the "classic" characteristics of the loggerhead turtle (Jones et al. 2011)

2.1.2 Nutrition

Leatherbacks are carnivores and feed only from soft bodied gelatinous invertebrates. Their mouth has two sharp teeth on the upper beak (Robinson and Paladino 2013). They travel thousands of kilometres to reach feeding grounds. Jellyfish are their main source of food for adults. The turtles eat daily 65 to 120 kg of jellyfish (Jones et al. 2012), while young turtles feed on algae and plankton. This plays an important role in the regulation of biodiversity (Spotila and Tomillo 2015).

2.1.3 Reproduction

Females only return to the place where they were born to lay their eggs. Males never return to their birthplace and mating has never been observed (Jones et al. 2011). Since young turtles are difficult to observe, the age of sexual maturity of leatherbacks is uncertain. Jones et al. 2011 was able to reduce the incertitude in between 9 and 15 years of age. The average of the studies made on the subject is approximately 13 to 14 years old (Zug and Parham 1996; Stewart et al. 2007).

The annual timing of nesting seasons varies geographically (Eckert 2012). Laying takes place from September to March in the Pacific Ocean and from March to July in the Atlantic Ocean with a peak in May and June (Spotila and Tomillo 2015). The turtle goes back to the beach where it was born and can migrate distances of more than 12,000 kilometres per year, which is greater than any distance travelled by any other marine species of this size (Hays and Scott 2013). After this long journey, the female turtle digs a hole (see Figure 2.2), and lays about 100 eggs before plugging the hole and returning to the ocean (Robinson and Paladino 2013). The female stay in near shore waters and lay a hundred eggs each, up to 12 times in a single nesting season. This occurs every 10 to 14 days (Spotila and Tomillo 2015; Luschi and Hays 2003). The nesting success vary between 50 and 90% and reflects the effect of beach conditions such as erosion, waves, debris, sand dryness and predators (Eckert 2012). The female turtle achieves this journey every 2.5 years as an average (Rivas et al. 2016). Incubation lasts 60 to 70 days. Research shows that if a turtle's eggs incubate below 27°C, the turtles will be males. If the eggs incubate above 31°C, however, the hatchlings will be females (Laloë et al. 2014; Ewert et al. 1994).

Figure 2.2: Leatherback turtle laying eggs in Guadeloupe.

2.1.4 The life cycle

Figure 2.3 shows the generalized life cycle for leatherbacks as there are some important differences between species. The first instinct of the newborn will be to move towards the brightest point, i.e. the ocean, which reflects the sun rays or the moonlight (Freund 2017). When it reaches the sea, it begins to swim vigorously away from the beach (Carr 1967). This vigorous swimming is called "swimming frenzy" (Wyneken and Salmon 1992) and the aim is supposedly to avoid predator-infested coastal waters (Salmon et al. 2009) and join the main offshore current (Hamann et al. 2007). All turtles species hurry to a pelagic, i.e. open sea, environment when they are born, only leatherbacks are staying offshore while other species return to coastal waters to spend at least part of their lives (Robinson and Paladino 2013). After a few days, hatchlings run out of energy and begin a more mysterious and very poorly known period, "the lost years" (Carr 1986). It is assumed that juveniles tend to remain in the open sea where they feed on pelagic prey like jellyfish or plankton while they drift passively over large areas of ocean without settling in a specific site. They are sometimes transported thousands of kilometres from their natal beach by the large-scale movements of ocean currents (Shillinger et al. 2012; Hays and Scott 2013). A few years later, the turtles are strong enough to swim and join pelagic feeding areas. When they are approximately ten years old, it reaches the adult stage (Stewart et al. 2007) and sexual maturity.

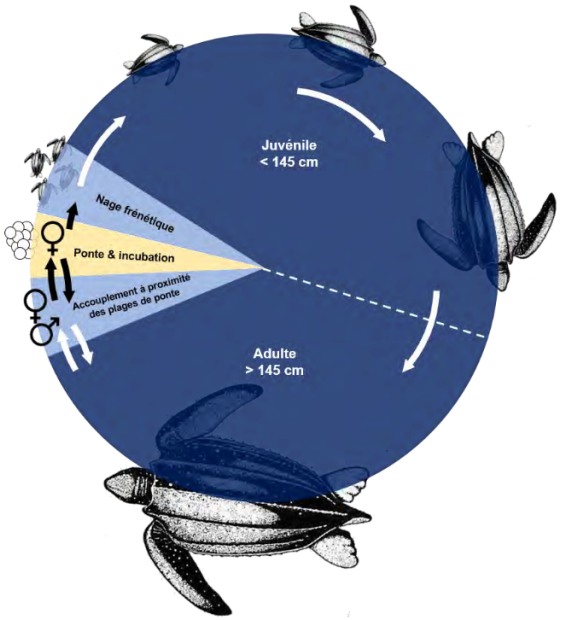

Figure 2.3: Simplified diagram of the standard leatherback turtle life cycle: size and environment occupied at different stages of development. The dark blue corresponds to the ocean environment, the light blue to the coastal environment and the yellow to the land environment where females lay their eggs (Lalire and Gaspar 2017)

2.2 Geographical region

On Earth, the leatherback turtle can be observed in all oceans below 60 degree of latitude (Spotila and Tomillo 2015). The main egg-laying areas, represented in red on Figure 2.4, are in America, on the east coast of Florida, the Caribbean Sea, Guyana and French Guyana, Suriname, west coast of Mexico and Costa Rica. In Africa, the Gulf of Guinea and the east coast of South Africa are main sites. India, Malaysia, Indonesia and west Australia are also main nesting sites. Some regions, once frequented by leatherback turtles, are now hardly or no longer frequented at all, such as Sicily, Turkey, Libya or Israel (Spotila and Tomillo 2015). In 1995, the estimation indicates a worldwide population of 34,500 females, which was an important decline from the 115,000 estimated in 1980 (DIC 2015). It is difficult to obtain an exact number concerning the total population of leatherback turtles on Earth. However, recent research estimates the amount between 35,000 (STC 2020) and 100,000 adults worldwide (DIC 2015).

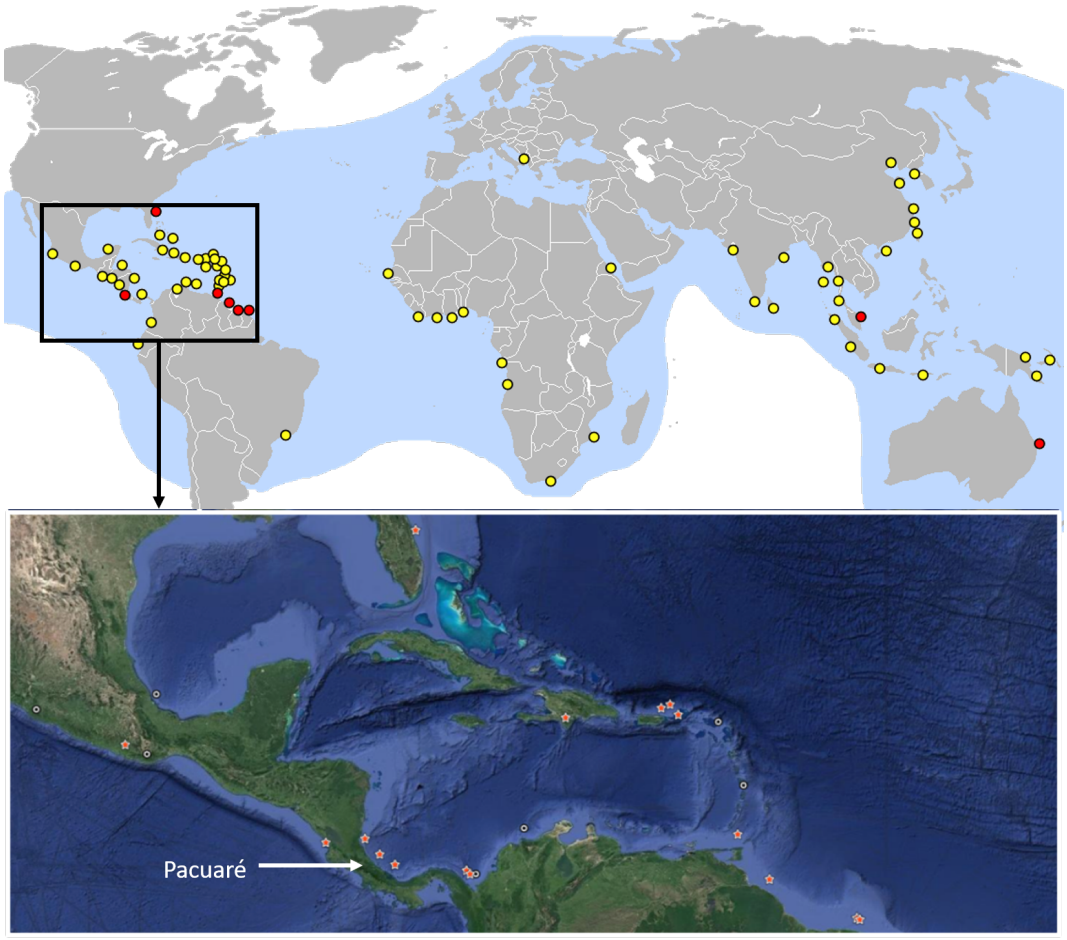

Figure 2.4: Main nesting locations of leatherback sea turtles on Earth and in the Caribbean Sea (STC 2020).

2.2.1 The Atlantic Ocean

The Atlantic Ocean today regroups nearly 80% of the global adult leatherback turtle population (DIC 2015), and can be split into 2 distinct groups:

- The east Atlantic population (A on Figure 2.5) is mainly based in the Gulf of Guinea. The population has between 15,000 and 41,000 reproductive females, the largest population of leatherback turtles in the world. After some monitoring, their trajectories show that they migrate and feed throughout the South Atlantic (Brazil), but no migration in the North Atlantic has yet been observed (Fretey et al. 2007; Witt et al. 2009).
- The northwest Atlantic population (B on Figure 2.5) from French Guiana to Florida, with Central America and the Caribbean Sea. Most of the main egg-laying sites have been monitored for more than 10 years. This population is estimated at approximately 24,000 reproductive females. Satellite tracking has shown that northwest Atlantic turtles generally migrate throughout the North Atlantic for food, but no trans-equatorial migration towards the South Atlantic has been observed (Wallace et al. 2013; Fossette et al. 2014).

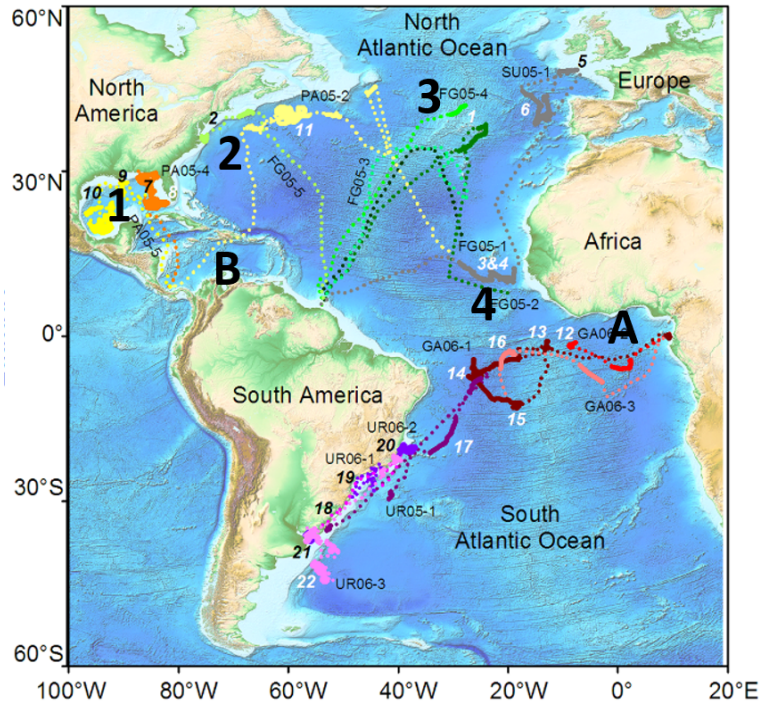

Figure 2.5: Migration routes of 16 leatherback turtles in the Atlantic Ocean for 3 years. It shows the 4 main sites of transit or migration and the migratory routes used by the Atlantic leatherback populations (Fossette et al. 2010).

In the North Atlantic Ocean, the migratory routes used by leatherback turtles are diverse and have been analysed for the last 15 years. Four places in particular are the main sites of transit or migration of leatherback turtles because of their abundance of food (jellyfish, plankton) and favorable temperatures. They are represented on Figure 2.5 (1,2,3,4).

1. The Gulf of Mexico and Florida, especially for turtles from Central America (Evans 2007).

2. The coasts of North America and Canada (Fossette et al. 2010).

3. The offshore habitats that extend from the west coast of Canada (between 30N-50N) to off the coast of Spain and northwest Africa (Fossette et al. 2010).

4. The eastern edge of the Atlantic Basin, which extends from the coast of Mauritania to the Gulf of Guinea (Fossette et al. 2010).

Dispersal follows a clockwise circulation around the North Atlantic Subtropical gyre (Lalire and Gaspar 2019). In 2003, STC 2020 began tracking adult female leatherback turtles from nesting beaches in Costa Rica and Panama and the simulation made afterwards confirms their dispersion (Lalire and Gaspar 2019). Turtles from the Caribbean Sea migrate into the Gulf of Mexico with the main Caribbean Current (1 on Figure 2.6). Then, they go along the coast of Florida, as well as into Canadian waters with the Gulf Stream (2 on Figure 2.6). Afterwards, they cross the Atlantic towards Europe (3 on Figure 2.6), where leatherback find the Azores, the coast of Portugal, Morocco and even the Mediterranean Sea, known to be feeding areas rich in jellyfish in particular (Evans 2007). They finally reach the Mauritanian upwelling area with the Canary Current (4 on Figure 2.6).

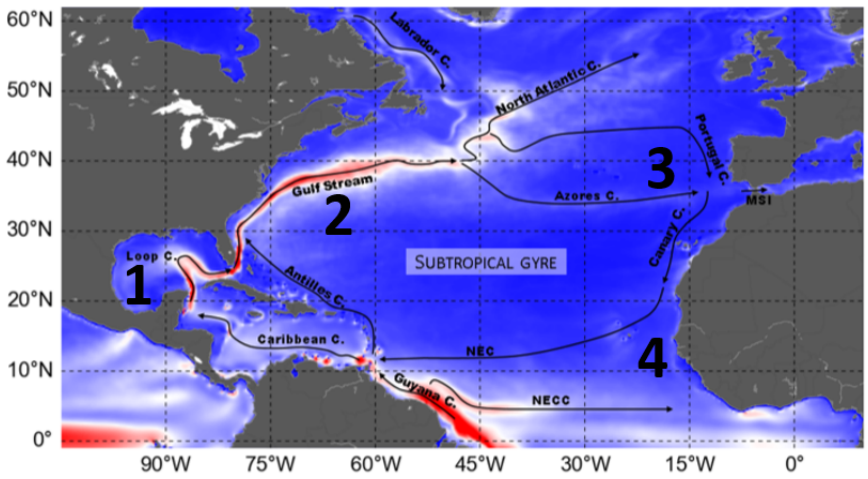

Figure 2.6: Main ocean currents in the North Atlantic Ocean (Lalire and Gaspar 2019)

2.2.2 The Caribbean Sea

Population

Let us take a closer look at the Caribbean Sea area. Figure 2.4 shows the main sites of this region like Trinidad and Tobago with approximately 6,000 females, Columbia and southeast Panama with 1,000 females and Puerto Rico with less than 1,000 females (Spotila and Tomillo 2015). A study by the Caribbean Conservation Corporation (STC 2020) estimated that the area between the Nicaragua-Costa Rica border (which contains Pacuaré Beach) and just south of Chiriquí Beach, Panama, represents the fourth largest reproductive population of leatherback turtles in the world. Data also suggest that this population of leatherback turtles may have been declining since 1995. The Caribbean coast of Costa Rica is part of an almost continuous nesting beach that extends from north Nicaragua to south Panama (Hoover et al. 2017). This long nesting beach is being visited by approximately 2000 to 4,000 nesting leatherback females, which lay 8,000 to 15,000 nests each year (Eckert et al. 2020) including 1000 nests on average on Pacuaré Beach (Rivas et al. 2016), making it an important rookery.

Location

Pacuare Nature Reserve is situated in the Limon province. Pacuare Beach is a 5.7 kilometer long beach in Costa Rica. The Figure 2.7 shows the location of the Pacuare Nature Reserve in the Caribbean Sea and the surrounding beaches that have been involved in the protection of leatherback turtles. Their efforts have been rewarded as this set of beaches represents the 4th highest breeding population in the world. Protection of the nesting beaches and associated conservation efforts have improved the population patterns of some of the larger colonies. The turtle monitoring project in the Pacuare Nature Reserve is one of the three oldest in the Caribbean and is being active since 1994. It is a very important rookery in Central America since it has an average density of 142 nests per km, probably the highest in the Caribbean region (Rivas et al. 2016). Long-term conservation efforts in the Reserve have significantly reduced hunting and helped to maintain a high level of hatching. Female leatherback turtles come to lay eggs on the beach during the months of March, April, June and July (Rivas et al. 2016).

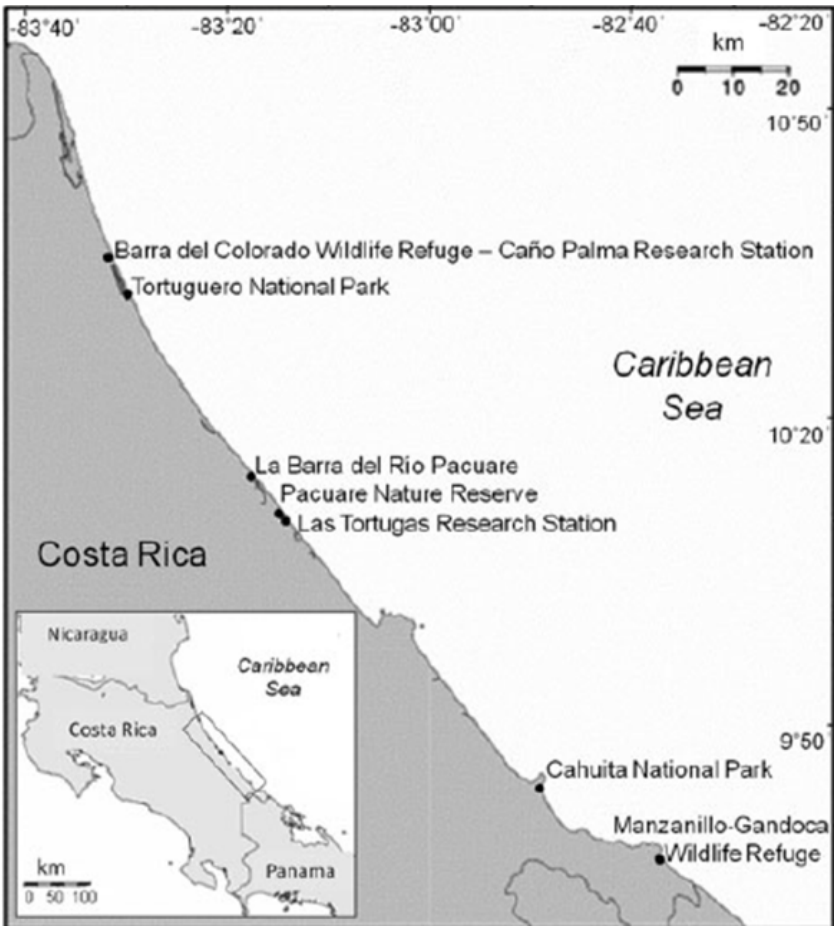

Figure 2.7: Location of the Pacuare nature reserve in the Caribbean Sea. Starting point for field data collection and numerical simulations (Rivas et al. 2016).

2.3 Tools to study turtles dispersion

Methods used on marine species are increasingly problematic when these species travel long distances, such as sea turtles and especially the leatherback turtle, which is the most highly migratory species between turtles (Hays and Scott 2013). Even juvenile turtles travel these long migrations with the currents (Shillinger et al. 2012) (Bolten and Witherington 2003). The main objectives of monitoring turtles today are to understand how they behave and how active they are in the current. This will allow us to better understand the distribution of population and prevent the disappearance of declining populations.

The main methods used in studies on leatherback turtles are satellite telemetry, acoustic tracking, and numerical simulation.

2.3.1 Satellite telemetry

Satellite telemetry is the placement of satellite tags on leatherback turtles. It is a recent, irreplaceable tool that made it possible to identify the migration routes and feeding areas of adult turtles (Fossette et al. 2010). Satellite telemetry provides accurate data during several months. However, it also has many limitations (Lalire and Gaspar 2017):

- The equipment is expensive.
- The number of turtles monitored and the volume of data is limited and therefore subject to observation errors.
- Attaching a tag to a turtle could change the turtle's behaviour.
- The size of the tags prevents their deployment on small individuals, e.g. hatchlings.

However, attaching methods have evolved over time to resolve these last two limitations. Notably after Fossette et al. 2008 proved for the first time that satellite transmitters fixed on harnesses (Figure 2.8 B.), which was the most used method until then, had an impact on the turtle's health and especially on its swimming behaviour. In general, all hard harnesses should be avoided since they may alter the shape of the carapace when the turtle grows (Mansfield et al. 2012). Therefore, the carapace-attached method is recommended, it consists in fixing the satellite transmitter directly to the carapace (Fossette et al. 2008). More precisely, the neoprene-silicone attachment over an acrylic base-coat (Figure 2.8 A.), is the best attachment method for juvenile turtles according to Mansfield et al. 2012.

The small size and weight of the hatchlings as well as their rapid growth makes tracking by satellite tag very difficult for small turtles (Shillinger et al. 2012). The aim is to achieve minimum energy costs during transport and attachment. It is assumed that the impact is negligible when the tag reaches a tag to body weight

ratio of 2-3% (Vandenabeele et al. 2012). Remarkably, the newly born turtle is only 6 centimeters long on average and weights only 46 grams. During the first 2 years, it grows an average of 32 centimeters a year in straight carapace length (SCL) (Jones et al. 2011) and decreases to 8 centimeters a year at the end of his juvenile cycle (Zug and Parham 1996). While adult turtles gain on average only 1 centimeters each year (Rivas et al. 2016). The challenge at the moment is to track turtles smaller and smaller and for longer and longer. This is were acoustic tracking comes in.

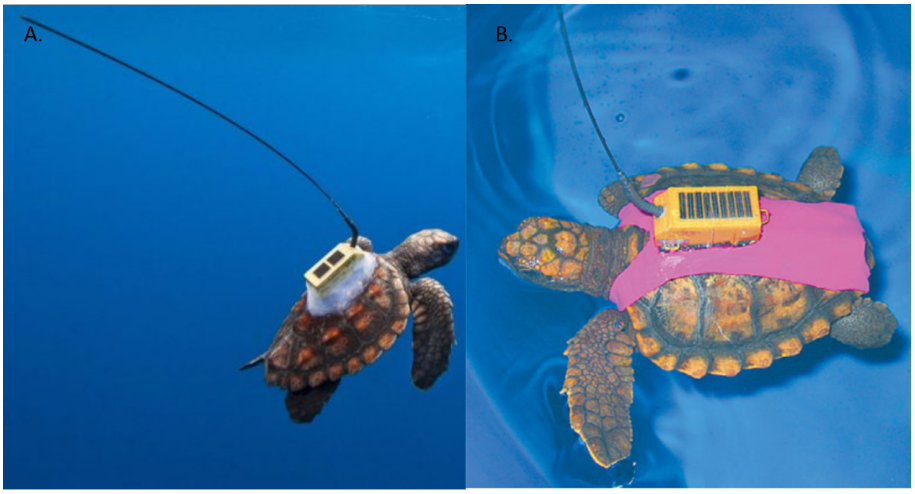

Figure 2.8: A. Direct carapace attachment method with acrylic-base coat and neoprene-silicone strips (TAMAR 2017) B. Indirect harness attachment method (Mansfield et al. 2012)

2.3.2 Acoustic tracking

Acoustic tracking is the placement of an acoustic transmitter tag on leatherback turtles. Acoustic tracking enables to track much smaller turtles than satellite telemetry. To track the turtles during their first days new lightweight miniature transmitters' tags are used. However, when tracking, the acoustic receiver must be on a boat close to the acoustic transmitter attached to the turtle. Indeed, the signal emitted by the turtle's tag does not have a long range. Therefore, the turtle have to be followed by boat. This method is labour intensive, takes into account a small sample size and is limited to hours of light when turtles hatch mainly at night. Scott et al. 2014 was able to collect data until the first 15 kilometers off the coast. As for satellite telemetry, attaching the acoustic transmitter on the back of the turtle must also be done without harness (Fossette et al. 2008).

Several studies demonstrated the efficiency and the lightness of the Vemco V5. It disturbs the turtle the least in its swimming behaviour (Thums et al. 2013; Scott et al. 2014; Hoover et al. 2017). When tracking a turtle, it is possible to track the turtle by GPS and visual tracking or only by GPS. No visual tracking involves the

use of a Vemco V5 tag (Figure 2.9 A.) directly attached to the bottom of the turtle and weighing only 0.65 grams (Scott et al. 2014). It is attached with a Vetbond binding agent that dissolves after a few days if the turtle is not recuperated. The turtle is then only tracked by GPS. The other option is visual tracking in addition to GPS tracking. The figure 2.10 below shows the classical visual tracking technique made by Gearhaert in 2011. It consists of a 1 cm^2 piece attached to a 1.5 to 2 meters long wire attached to two floats to which is attached the acoustic tag that transmits the positions. The whole weighs 7 grams but is obviously not entirely carried by the turtle. A binding agent, called Velcro can be easily removed when the turtle is collected at the end of the study. The acoustic tag Vemco V5 and the Velcro binder are currently the most effective device to track turtles in the short and medium term (Hoover et al. 2017).

Such studies will be particularly important to provide data to improve and validate models of migration and dispersal of young turtles developed by numerical simulation.

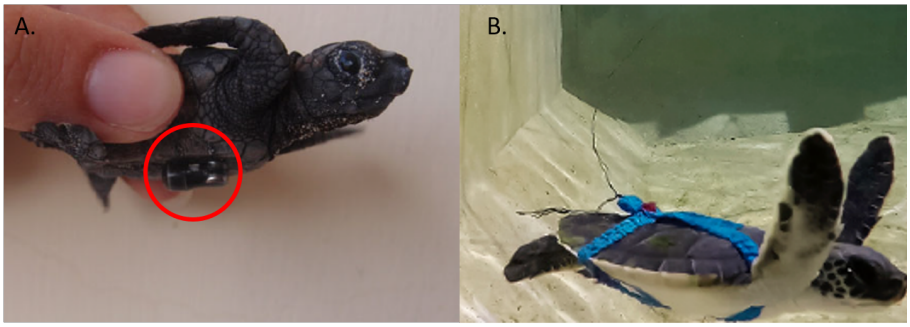

Figure 2.9: A. Vemco V5 nano tag (miniaturized) glued with Vetbond to the bottom of the turtle (Scott et al. 2014) B. Harness attachment method (Hoover et al. 2017)

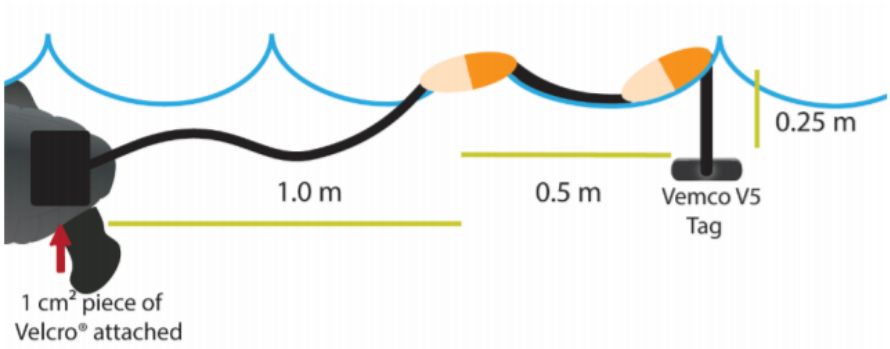

Figure 2.10: Acoustic transmitter Vemco V5 tag with Velcro® attachment method modified from Gearheart et al. (2011) (Hoover et al. 2017).

2.3.3 Numerical simulation

Understanding the mechanisms of turtle movements will improve our prediction of population dynamics, habitat occupation and manage species. Researchers highlight the usefulness of numerical simulation to increase the knowledge especially on the early life of marine turtles (Hamann et al. 2011) (Patterson et al. 2008). The spatial distribution of turtles can also help us in the establishment of areas where fishing is restricted or prohibited. However, areas are very difficult to determine because of the large migrations and movements that turtles undertake each year (Hamann et al. 2010).

Data on the movements of individuals are often not long enough or subject to errors. After satellite telemetry or acoustic tracking which lasts a few hours for young turtles or a few months for adult turtles, numerical simulation links field data to ocean motion, depth, currents or wind and enables to extrapolate the behaviour of the turtle on a larger period. The field data is an important way to validate the results and improve the accuracy of the simulations. Indeed, the single model is not sufficient to confirm a hypothesis. It must be possible to confirm its results with tangible evidence obtained otherwise (Jonsen et al. 2013). For example, observations of stranded turtles in specific locations or turtles caught by fishing nets.

2.3.4 State of the art in modelling marine turtles dispersion

Several studies have already been carried out to model the behaviour of marine turtles whatever the species, their age or the region.

Very little is known of the approximately ten years between the time the turtle leaves its egg-laying beach and when it returns to lay eggs years later. During this period, turtles are difficult to track and it led to the enigmatic period of the lost years. The hypothesis of passive drift has long been accepted and the studies by Carr 1967 and Carr and Barkau 1980 are the origin of this hypothesis. Archie Carr is considered to be the most influential pioneer in understanding and interpreting the lives of sea turtles. He assumed that some turtles, after their frenetic swimming, stop swimming and let themselves drift with a pile of algae which constitutes a micro-habitat with food, a warmer temperature and which hides them from certain predators. If the turtle doesn't find algae, Carr assumed that the currents would sooner or later bring the turtles to feeding areas. Turtles are able to memorize the feeding areas they encountered in their juvenile stage and return to them as adults. Discoveries of turtles stranded downstream of nesting beaches, their sizes and spatial distribution compared to drifter or other passive organisms have led to confirm that turtles size grew with ocean currents and confirmed the hypothesis of passive migration used by many researchers after him (Bolten and Witherington 2003). But is it the only dispersal mechanism for juvenile leatherback turtles? The answer to that question is clearly no. Carr's studies have identified the main areas of marine turtle migration. However, it needs to be improved.

Gaspar et al. 2012 went beyond the passive behaviour of the juvenile turtle via numerical simulation in the North Atlantic Ocean. They observed large numbers of juvenile turtles being caught by longline fisheries in areas where it was normally impossible for the turtles to end up with passive behaviour. In winter, water temperatures fall below the minimum temperature tolerated by juvenile turtles which made the turtles move to lower, and therefore warmer, latitudes. Then, they returned to higher latitudes in the spring. Putman et al. 2012 showed that an extra swimming component helped the turtles in reaching feeding areas and encounter favourable temperatures. Large number of adults have been observed in feeding grounds that they would never have encountered and therefore, would never have returned to them as adults, if they had not swam on their own. In addition, the age of the leatherback turtles observed in these areas are not corresponding and they would have died on the way because the water is too cold for juvenile turtles. More recently, Mansfield et al. 2012 made advances on small tags to track individuals as young as a few months old. He used these findings in 2014 (Mansfield et al. 2014) and 2015 (Putman and Mansfield 2015) by capturing wild turtles between one and two years old. Putman and Mansfield 2015 conclusively determined that these turtles do not behave like passive drifters. In almost all cases, the drifter trajectories are not representative of turtle trajectories (Putman and Mansfield 2015). Christiansen et al. 2016 made a similar conclusion in 2016. **Due to these inconsistencies and due to the fact that turtles manage to escape from cold waters and meet places full of food, we know that during the first years of their life, turtles are mainly driven by currents but from a certain point they have an active behaviour that adds up to the current.** It proves the necessity to go beyond the classic assumption of passive drifting modelling for the turtle dispersion during the "lost years". Many aspects have yet to be determined and remain a mystery. Given the latest findings that one and two years old turtles also have active behaviour, is this behaviour present from birth? And what factors motivate this behaviour, habitat, temperature, food, magnetic field or waves direction ?

In 2017 and 2019, Maxime Lalire and Phillipe Gaspar continued the study. **Although oceanographic currents are still the main factor shaping the dispersion of juvenile turtles, they created a model that takes into account favourable habitat criteria that orients the turtle and gives it a certain speed** (Figure 2.12). In this case, the turtle behaviour is motivated by food and temperature. They confirmed seasonal migrations; they swim south to warmer waters as winter approaches and return to higher latitudes where food is abundant in the spring. More surprisingly, they have a movement of juvenile turtles against the prevailing ocean currents (Gaspar and Lalire 2017; Lalire and Gaspar 2019).

Wildermann et al. 2017 studied the movement during the early life stages of juvenile turtles and how it influences the distribution of their population. **They are the first to include a constant swimming component to passive drift to counter the influence of the current.**

Several authors according to, Lalire and Gaspar 2017, have added to the passive drift a swimming component oriented according to the position of the simulated individuals. The aim of these simulations was to reproduce an innate response of juvenile turtles to the characteristics of the Earth's magnetic field. Indeed, studies suggests that hatchling turtles orient themselves against the waves during the swimming frenzy (Wyneken and Salmon 1992). Then, **when they grow and become active in the currents, juvenile and adult turtles are able to maintain direction using different sources of directional information, two of which we know : visual cues and magnetic field** (Avens and K. Lohmann 2003). Turtles can detect subtle differences in two characteristics of the magnetic field that vary around the globe : inclination and intensity. The unique combination of these features could help turtle navigate (Lohmann et al. 1997) and find their natal beach (K. Lohmann et al. 2013).

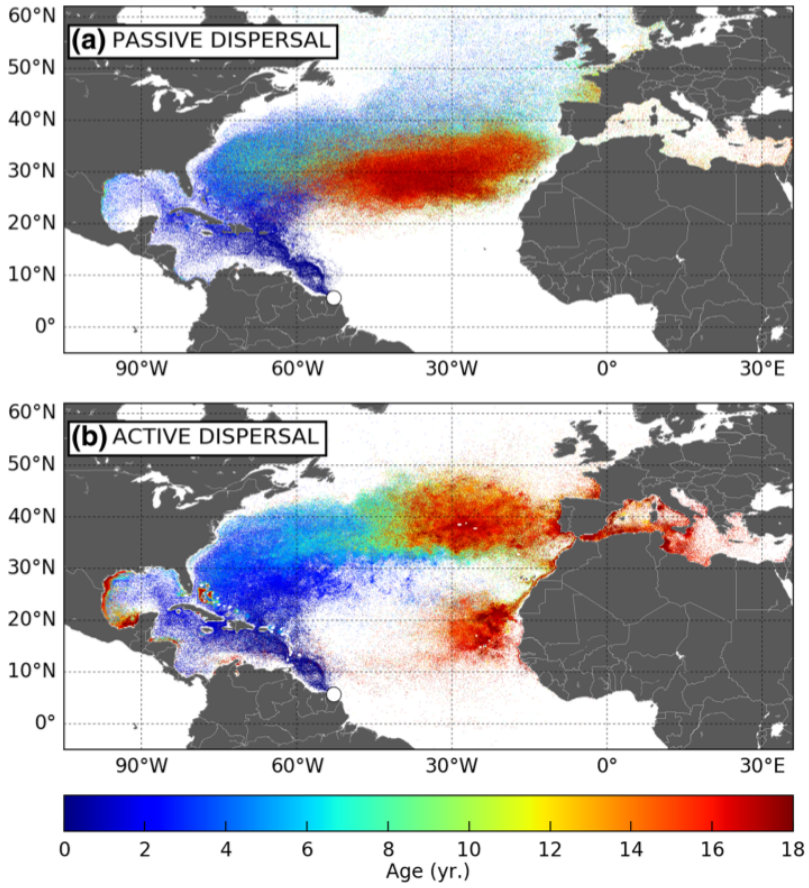

Figure 2.11: The numerical simulation result obtained by M. Lalire and P. Gaspar during their study of the passive and active behaviour of turtles on an 18 year old simulation. First model based on favourable habitat criteria (food, temperature) that orient the turtle and give it a certain speed. (Lalire and Gaspar 2019).

Chapter 3

Methods

My method will be divided into two important parts. As explained previously, I received two sets of data of turtle positions from the NGO upwell.org. They were collected, in 2016 and 2018, by acoustic tracking of leatherback hatchlings from the beach of the Natural Reserve of Pacuare in Costa Rica and during the first hours at sea. I also obtained data on passive floats or "drifters" released along each turtle track. They were used to obtain the immediate currents that the turtle encounters. The few first days of the turtles is characterized by a major energy expense, called swimming frenzy. Once this frenetic swimming period is over, the turtle has exhausted its energy reserves and is drifting passively (presumably) for a long time. The first part will be the analysis of the NGO data, select an amplitude of speed and a direction as a function of time. Considering the analyses and previous studies on the subject, several possible scenarios of turtle's behaviour will be tested. Once these scenarios have been determined, the second part will be the numerical modelling of the dispersal of juvenile leatheback turtles for two months from the beach of Pacuaré in Costa Rica and more widely in the Caribbean Sea.

3.1 Analyzing leatherback turtle behaviour

3.1.1 Data from the NGO

Turtles

In order to analyse the swimming behaviour of the turtles and be able to implement it in our model afterwards, Hoover (2016) and Upwell.org (2018) captured 43 turtles that emerged from the nesting beach between 20 August 2016 and 3 September 2016, and 52 turtles between 27 july 2018 and 12 august 2018. Each turtle was released at a location 400 meters from the shore in front of the hatcheries. Then, the turtles were tracked individually at a distance of 10 to 20 metres in a small boat using an acoustic receiver. The receiver recorded the positions and the data was downloaded to reconstruct the leatherback turtles' movement patterns. The data received by the NGO in 2016 covered about 80 to 120 minutes for each turtle with data being taken every 5 minutes. The method used in 2018 was similar but due to weather conditions and hatchling availability, the period during which all positions were recorded was more variable, generally between 30 and 120 minutes. At the end of the tracking period for each trial, the hatchling turtle was recovered, the acoustic transmitter removed, and the turtle was released to the wild. There were no evident damages, marks, or lesions from this attachment method (Hoover 2017).

Drifting floats

In order to analyse the immediate current the turtles encounter and be able to implement it in our model afterwards, a number of drifting floats were released (40 in 2016 and 50 in 2018). The two years had similar methods. In 2016, two types of drifting floats were used to obtain data on sea surface currents. A drifting float, "Microstar Drifter", was deployed at the beginning of the turtle track. The float was equipped to broadcast position coordinates every five minutes. A secondary float, the "GPS Drifter" was launched when possible about halfway (1 hour) down the track of the turtle. This provided a better estimate of the immediate currents the turtles were experiencing as the turtles moved offshore. The two drifting floats were collected at the end of each turtle's trajectory.

The first drifting float, **Microstar drifter** (Figure 3.1 A), was equipped with a GPS unit that used the iridium short burst data service to broadcast location coordinates every five minutes. To provide estimates of surface flow, the drifter's drogue was composed of a radar reflector with its centre at a depth of one meter vertically in the water. This drifter is supplied by Pacific Gyre (Pacific Gyre 2017).

The second drifting float, **GPS drifter** (Figure 3.1 B), consisted of an aluminum radar reflector with 80 cm of parachute rope attached to a 20 cm diameter trawl float. The centre of the drogue sat one meter from the water's surface, similar to the Microstar drifter. A piece of wood fixed to the top of the float had a mobile phone attached in a waterproof bag. A GPS application was started for each drifter to provide locations (Hoover 2017).

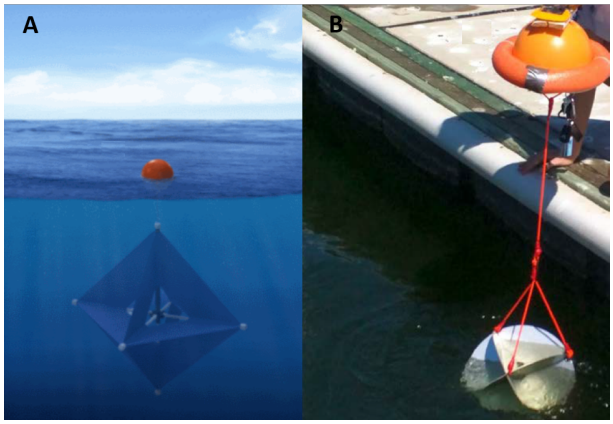

Figure 3.1: Representation of the Microstar Drifter (A) (Pacific Gyre 2017) and the GPS Drifter (B) (Hoover 2017) used to collect data on the immediate current.

Transmission equipment

In each case, 2016 and 2018, the hatchlings were released and tracked individually with a Vemco VR100 acoustic receiver and a VH180-D-10M directional hydrophone. The turtles were equipped with a Vemco V5 acoustic transmitter attached to the turtle with a line of 2 meters, two floats and a 1 cm^2 Velcro binding agent glued to the carapace with a Vetbond glue (see Figure 3.2) Based on various studies on the subject and explained previously, this is the latest and most effective technology.

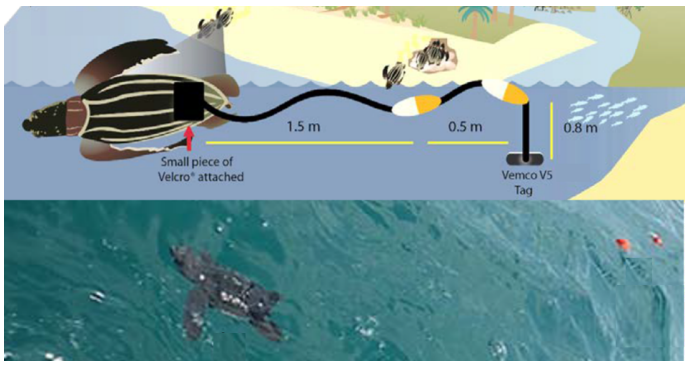

Figure 3.2: Representation of the Velcro attached to the shell of the turtle (A), the floats (B) and the turtle acoustic transmitter Vemco V5 (C) (Hoover 2017).

Figure 3.3 shows the three different behaviours following the three devices :

- The Microstar drifter released at the same time as the turtle enters the water.
- The GPS drifter released at the same place as the turtle after one hour.
- The turtle which will tend to go more offshore than the drifters.

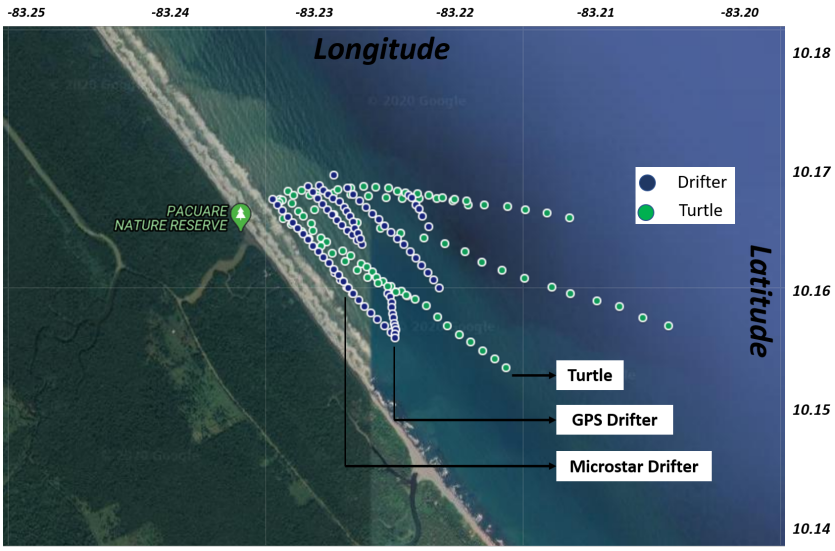

Figure 3.3: Turtles and drifters followed during the day of August 30, 2016.

Stokes drift

Juvenile turtles and even more hatchlings that have just emerged from their nests have a diving capacity limited to a maximum of three minutes and only a few meters deep (Wyneken and Salmon 1992; Spotila and Tomillo 2015). Therefore, they are presumably subjected to the Stokes drift. The Stokes drift [1] is an effect related to the waves of the current. The Stokes drift can be represented by the motion of a particle transport associated with the propagation of a wave in the ocean. This transport can be interpreted as the water transported between the wave lows and the wave peaks. Although the waves' motion is periodic, surface gravity waves involves a net drift in the direction of wave propagation (Van den Bremer and Breivik 2018). Therefore, on top of my hydrodynamic model, I'm going to add Stokes drift which is similar for 2016 and 2018. The Stokes drift is always in the direction of the surface waves. Near Pacuaré, it is more or less perpendicular to the coasts and will push the turtles to strand on the coasts throughout their journey. Which happens to the floats whereas the turtles move towards the open sea. The amplitude of the Stokes drift can reach 0.14 m/s in the Caribbean Sea, which is not negligible.

[1] A representative animation of the effect of the Stokes drift can be found on the web page http://www.physics.unlv.edu/ jeffery/astro/waves/water_waves.html

3.1.2 Preliminary analyses of the data collected

As illustrated in the context of Chapter 2 and more precisely on Figure 2.7, the Pacuare Nature Reserve in the Caribbean Sea is the starting point for field data collection and numerical simulations. Figures 3.4 and 3.5 show the raw data, for years 2016 and 2018, formatted on a map to better visualize what is provided. From the data, the aim is to deduce the behaviour of the turtle as a function of time.

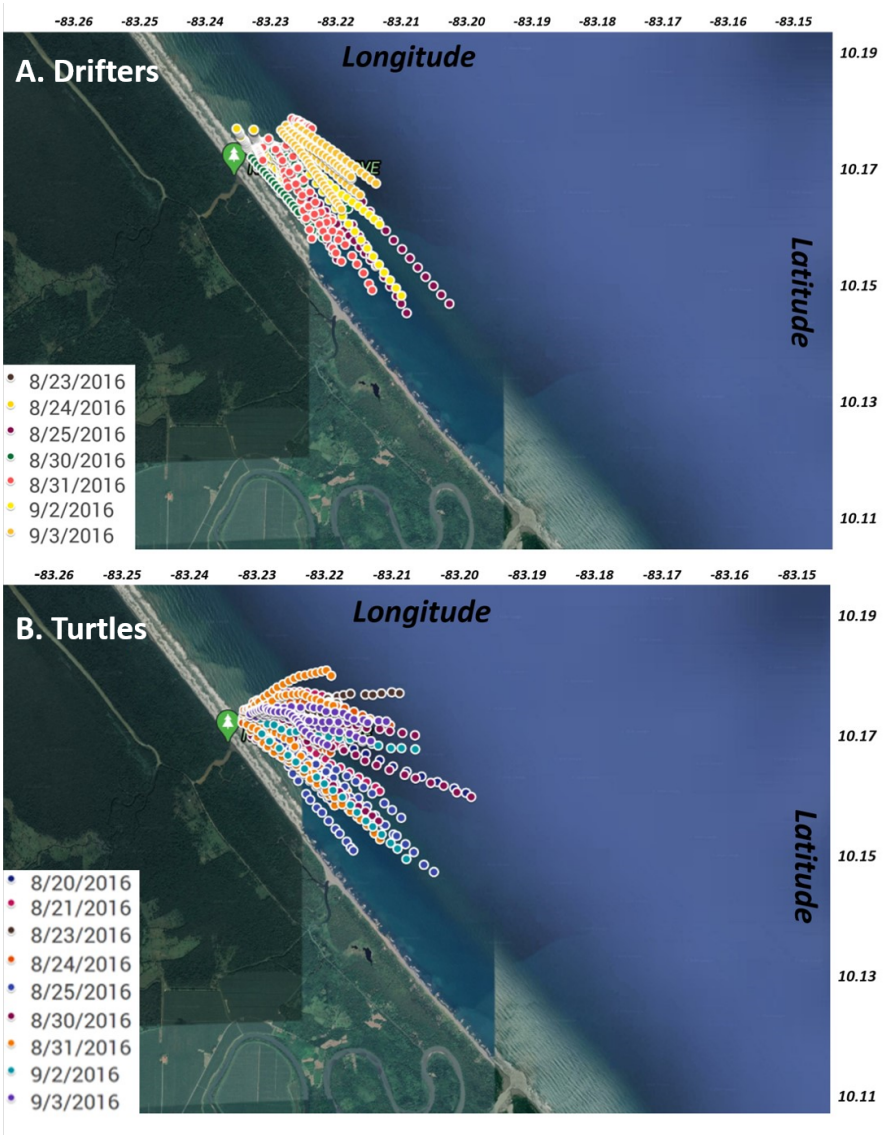

Figure 3.4: Dispersal of 40 drifters (A) and 42 turtles (B) at Pacuare Beach in Costa Rica between 20 August and 3 September 2016.

Each colour represents one day of measurement, so each colour correspond to 1 to 5 turtles or drifters. Each point represents a measurement of the position at a 5-minute interval. The 94 turtles were each tracked for approximately 80-90 minutes. Drifters, on the other hand, were tracked for 80-90 minutes in 2016 and discontinuously for only 30 minutes in 2018.

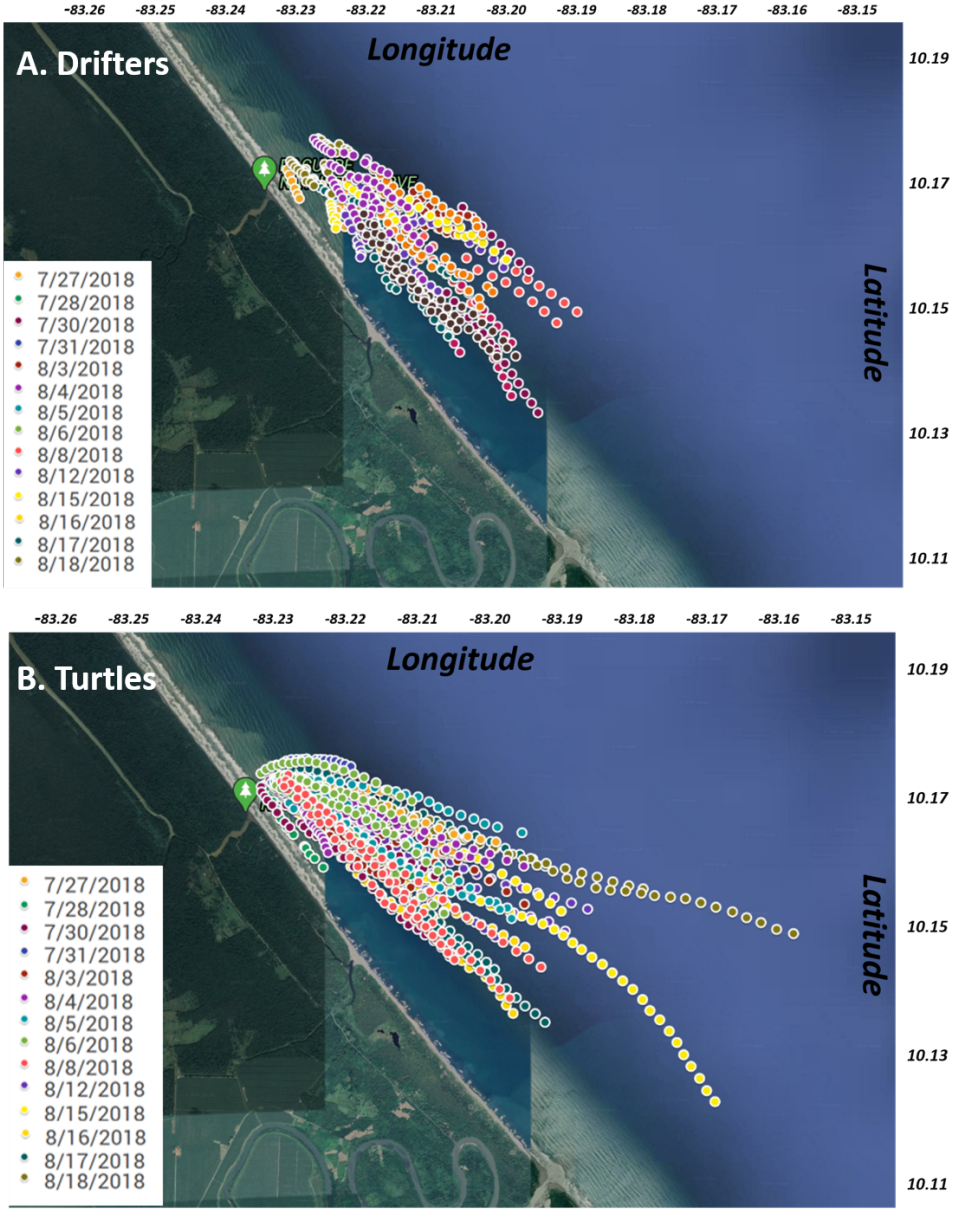

Figure 3.5: Dispersal of 50 drifters (A) and 52 turtles (B) at Pacuare Beach in Costa Rica between 27 july and 12 august 2018.

The manipulation of a large number of data in an excel table was an important part of the pre-analysis work, especially to sort them. In 2016, the GPS coordinates were given. From these coordinates the velocity amplitude, distance travelled and bearing were already measured for each time interval for each turtle and drifter. The velocity components, u (east-west) and v (north-south), could therefore be calculated using a simple trigonometric formula. Although it had already been measured, I confirmed the data obtained by taking only the GPS coordinates and calculating myself each data (velocity components, distance and bearing). In 2018, all data, even the velocity components u and v, were given. From the GPS coordinates, I also confirmed the data given. I excluded the data with an excessive speed (more than 2 m/s), or an impossible direction. These extreme data were either obtained between a turtle or drifter transition. They could also be obtained due to the turtles being predated by tarpons or frigate birds, which are the major predators in Pacuaré (Hoover 2017). Even the waves created by the boat and difficulties of visual tracking could also lead to these extreme data.

In the the study at the Pacuare Nature Reserve in 2016, the mean weight of the leatherback turtles tagged was 42.5 g with a mean carapace width of 42 mm and length of 60 mm. Figure 3.6 shows the average hatchling bearing of 109°, a southeast trajectory. I calculate the classic cardinal bearing and the bearing with reference to the beach. Mean speed of hatchlings was 0.40 m/s $\pm$ 0.15 m/s. The distances travelled was maximum 4 km (121 m for each time interval) and 3 km (92 m for each time interval) for turtles and drifters, respectively. The mean drifter bearing was 137° with an average speed of 0.27 m/s for Microstar, and 0.33 m/s for GPS drifter. The mean water temperature was 30°C.

In 2018, an average hatchling bearing of 120° was recorded, a southeast trajectory. Mean speed of hatchlings was 0.58 m/s $\pm$ 0.17 m/s. The distances turtles travelled were maximum 8 km with a mean of 187 meters for each time interval. The tracking time of the turtles was very variable in 2018, it could vary from 30 minutes to 3 hours. For drifters, the tracking time exceeded only rarely 40 minutes and the mean distance travelled was 172 meters for each time interval. The mean drifter bearing was 131° with an average speed of 0.55 m/s. From Figure 3.6, we can confirm that the currents in 2018 are more important than in 2016. Indeed, the current brings the turtles to farther distances and makes them move faster.

Turtles	Unit	2016	2018
Over ground speed	[m/s]	0.4 ± 0.15	0.58 ± 0.17
Distance	[m]	121 ± 54	187 ± 78
Bearing (cardinal)	[°]	109 ± 28	120 ± 14
Bearing (beach)	[°]	33 ± 28	22 ± 14

Drifters	Unit	2016	2018
Over ground speed	[m/s]	0.31 ± 0.21	0.55 ±0.3
Distance	[m]	92 ± 64	172 ± 88
Bearing (cardinal)	[°]	137 ± 20	131 ± 28
Bearing (beach)	[°]	6 ± 20	12 ± 28

Figure 3.6: Tables of averages and standard deviation over the 5-minute intervals for turtles and drifters respectively. Based on data provided by Upwell for 2016 and 2018 on a total of 94 turtles and 90 drifters.

3.1.3 Total, passive and active behaviour

We can distinguish three behaviours defined as passive, active and total. For the continuation of this thesis, active behaviour will be defined as the swimming behaviour of the turtle, i.e. independently of the current they face. On the other hand, passive behaviour will be defined as the drifting behaviour driven solely by the currents, i.e. when the turtle does not swim. The total behaviour is obtained from the sum of the active and the passive behaviour.

The turtle positions provided by Upwell represents the total behaviour, i.e. the sum of the currents (passive) and the swimming behaviour (active). The active behaviour, especially the active speed and direction are the most interesting to calculate because it will allow us to parametrize the turtle's behaviour in the numerical model. To determine the active swimming speed, we must subtract the passive velocity components (u,v) from the total velocity components (u,v).

As the drifter moves away from the turtle, it does not exactly represents the current the turtle is facing. I will make the hypothesis that even though the drifter moves away from the turtle, the difference remains negligible at a few hundreds meters maximum. As soon as we launch a new drifter (GPS drifter), halfway along the turtle's track, I will take this new, more accurate data into account. We will notice in the following graphs that the currents remain stable and thus confirm the hypothesis.

3.1.4 Swimming behaviour analysis

In 2016, data from 31 out of 42 turtles have been collected with drifter and for more than 80 minutes. We assume this is sufficient to draw robust conclusions. In 2018, the 50 drifters were used for a maximum of 30 to 40 minutes. Moreover, we have very little data on the first 30 minutes of the 52 turtles since the drifters were launched later. No turtle was tracked for as long as 80 minutes and often when two drifters were launched successively on the same turtle there was a significantly time gap. Due to the lack of constant and continuous collected data in 2018, I cannot use them as the one from 2016. They will be used to confirm or refute the results obtained for 2016.

Speed

The active swimming speed, also called in-water swimming speed (red in Figure 3.7 and 3.8), is obtained by subtracting the surface currents (blue on Figure 3.7 and 3.8) from the measured speed of the turtle (Gaspar et al. 2006; Fossette et al. 2010). The total speed, also called over-ground swimming speed (black in Figure 3.7), is the apparent speed of the turtle moving through the water, which includes the turtle's movements and the drift of the currents.

Figures 3.7 and 3.8 shows the average speed as a function of tracking time for the passive, active and total speed. The total speed increases from 0.40 m/s to 0.45 m/s with an overall average of 0.40 m/s. The passive speed remains more or less stable, around 0.30 m/s. **The active swimming speed remains constant between 0.20 and 0.30 m/s with an overall average of 0.25 m/s.** Figure 3.7 gives an overall view of the three speeds. In 2018 (Figure 3.9), the average and standard deviation are confirmed even with a current that is much more intense (0.52 m/s).

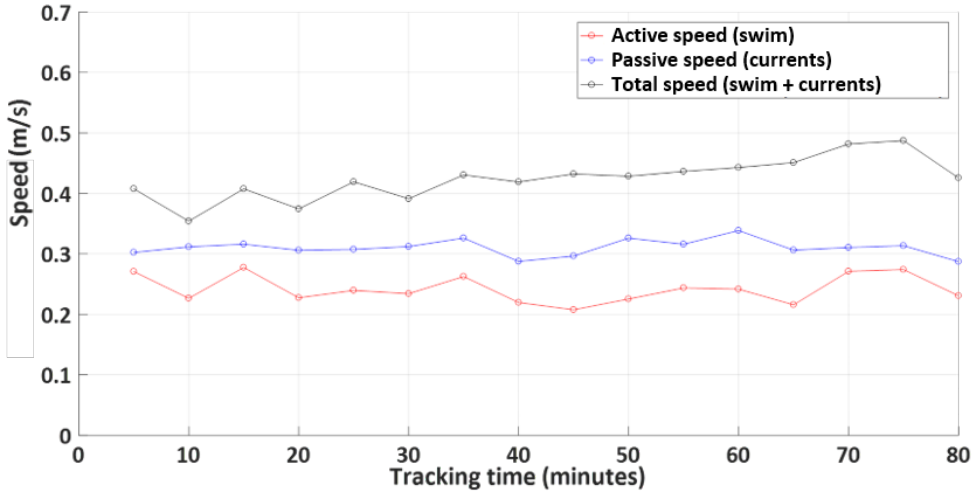

Figure 3.7: Average speed over all turtles and drifters since release for total speed (black), passive speed (blue) and active swimming speed (red) in 2016.

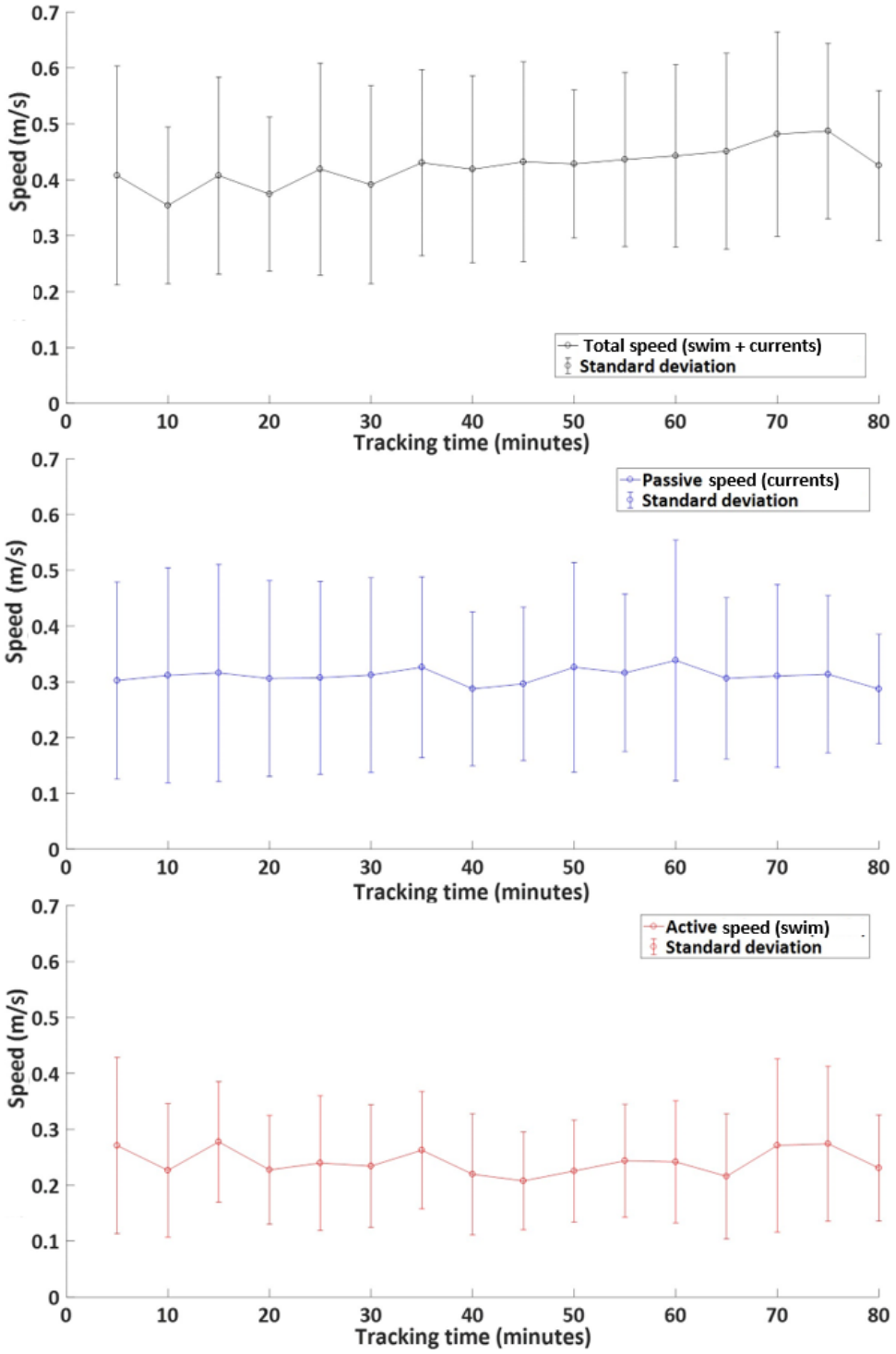

Figure 3.8: Average speed and standard deviation over all turtles and drifters since release in water for total speed (black), passive speed (blue) and active swimming speed (red) in 2016.

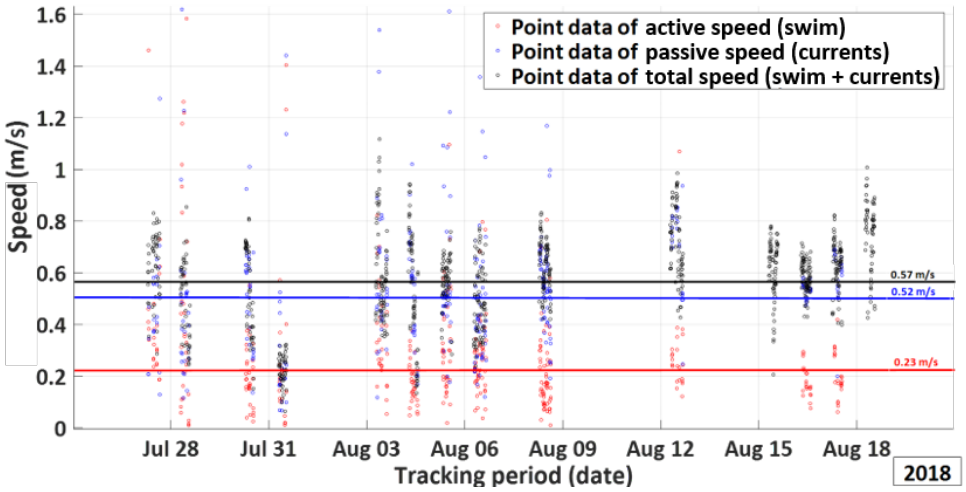

Figure 3.9: Point and average data speed over all turtles and drifter for total speed (black), passive speed (blue) and active swimming speed (red) in 2018.

Direction

Velocity components (u,v) are also used to study the angles of the total direction (black on Figure 3.10) and passive direction (blue on Figure 3.10) as a function of time. In order to obtain the active swimming direction (red on Figure 3.10), it was necessary to use a trigonometric tangent function between u and v obtained for the active swimming speed. For practical reasons, I used the nesting beach as reference for the direction.

Similarly to the speed, Figure 3.10 shows each behaviour individually with its standard deviation. The average passive direction (currents) remains more or less stable between 0° and 20° and pushes the turtle slightly offshore to the east as the current is not parallel to the coast. The overall average current angle for 2016 is 5°. There is a slight decrease in total direction which starts around 50° and gradually decreases towards 30°. The overall average is 33°. **For the average active swimming direction, there is an almost linear decrease from 100° to 71° and its overall average is 82°.** The turtle seems to swim away towards the open sea and then approach the current as we move forward in time.

Figure 3.12 represents the raw data obtained by Upwell for 52 turtles in 2018. The overall average of the angle of active swimming of 63° is not fully confirmed by 2016 data. However, in 2018, the drifters' tracking started 30 minutes and sometimes even 1 hour after the turtles' tracking. If we assume that the angle continues to decrease slightly until it reaches the direction of the current, it is quite possible that the turtles during began to swim perpendicular to the beach and afterwards decreased with time.

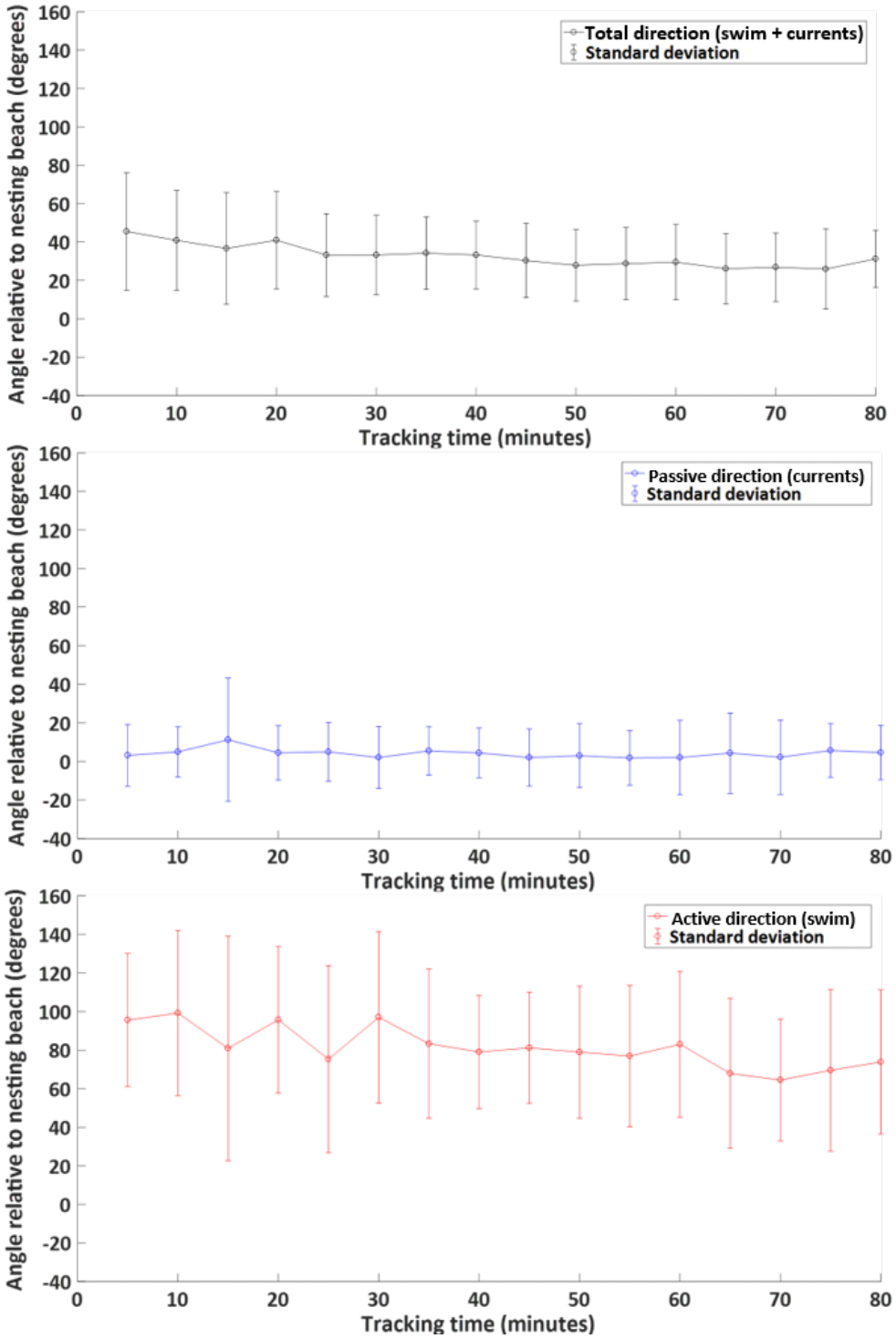

Figure 3.10: Average angle relative to the nesting beach and standard deviation over all turtles and drifters since release in water for total direction (black), passive direction (blue) and active swimming direction (red) in 2016.

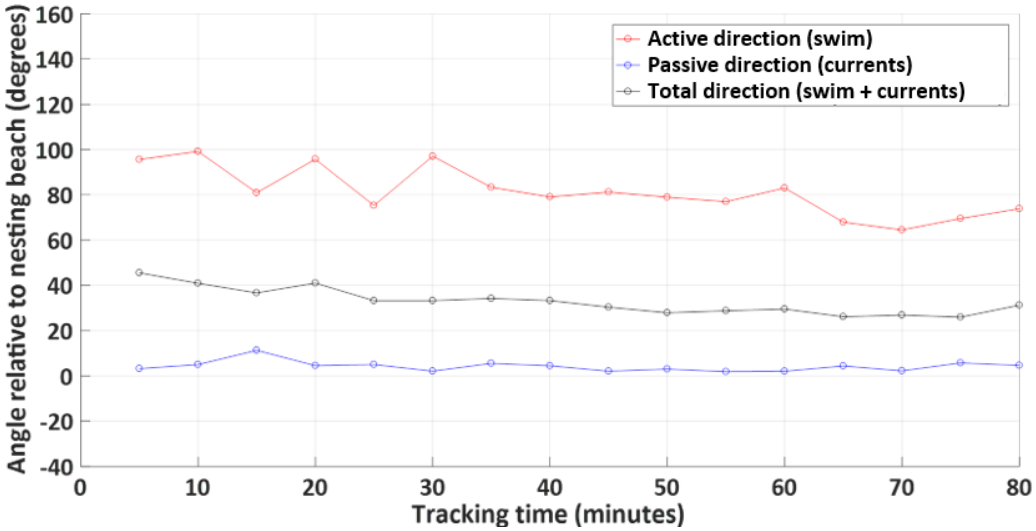

Figure 3.11: Average angle relative to the nesting beach over all turtles and drifters since release in water for total direction (black), passive direction (blue) and active swimming direction (red) in 2016.

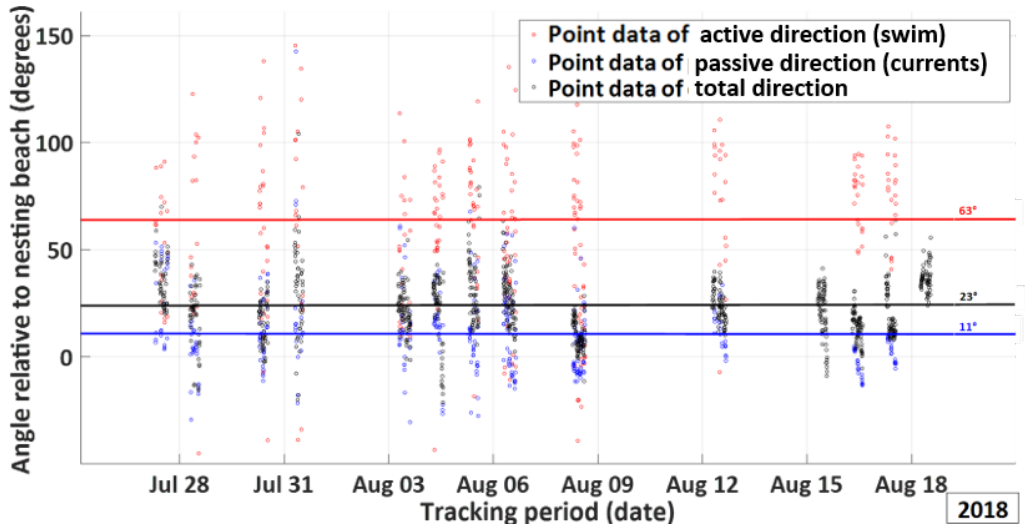

Figure 3.12: Point and average data angle relative to the nesting beach over all turtles and drifters since release in water for total direction (black), passive direction (blue) and active swimming direction (red) in 2018.

Summary and comparison with Hoover

Figure 3.13 shows a summary of the main parameters for each behaviour :

Active behaviour	Unit	2016	2018
In water speed	[m/s]	0.25 ± 0.12	0.23 ± 0.14
Bearing (beach)	[°]	82 ± 41	63 ± 54
Passive behaviour	**Unit**	**2016**	**2018**
Over ground speed	[m/s]	0.30 ± 0.18	0.52 ± 0.21
Bearing (beach)	[°]	5 ± 19	11 ± 23
Final behaviour	**Unit**	**2016**	**2018**
Over ground speed	[m/s]	0.40 ± 0.18	0.57 ± 0.17
Bearing (beach)	[°]	33 ± 28	23 ± 14

Figure 3.13: Averages and standard deviation of active, passive and final behaviour of the data provided by the NGO Upwell.org for 2016 and 2018.

Before going any further, I must compare these parameters with the results obtained by Aimee Lynn Hoover. Indeed, she made a thesis in 2017 with three main objectives including the analysis and data recovery of the same 42 hatchlings turtles on the beach of Pacuaré in 2016 (Hoover 2017). Overall, the data are very similar for the final and passive behaviours. Speeds vary by maximum 1% and angles by maximum 5%. Although minimal, these errors can be explained by the extreme values that I rejected and that she kept. This confirms a lower standard deviation for me.

However, there is one big difference, the active behaviour. Indeed, she gets an active speed of 0.48 ± 0.20 m/s and I obtained 0.25 ± 0.12 m/s for 2016. I have the advantage of having the 2018 data. Indeed, the 2018 data already provides the components u and v for the active, passive and final behaviour. Therefore, unlike 2016, it was not necessary to calculate the active swimming components u and v. After getting results for 2016, I used the same calculation method for 2018. My personal results for 2018 were the same as those provided by Upwell. Therefore, the method used for 2016 is consistent. The second reason that allows me to be confident in my results, is the documentation. In fact, the documentation and especially the papers of (Davenport 1987; Wyneken and Salmon 1992), and almost all papers since then (Hamann et al. 2011; Wildermann et al. 2017) take into account a swimming frenzy with an active speed of 0.30 m/s. To be more confident in my result, since we have similar average results for the passive and total behaviour, I used the averages obtained to deduce the approximate active swimming speed and angle. Even with extreme values, I obtained a maximum active swimming speed of 0.27 m/s and an angle of 89° which matches my results.

3.1.5 Swimming frenzy: my choice of parameters

After hatching, the swimming frenzy behaviour, common to all species of marine turtles, was first observed with Deraniyagala 1930 and analysed in the 1980s and early 1990s by Davenport 1987 and Wyneken and Salmon 1992. These two studies of 1987 and 1992 inspired the swimming frenzy of most of the simulations made afterwards. The supposed goal of this frenetic swim is to escape the moving waters full of predators near the coast and join the main ocean currents (Wyneken and Salmon 1992; Hamann et al. 2007; Salmon et al. 2009)

Duration

The swimming frenzy, according to Salmon and Wyneken 1987, authors of countless studies on sea turtles, is continuous during 24 hours. They completed their study by adding, in the 1990s (Wyneken and Salmon 1992), that they continue to swim frenetically for a few days saving energy during the night according to Figure 3.14.

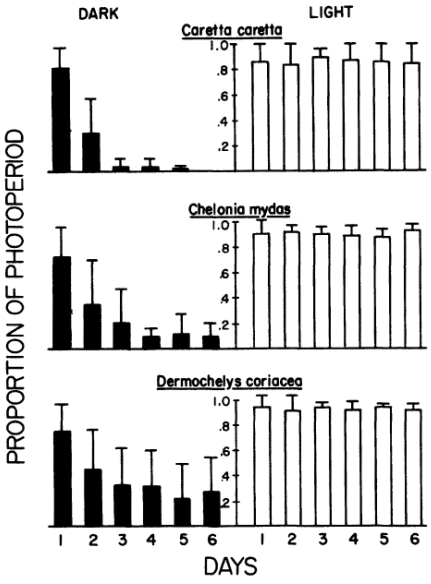

Figure 3.14: Pattern of swimming frenzy activity during the six first days of three species of sea turtles : the loggerhead (Caretta caretta), the green turtle (Chelonia mydas) and the leatherback (Dermochelys coriacea) (Wyneken and Salmon 1992)

Figure 3.14 shows the duration of activity during the day and the night according to the different species of turtles. There is a great contrast between day and night. Indeed, the activity at night decreases drastically after the first 24 hours, while the activity during the day seems to remain more or less stable. There could be several reasons to this : immobility at night helps avoiding predator detection and hatchlings expense less energy to search food when it cannot easily be located (Dalton 1979). The turtles have globally a similar behaviour between species with the leatherback

turtle being the most active during the day. Since then, depending on the different studies, the species and the offshore currents nearby, the swimming frenzy varies from three to six days, most of them lasts three days (Hamann et al. 2011; Wildermann et al. 2017). For ease in numrical simulations, swimming frenzy has always been simulated continuously without interruption at night. **The swimming frenzy in my numerical simulation will vary from 3 to 6 days.**

Speed

As mentioned before, documentation confirms the active swimming speed observed in 2016 and 2018. The speed during swimming frenzy vary from 0.23 m/s to 0.36 m/s (Davenport 1987; Salmon and Wyneken 1987; Wyneken and Salmon 1992; Witherington 1991) Since then, depending on the different studies, the swimming frenzy speed was constant during the swimming frenzy and taken around 0.28 m/s (1 km/h). Considering Figures 3.7, 3.8 and 3.9, I obtained a stable curve with an average of 0.25 m/s and 0.23 m/s for 2016 and 2018, respectively. **Therefore, I decided to keep a constant swimming frenzy speed of 0.24 m/s, and a standard deviation of 0.12 m/s during the entire duration of the swimming frenzy. Which is at midway between the average data of 2016 and 2018.**

Direction

First, the hatchling is attracted to the bright ocean, which reflects the moonlight or sunlight (Nagelkerken et al. 2003). After entering the ocean the hatchlings orient seawards by swimming into the surface waves (Salmon and Wyneken 1987; Wyneken and Salmon 1992). According to observations, the first hour of swimming of the turtles is perpendicular to the surface waves (K. Lohmann and C. Lohmann 1995; Manning et al. 1997). The first studies carried out since then have almost always assumed an entire swimming frenzy against waves. However, Hamann et al. 2011 used a swimming frenzy orientated against the surface waves during the first hour and then, parallel to the direction of the current (Hamann et al. 2011).

A complete swimming frenzy against waves is quite possible since I have an average angle of active swimming of 82° in 2016. However, considering my observations, I should not reject the hypothesis that the turtle decreases its direction to reach the direction of the current. Moreover, the average of 63° obtained in 2018 which have been calculated later on the track of the turtle is in agreement with the decrease of the angle of swimming of the turtle. Several scenarios of turtle behaviour will be considered in the numerical model in order to test all hypotheses. All scenarios will be defined in more detail on page 40 and 41. Therefore, I will have two scenarios to consider :

- The turtles swim perpendicularly to the waves during the swimming frenzy.
- The turtles swim one hour perpendicularly to the waves and then their angle decreases progressively until it reaches the current's angle.

3.1.6 The following months: passive or active behaviour ?

After burning off all their energy, the turtles find themselves far from the coasts, in the open sea. This is where their oceanic development phase starts. During this phase, there is no doubt that current remains a major component of the movement even for older, more powerful individuals (Gaspar et al. 2006) and long term simulations have already proven their effectiveness (Fossette et al. 2010; Gaspar et al. 2012). **However, it is becoming increasingly evident that the final dispersion of hatchlings can be influenced even with a little active swimming component in these important currents.** Therefore, it can influence future population dynamics (Putman et al. 2012; Shillinger et al. 2012; Scott et al. 2014; Putman and Mansfield 2015). Given that the active behaviour of the turtle is discovered earlier and earlier (Putman and Mansfield 2015), why couldn't the turtle be active from the beginning of its life? Even a minimal speed could have a beneficial effect on its distribution. Wildermann et al. 2017 was the first to add a active swimming speed to hatchlings. After the classic three days swimming frenzy, either the swimming behaviour was stopped and they drifted passively or they swam directionally with a constant speed. She obtained surprisingly good results for the active speed compared to the passive drift. Therefore, I will add two scenarios :

- Post-frenzy swimming activity of 0.04 m/s for the entire simulation (scenario D).
- Post-frenzy swimming activity of 0.08 m/s for the entire simulation (scenario E).

3.1.7 Scenarios and evaluation method

Each scenario simulation will release a total of 500,000 virtual turtles from the beach of Pacuaré, Costa Rica. An indicator of the success of each scenario will be the percentage of turtles that will strand on the beach. My hypothesis is that turtles disperse instinctively to survive as much as possible. The lowest the ratio of stranded turtles, the better the scenario's dispersal. The scenarios will be discussed and compared to find the most plausible turtle dispersion. The further in the simulation, the greater the uncertainty on the turtle dispersal increases. This is why **I will stop after 1, 2, 3, 4, 6 and 8 weeks to show the evolution of the dispersion, the probability of presence and the stranded turtles' ratio for each scenario.** Several swimming frenzy parameters remain constant among the scenarios:

- The active speed based on the average of the 2016 and 2018 field data, 0.24 m/s $\pm$ 0.12 m/s.
- The standard deviation of the active direction based on field data 40°
- The duration according to previous studies will vary between 3 and 6 days.

Scenario A

The 'Classic" scenario has no great particularity, it is the most probable and widespread scenario according to previous studies. In this scenario, I chose a swimming frenzy scenario where the turtles swim against the waves, represented by the Stokes drift. After the swimming frenzy, the turtle is drifting passively.

Scenario B

The "No Stokes" scenario is very similar to scenario A. However, according to some observations (Wyneken and Salmon 1992; Spotila and Tomillo 2015), the successive shallow dives that the turtle makes during swimming frenzy is useful to avoid the effect of the Stokes drift. Indeed, I assume the turtle returns to the surface to breathe and orient itself against the waves and then dives to avoid the effect of the Stokes drift that bring it back to the coast.

Scenario C

The "Decrease" scenario shows whether it is possible for the turtle to swim perpendicularly to the beach and then linearly decrease its direction to reach the direction of the current at the end of the swimming frenzy. This behaviour can be extrapolated from the different observations made during the 80 minutes of turtle tracking in 2016. Hamann et al. 2011 used a similar swimming frenzy. Similarly to scenario A, the turtle is drifting passively after swimming frenzy.

Scenario D and E

The "Active swimming 1" and "Active swimming 2" scenarios are the same as Scenario A with a little constant active speed added after the swimming frenzy and for the rest of the simulation. I considered this constant speed with an amplitude of 0.04 (scenario D) and 0.08 m/s (scenario E) similar to Wildermann et al. 2017. I presumed that the direction of the active swimming is against waves (or Stokes drift). In my opinion, at this early life stage, they don't use magnetic field yet and their only visual cues are the waves. Since the turtle is near the surface, it easy for it to locate itself in front of the waves.

Scenario F

The "Random" scenario is a base scenario that I will compare to the others. Indeed, this scenario will consider a random and constant direction chosen between 0 ° and 180 ° from the beach. The turtle will keep this direction during all the swimming frenzy. The purpose of this scenario is to demonstrate the innate instinct of the turtles to orientate themselves and have the maximum chance of survival. It is a basis for comparison.

2016									
N°	Scenarios				Swimming frenzy parameters			Post frenzy parameters		
	Name	Start	End	Stokes	Speed (ms^{-1})	Direction (°)	Duration	Speed (ms^{-1})	Direction (°)	Duration
A	Classic	20/08	20/10	Yes	0.24 ± 0.12	Waves $\pm$ 40	3 to 6 days	/	/	/
B	No Stokes	20/08	20/10	No	0.24 ± 0.12	Waves $\pm$ 40	3 to 6 days	/	/	/
C	Decrease	20/08	20/10	Yes	0.24 ± 0.12	Decreasing $\pm$ 40	3 to 6 days	/	/	/
D	Active swimming 1	20/08	20/10	Yes	0.24 ± 0.12	Waves $\pm$ 40	3 to 6 days	0.04	Waves	54 to 57 days
E	Active swimming 2	20/08	20/10	Yes	0.24 ± 0.12	Waves $\pm$ 40	3 to 6 days	0.08	Waves	54 to 57 days
F	Random	20/08	20/10	Yes	0.24 ± 0.12	Random constant	3 to 6 days	/	/	/

2018									
N°	Scenarios				Swimming frenzy parameters			Post frenzy parameters		
	Name	Start	End	Stokes	Speed (ms^{-1})	Direction (°)	Duration	Speed (ms^{-1})	Direction (°)	Duration
A	Classic	27/07	27/09	Yes	0.24 ± 0.12	Waves $\pm$ 40	3 to 6 days	/	/	/
B	No Stokes	27/07	27/09	No	0.24 ± 0.12	Waves $\pm$ 40	3 to 6 days	/	/	/
C	Decrease	27/07	27/09	Yes	0.24 ± 0.12	Decreasing $\pm$ 40	3 to 6 days	/	/	/
D	Active swimming 1	27/07	27/09	Yes	0.24 ± 0.12	Waves $\pm$ 40	3 to 6 days	0.04	Waves	54 to 57 days
E	Active swimming 2	27/07	27/09	Yes	0.24 ± 0.12	Waves $\pm$ 40	3 to 6 days	0.08	Waves	54 to 57 days
F	Random	27/07	27/09	Yes	0.24 ± 0.12	Random constant	3 to 6 days	/	/	/

3.2 Numerical modelling

Direct observations and short-term experiments remain the best method to obtain field data for hatchlings. After having done these, we have to extrapolate these data and use numerical models.

3.2.1 SLIM

Second-generation Louvain-la-Neuve Ice-Ocean Model or SLIM is a "multi-scale model of the land-sea continuum" (UCL 2020). SLIM is an unstructured-mesh hydrodynamic model that can simulate flows from rivers to the coastal oceans. It is based on the discontinuous Galerkin finite element method and allows great flexibility and adaptability, even for very complex coastlines and bathymetry. I used the SLIM2D module to model my water environment. The model solves the depth-averaged shallow water equations for the surface elevation and the horizontal velocity. I used SLIM's Lagrangian particle tracker to simulate the transport and SLIM's Eulerian transport model to simulate the dynamics of the turtles (UCL 2020).

3.2.2 Framework to generate the hydrodynamic model

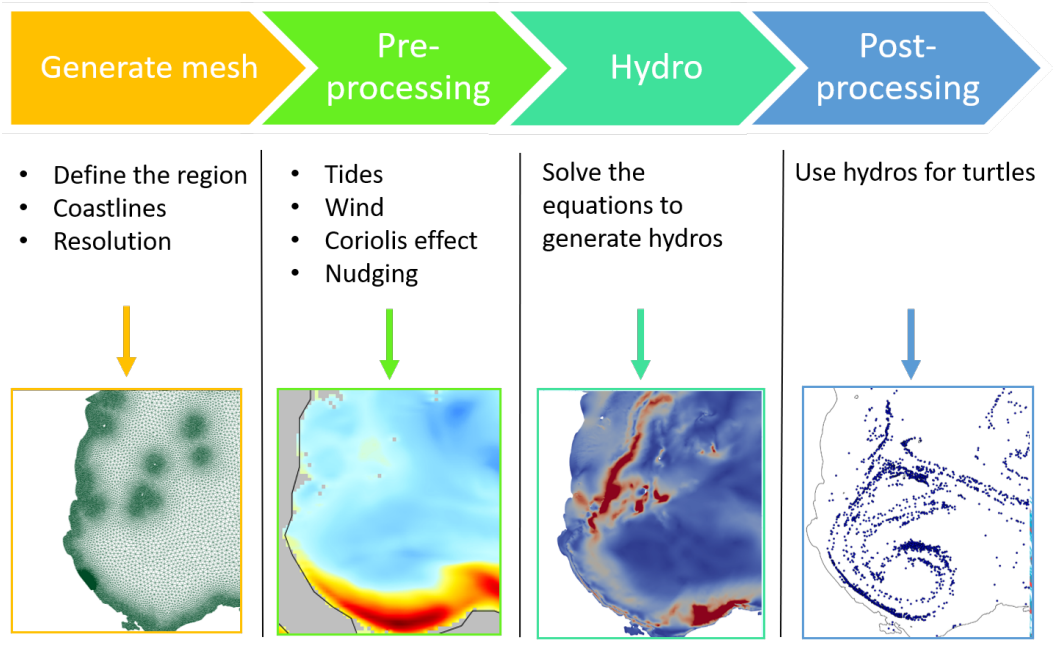

Figure 3.15: Framework to generate my hydrodynamic model.

Generate a mesh

The first step is choosing a geographical region and defining its boundaries. I chose a region of 2000 km west-east and 1000 km north-south in the Caribbean Sea (Figure 3.16). Next, I had to define the open borders (O), where a flow of water continuously enters and/or exits, and the closed borders (C), the coasts where no water flow passes. Finally, I added a marker for the nesting beach (B) which is the start point of the numerical model. My resolution is based on two factors, the distance to the nesting beach and the distance to the coast. The mesh resolution ranges from 100 m near Pacuaré, 2 km near any coast, to 20 km far away from the coasts. Figure 3.16 shows the mesh which contains 287 000 elements and 145 000 nodes.

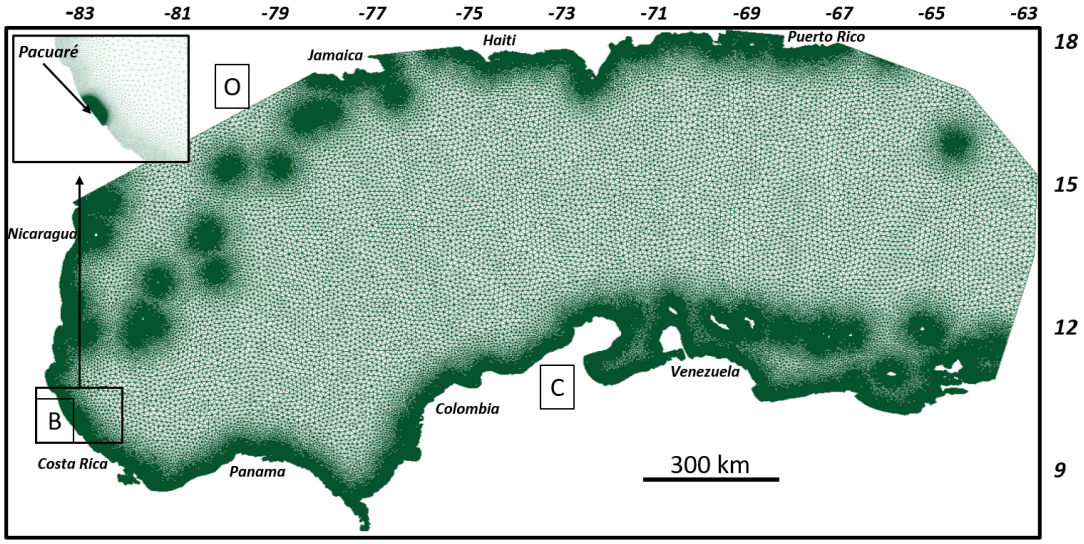

Figure 3.16: Mesh of the Caribbean Sea, basis of the hydrodynamic model. Examples of open borders (O), closed borders (C) and the Pacuaré nesting beach (B).

Pre-processing

Preprocessing is the stage during which all the variables involved are researched. The model equations can be forced by wind, tides, coriolis, and large-scale currents from a global ocean model. The bathymetry was defined by the Arcgis file created to generate the mesh. The coriolis factor is a simple formula that represents the effect. Then, I added the wind found on the site of the Climate Data Store (DTS). Finally, for the tides and the water heights, I had to find them in the HYCOM data. Mercator data were used in deep offshore water and to add the Stokes drift.

Stokes drift

The amplitude and direction of the Stokes drift are represented on Figure 3.17. It reaches peaks of 0.14 m/s and is globally directed westward. In the bay in front of Pacuaré, the Stokes drift amplitude reaches peaks of 0.075 m/s. The resolution of the Mercator data doesn't guarantee accuracy for the Stokes drift along the coast and have therefore be set to 0. As explained previously, the Stokes drift is in the direction of the waves. It have been set as the reference direction for majority of the scenarios. Since the Stokes drift have been set to 0 along the coast, when the amplitude of the Stokes drift is less than 0.01 m/s, the turtle goes perpendicular to the coast of Pacuaré.

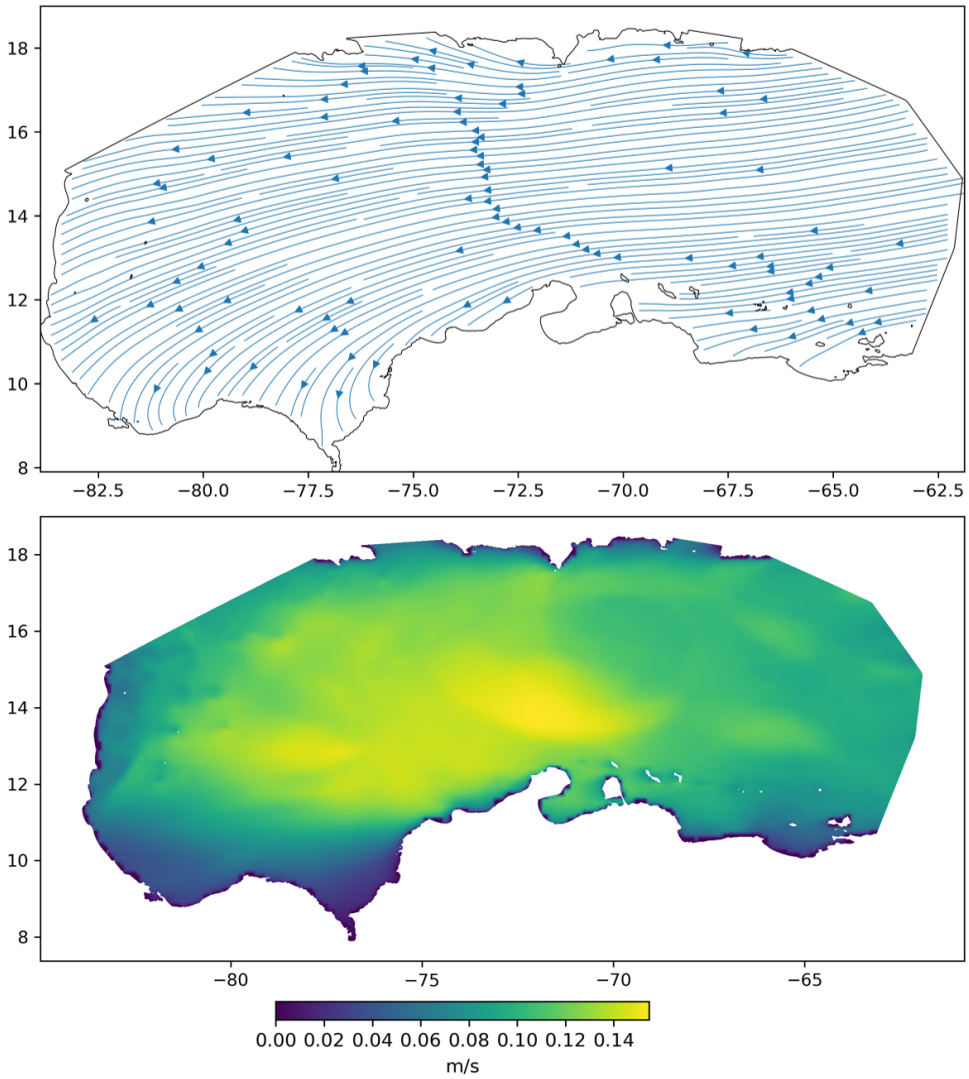

Figure 3.17: Mean Stokes drift direction and amplitude for the two months simulation period of 2016.

Generate the hydrodynamic model

The last step to generate the hydrodynamic model is parameterization. After creating the files of the different factors involved, I had to add the initial conditions in order to let SLIM solve the shallow-water equations. The model parameterization consists also in constant coefficients such as Manning for bottom roughness or Smagorinski for momentum diffusion. First, the shallow-water equations solved by SLIM compute the sea surface elevation n and the depth integrated mean velocity u :

$$\frac{\partial dn}{\partial dt} + \nabla \cdot (H\underline{u}) = 0 \tag{3.1}$$

$$\frac{d\underline{u}}{dt} + \nabla \cdot (\underline{u}\underline{u}) = -f \cdot \underline{u} - g\nabla n - Cd\|\underline{u}\|\underline{u} + \frac{\tau}{\rho H} + \frac{1}{H}\nabla \cdot [Hv(\nabla \underline{u})] \tag{3.2}$$

where in the same order we can find the total water column depth $H = h + n$, the mean depth h, the Coriolis acceleration f, the gravitational acceleration g, the bottom stress coefficient Cd (equation 3.3), the surface wind stress τ (equation 3.4), the water density ρ and the diffusivity coefficient of Smagorinski v (equation 3.5).

$$Cd = \frac{n^2 g}{H^{4/3}} \tag{3.3}$$

where n equals 0.03 $\mathrm{sm}^{-1/3}$ and is the Manning coefficient

$$\tau = 10^{-3}\left(0.63\|\underline{w}\| + 0.66\|\underline{w}\|^2\right)\underline{w} \tag{3.4}$$

where $\underline{w}$ is the wind velocity obtained from the Climate Data Store (CDS).

$$v = (0.1\Delta)^2\sqrt{(\nabla\underline{u} + \nabla\underline{u}^T) : (\nabla\underline{u} + \nabla\underline{u}^T)} \tag{3.5}$$

Afterwards, the boundary conditions have to be imposed. These conditions depend on whether it is closed or open boundaries. For open boundaries, the flow of water depends on tides and data provided by HYCOM, which are added to the model.

Figure 3.18 shows the the hydrodynamic model obtained. There is a gyre, a vortex that occurs near the coasts of Costa Rica and Panama, in front of the beach of Pacuaré. There is also a powerful current that flows along the coasts of Costa Rica and Panama. This current is stronger in 2018 than 2016 which confirms the drifters data. In 2016, this current goes predominantly towards Columbia with some going in the bay between Panama and Columbia. In 2018 this same current, coming from the coasts of Costa Rica and Panama, will tend to stop at the bay between Panama and Columbia with a part going directly offshore and an other part staying in the bay. It is difficult to predict what will happen offshore with rather random directions but mainly directed towards the west. Given the constancy of the current along the coast of Pacuaré in the data and the hydrodynamic model, I made the hypothesis that the turtles were not influenced by high and low tides. The current is always directed towards the south-east.

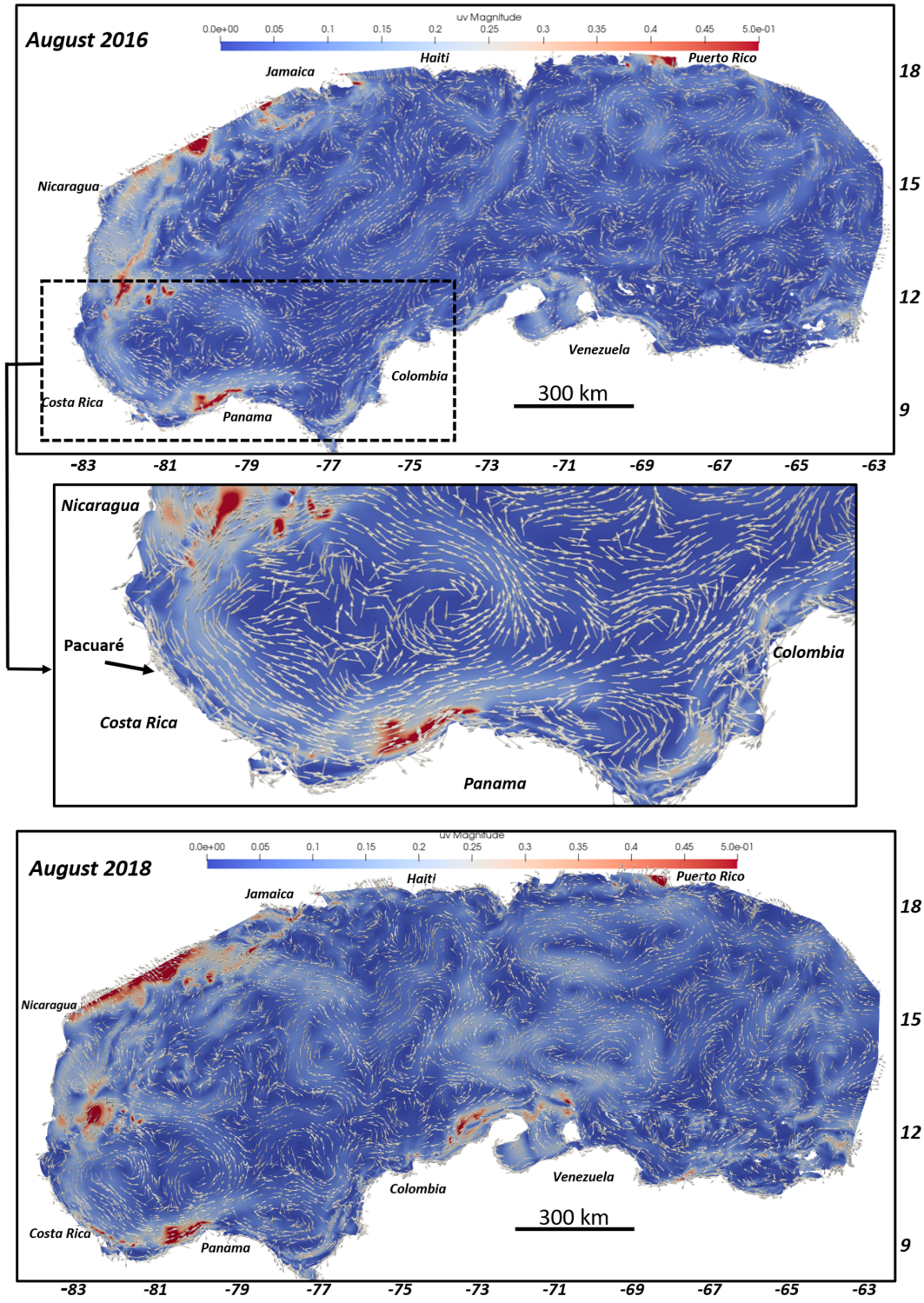

Figure 3.18: Hydrodynamic model of the Caribbean Sea with amplitude and direction of the surface currents in August 2016 and 2018.

3.2.3 Post-processing

The two hydrodynamic models previously developed are three months models from August 1, 2016 to October 30, 2016 and from July 1, 2018 to September 30, 2018. The first turtles were followed on 20 August and 27 July for 2016 and 2018, respectively. I decided to start my models earlier so that they have time to converge which lasts 1 to 2 weeks according to my information. The first step of post-processing will be the validation of these models. And then, I will start to use SLIM's particle tracker for different turtle behaviours.

Validation

To assess the model accuracy, it has to be validated with respect to field observations. Here we used the World Sea Levels site (JRC 2020). I have taken, as seen in the figure below, a measurement of the height of the water level offshore of the island of San Andrés (Columbia) which is in the middle of the bay in front of the beach of Pacuaré (Figure 3.19). I extracted the water heights provided by my numerical model and those given by the WSL site (JRC 2020) for a period of 15 days from August 1 to 15, 2016. Since the two data ranges may have different references, I took the average of these two data ranges and for each point, I subtracted the appropriate average. This allowed me to have the same common reference for both data ranges which is 0. Then, I superposed the two graphs and obtained Figure 3.19. Interestingly enough, my hydrodynamic model takes 7 to 8 days to converge. Indeed, the margin of error gets smaller as time goes by. We notice the effect of the tides which makes the water level vary by 0.4 meters.

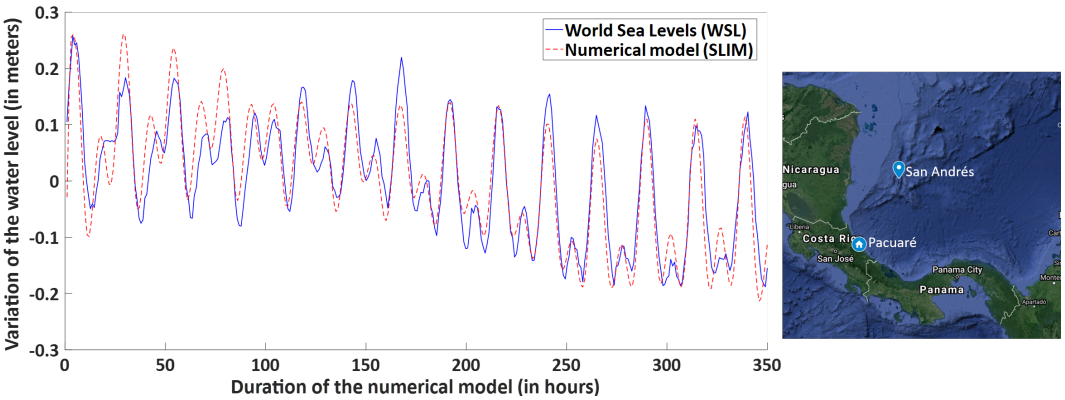

Figure 3.19: Validation of the first 15 days of the hydrodynamic model with sea levels from San Andrés (Columbia).

Tracker

The tracker consists in particles launched from a starting point in the domain, and the start-end date of the simulation. The simulation start dates, 20 August 2016 and 27 July 2018, are the first days of turtle tracking on field in Pacuaré, Costa Rica. The end dates will be 20 October 2016 and 27 September 2018, respectively. As mentioned before, the other parameters added to the tracker are the duration, speed, direction of active behaviour during swimming frenzy. As well as the duration, speed and direction of the "post frenzy" active behaviour, during the the rest of the simulation.

Chapter 4

Results

From the 500,000 virtual turtles launched from Pacuaré, my simulations indicated the distribution of the amount of turtles per km^2 in every element of my mesh. Finally, this amount was divided by 500,000 to obtain the probability of presence per km^2. Because turtles are stranding throughout the simulation, the integral of this distribution (equal to 1 in the beginning) decreases gradually. The overall results of the percentage of stranding turtles after 1, 2, 3, 4, 6, 8 weeks are given in table form in Chapter 4. The "total" in the table indicates the percentage of turtles that stranded after the two months of simulation. The maps of probability of presence for each of the twelve scenarios A, B, C, D, E and F for 2016 and 2018 can be found from page 74 to 86 in Appendix A and B. Similarly, illustrations of the dispersion simulation were taken after 1, 2, 3, 4, 6, and 8 weeks.

The purpose of Chapter 4 is to present and describe the simulation results obtained before discussing them in more details in Chapter 5. I divided the chapter into 3 parts. Firstly, the table display the numerical results obtained. I comment the results after the first week and the final results, after two months. Secondly, the results of each scenarios between week 1 and week 8 are given and compared. The scenarios are split in passive dispersion and active dispersion. Based on these, the scenario that guarantees the most optimal dispersion is chosen. The last part, dispersion, compare the progress of the dispersion in 2016 and 2018.

As a reminder of the parameterization of each scenario, the reader may wish to use the table on page 41 when analyzing the results table or the images of simulation.

4.1 Results table

The table on next page shows the results for scenarios A, B, C, D, E and F. The 2018 results are significantly higher compared to those of 2016, which may be due to the stronger currents near the Bay of Pacuaré.

For both years, the best swimming frenzy results (week 1) are obtained by the active swimming scenarios (D and E) with 0.05% of stranded turtles after week 1. The amplitude of the active component doesn't matter since the results of the two scenarios after week 1 for either 2016 and 2018 are equal. The third best is the No Stokes scenario (B) which have 0.08% and 0.60% of stranded turtles for 2016 and 2018, respectively. Then comes the Classic scenario (A) with 0.15% and 0.73% and the Decrease scenario with 0.34% and 0.92% for 2016 and 2018, respectively. Unsurprisingly, the Random scenario comes last and its percentage don't vary much from one year to the other, approximately 14% of turtles strand after only one week.

As a reminder, the swimming frenzy parameters for scenarios A, D and E are identical. The percentage differences are due to the differences between the first three days and from the third to the seventh day. Indeed in all three scenarios, the first turtles stop their swimming frenzy on day three and begin their post frenzy behaviour. Consequently, until day three all three scenarios have the same percentage of stranded turtles, and between day three and day seven, a larger number of turtles strands for the Classic scenario (A) than for the active scenarios (D and E). Which is not surprising because their active component takes them far from the coast.

The results after one week and after two months are linked since the order remains unchanged. Concerning the final results, the first impression for both years is that the best scenarios are the active swimming scenarios (D and E). Even after swimming frenzy, they lose a very low amount of turtles with final percentages of 0.19% and 1.53%. Then comes the No Stokes scenario (B) with 3.79% and 32.59% for 2016 and 2018, respectively. The Classic scenario (A) which is the most widespread in the studies comes fourth for 2016 and 2018 with 4.29% and 41.68%, respectively. The Decrease scenarios (C) are fifth for 2016, 5.46% and 2018, 50.06%. The Random scenarios (F) takes into account no innate behaviour of the turtle to orient itself and is indeed the worst of all scenarios with incredibly high results of 29.88% and 61.93%. This implies that out of 500,000 virtual turtles launched from Pacuare beach on 27 July 2018, only less than 200,000 did not strand after two months of simulation.

I have also extracted another type of result, the total percentage of turtles escaping from the domain. The totality of turtles escaping from the domain does so through the open border between Nicaragua and Jamaica towards the north of the Caribbean Sea to the Gulf of Mexico. **Two scenarios have a significant number of turtles escaping from the domain, the active swimming scenarios of 2016 with 5.64% and 4.65%. The other ten scenarios, including all those of 2018, have no turtles escaping the domain.**

2016									
Scenarios		Stranded turtles (%)							Turtles leaving the domain (%)
N°	Name	Week 1	Week 2	Week 3	Week 4	Week 6	Week 8	Total	Total
A	Classic	0.15	1.59	2.74	2.82	3.22	3.99	4.29	0
B	No Stokes	0.08	1.43	2.48	2.54	2.75	3.54	3.79	0
C	Decrease	0.36	1.86	3.13	3.28	4.12	4.92	5.46	0
D	Active swimming 1	0.05	0.90	1.35	1.39	1.48	1.52	1.53	5.64
E	Active swimming 2	0.05	0.87	1.32	1.33	1.35	1.48	1.53	4.65
F	Random	14.36	16.60	21.11	22.79	27.01	29.05	29.88	0

2018									
Scenarios		Stranded turtles (%)							Turtles leaving the domain (%)
N°	Name	Week 1	Week 2	Week 3	Week 4	Week 6	Week 8	Total	Total
A	Classic	0.73	6.98	15.30	16.67	20.13	30.43	41.68	0
B	No Stokes	0.60	5.17	10.45	11.36	13.92	23.70	32.59	0
C	Decrease	0.92	11.01	21.83	23.37	31.53	44.16	50.06	0
D	Active swimming 1	0.03	0.15	0.18	0.19	0.21	0.73	0.76	0
E	Active swimming 2	0.03	0.14	0.18	0.19	0.19	0.19	0.19	0
F	Random	14.70	28.58	40.38	43.52	49.61	56.68	61.93	0

4.2 Scenarios

I examined the intermediate results using the illustrations taken in week 1, 2, 3, 4, 6 and 8. The illustrations provide the distribution of probability of presence during the simulations. During the simulation, the turtles strand along the beaches of Costa Rica, Panama and Colombia. For simplicity of visualization, I created five turtles' stranding areas (Figure 4.1). These are the coastlines where the turtles strand in their two-month journey. For each scenario, I defined the stranding zones according to the turtles' advance, week 1 until week 8, and the relevant remarks about the degree of these strandings.

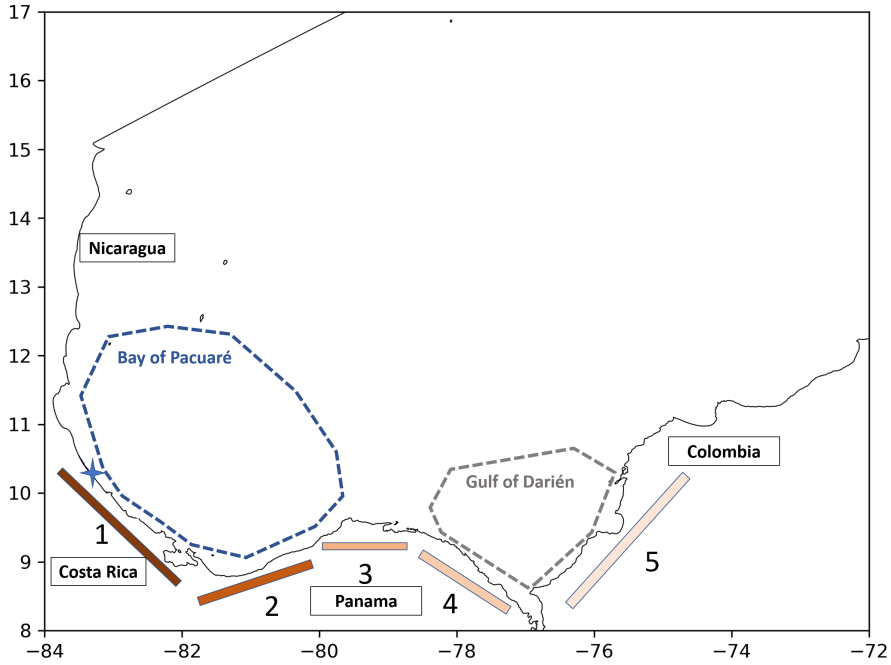

Figure 4.1: Reference number and position of the main stranding areas for turtles along their two-month journey. Personal illustration made with SLIM.

Zone 1 is located along the coast of Pacuaré in Costa Rica (blue star in Figure 4.1) and up to the border of Panama. Zone 2 goes from the border of Costa Rica to the north of Panama. Zone 3 is the northern tip of Panama. Zone 4 and 5 are located respectively in Panamá and Colombia. They make the edges of the Gulf in between the 2 countries, called Gulf of Darién. The bay formed by the coastlines of Nicaragua, Costa Rica and Panama on the west side of Figure 4.1 will be called the Bay of Pacuaré for the rest of the thesis.

4.2.1 Passive dispersion

The following table shows the similar stranding zones of the three passive scenarios, scenario A (Appendix A.1, B.1), B (Appendix A.2, B.2) and C (Appendix A.3, B.3). Indeed, whether in 2016 or 2018, the passive scenarios have turtles stranding in all five zones of the domain. In 2018, the zones are reached faster than in 2016.

Scenarios A, B, C	Week 1	Week 2	Week 3	Week 4	Week 6	Week 8
2016	1	1	2	3	3,4,5	3,4,5
2018	1	1,2	1,2,3	1,3,4	1,2,3	1,2,3,4,5

Zone 2 appears to be the most important zone for turtle strandings. This is especially true for 2018. The currents bring the turtles eastwards. In addition, the Stokes drift brings the turtles back to the coast. The stronger the currents are, the closer the turtles will be to this area and the more likely they will strand. The swimming frenzy of the scenario B benefits the most the turtles' placement. Indeed, avoiding Stokes drift is sort of having a stronger speed offshore. Compared to scenarios A and C, the turtles go further offshore and avoid more easily zone 2. This explains the difference with scenario A and C for the first 3 weeks. The stronger the currents, the greater the benefit of avoiding the Stokes drift. The swimming frenzy of scenario C does not benefit the turtles' placement. Indeed, it decreases the turtles direction linearly to the current, which brings the turtle near zone 2. This is why from week 1 to week 3, there is major increase in the turtles' strandings.

From week 3 to week 6, the turtles disperse globally northwards and come back to the Bay of Pacuaré for the second time, they also begin to enter the Gulf of Darién between Panama and Columbia. Consequently, during this period in 2016 and 2018, there is a slower growth in the turtles' strandings. Nevertheless, from week 6 to the end of the simulation, in 2016, the turtles are mainly stranding on the two edges of the Gulf of Darién. In 2018, as the turtles return for another loop around the gyre near Pacuaré, they are mainly stranding in the same zone 2. Therefore, especially in 2018, there is an important growth from week 6 to the end of the simulation.

4.2.2 Active dispersion

The little swimming component added to the turtles' behaviour has a huge impact on their dispersal. Scenarios D (Appendix A.4, B.4) and E (Appendix A.5, B.5) also show the influence of the magnitude of the active component on the success of the dispersion. In 2016, the percentage evolution is continuous with a peak between week 1 and 2. In 2018, the percentage is very low during the entire simulation with a peak between week 6 and 8 for scenario D. They are the only scenarios with a lower percentage of stranded turtles for 2018 than for 2016.

Scenario D, E	Week 1	Week 2	Week 3	Week 4	Week 6	Week 8
2016	1	1	/	/	/	/
2018	/	/	/	/	2	/

4.2.3 Best scenario

Figure 4.2 and 4.3 show the scenario E for 2016 and 2018, respectively. This scenario is worth highlighting because it allows an optimal dispersion for both 2016 and 2018.

Their swimming component makes it possible to avoid the trap of stranding zone 2, which, especially in 2018, is very deadly. In spite of the intensity of these currents, the swimming component applied to the turtle in 2018 makes it possible to increase the number of stranded turtles between week 1 and week 3 by only 0.15%. Whereas for the other scenarios the percentage increases by several tens of percent. For 2016, the swimming component is also advantageous but to a lesser extent. Indeed, between week 1 and week 3, the percentage of turtles increases by 1.3%. Whereas for the other scenarios the percentage increases by 2 to 3%. The post frenzy swimming component appear to be advantageous and even more in strong currents.

Assuming that turtles have a survival instinct that allows them to disperse in order to increase their chances of survival, the best scenario is a combination of scenario B during the swimming frenzy and the scenario E during the following weeks. Indeed, compared to the scenario A, the avoidance of the Stokes drift allows a better dispersion afterwards.

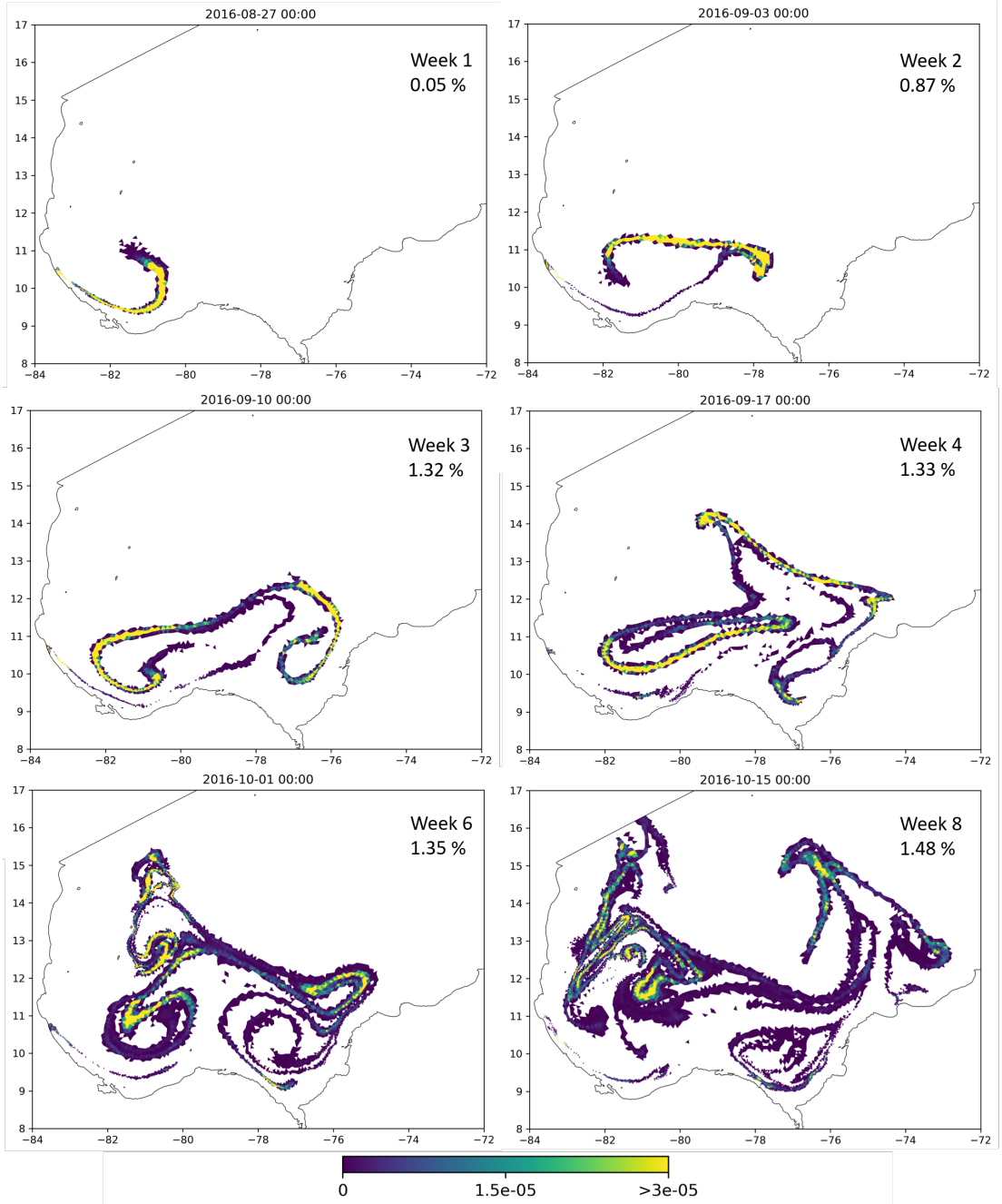

Figure 4.2: Scenario E. Dispersion and probability of presence of leatherback hatchlings on a eight weeks simulation from Pacuaré, Costa Rica in 2016. The percentage indicates the stranding rate of turtles so far in the simulation.

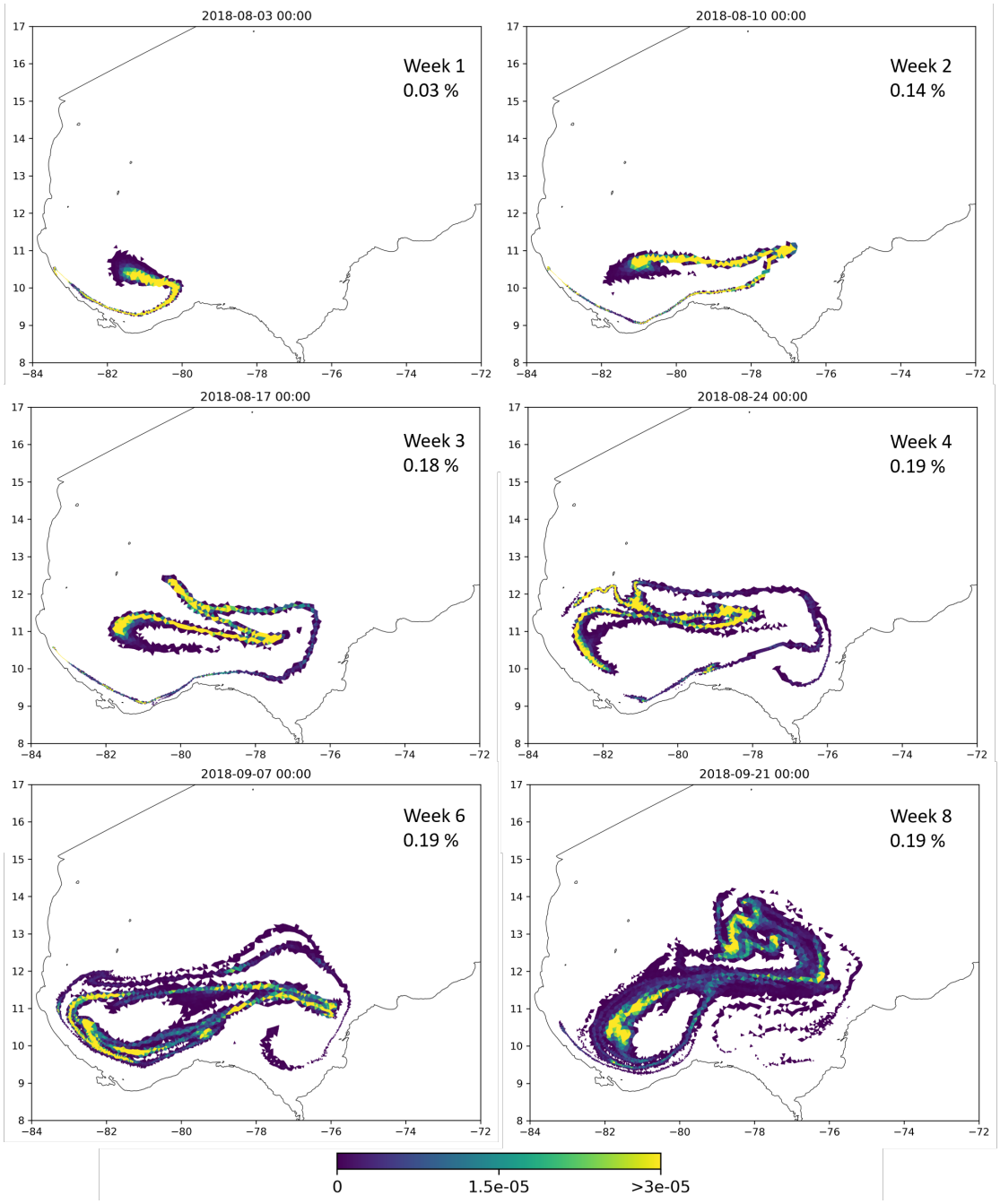

Figure 4.3: Scenario E. Dispersion and probability of presence of leatherback hatchlings on a eight weeks simulation from Pacuaré, Costa Rica in 2018. The percentage indicates the stranding rate of turtles so far in the simulation.

4.3 Global dispersion

The aim of this section is to compare the illustrations and the dispersion of the turtles.

4.3.1 Swimming frenzy

Figure 4.4 and 4.5 show illustrations of the simulation for each scenario after 7 days. The swimming frenzy varies from 3 to 6 days depending on the turtles. Therefore, the illustrations of the scenarios A, D and E, which have the same swimming frenzy parameters, are very similar. Nevertheless, scenario B is very similar to the other 3 previously mentioned. In scenario B, No Stokes drift is applied because of the ability of the turtle to avoid it. However, the turtles' dispersion don't vary. Scenario C has a dispersion that covers a wider area with turtles going further east. In spite of the percentage, this scenario positions the turtles unfavorably for later stages. Indeed, turtles are near the coasts and a large number will strand in the next few days of the simulation. For Scenario F, since all turtles take a random direction between 0° and 180° from the beach, the dispersion covers a much larger area.

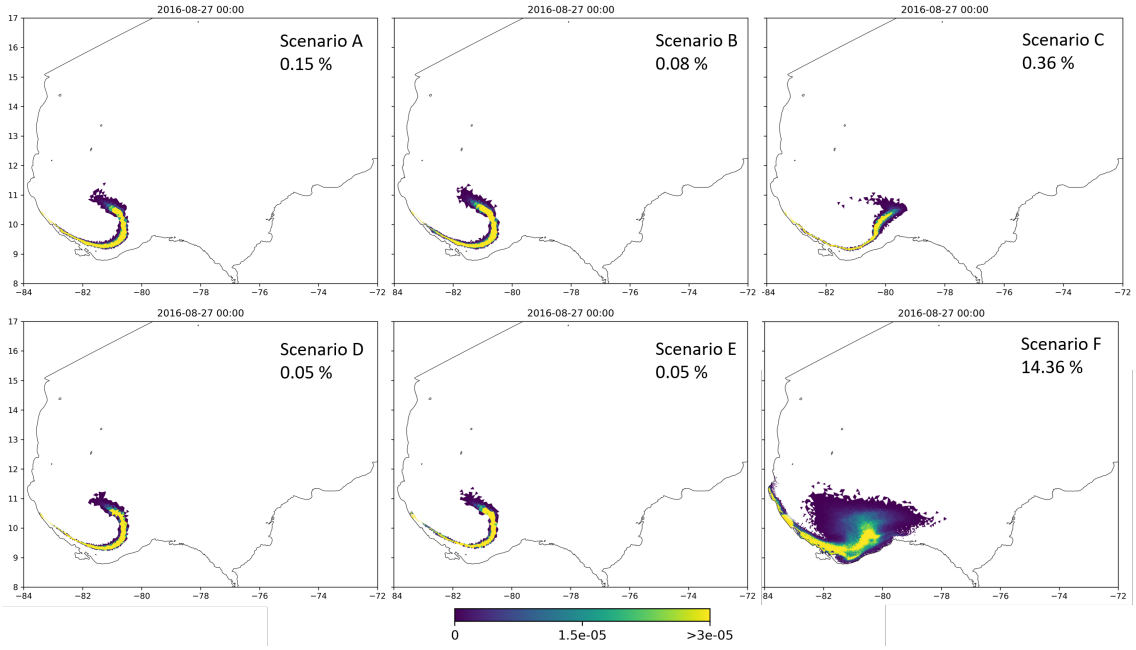

Figure 4.4: Dispersion and probability of presence of leatherback hatchlings on a one week simulation from Pacuaré, Costa Rica in 2016. The percentage indicates the stranding rate of turtles so far in the simulation.

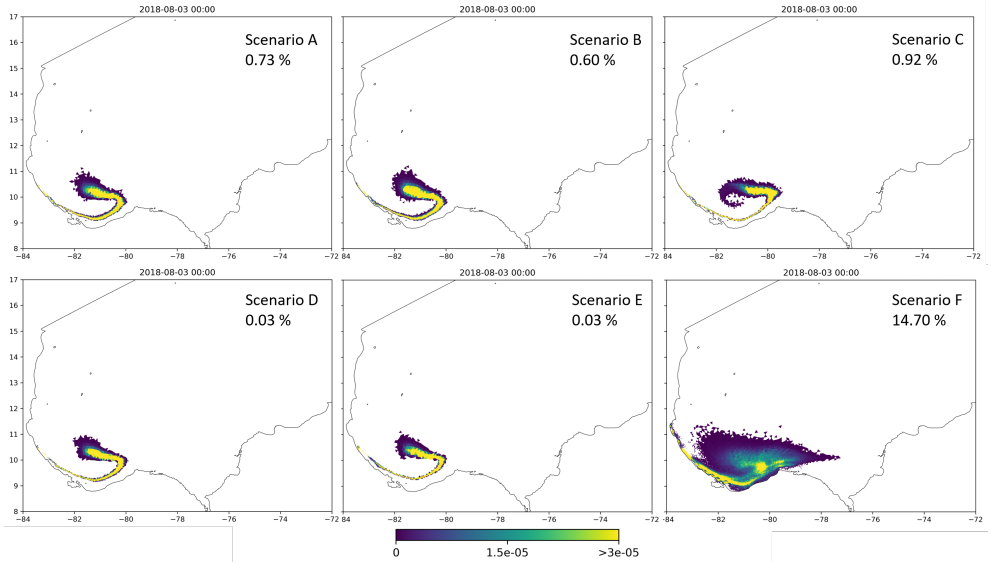

Figure 4.5: Dispersion and probability of presence of leatherback hatchlings on a one week simulation from Pacuaré, Costa Rica in 2018. The percentage indicates the stranding rate of turtles so far in the simulation.

4.3.2 Currents

After their swimming frenzy and during the first months, except for scenarios D and E, the turtles drift with the current. Nevertheless, the additional swimming component does not fundamentally change their dispersion which is mainly driven by the current. Therefore, the overall dispersion of all scenarios remains similar. However, the dispersion differs from one year to the next.

In 2016, the turtles leave the Pacuaré beach, head towards the northern tip of Panama where filtration takes place, part of the current carries the turtles into the gyre and brings them back westwards into the initial bay, in front of the Pacuaré beach. The other part of the turtles continue on their way and go westward to the edge of the Gulf of Darién. From week 3, the first turtles having been to the west, have already gone around the gyre and are coming back to the east while the other turtles going east definitely enter the Gulf of Darién between Panama and Colombia. Figure 4.6 shows that from the fourth week, a third group is formed. Indeed, the currents lead the turtles nortwest, heading to the Gulf of Mexico.
In 2018, after a week, the turtles were already further away and have not enough momentum to pass over the northern tip of Panama. This explain the huge losses made by scenarios A, B, C and F in zone 2. Scenarios D and E, on the other hand, have an additional swimming component, which I assume helped them to avoid stranding in this zone. Regarding dispersion in week 2, it is similar to 2016. Indeed, two groups are formed. One group is forming to return to the gyre of the Bay of Pacuaré and another is moving further east. However, these two groups remain

northward in comparison to 2016. In week 3, they are merging in one big group. Figure 4.7 shows that from week 4, the turtles follow other currents further north and are only beginning to re-enter the gyre near Pacuaré. Unlike 2016, very few turtles enter the Gulf of Darién.

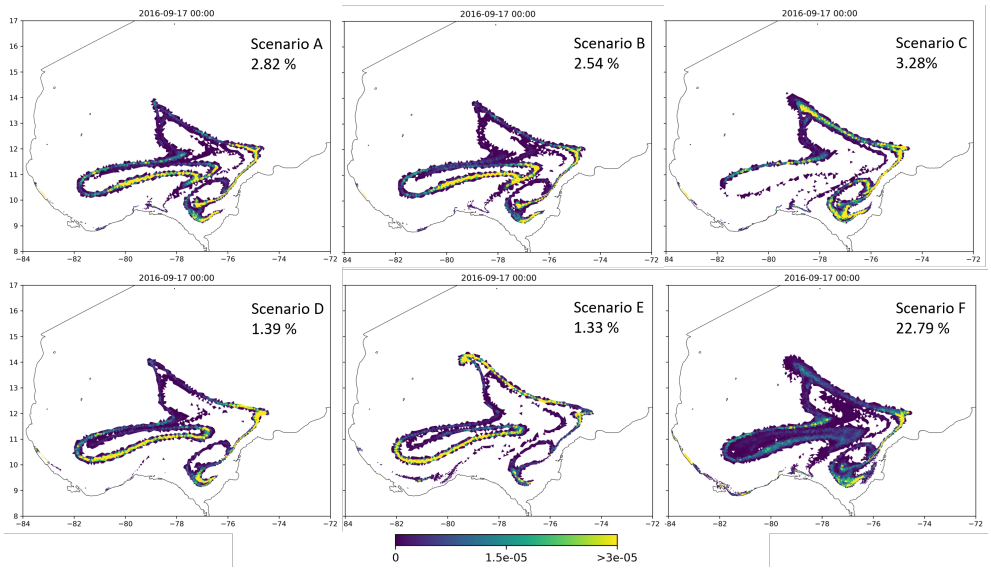

Figure 4.6: Dispersion and probability of presence of turtles on a four weeks simulation from Pacuaré in 2016. The percentage indicates the stranding rate of turtles in the simulation.

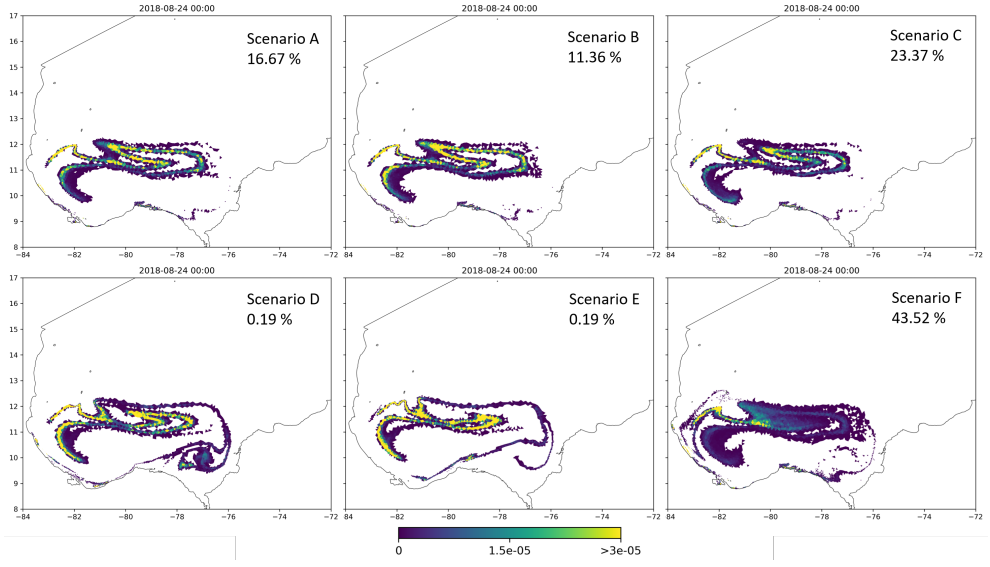

Figure 4.7: Dispersion and probability of presence of turtles on a four weeks simulation from Pacuaré in 2018. The percentage indicates the stranding rate of turtles in the simulation.

4.3.3 End of simulations

In 2016, during week 6, turtles break off from the group in the bay of Pacuaré and go towards the Gulf of Mexico. At the end of the simulation (see Figure 4.8), the group in the bay of Pacuaré and the group in the Gulf of Darién decrease to the benefit of the group north. The passage to the north towards the Gulf of Mexico gradually starts to strengthen and I expect many turtles will leave the area in the following months.

In 2018, the dispersal forms one homogeneous group. From week 4, all the turtles form a loop from the bay of Pacuaré until the north of the Gulf of Darién without entering into this last (see Figure 4.7). Gradually, the turtles rotate, and are distributed between the area of Pacuaré bay and the middle north of the two bays without spreading much more (see Figure 4.9).

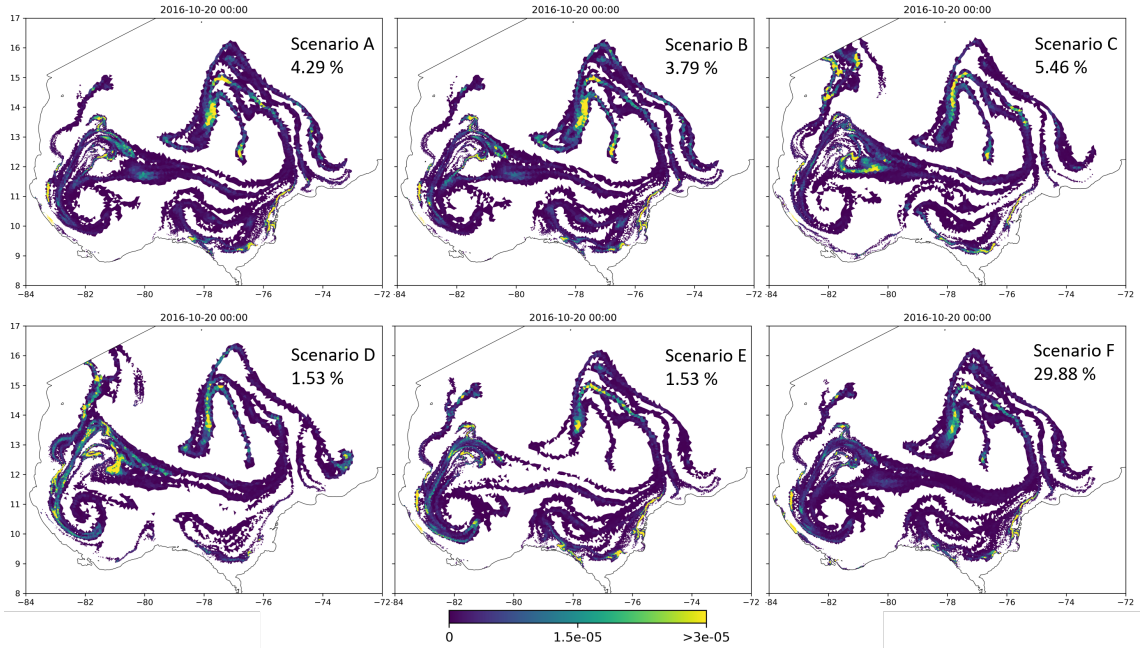

Figure 4.8: Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2016. The percentage indicates the stranding rate of turtles so far in the simulation.

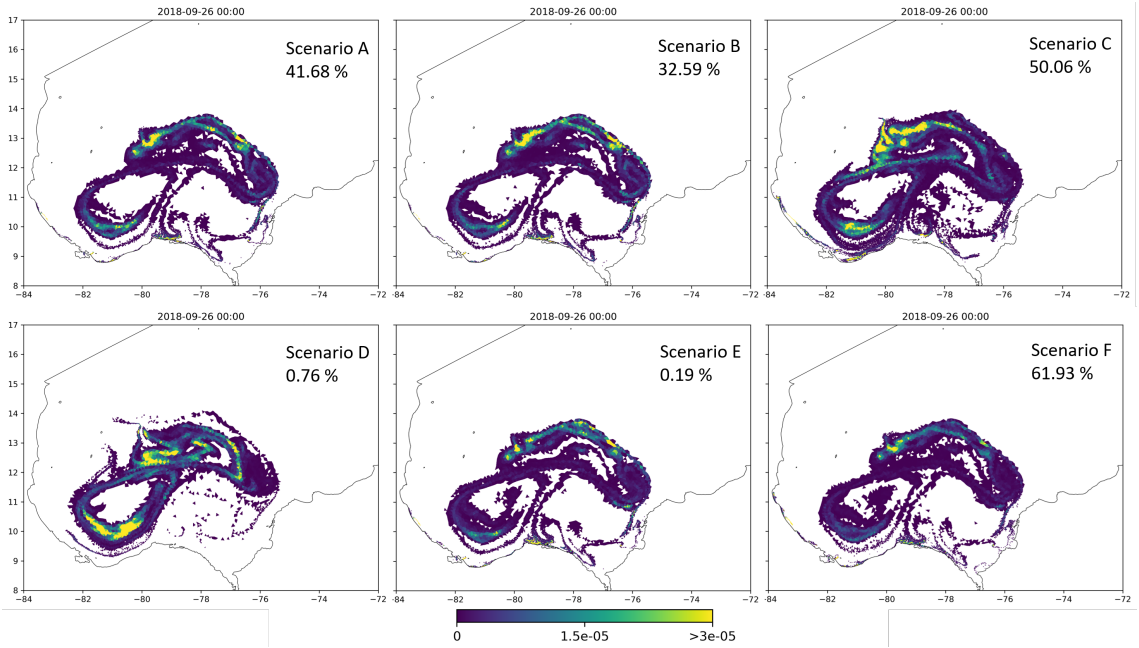

Figure 4.9: Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2018. The percentage indicates the stranding rate of turtles so far in the simulation.

Chapter 5

Discussion

Chapter 5 is divided into four parts. Each part considers one aspect of the results of chapter 4 and previous studies on the subject.

The first part defines the impact of the swimming frenzy parameters, during the first days and on the overall distribution of turtles further on in the simulation. The second part debates the advantage of active swimming over passive drift. For active swimming, the effect of the magnitude and direction are discussed, as well as the particular innate instinct of the turtle. The third part concerns the dispersion of the turtles throughout the two months of simulation, the influence of annual currents, and the possible generalization of these simulations. I also argue about the management of the fisheries and efforts to be made in certain areas. The last part concerns the limitations of my work and the possibilities for further research.

In reading the discussions in this chapter, the reader may wish to turn to the images of simulation results presented from page 74 to 86 in Appendix A for 2016 and Appendix B for 2018. It is recommended to use page 41 as a reminder of the parameterization of each scenario.

5.1 The effect of swimming frenzy behaviour on the overall dispersal

Importance of swimming frenzy on overall dispersal

In order to determine the importance of the early first days on the overall dispersal of turtles, the four scenarios Classic (A), No Stokes (B), Decrease (C) and Random (F) are useful to compare since they have four different swimming frenzy parameters and a similar post frenzy passive drift. Based on my end of simulation illustrations, scenario A, B and C are similar. In fact, the turtles' overall dispersal remains mainly driven by currents with an annual variability depending on the intensity and direction of the current for each year.

Upon closer inspection, several dispersion differences can be identified along the two months journey:

1. The turtles of scenario C don't return to the bay of Pacuaré and tend to stay very dense in the Gulf of Darién until week 6 in 2016, unlike scenarios A and B.

2. The most striking example is scenario F, the turtle randomly hold a same direction between 0 and 180° during the swimming frenzy. The dispersion varies considerably in comparison to the three other scenarios with a much wider area and a remarkable amount of stranded turtles.

3. From one scenario to the other, the stranding percentage differs depending on the stage of the simulation.

Without a doubt, the model predicts that the direction, speed and duration of the swimming frenzy determine the future of the turtles' dispersion. Recently, Diane et al. 2020 confirm these results : "The swimming frenzy as well as variability in oceanic conditions strongly influenced dispersal of virtual hatchlings. Furthermore, variability in oceanic conditions dispersed virtual hatchlings into different areas where threats, like fisheries bycatch, might also influence their survival."

Direction : The linear decreasing hypothesis

The swimming frenzy of scenario C, in which the direction decreases from perpendicular to the waves to in the current, leads to a distribution that brings the turtles closer to the coast. And with strong currents, as in 2018, this distribution causes heavy losses. Hamann et al. 2011 made similar scenarios with the turtles swimming first perpendicular to the current for one hour, and then parallel to the current during the rest of the swimming frenzy.

Questions remain about the turtle's ability to swim and orient itself in a large volume of water as the directions of the current can be different depending on the depth the turtle is at. Indeed, in all the other scenarios, the turtle remains at the surface, feels the effect of the waves and orientates itself against the waves. This, in order to not be carried away and join the coast. The justification is easier. Moreover, according to some observations the turtles swim already one hour against the waves and could easily continue this way (Salmon and Wyneken 1987; Wyneken and Salmon 1992; K. Lohmann and C. Lohmann 1995; Manning et al. 1997). Since my hypothesis based on the field observations of the NGO is not confirmed by numerical modelling and has a higher percentage of turtles stranding than the classical scenario (50.06% vs 41.68% in 2018) , I reject this hypothesis. Therefore, my model suggests a swimming frenzy perpendicular to the waves. But do turtles manage to avoid the effect of the Stokes drift ?

Speed : Stokes drift avoidance hypothesis

The hypothesis of scenario B was first mentioned by Wyneken and Salmon 1992 and several observations were made afterwards (Spotila and Tomillo 2015). Many small, repeated and shallow dives take place during swimming frenzy and it would be conceivable that through this the turtle innately could defend itself against the Stokes drift which clearly disadvantages the turtles dispersion. My model suggests that avoiding Stokes drift is equivalent to having a stronger swimming component against the waves during swimming frenzy and indeed, this greatly benefits the dispersion later on. Compared to scenario A, both for 2016 and 2018, the simulations confirm a better future dispersal. However, I based my hypothesis solely on observations made by Wyneken and Salmon 1992; Spotila and Tomillo 2015. Indeed, the ability of hatchlings to avoid the Stokes drift is unproven. A field study on how the Stokes drift affect the turtles' behaviour and its influence considering the turtles' depth would be interesting to confirm this hypothesis.

5.2 The importance of active swimming

Passive drift versus active hypothesis

My simulations confirm the first results of Wildermann et al. 2017 on the subject and prove that even a small component added to the turtle's passive behaviour increases drastically chances of survival and increases success of dispersal. Especially for 2018, the unexpected difference between the active hypothesis (scenario D and E) and the passive drift hypothesis (scenario A,B and C) shows that the turtle's active behaviour is almost mandatory. Without this active swimming, up to half of the turtles would die prematurely. Whereas in 2016, the active behaviour does not have as much influence, it is still better than passive drifting. Moreover, the two years, 2016 and 2018, have different intensities and directions of currents. I assume that the stronger the currents along the coast of Pacuaré are, the more the turtle needs this active behavior and its importance varies from one year to the other. The further we move forward in time, the more we can prove that turtles are active at an earlier stage in their life. In my opinion, active behaviour, no matter how small the turtles are, is essential for turtles even as young as a few days to find food, comfortable habitats or to avoid stranding on beaches.

Aside from the stranding rate on the beaches, an active swimming component (scenario D and E) does also have an impact on the dispersion of turtles. Compared to the Classic scenario (A), in 2016, the Gulf of Darién is less dense in turtles and much more turtles leave the Caribbean basin to go towards the Gulf of Mexico. In 2018, despite a significant difference in stranding rate, the active swimming did not have as big an impact since the dispersion remains homogeneous along the simulation.

Magnitude of the active swimming

The results show that, no matter the magnitude of the active swimming, 0.04 m/s or 0.08 m/s, the success rate is not significantly higher. We conclude, regardless of the direction and intensity of the currents, that a small active swimming component of 0.04 m/s is sufficient to increase drastically the turtles' dispersion success rate. Questions remain about the turtle's ability to swim in a continuous constant manner during all the post frenzy simulation. An alternative would be that the turtle adopts a passive drift unless close to the coasts, then, engages in a much more important active behavior to return again offshore. Moreover, similarly to the swimming frenzy (Wyneken and Salmon 1992; Dalton 1979), the turtle probably rests at night to avoid predators and because very little food is visible.

Direction of the active swimming

Evidence suggests that hatchlings use three different sets of cues to maintain orientation during their migration offshore. They initially use the visual light of the moon or sun reflecting on the sea when leaving their nest. Second, the detection of wave direction during the swimming frenzy (Wyneken and Salmon 1992; Spotila and Tomillo 2015). The turtles, being without landmarks in the ocean, and assuming that they already orient themselves against the waves during swimming frenzy, it seems consistent that the turtle reuses waves for orientation throughout post-frenzy behaviour. Finally, from a certain aget, they use a combination of visual and magnetic signals to orient themselves in the open ocean (K. Lohmann and C. Lohmann 1996; Avens and K. Lohmann 2003; Hays et al. 2010; K. Lohmann et al. 2013).

The innate instinct

Sea turtle hatchlings have one of the most effective innate behaviour of all animals. They hatch and during several hours, dig their way out of the buried hatchery. They instinctively time themselves to emerge at night when they are the safest. Once at sea, the turtle has a mysterious innate instinct that increase its chances of survival by swimming in a specific direction. As shown a contrario in scenario F, the swimming during the first hours will determine their dispersion. Indeed, adopting a random direction as in scenario F, from their birth beach would get only 40 to 70 % of the population to survive, leaving the rest stranded on the beaches. This instinctive behaviour guides the swimming frenzy period, get the turtles out of the coastal predator infested waters and helped them reach the main offshore currents (Salmon et al. 2009).

Strandings

The coast of Pacuaré beach between Costa Rica and Panama goes from Tortuguero, Limon, Chiriquí beach to Bocas del Toro. Studies estimates up to 15,000 nests of leatherbacks each year in this region (Eckert et al. 2020). 500,000 virtual turtles were released during my simulations in order to have a fairly representative probability of turtle presence. The future of each turtle is uncertain and can vary greatly from one turtle to another. The five main turtle stranding areas have been defined in Chapter 4. In a year with very strong currents, turtles would come ashore in large numbers on the Panamanian coast, in zone 2. However, we have found no reports of strandings of turtles near the Panamanian and Costa Rican coasts. The turtles may go undiscovered, or be eaten by birds or other predators once close to the coast. However in 2018, assuming a passive drift, several hundreds or even thousands of hatchlings would have stranded according to scenario A. This further increases the likelihood that the turtle has an active swimming behaviour.

5.3 Dispersal of turtles from Pacuaré on a two months simulation

The main objective of this thesis was the dispersal of turtles from Pacuaré on a two months simulation. The findings are discussed here.

As the simulation progresses, the turtles find themselves further east along the coasts of Costa Rica, Panama, Columbia, the Gulf of Darién and the gyre in front of Pacuaré. Indeed, currents bring the turtles until the southern Caribbean major upwelling system that brings nutrients to the surface such as phytoplankton, zooplankton and chlorophyll. The upwelling system extends from the Isthmus of Panama, Colombia and Venezuela (Eckert et al. 2020). It is the main nutrients source that support the biological productivity in this oligotrophic sea (Digna et al. 2013). However, feeding areas for turtles are still not well understood, especially in the southern Caribbean where only few long-term projects have gathered information (Barrios-Garrido et al. 2020).

My simulations suggest that currents bring progressively the turtles towards the northwest. Indeed, turtles reaching quickly the Gulf of Darién, later tend to disperse further north, leaving it with a low density. Turtles that manage to escape from the gyre in front of Pacuaré will tend to go further north as well. All turtles are gradually leaving the coasts to go towards the north of the Caribbean Sea towards the Gulf of Mexico. The Caribbean coastline of Central America from Mexico to Panama is 3875 km long, contains the Mesoamerican Barrier Reef System, and provides countless estuaries, nearshore islands, coral reefs, deep-ocean habitats and foraging areas for sea turtles (Eckert et al. 2020). By staying in this region, the turtle should have a tolerable temperature, a sufficient food supply, and therefore a higher survival ratio as long as it avoids the poaching and intensive fisheries that are very common.

After a few months or years, I suppose, almost all turtles should have left the domain and go towards the Gulf of Mexico. Indeed, the turtles present in the gyre near the coasts of Costa Rica and Panama remain present until the end but with a lower density over time, consolidating the northward movement to the north of the Caribbean Sea. The Gulf of Mexico is a known multi species migratory corridor and foraging zone. Some post nesting leatherback females from Costa Rica were observed there (Eckert et al. 2020). Young turtles have to strengthen for a few years by staying in this area with favourable temperatures and feeding grounds. Indeed, if the turtles catch too early the Gulf Stream and leave the north Caribbean region and the Gulf of Mexico to go further north towards the Florida and Canada coasts, the low temperatures at these latitudes will kill the turtles too young and weak to survive.

My simulations give the probability of presence, of leatherbacks born on the beach of Pacuaré, for a specific time and location. The dispersion from one year to the other varies according to the oceanic conditions. A global simulation in order to generalize the dispersion for future years is needed. The aim is to prevent the fishing of leatherbacks. For 2016 and 2018, the major density of turtles after one month is between longitude -82 and -75 and latitude 9 and 13. After more than two months, the dispersion becomes more and more extensive and the high density area is between longitudes -84 and -74 and latitudes 9 and 15. There is little risk of fishing a leatherback turtle from Costa Rica or Panama beyond longitude -74.

Off the coasts of Nicaragua, Costa Rica, Panama and in the Bay of Pacuaré is a gyre that doesn't vary from year to year. Along the coasts of Costa Rica and Panama, the direction of the current is always towards the southeast. Since it is the same current each year, a generalization of the dispersion of the turtles from Pacuaré to the nesting beaches located in the south of Costa Rica and the north of Panama, which represent 10,000 more nests, could be possible. Indeed, the turtles will presumably, be caught in the same currents and thus form a similar dispersion. Furthermore, it is very likely that leatherbacks from Puerto Rico, Martinique and Trinidad and Tobago reach the region of Western Caribbean Sea as well as the sea currents are towards the northwest. For the probability maps of leatherback presence to be accurate, they have to be overlapped with the probability maps of other nesting beaches in the Caribbean region.

5.4 For further research

The development of nano-tags to track smaller turtles is essential to confirm the numerical simulations. Indeed, the development, notably by Mansfield et al. 2012 and Scott et al. 2014, put us on the way of discovering the turtle's behaviour in the mysterious period of the lost years. The study highlights the importance of considering active behaviour when simulating the early dispersal of marine turtles. There is no doubt that both similar simulations on early dispersal and tracking neonates with tags, will greatly enhance our understanding about the least known and most deadly period of the turtle's life. One of my limitations would be that my model doesn't consider a discontinuous swimming frenzy as suggested by (Wyneken and Salmon 1992) during day and night. Moreover, no field observations are provided for hatchlings in the open sea. Observations of stranded hatchlings or catches of hatchlings would confirm or refute my hypothesis.

As explained before, evidence suggests that hatchlings use three different sets of cues to maintain orientation during their migration offshore, visual cues, waves and magnetic field. Experiments have demonstrated that turtles can change their orientation based initially on waves to a an orientation by a magnetic compass. Adult sea turtles use the earth's magnetic field as a source of world-wide positional information. The navigation behaviour of sea turtles is linked to a complex interplay between ocean circulation, visual cues and geomagnetic dynamics (Avens and K. Lohmann 2003; Putman et al. 2015). Some factors have never been tested like the influence of sound, smell or wind direction on the turtles' movement.

For further research and especially to avoid fishing leatherback hatchlings in the Caribbean Sea, a model from May, the start of the birth period, until April of the following year, covering all leatherback nests in the Caribbean Sea should be analyzed. Indeed, the main leatherback nesting area are Puerto Rico, Trinidad and Tobago, Martinique, Costa Rica and Panama. The simulation might consider differences in the amount of virtual turtles depending on the importance of the nesting beaches. Furthermore, the model could include departures at different times and locations and would furnish an almost exact dispersion and probability of presence at a given time of the year.

For further research, this study confirms the strong influence of annual variability of oceanic conditions (Okuyama et al. 2009; Hays et al. 2010; Putman et al. 2012) and highlights the importance to take into account two different years. For the first months of a turtle's life, future models would be greatly enhanced by considering the inter annual influence and the active component since these factors have a great importance on the turtle's dispersal.

Chapter 6

Conclusion

After observing a hatchling turtle crawling to the water, the hatchling will only be seen again after ten years, when it returns to the same beach to lay eggs as an adult. During this poorly documented and unknown period, "the lost years", the turtle must struggle to survive. The early life stage determine the future dispersion of turtles and can help their conservation. Since recently, there is increasing evidence that young sea turtles do not drift in a purely passive manner and that an additional swimming component should be added. This knowledge gap has narrowed to the first year of the early life of juvenile sea turtles.

This research provide a global review on the behaviour pattern of turtles during their early dispersal, particularly, in the southwest region of the Caribbean Sea from the nesting beach of Pacuaré, Costa Rica. The offshore distribution of the leatherback turtles was favoured by the local oceanic conditions offshore of the coast of Costa Rica, Panama, Columbia and more widely, in the gyre in the Bay of Pacuaré and the Gulf of Darién. The oceanic conditions vary from one year to the next which influence the turtles dispersal. The northward movement that brings the turtles gradually towards the north of the Caribbean Sea and the Gulf of Mexico is common to both years studied. Moreover, no turtles are going beyond longitude -74. However, in 2016, the currents force progressively a more extensive dispersion with turtles already leaving the domain towards the Gulf of Mexico after two months. In contrast, the 2018 oceanic conditions favour a more homogeneous dispersion with all the turtles staying in the Southwestern Caribbean but with reduced densities in the Gulf of Darién.

The swimming frenzy parameters, duration, speed and direction, also play an important role in the distribution of hatchlings during their two first months of life. According to my model, the widespread classic scenario of a three to six days swimming frenzy with a direction against waves is the most plausible. However, regarding speed, the turtle's ability to avoid Stokes drift by making small dives during swimming frenzy could lead to a better dispersion and requires further research.

After swimming frenzy, the active swimming behaviour of the turtles have strong effects on their survival rates depending on the oceanic conditions. Indeed, the model suggests that **post frenzy swimming efforts could bring the survival rate from 58.32 % without active component to 99.81 % with an active component**. Furthermore, the magnitude of this active component does not have a significant importance. In fact, considering the survival rate, the difference between an 0.04 m/s and an 0.08 m/s active component vary from 0% in 2016 to 0.57% in 2018. **These results highlight that even a small active component could have significant influence on the success of the turtles dispersal.** As explained in chapter 5, the supposed direction of the turtle as being opposed to the waves has never been verified but seems the most probable. The model draw robust conclusions about the ability of the turtles to be active in current even during their first months at sea. Their direction and intensity could be important parameters to consider in future studies of leatherback turtle dispersal.

This research also underlines the necessity of using hydrodynamical models to study the behaviour of turtles. Whether during swimming frenzy, the lost years or for turtle migrations during their lifetimes, numerical models will help modelling habitat dispersal and better understanding the distribution of populations in order to prevent the disappearance of declining populations and ensure the future of stable populations. The combined knowledge about the species biology and field data as well as a high resolution numerical model will enhance the comprehension of the influence of the changing oceanic conditions on this endangered and highly migratory species.

Appendix A

Simulation results for 2016

A.1 Scenario A

The 'Classic" scenario has no great particularity, it is the most probable and widespread scenario according to previous studies. In this scenario, I chose a swimming frenzy scenario where the turtles swim against the waves, represented by the Stokes drift. After the swimming frenzy, the turtle is drifting passively.

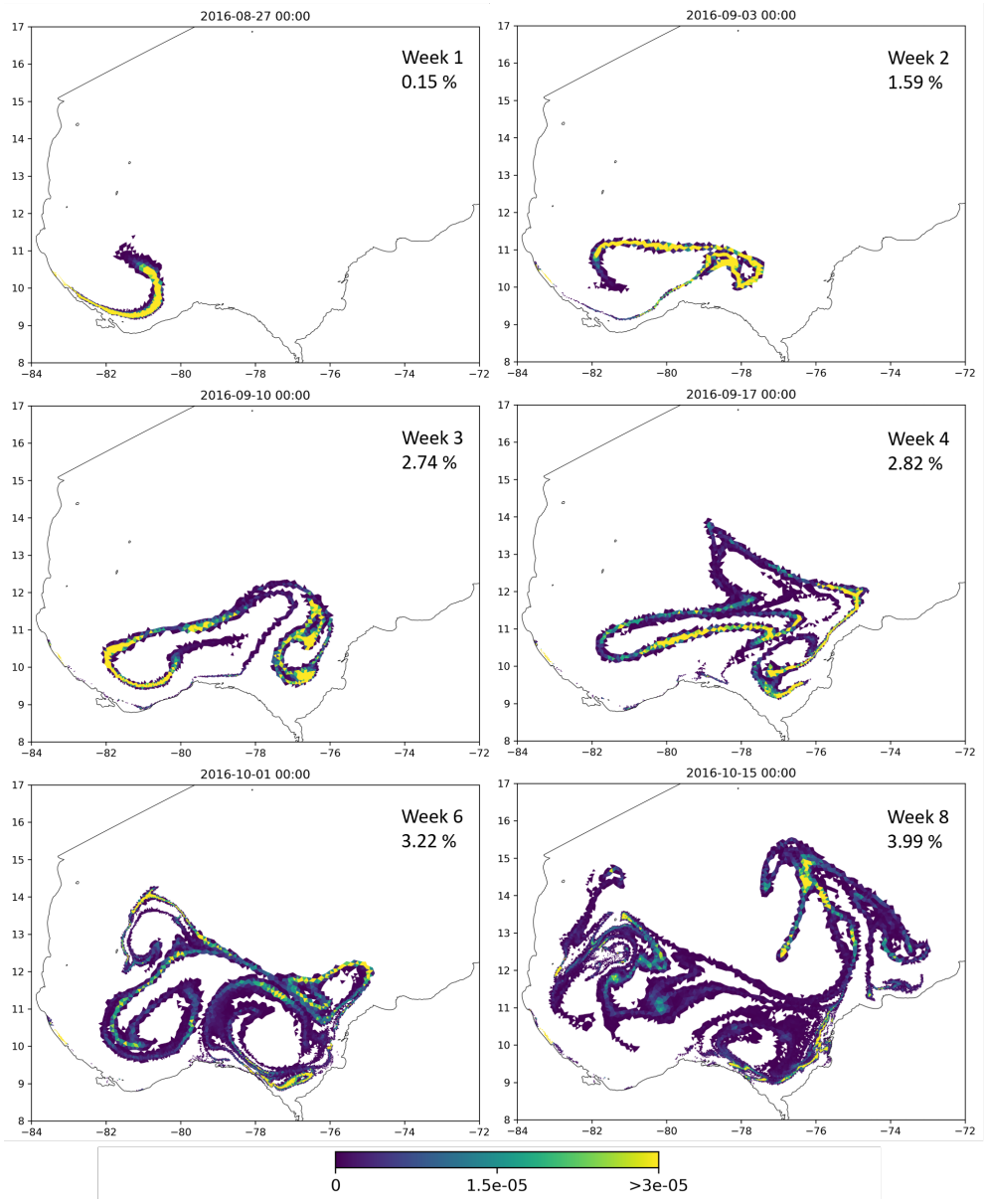

Figure A.1: Scenario A. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2016. The percentage indicates the stranding rate of turtles so far in the simulation. The percentage indicates the stranding rate of turtles so far in the simulation.

A.2 Scenario B

The "No Stokes" scenario is very similar to scenario A. However, according to some observations (Wyneken and Salmon 1992; Spotila and Tomillo 2015), the successive shallow dives that the turtle makes during swimming frenzy is useful to avoid the effect of the Stokes drift. Indeed, I assume the turtle returns to the surface to breathe and orient itself against the waves and then dives to avoid the effect of the Stokes drift that bring it back to the coast.

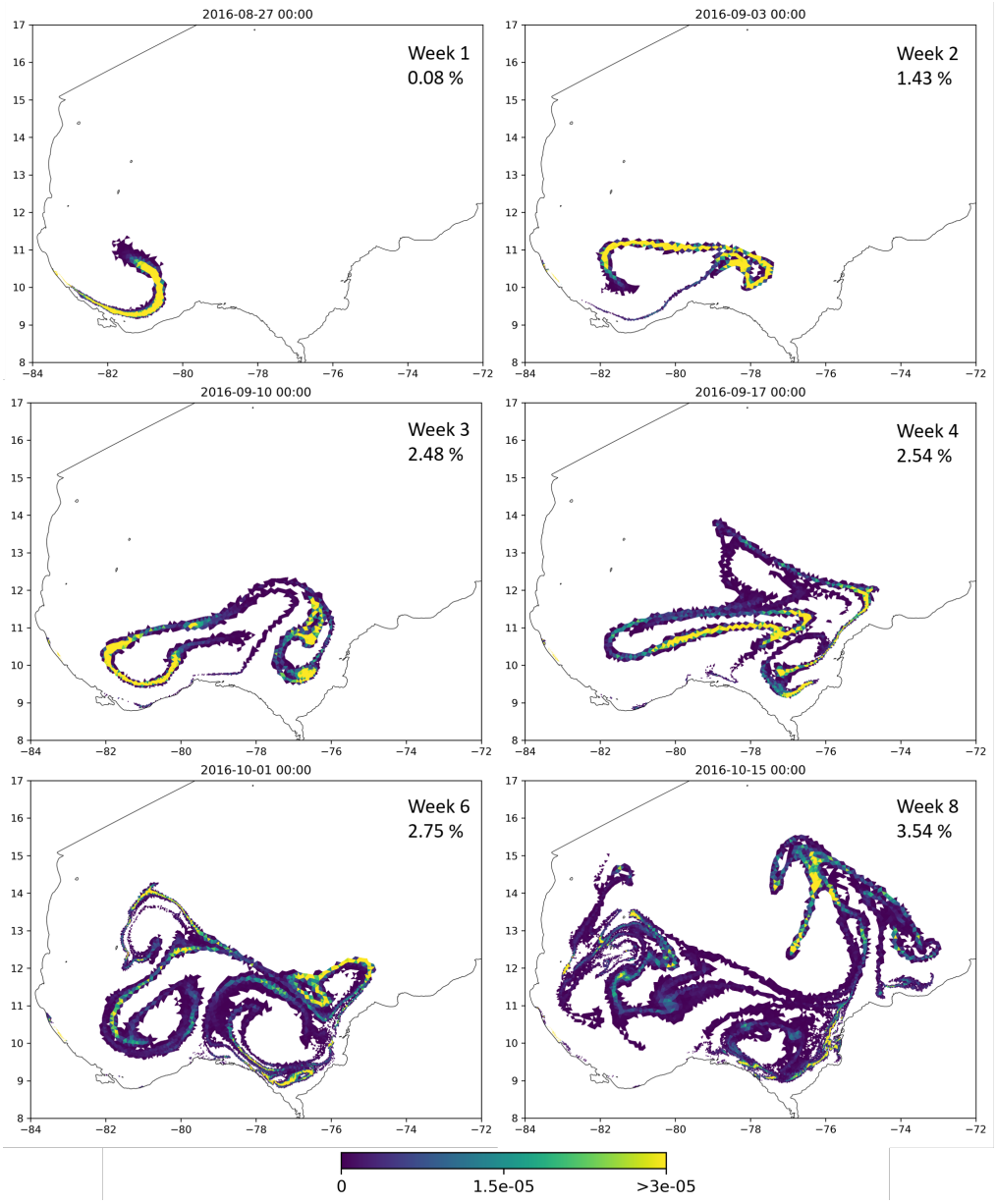

Figure A.2: Scenario B. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2016. The percentage indicates the stranding rate of turtles so far in the simulation.

A.3 Scenario C

The "Decrease" scenario shows whether it is possible for the turtle to swim perpendicularly to the beach and then linearly decrease its direction to reach the direction of the current at the end of the swimming frenzy. This behaviour can be extrapolated from the different observations made during the 80 minutes of turtle tracking in 2016. Similarly to scenario A, the turtle is drifting passively after swimming frenzy.

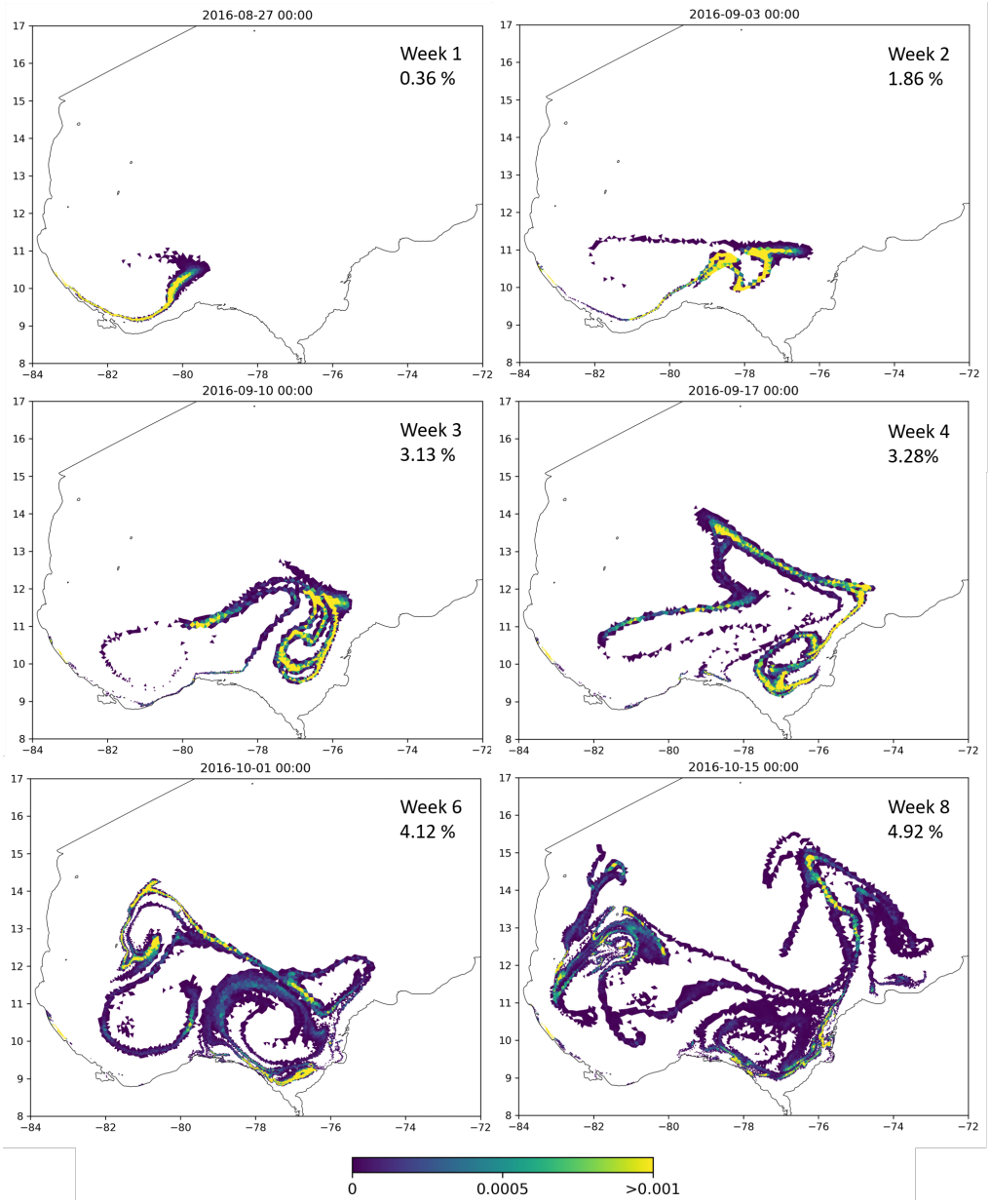

Figure A.3: Scenario C. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2016. The percentage indicates the stranding rate of turtles so far in the simulation.

A.4 Scenario D

The "Active swimming 1" scenario is the same as Scenario A with a little constant active speed of 0.04 m/s added after the swimming frenzy and for the rest of the simulation. I presumed that the direction of the active swimming is against waves (or Stokes drift). In my opinion, at this early life stage, they don't use magnetic field yet and their only visual cues are the waves. Since the turtle is near the surface, it is easy for it to locate itself in front of the waves.

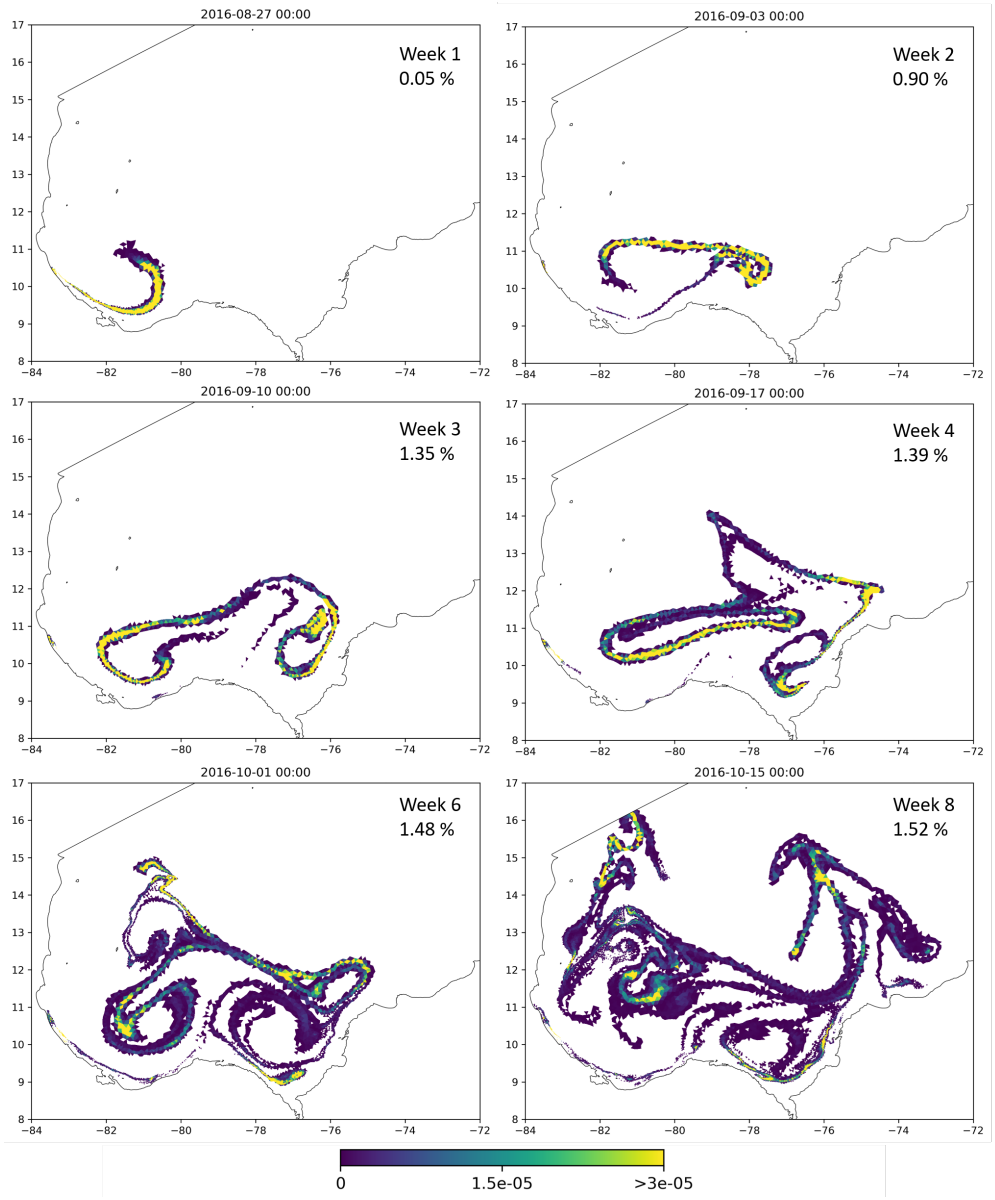

Figure A.4: Scenario D. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2016. The percentage indicates the stranding rate of turtles so far in the simulation.

A.5 Scenario E

The "Active swimming 2" scenario is the same as Scenario A with a little constant active speed of 0.08 m/s added after the swimming frenzy and for the rest of the simulation. I presumed that the direction of the active swimming is against waves (or Stokes drift). In my opinion, at this early life stage, they don't use magnetic field yet and their only visual cues are the waves. Since the turtle is near the surface, it is easy for it to locate itself in front of the waves.

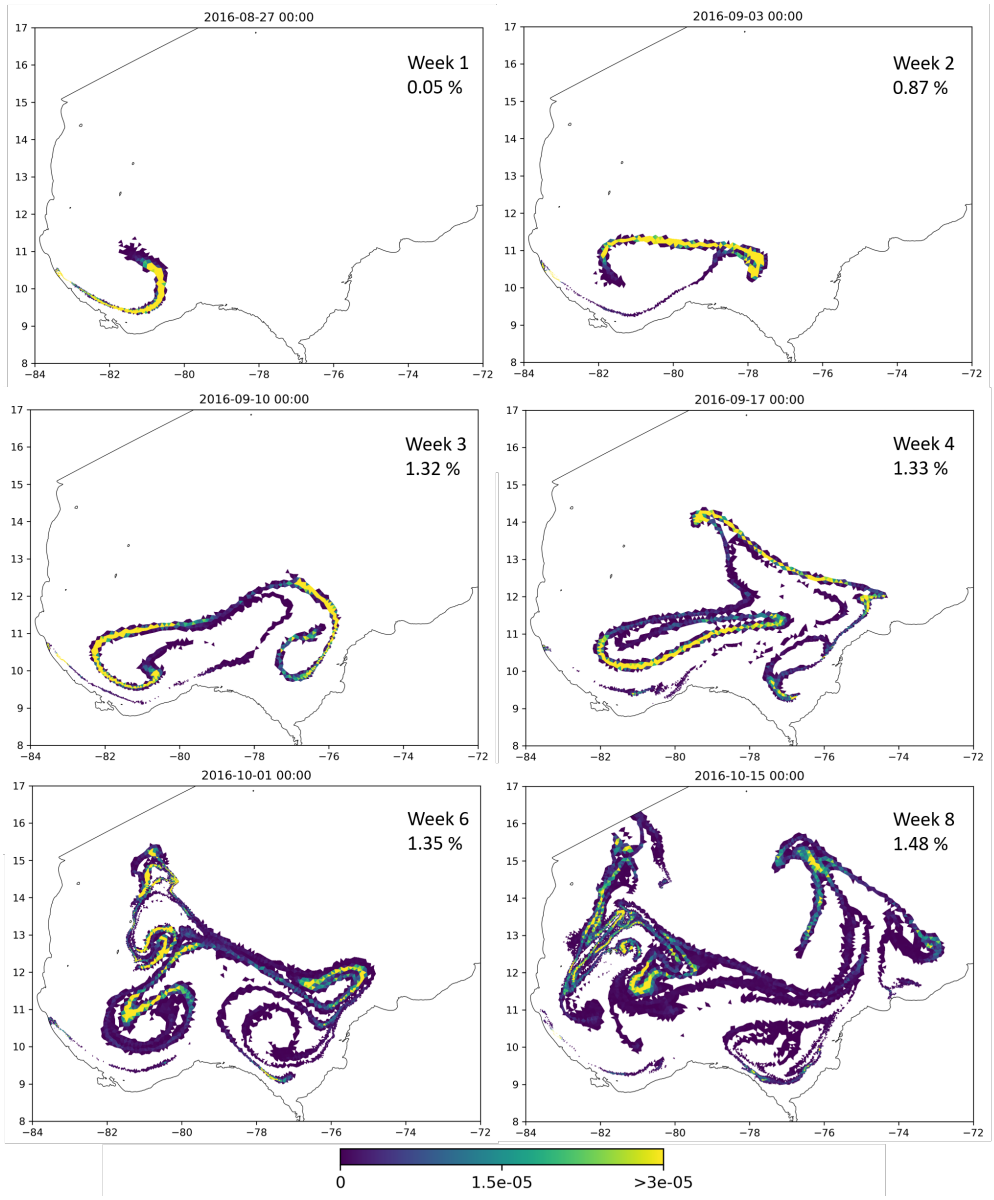

Figure A.5: Scenario E. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2016. The percentage indicates the stranding rate of turtles so far in the simulation.

A.6 Scenario F

The "Random" scenario is a base scenario that I compare to the others. Indeed, this scenario considers a random and constant direction chosen between 0 ° and 180 ° from the beach. The turtle keeps this direction during all the swimming frenzy. The purpose of this scenario is to demonstrate the innate instinct of the turtles to orientate themselves and have the best chance of survival. It is a basis for comparison.

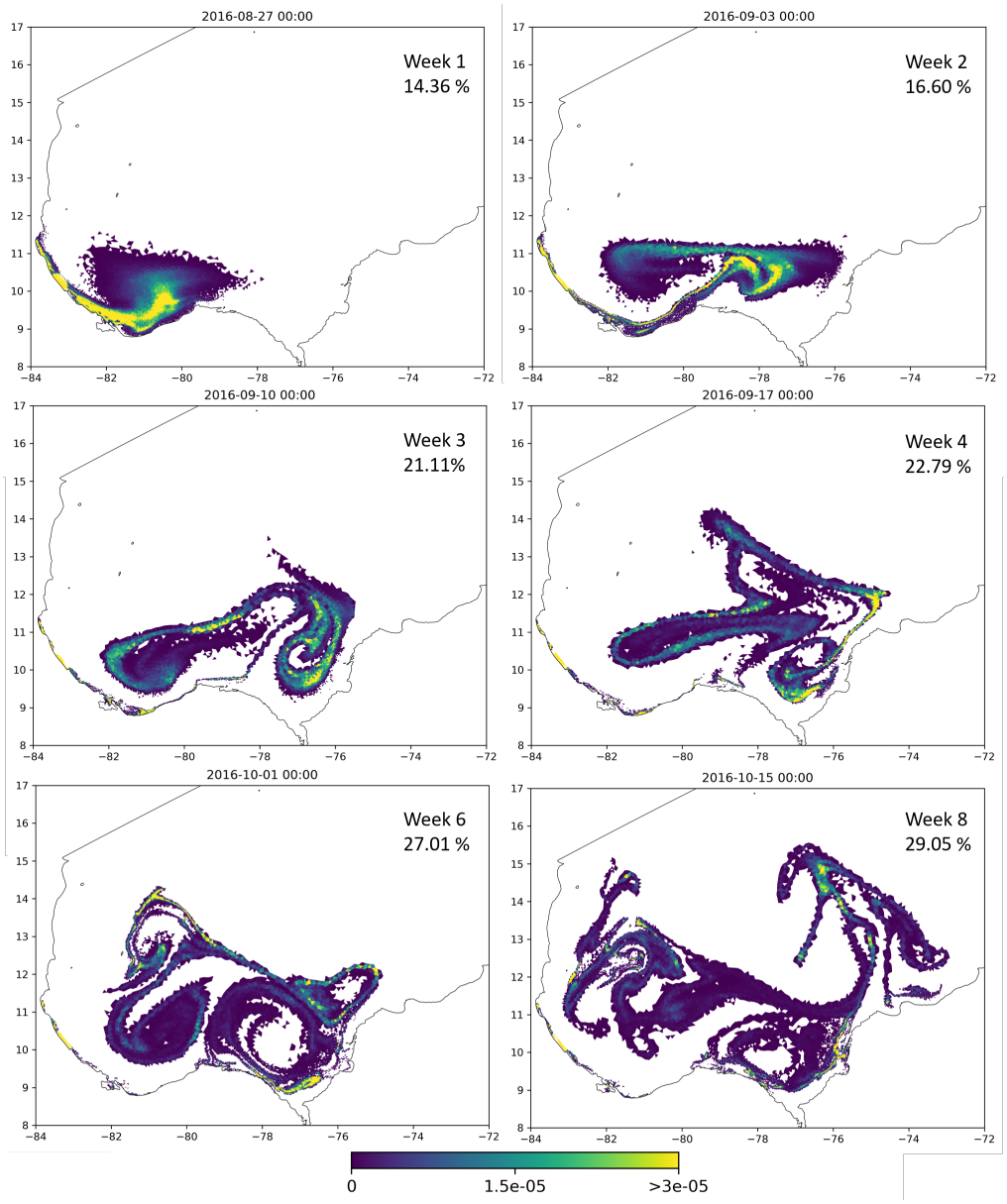

Figure A.6: Scenario F. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2016. The percentage indicates the stranding rate of turtles so far in the simulation.

Appendix B

Simulation results for 2018

B.1 Scenario A

The 'Classic" scenario has no great particularity, it is the most probable and widespread scenario according to previous studies. In this scenario, I chose a swimming frenzy scenario where the turtles swim against the waves, represented by the Stokes drift. After the swimming frenzy, the turtle is drifting passively.

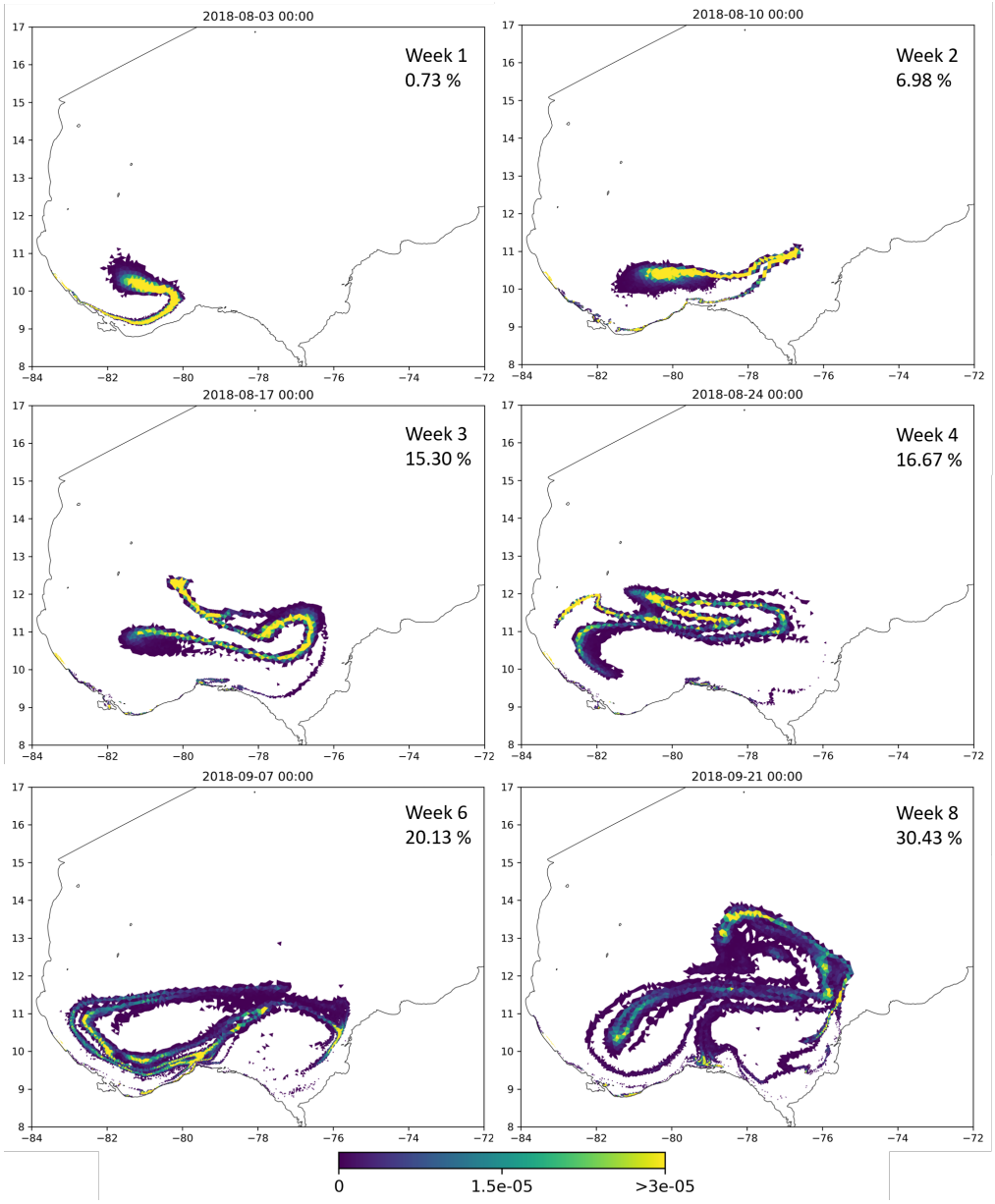

Figure B.1: Scenario A. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2018. The percentage indicates the stranding rate of turtles so far in the simulation.

B.2 Scenario B

The "No Stokes" scenario is very similar to scenario A. However, according to some observations (Wyneken and Salmon 1992; Spotila and Tomillo 2015), the successive shallow dives that the turtle makes during swimming frenzy is useful to avoid the effect of the Stokes drift. Indeed, I assume the turtle returns to the surface to breathe and orient itself against the waves and then dives to avoid the effect of the Stokes drift that bring it back to the coast.

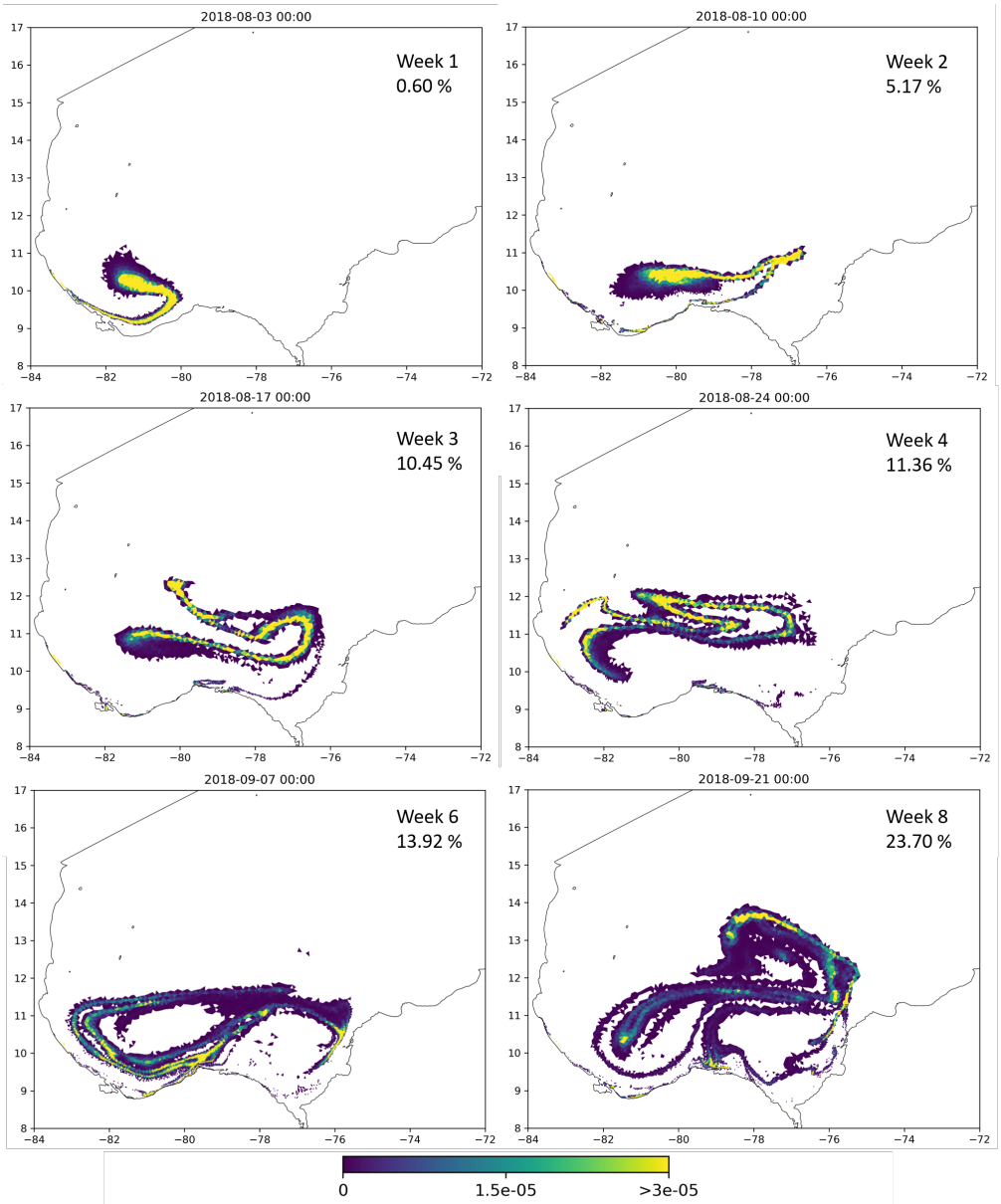

Figure B.2: Scenario B. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2018. The percentage indicates the stranding rate of turtles so far in the simulation.

B.3 Scenario C

The "Decrease" scenario shows whether it is possible for the turtle to swim perpendicularly to the beach and then linearly decrease its direction to reach the direction of the current at the end of the swimming frenzy. This behaviour can be extrapolated from the different observations made during the 80 minutes of turtle tracking in 2016. Similarly to scenario A, the turtle is drifting passively after swimming frenzy.

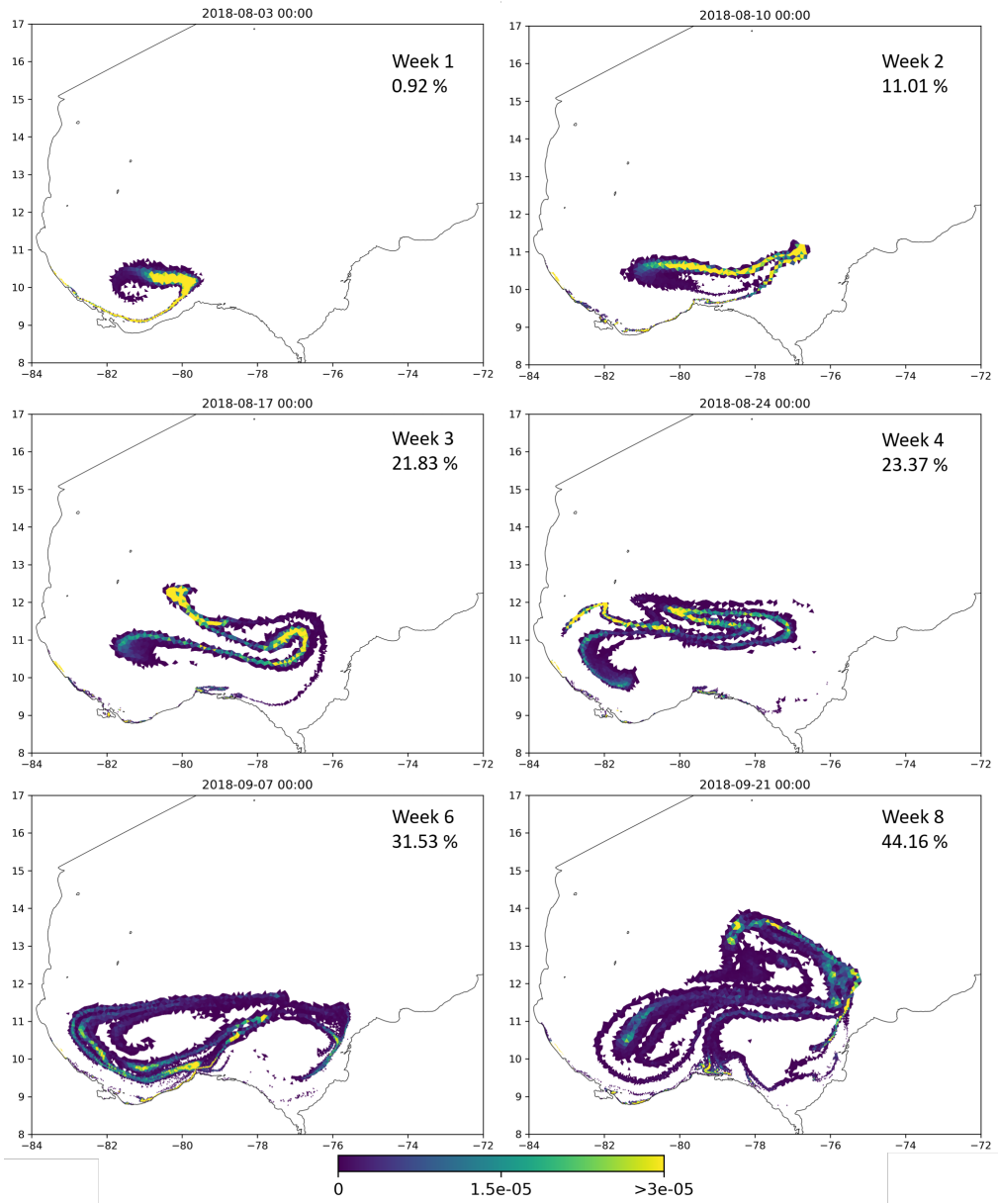

Figure B.3: Scenario C. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2018. The percentage indicates the stranding rate of turtles so far in the simulation.

B.4 Scenario D

The "Active swimming 1" scenario is the same as Scenario A with a little constant active speed of 0.04 m/s added after the swimming frenzy and for the rest of the simulation. I presumed that the direction of the active swimming is against waves (or Stokes drift). In my opinion, at this early life stage, they don't use magnetic field yet and their only visual cues are the waves. Since the turtle is near the surface, it is easy for it to locate itself in front of the waves.

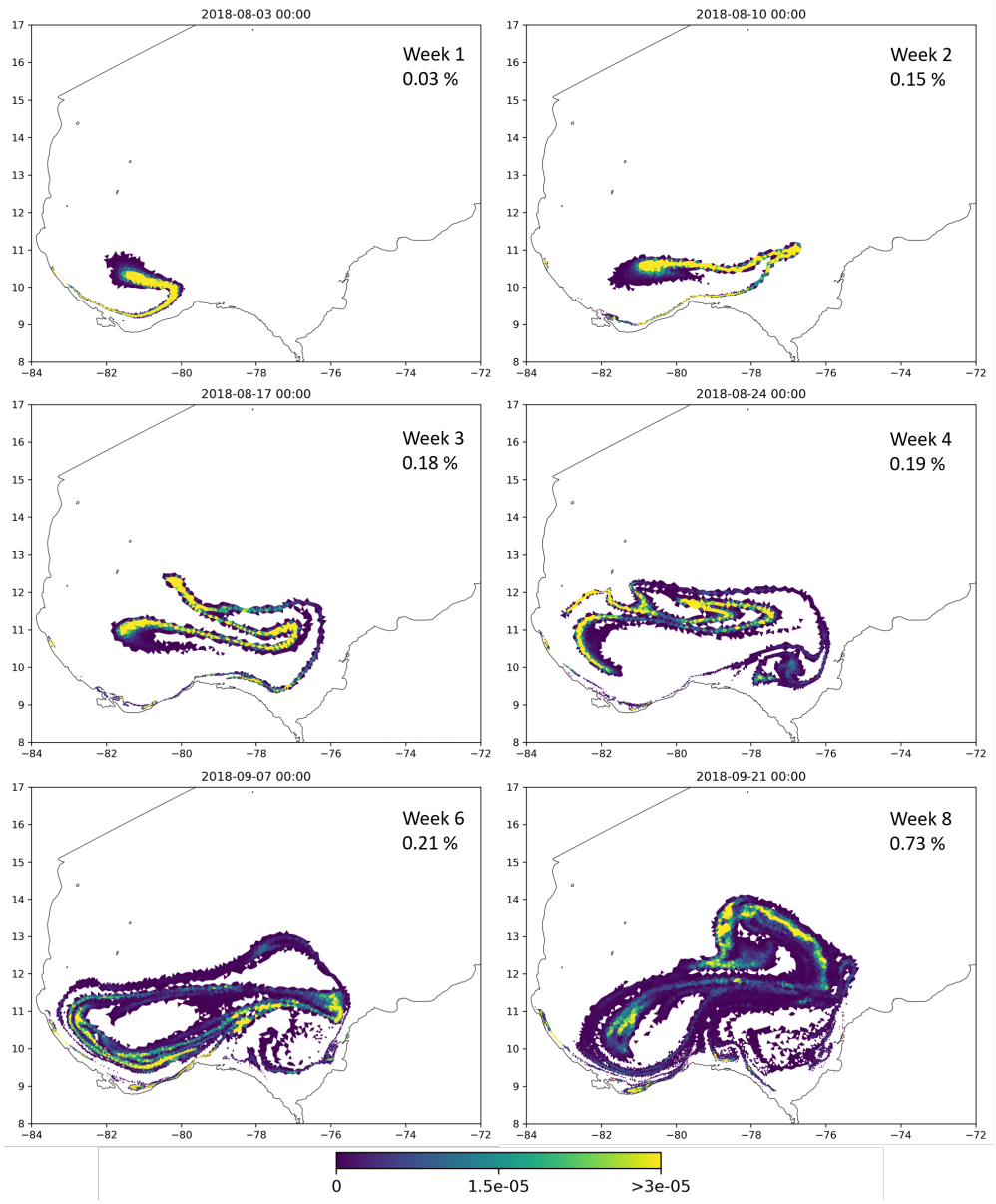

Figure B.4: Scenario D. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2018. The percentage indicates the stranding rate of turtles so far in the simulation.

B.5 Scenario E

The "Active swimming 2" scenario is the same as Scenario A with a little constant active speed of 0.08 m/s added after the swimming frenzy and for the rest of the simulation. I presumed that the direction of the active swimming is against waves (or Stokes drift). In my opinion, at this early life stage, they don't use magnetic field yet and their only visual cues are the waves. Since the turtle is near the surface, it is easy for it to locate itself in front of the waves.

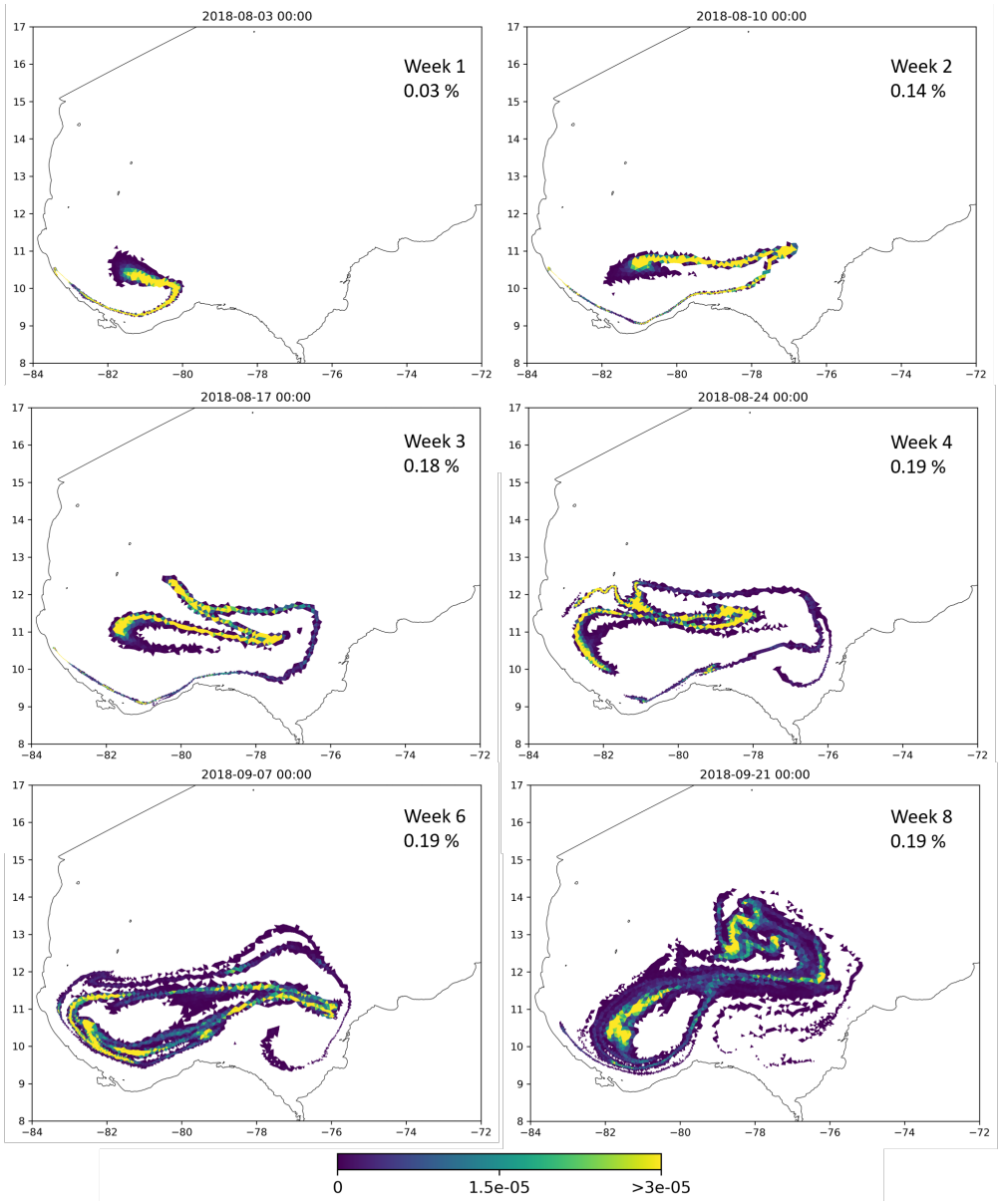

Figure B.5: Scenario E. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2018. The percentage indicates the stranding rate of turtles so far in the simulation.

B.6 Scenario F

The "Random" scenario is a base scenario that I compare to the others. Indeed, this scenario considers a random and constant direction chosen between 0 ° and 180 ° from the beach. The turtle keeps this direction during all the swimming frenzy. The purpose of this scenario is to demonstrate the innate instinct of the turtles to orientate themselves and have the best chance of survival. It is a basis for comparison.

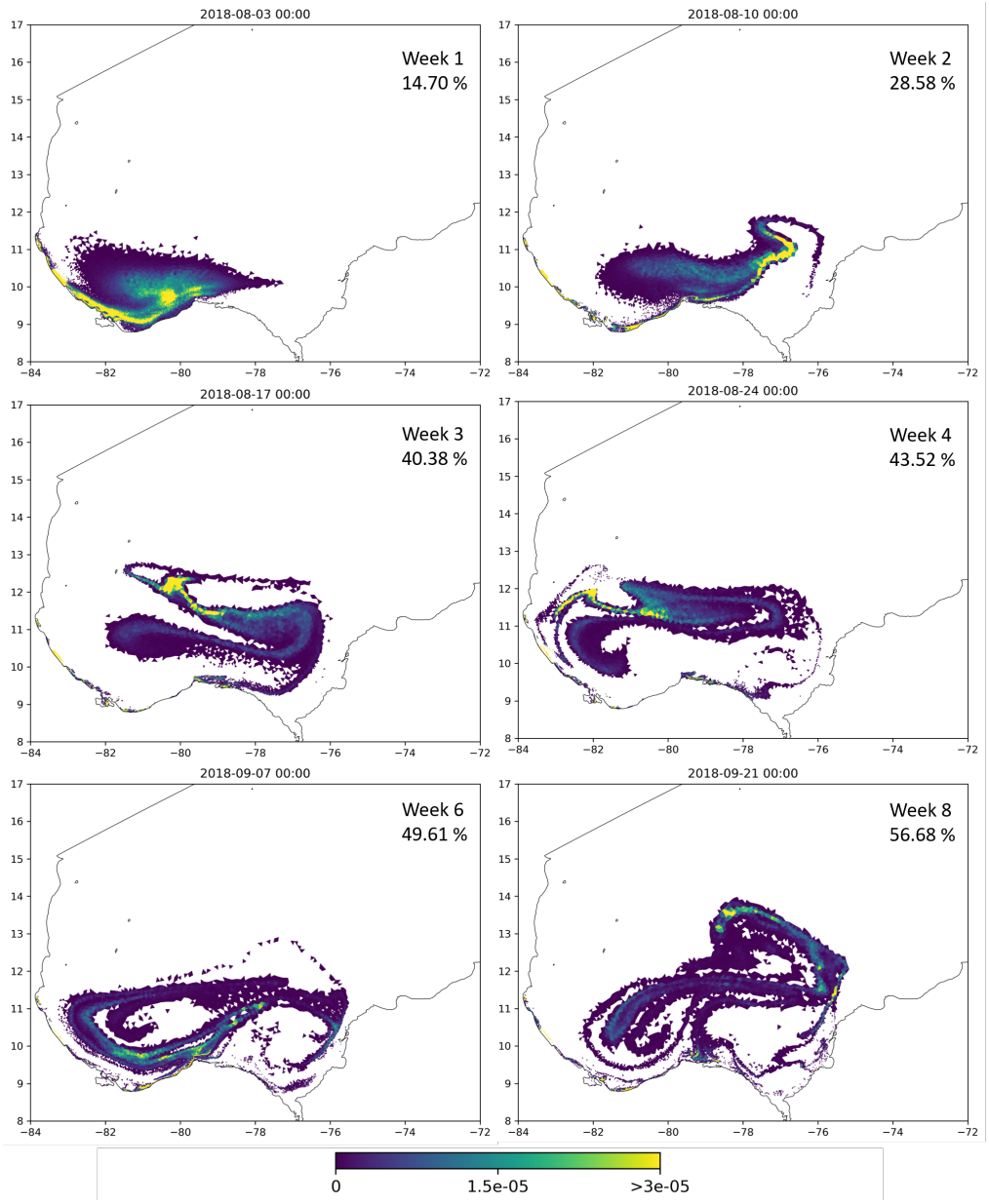

Figure B.6: Scenario F. Dispersion and probability of presence of leatherback hatchlings on a two months simulation from Pacuaré, Costa Rica in 2018. The percentage indicates the stranding rate of turtles so far in the simulation.

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