Movements and Behavior of the East Pacific Green Turtle (*Chelonia mydas*) from Costa Rica

A Dissertation

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by

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Dedication

To all the people that walk sea turtle beaches every night.

Para la gente que todas las noches patrulla playas de tortugas.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Movements and Behavior of the East Pacific Green Turtle (*Chelonia mydas*)
from Costa Rica

Gabriela S. Blanco

Supervisor: James R. Spotila, PhD

I attached satellite transmitters to study the movements and behavior during internesting and migration of East Pacific green turtles nesting on Nombre de Jesús and Zapotillal. Prior to transmitter attachment we preformed an ultrasound scan to determine the turtle's reproductive status. I obtained information on geostrophic surface currents to simulate the dispersion of hatchlings emerging from Nombre de Jesús. I determined the Estimated clutch frequency ($ECF_{U:}$ mean ± SD) 5.13 ± 1.32 using ultrasound, which was an effective technique to determine the reproductive effort of turtles. Turtles spent the 12 day internesting period in the nearby waters off the nesting beach using mainly an area of 4.5 km^2. Depths of dives and depth of water in the area indicated that the turtles dove to the bottom to rest during the day and rested at the surface during the night. After the nesting season, some turtles moved to their foraging areas in Gulf of Papagayo and the Santa Elena Bay, close to the Gulf of Fonseca, and in inshore waters of Panama. During migration the turtles dove mainly to a depth of 5 m or less. During foraging most of the dives were between 5 and 10 m depth. I found three different scenarios for possible hatchling dispersion: 1-hatchlings could be transported offshore and after three months pushed back closer to the coast, 2- hatchlings could be transported north or south remaining along the coast and, 3-hatchlings could be transported to waters offshore still within the Eastern Tropical Pacific (ETP). East Pacific green turtles remained their entire

life within the waters of the ETP including females, which carry out limited to-long-distance migrations (5 to 1091 km). The unique characteristics of the area disperse hatchlings to productive areas providing them with enough resources to grow at the early life stages and move to adult foraging areas also in the ETP. The coastal nature of their movements and the high concentration of turtles off the nesting beach make them vulnerable to artisanal fisheries. That, together with intense poaching that occurs on the nesting beach indicates that this population may soon face extinction.

Chapter 1: Introduction

Sea turtles are widely distributed, occurring in neritic and oceanic environments around the world, but their nesting beaches are restricted to tropical and subtropical areas (Pritchard 1997). The seven species of sea turtles share a common generalized life cycle that includes long periods at sea away from the nesting areas (Carr 1987). Reproductively active female sea turtles migrate to nesting beaches to lay eggs; this process takes several months for each individual.

During a single reproductive season turtles nest repeatedly with variable internesting times between consecutive clutches (Miller 1997). Prior to nesting pre-ovulatory follicles develop in the ovaries and are then ovulated into the oviductal tract (Rostal et al. 1990, Rostal et al. 1996) where the sperm is stored and fertilization takes place (Gist and Congdon, 1998). After this process the albumin layers and the shell are deposited (Rostal 2007). At the culmination of this phase, turtles emerge onto the nesting beaches and lay their eggs. Meanwhile in the ovary, there are still enlarged follicles that will be ovulated and shelled for the following nesting event. The process takes place during the internesting interval and is repeated until the end of the nesting season when the eggs are depleted.

In general, during the internesting period sea turtles congregate in areas along the coast relatively close to the nesting beaches, moving back to the nesting beaches just a few days prior to the nesting event (Fossette et al. 2007, Schofield et al. 2009, Shillinger et al. 2010). The behavior of female turtles during internesting is driven by energy optimization due to the high coast of crawling onto the beach and laying eggs (Wallace et al. 2005); as a result they spend most of the time resting on the seabed (Hays et al. 1999).

After several weeks of incubation hatchlings emerge from the nest, enter the surf and swim to oceanic areas (Bolten et al. 1998). The oceanic stage of sea turtles has been referred to as “the lost years” (Carr 1982) a stage that can last for several years. In a later juvenile stage sea turtles move to the adult foraging areas where they stay and reach sexual maturity and start to carry out migrations to and from the nesting beaches (Bolten 2003). This is true for all sea turtle species but for the flatback turtle (*Natator depressa*) which is the only sea turtle species that lacks an oceanic phase in its life cycle (Walker and Parmenter 1990) and the leatherback turtle (*Dermochelys coriacea*) which is pelagic all its life (Bolten 2003).

Another feature common to all sea turtles is migration. Migration in sea turtles is driven by the balance of the cost of residing at a given location versus the benefit of moving (Morreale et al. 2007). For example, turtles in foraging areas need to migrate to tropical and subtropical beaches to ensure the proper development of eggs and survival of the hatchlings. However, food availability in the surroundings of the nesting beaches is not always optimal for adult survival (Hays et al. 1999).

Due to the pelagic habits of sea turtles, studying their migration has been challenging (Myers et al. 2006). Different methodologies have been applied to determine the migration of these reptiles. Eckert and Eckert (1988) analyzed time of colonization as well as the age of the barnacle communities that live on sea turtle’s carapaces. Green (1984) and Alvarado and Figueroa (1992) used tag return to study the migration of turtles. The mark-recapture technique provided information on movements (point to point) but no data on migratory pathways (Byles et al. 1995).

Satellite telemetry was used in several studies recovering data on diving behavior (Hays et al. 2000, Hays et al. 2002, Eckert 2006, Fossette et al. 2007, Blumenthal et al. 2009), and migratory paths (Morreale et al. 1996, Cheng 2000, Eckert 2006, Seminoff et al. 2008, Shillinger et al. 2008) of sea turtles. More studies are including telemetry because it gives information on the geographic location of the animal, as well as other behavioral and environmental information (Tremblay et al. 2006). Therefore, electronic devices play an important and increasing role in the study of marine turtles (Myers et al. 2006)

Sea turtle migrations can be fairly extensive. Pacific leatherback turtles nesting in Costa Rica migrate into the South Pacific off Chile and Peru (Morreale et al. 1996, Shillinger et al. 2008). Green turtles (*Chelonia mydas*) nesting on Ascension Island travel to feeding grounds along the coast of Brazil (Hays et al. 2002), and olive ridley turtles (*Lepidochelys olivecea*) nesting in northwestern Australia migrate between 180 and 1100 km to their feeding grounds (Whiting et al. 2007). Some juvenile loggerheads (*Caretta caretta*) traverse the entire Pacific Ocean during developmental migrations; traveling from nesting beaches in Japan and Australia to foraging areas in Baja California (Bowen et al. 1995). When they reach sexual maturity they return to the western Pacific where they remain the rest of their life (Nichols et al. 2000). In the Eastern Pacific, green turtles nesting in the Galapagos Islands migrate to the coast of Central America and to oceanic areas in the Eastern Tropical Pacific (Seminoff et al. 2008).

Conservation of sea turtles is vital for marine and terrestrial ecosystems, which are significantly affected by these reptiles (Bouchard and Bjorndal. 2000). Their ecological role consists in being consumers, prey, hosts for parasites, substrate for epibionts, nutrient transporters and modifiers of the landscape (Bjorndal and Jackson 2003, Heithaus et al. 2007). All sea turtle species are in the Red list of threatened species ranging from vulnerable to critically endangered (IUCN 2010). For several decades, people have harvested eggs and adults (Seminoff 2004, Santidrián-Tomillo et al. 2008), these activities continue until today in unprotected areas. In addition, numerous populations have declined because of several interactions with fisheries, both industrial and artisanal (Lewison et al. 2004, Spotila et al. 2000, Troëng et al. 2004). One of the main problems that sea turtles are facing at present is the loss of marine ecosystems and nesting beaches through pollution, over-fishing and development of nesting sites (Bjordnal et al. 2003). The new threat faced by sea turtles is global warming, because at very least an increase in incubation temperatures may lead to female biased populations and will increase levels of egg mortality (Spotila 2004).

East Pacific green turtles (*Chelonia mydas*) (also known as black turtles) belong to distinct breeding populations of this Endangered Species (IUCN 2010) and inhabit waters in tropical and sub tropical regions throughout the Eastern Pacific (Seminoff et al. 2002b). In general, green turtles forage in coastal areas, estuaries, lagoons (Seminoff et al. 2002b) and near shore insular habitats (Amorocho and Reina 2007). Their diet is mainly sea grass and red and green algae. However, in the Pacific they also eat invertebrates and gelatinous prey (Seminoff et al. 2002a, Seminoff et al. 2006, Quiñones et al. 2010). In the Eastern Pacific, their range extends from the U.S. West Coast to Chile and the Galapagos Islands. The most important nesting grounds in the eastern Pacific are reported to be in Michoacán, Mexico (Alvarado and Figueroa 1992) and the Galapagos Islands, Ecuador (Green 1984). Although green turtles are common along the Pacific coast of Central America, limited information exists on population characteristics and number of individuals nesting on those sites (Richard and Hughes 1972, Cornelius 1976).

Although few scientific data are available for East Pacific green turtles in Costa Rica it appears to host an important population along the coast of Guanacaste on the Nicoya peninsula (Richard and Hughes 1972, Cornelius 1976). Nesting there occurs mainly on Nombre de Jesús and Zapotillal beaches and in lower numbers on beaches along the North of the Nicoya peninsula. Nombre de Jesús and Zapotillal are located north of Parque Nacional Marino Las Baulas (PNMB), created to protect leatherback turtles, but these beaches lie just outside its area of protection. Because of the lack of official status, poaching of eggs, presence of tourists on the beach and small artisanal vessels fishing in the nearby waters are common.

Both the potential conservation gaps and the potential importance of this unstudied breeding population motivated the present research. The main focus of this dissertation was to study the movements and behavior of adults and hatchlings of East Pacific green turtles from Costa Rica during different stages of their life. Through this effort I intended to contribute to the general knowledge of sea turtle life cycles and to identify areas in need of protection.

In Chapter 2, I identified high use internesting areas for turtles nesting on Nombre de Jesús and Zapotillal beaches. I also determined the diving behavior and vertical habitat use of the turtles. This information allowed me to highlight hot spots for conservation of sea turtles in Northwestern Costa Rica.

In Chapter 3, I studied the reproductive status of East Pacific green turtles to assess their clutch frequency and the duration of the internesting period to have a better understanding of the nesting habits of this population.

In Chapter 4, I described the post nesting movements and behavior, and identified foraging areas for the Costa Rican green turtles. I also analyzed oceanic characteristics that may influence the movements and behavior of the turtles.

Finally, in Chapter 5, I estimated the dispersion of hatchlings emerging from Nombre de Jesús in their post-hatchling stage by modeling currents in the Eastern Tropical Pacific.

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Chapter 2: Diving behavior and movements of the East Pacific green turtle (*Chelonia mydas*) during internesting in Costa Rica

Abstract

We attached hydrodynamic satellite transmitters by tether to 13 East Pacific green turtles nesting on Nombre de Jesús and Zapotillal beaches to identify movements and diving behavior, and to determine high use internesting areas in need of protection in northwestern Costa Rica. Tracking duration ranged from 5-39 days. A fixed Kernel density analysis showed that high use areas during internesting periods were close to the nesting beaches; utilization distribution polygons of 50 and 95% included 4.5 and 53.9 km^2 respectively. Turtles performed short dives (2-10 min) mainly in the upper 10 m of the water column. U-shaped dives were shallow (3-5 m) and their modal duration ranged from 8 to 23 min. These were probably animals resting at the bottom. Strong diel patterns occurred in diving behavior during internesting with a significantly larger amount of time spent at the surface during the night. The proportion of U-dives was negatively correlated with surface time at night suggesting the turtles were floating at the surface as a resting strategy and resting at the bottom during the day. The combination of movement and behavioral data suggested that the turtles were staying near the nesting beach relatively inactive during the internesting period. The depths of U-dives and depth of water in the area indicated that the turtles used calm shallow areas to rest between successive nesting events. This high concentration of nesting turtles and the lack of long distance movements during internesting indicated the extensive use of the area by resting turtles. This behavior was probably representative of the behavior of the whole population,

which indicated that this small area was of great importance for East Pacific green turtles and likely a crucial location for conservation of this population.

Introduction

Marine animals spend most of their life in the ocean away from shore, which makes it difficult to obtain direct observations of their behavior. Recently modern technologies have allowed scientists to collect much more information on the ecology and natural behavior of marine vertebrates (Wolcott 1995, Cooke et al. 2004, Altmann and Altmann 2003). In particular, satellite telemetry has been widely used to analyze the movements, behavior and physiology of marine mammals (Mate et al. 1999), fish (Block et al. 1998), sea birds (Jouventin et al. 1994) and sea turtles (Morreale et al. 1996, Hays et al. 2000, Eckert 2002, Seminoff et al. 2008, Shillinger et al. 2010).

Specifically, satellite telemetry and deployment of data loggers have helped us understand different dive patterns in sea turtles involving depths, durations and ascent and descent phases. These patterns vary widely within species and their immediate environments. Several studies indicate that sea turtles display different dive types associated with different life history phases (Minamikawa et al. 1997, Hays et al. 1999, Hochscheid et al. 1999, Houghton et al. 2002). Whereas leatherback turtles (*Dermochelys coreacea*) dive at an average maximum depth of 108 m during the internesting period off northwestern Costa Rica (Shillinger et al. 2010) green turtles (*Chelonia mydas*) in the Mediterranean only dive as deep as 25 m (Hochscheid et al. 1999) and loggerheads (*Caretta caretta*) use an average depth < 20m during the internesting (Houghton et al, 2002). In addition, data loggers have revealed that different dive shapes are related to a sea turtle's underwater behavior (Minamikawa et al. 1997, Hays et al. 2000, Houghton et al. 2002, Seminoff et al. 2006). Six types of dives have been recognized. Type 1 or "U" dives are associated with resting behavior (Houghton et al. 2002, Hays et al. 2000) and stationary foraging (Seminoff et al. 2006); Type 2 or “V” and Type 6 (W-shaped) dives indicate underwater exploratory surveys or turtle orientation; Type 4 or “S” dives may relate to energy savings while returning to the surface using positive buoyancy (Hochscheid et al. 1999). Finally, Types 3 and 5 have been linked to foraging activity (Seminoff et al. 2006). Different dive types have been recognized during the internesting in sea turtles (U-dives, V-dives, S-dives) but the predominant dive during that period is the U-dive (Hays et al. 1999, Hochscheid et al. 1999, Houghton et al. 2002).

The behavior of turtles during the internesting period appears to be driven by energy optimization. For example, lack of food availability in some reproductive areas causes turtles to spend most of the time resting during the internesting period (Hays et al. 1999, Reina et al. 2005). On the other hand, some populations forage during internesting (Houghton et al. 2002, Fossette et al. 2008, Tucker and Read 2001). These differences are related to the conditions of the nesting grounds (Hays et al. 2002a).

The green turtle is listed as endangered by the IUCN. In particular the population in the Eastern Pacific is classified as endangered by the US and considered highly vulnerable to extinction. The decline in the eastern Pacific was due to harvest of eggs and adults, habitat degradation at nesting beaches and feeding grounds and by-catch from fisheries in the ocean (Seminoff 2004)

The objective of this study was to examine the movements and identify the dive behavior of green turtles during internesting periods, as well as to determine their vertical habitat use along the Pacific Coast of Costa Rica. To our knowledge, this is the first study on internesting movements and behavior of the East Pacific green turtle. These data will help elucidate high use internesting areas in need of protection in northwestern Costa Rica.

Materials and Methods

Study site

To monitor individual East Pacific green turtles, we deployed 13 ARGOS-linked satellite transmitters from August 2007 to October 2007 and an additional one in November 2009. The study took place at three nesting beaches on the Nicoya Peninsula in Northwest Costa Rica. We attached 12 transmitters on turtles on Nombre de Jesús (10° 23' 30" N; 85° 50' 07" W), a 1 km stretch of beach and on its neighboring 700 m beach, Zapotillal (10° 23'48"N; 85°49'48"). These beaches hosted an important aggregation of nesting green turtles (~15 turtles/night during peak season) and were located just north of Parque Nacional Marino Las Baulas (PNMB), which was created to protect leatherback turtles (*Dermochelys coriacea*), but they were just outside its area of protection. Therefore, poaching of eggs, presence of tourists on the beach and small artisanal vessels fishing in nearby waters were common. We also attached one transmitter on a green turtle on Playa Ventanas a 1.1 km stretch beach in PNMB where green turtles sometimes nest as well.

Turtle measurements

To intercept the turtles we patrolled Nombre de Jesús, Zapotillal and Playa Ventanas at night. Each turtle encountered on the beach was scanned for a Passive Integrate Transponder (PIT tag). If they did not have one, we injected a PIT tag into the right front flipper for later identification. We measured the curved carapace length, CCL +/- 0.5 mm of every tagged turtle with a flexible meter tape and we checked them for scars or lesions. Additionally some of the turtles were scanned with ultrasound to assess their reproductive status, enabling us to see future clutches (Chapter 3)

Satellite transmitter attachment

Sea turtles have a streamlined shape that minimizes hydrodynamic disturbance when they are moving through the water. This characteristic undoubtedly minimizes energy expenditure while they swim. Therefore, any disturbance in the shape of the turtle will cause flow separation increasing drag (Schlichting 1979, Denny 1993), and consequently increasing energy expended by the turtle (Watson and Granger 1998).

Two different methodologies have been used to attach satellite transmitters to sea turtles: lying on the carapace and trailing behind the turtle. Commonly for hard-shelled turtles a rectangular transmitter is attached to the anterior top-most part of the carapace (Plotkin et al. 1995, Balazs et al. 1996, Papi et al. 1997, Hays et al. 1999). However, this placement increases drag due to the disturbance of the carapace’s shape potentially causing a 13% increase in travel time and increasing energy consumption by 13 to 27% (Watson and Granger 1998). For this method drag is even greater when the transmitter is placed more anteriorly on the carapace where they are commonly attached (Logan and

Morreale 1994). Another method is to attach the transmitters using a tether, a technique first developed by Standora et al (1982) and modified by Morreale et al (1996) and Morreale (1999). In this technique the transmitter trails behind the turtle without disturbing shape and flow across the carapace. The buoyant and hydrodynamic transmitter follows closely behind the turtle and floats with the antenna out of the water when the turtle rises to the surface. A further benefit to this technique is that the attachment can be performed in a short period of time with minimal disturbance of the turtle's natural behavior while it is on the beach. The main disadvantage of this technique is the potential for shorter duration of tracks due to the smaller batteries and the shedding of the transmitter when the tether breaks. Balancing all of these factors we opted to use tether transmitters for this study.

When we determined that a turtle was suitable for attachment we cleaned the marginal posterior scute of the carapace with 70% alcohol, and made a 3 mm diameter incision with a sterile electric drill bit (battery-powered electric drill). Immediately after the incision we applied lidocaine and betadine antiseptic solution and inserted sterile surgical tubing into the small hole through the overhanging edge of the scute. We positioned plastic buttons with Y shaped holes above and below the carapace to avoid friction and wearing damage to the carapace. The transmitter was connected to the buttons on the carapace by a flexible lanyard (monofilament fishing line, 400 lb test) that passed through the holes and was secured to itself with a corrosive metal crimp. To avoid entanglement or long-term impediment of the turtles, we placed in line swivels and crimps that would breakaway with corrosion (Figure 2.1). The attachment process took from 7 to 15 min for all turtles and was performed when the turtle was covering the nest after laying eggs, thus minimizing the impact on its nesting behavior.

Satellite transmitters

We attached transmitters to 13 female green turtles at Nombre de Jesús, Zapotillal and Playa Ventanas (Table 2.1) to track their movements and analyze diving behavior. The satellite transmitters (Wildlife Computers Mk-10 PAT Pop up archival transmitting tag) were configured to transmit opportunistic transmissions, so we could obtain real time location data.

We customized the satellite tags with a buoyant case made out of syntactic foam. Satellite transmitters weighed ~115 g (≈ 0.2 % of the turtle mass), had a hydrodynamic shape and were tethered behind, all resulting in minimized drag. The transmitter's positive buoyancy was 36 g, enough to bring the antenna of the transmitter out of the water each time the turtle surfaced but very minimal for adult green turtles. We programmed the tags with duty cycles of 10 h on / 14 h off (0:00-9:00 h/ 10:00-23:00 h local time) to optimize battery life. The transmitter sampled and summarized dive depth, dive duration and time at depth data in categorized bins: Dive depth: 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 75, 100 and 200 m; Dive duration; 2, 5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80 and 90 min.

Dive and movement analysis

The location of the animals and the summarized satellite messages were transmitted via the Argos system. To analyze the areas used by the turtles we performed a

Kernel Density Analysis using ArcGIS and Home Range Tools for ArcGIS (Rodgers et al. 2005). We performed a fixed kernel density analysis using the least-squares-cross-validation method (LSCV) to calculate the smoothing factor. The core areas were determined by 25, 50, 70 and 95 % Utilization Distribution (UD).

We analyzed the daily displacement of the turtles by calculating the distance between all points travelled in a given day. We then calculated the total movement in the first 10 days after a successful nesting event. We used 10 days because it was the shortest internesting time recorded in this study to have a representation during the internesting. We also compared turtle size (CCL) to the distance covered in 1 and 10 days, to analyze if the size of the turtle had an influence on displacement.

We analyzed diving behavior of turtles from the summarized dive information obtained from the Argos messages and from the more detailed data retrieved from satellite transmitters that were later recovered.

The summarized dive information allowed us to calculate the percentage of dives accumulated in 4 hour period at different depths for all turtles and the average duration of dives, although these data did not allow us to determine the specific number of dives that the turtles performed during the tracking period.

We were able to later retrieve four satellite transmitters, which archived complete detailed information on the animal's diving behavior including every dive performed by the turtle during the tracking period (date, time, water temperature, dive depth, duration, bottom time, surface time, etc). This allowed us to identify, analyze, count and classify individual dives.

From the retrieved satellite transmitters we analyzed the relation between the total duration of dives and their depth. Also, we specifically separated the U-dives from the total dives. These dives were characterized by a steady descent phase followed by a period of time at a constant depth followed by a steady ascent phase (Hochscheid et al. 1999). U-dives are commonly related to resting behavior, which appears to be the main activity during the internesting period of sea turtles. To identify U-dives we calculated the relation between total duration of an individual dive and the time at the bottom. If the time at the deepest depth was 90% or more of the dive, it was considered a U-dive (Hays et al. 1999). We calculated the proportion of U-dives at depth and their duration for every turtle. We calculated the proportion of U-dives in relation to all other dives for individual turtles. Additionally, we studied the behavior of turtles during the day and night. Based on the hours of light in the study area 05:30 to 17:30, night corresponded to 17:30 to 05:30. We calculated and compared the surface time for each turtle during day and night and also compared it to the percentage of U-dives performed by each turtle. All statistical analyses were performed using SPSS. Data are reported as mean ± SD.

Internesting Interval

From tagged individuals, we calculated the observed internesting period (OIP) as the number of days between observed successful nesting events (Reina et al. 2002). The mean reported internesting interval for green turtles is 12 days (ranging from 10-17days) (Miller 1997) therefore data where the observed interval was higher than 17 days were excluded from the analysis.

Additional observations

We made observations of activity on the beaches including presence of tourists and illegal egg collectors (poachers). We also recorded the presence of fishing activity in the area and the occurrence of male and female green turtles near the nesting beaches.

Results

In all, we attached satellite transmitters to 13 turtles with CCL from 82.0 to 89.5 cm (mean ± SD = 84.9 ± 2.5 cm). Duration of satellite attachment for all internesting turtles ranged from 5 to 39 days (mean ± SD = 19.3 ± 3.2 days) (Table 2.1).

Several transmitters were removed by egg collectors at night and moved to different localities of Costa Rica. Others were taken by fisherman in the ocean. On two separate occasions the transmitters were brought to land by artisanal fishing boats. Those transmitters were transported to a small fishing village, and it was not possible to recover them. Before transmissions ended we did track one transmitter as it moved around Guanacaste, but we could not catch up to it for recovery. In general, premature release was due to the transmitter releasing itself through a failure in the popup emergency release mechanism and to its removal from the turtle by people.

Internesting areas

Observed internesting periods exhibited a mean of 12 days (range 10-15 days, N = 25. Internesting areas ranged from north of Brasilito Bay to Playa Langosta in PNMB in the south (Figure 2.2) both within 15 km of the nesting beach. Turtles spent most of the time in waters even closer to the nesting beaches during internesting, limiting their travel to 1-4 km off the nesting beaches. Kernel density analysis showed UD polygons of 25, 50, 75 and 95% included 1.6, 4.5, 9.4 and 53.9 km^2 respectively (Figure 2.2). Notably approximately 39% of the 25% UD was contained within the Bay of Nombre de Jesús, 34% corresponded to the Bay of Zapotillal and the remaining 27% was in the southern part of neighboring Conchal Bay. One of the turtles showed a broader movement swimming 50 km south of the nesting beach. All the turtles tagged in the present study were between nesting emergences; we recorded the majority of these turtles nesting at least once more through satellite locations and direct beach observations. Additionally, some of these turtles were scanned with ultrasound as part of a different study. This enabled us to see more future clutches (Chapter 3).

During internesting the mean daily distance travelled by turtles was 4 ± 3 km Mean distance covered in 10 days was 52 km. There were no significant correlations between daily displacement of turtles and the CCL ($p = 0.119$) and the movements in 10 days and CCL ($p = 0.233$).

Diving behavior

Of all dives, during internesting 69% were performed in the first 5 m of the water column with an additional 20% to depths between 5 and 10 m (Figure 2.3a). Likewise, most dives were of short duration, between 2 and 10 min (71%) (Figure 2.3b).

We retrieved four of the satellite transmitters, from which we obtained archival information on the detailed diving behavior for individuals. The total number of dives for each turtle was: Turtle 1 = 1375, Turtle 2 = 833, Turtle 3 = 725 and Turtle 4 = 3692.

Mean water temperature recorded by the transmitter during internesting was 27.5 ± 1.0 °C.

Even though we recognized different dive types (V-shaped dives, S- shaped dives, W- shape dives) in the dive profiles of the four turtles, we focused our analysis on U-dives because they were described as the predominant dive type that sea turtles perform during the internesting period (Hays et al. 1999, Hoscheid et al. 1999, Houghton et al. 2002) and they were the predominant dive type in our study.

The percentage of dives that were U-dives performed by the turtles were: Turtle 1: 21%, Turtle 2: 31.6%, Turtle 3: 9.9% and Turtle 4: 31.2%. The U-dives were characterized by shallow ultimate depths with 79.3% (± 9.2) of dives ranging between 3-5 m (Figure 2.4). The modal durations of dives were 8 min, 11.5 min, 15 min and 23 min for all four turtles respectively (Figure 2.5).

The relation between depth and duration was weakly explained by a regression for all four turtles (Figure 2.6). Dives were mainly performed in the first 10 m of the water column independently of their duration. Turtle 4 performed the deepest dive (110 m) in 10 minutes and the longest dive, 55 min to a depth of 18 m.

During the internesting period green turtles exhibited a strong diel pattern in their submergence behavior. Dive profiles exhibited that two turtles (1 and 3) spent a significant amount of time at the surface at night as opposed to turtles 2 and 4 (Figure 2.7) that spent most of their time diving. Overall, we found significant differences when comparing the surface time during day and night (ANOVA, F = 48.775, $df_{1,\ 17;}$ $p < 0.01$) (Figure 2.8).

We also compared the proportion of U-dives performed during the day and night with the time spent at the surface (Figure 2.9a). Turtles spent more time at the surface at night and more time performing U-dives during the day. Total time of entire tracking duration spent involved in those activities together (U-dives and surface time) was 73 % (± 4.73) (Figure 2.9b), which gave an indication of great amount of time spent resting during internesting.

Due to the differences in the total of U-dives between individual turtles; we compared the proportion of U-dives and the total time spent at the surface during the night (Figure 2.10). We found a strong negative regression despite the small sample size, between U-dives and surface time during the night ($r^2 = 0.930$, $p < 0.05$, $N = 4$).

Additional observations

We estimated that 90% of the eggs were taken by illegal egg collectors on Nombre de Jesús and Zapotillal beaches unless researchers or rangers were on the beach. We also observed 10 longlines on different occasions and several gill nets set up in the water within sight of the nesting beaches. Gill nets were set for durations of at least 12 h. Simultaneously with our study colleagues reported several green turtles hooked on longlines in the nearby Gulf of Papagayo near the nesting beaches. Male green turtles also were present in the area and we observed several copulating pairs of green turtles near the nesting beaches during both day and night.

Discussion

Our data indicated that the internesting interval for the East Pacific green turtle population nesting in Costa Rica was 12 days. It was shorter than the 14 days reported at Ascension Island by Carr et al. (1974) and at Tortuguero, Costa Rica (Bjorndal and Carr 1989). The internesting period is the time that it takes for the turtle to develop the next clutch, thus it is a direct representation of the ovulation, fertilization and shelling of the following clutch (Rostal 2007). Ovulation, fertilization and albumen deposition occur within the first 3 days after nesting (Wibbels et al. 1992) and in the remaining time the eggs are shelled in the oviduct.

Egg development is directly affected by temperature in the surrounding environment (Sato et al. 1998). Standora et al. (1982) reported water temperatures at Tortuguero between 27.5 and 28.5 ºC and Hays et al (2002b) reported water temperatures at Ascension Island close to 28ºC. The mean water temperatures from this study varied between 27.5 and 27.9 ºC. The similarity in the water temperatures of the three areas indicated that the shorter internesting interval of the green turtles in Costa Rica was not a result of higher temperatures. We believe that the difference in the duration of internesting interval may be related to differences in size of the turtles and number of eggs per clutch (Bjorndal and Carr 1989, Broderick et al. 2003, Wallace et al. 2006).

Internesting Movements

Satellite tracking indicated that the areas of importance during the internesting period of green turtles that nested on Nombre de Jesús and Zapotillal beaches were the waters off the nesting beaches in nearby Brasilito Bay (4 km north of the nesting beach).

Turtles mainly remained in a particularly small area (4.5 km^2- 50% UD) near the nesting beaches. The turtle that nested on Playa Ventanas used a broader area, but even this was a relatively small area, ranging from the nesting beach to 12.5 km south along the Nicoya Peninsula. These limited internesting movements underscore the importance of coastal waters near the nesting beaches.

Contrary to our findings, green turtles on the Caribbean coast of Costa Rica travel from 30 to approximately 100 km off shore during internesting (Tröeng et al. 2005). Our results also differ from the behavior described for leatherback turtles that nest at nearby PNMB that travel hundreds of kilometers during the reproductive season (Shillinger et al. 2010)

The mean daily distance traveled by the green turtle was 4.6 km. There was little variation between turtles, and these differences apparently were not related to turtle sizes as was reported for leatherback turtles (Eckert 2002). In contrast to overall movements, distances covered in a day for these green turtles were similar to the daily distance traveled by leatherback turtles at nearby PNMB (Shillinger et al. 2010)

Dive behavior

The binned data obtained from the satellite transmitters indicated that, during internesting, turtles dive mostly between depths of 2 and 10 m (90% of the dives) performing mainly short dives. The depth of the majority of the dives corresponded to the depth in the area where the turtles stayed during the internesting interval indicating that diving behavior of the turtles was mainly influenced by bathymetry of the internesting area and turtles mainly dove to the bottom. Along Nombre de Jesús the depth ranged from 0 to 3m in the first 300 m off the coast and depth increased to 10 m at 900 m away from the coast. Conditions were similar in Brasilito Bay reaching 10 m of depth at 1.3 km from the coast. The mean dive depth of this population was similar to the mean depth described for internesting green turtles in Ascension Island (Hays et al. 2000, Hochschied et al. 1999), and loggerheads in the Mediterranean (Houghton et al. 2002).

Dive data obtained from the transmitters that we recovered indicated that the predominant depth for U-dives ranged from 3 to 5 m reinforcing the assumption that these turtles rested mainly on the bottom. Turtles did more U-dives during the day than at night. U-dives are related to resting behavior because turtles remain at a fixed depth for a period of time; this depth often is the bottom (Minamikawa et al. 1997, Hays et al. 2000). U-dives have widely been considered to represent resting activity on the sea floor, although on occasion some other activities such as foraging or movement along the bottom may occur (Hochscheid, et al 1999, Seminoff et al. 2006). Although some populations do not forage due to lack of food in the internesting areas (Hays et al. 2000, Reina et al. 2005), other sea turtle populations do feed during the breeding season (Houghton et al. 2002, Fossette et al. 2008, Tucker and Read 2001). We could not observe our turtles in the water, so we cannot rule out foraging behavior. However, there is no seagrass, and little algae are present on the bottom in the area near the nesting beach (Reina et al. 2005, Bernecker and Wehrtmann 2009). Therefore, these turtles were probably resting at the bottom. Duration of U-dives varied with individual turtles from 8 to 23 min. There was no relationship between dive depth and dive duration for U-dives as found in other populations (Houghton et al. 2002), although we found a weak relationship between depth and duration including all dive types. In this study the turtles spent a relatively short proportion of the overall time carrying out U-dives in relation to other studies (Hays et al. 2000).

Green turtles in our study area spent a large amount of time at the surface and the majority of the surface time occurred at night. One individual spent the longest consecutive time at the surface (12 hours at night). A basking sea turtle can increase its body temperature almost 4 ºC by exposing a substantial portion of the carapace to the sun (Spotila and Standora 1985). Our study showed that turtles were at the surface at night so they were not basking, but rather were probably resting. Because floating at the surface during the day in the warm waters off the beach would cause an increase in their body temperature (Spotila et al. 1997) the turtles avoiding heating by diving to the bottom to rest during the day.

U-dives, probably related to resting behavior, mainly took place during the day and there was a strong tendency for the turtles to go to the surface when the sun set. There was a negative correlation between the total surface time and the percentage of U-dives performed during the internesting indicating that the turtles that lay on the surface more at night invested less time doing U-dives during the day. Combining the time turtles spent at the surface at night and in U-dives during the day it appeared that east Pacific green turtles invested 73 % (± 4.73) of their total time during the internesting interval resting while their eggs are being developed in the oviducts.

During internesting turtles need to save energy to yolk up and shell eggs, crawl to the beach and lay the eggs several times in the season. Green turtles in this study remained close to the nesting beach and rested most of the time during the internesting period. These behaviors reduced energy expenditure during the nesting season which could be a significant cost for reproduction (Wallace et al. 2005). During the reproductive season sea turtles mainly rely on stored lipids to support metabolism and reproduction (Hamann et al. 2002) especially in areas where food is not plentiful. The mechanism of floating at the surface for resting may be less costly in terms of energy than diving. It has been suggested that one of the adaptations for sea turtles to dive is to avoid predation (Lutcavage and Lutz 1997). However, by staying close to the beach this Costa Rica green turtle population may be less exposed to predation than other populations, which would allow it to rest at the surface for long periods of time at night.

Conservation Implications

Female green turtles spent the internesting period close to the nesting beaches in Northwestern Costa Rica and used the complete water column, which was very shallow. Males are present in the waters off the nesting beaches and we often observed mating in the waters off the beach. Therefore, several parts of the life cycle of this population are occurring in this small portion of Costa Rica and this area is of great importance for the conservation of this population. At the same time there was heavy fishing pressure in this area. On two occasions, transmitters were brought to land by artisanal fishing boats indicating that turtles were being captured by fisherman during the internesting period. In addition, we observed turtles caught on longlines nearby. Gill nets were common in the area.

During the course of this study we estimated that 90% of the eggs were taken in Nombre de Jesús and Zapotillal by egg collectors, unless biologists or rangers were on the beach and secretly relocated the clutches. Despite the Costa Rican law that prohibits the egg harvest on every beach in Costa Rica except Ostional (Spotila and Paladino 2004) poaching of eggs is very common in areas that are not protected within a National Park. East Pacific green turtles nest along the coast of Guanacaste in low numbers with more concentration in some beaches like Nombre de Jesús and Zapotillal. Moreover none of these beaches have law enforcement and there is little or no control over commercialization of eggs in the area.

At least four sea turtle species nest along the coast of Guanacaste, Costa Rica: olive ridley turtles (*Lepidochelys olivacea*), green turtles, leatherback turtles and hawksbill turtles (*Eretmochelys imbricata*) (Cornelius 1979). With all these species in danger of extinction, urgent action must take place in Costa Rica to save these important populations. The intensive poaching that is taking place on Nombre de Jesús may lead to a decline in the population as has already happened with the leatherback population in PNMB (Santidrián Tomillo et al. 2008). Because there is no previous information on the number of females nesting on these beaches, it will be difficult to determine if the impact of the egg poaching is already affecting these numbers. Nevertheless, it is essential that enhanced protection be provided both on the beaches and in the waters of Northwestern Costa Rica where there is a previously unreported large breeding population of the highly endangered East Pacific green turtle.

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Tables

Table 2.1: Attachment data for 13 eastern pacific green turtles (*Chelonia mydas*) during the nesting season in Costa Rica. All individuals included in the study were in their internesting interval. *Transmitters recovered after premature release. #Transmitters probably removed by fisherman.

ID	Attachment date	Beach	CCL (cm)	CCW (cm)	Days of transmission
1*	26-Aug-07	Zapotillal	87.5	79.0	10
2*	2-Sep-07	Zapotillal	82.0	80.0	8
3*	9-Sep-07	N. Jesús	89.0	84.0	5
4*	22-Oct-07	Zapotillal	82.0	76.0	29
5	25-Aug-07	N. Jesús	89.5	85.9	11
6	22-Oct-07	Zapotillal	86.1	83.0	39
7	22-Oct-07	Zapotillal	82.2	81.8	25
8	24-Oct-07	Ventanas	82.0	----	24
9#	27-Oct-07	Zapotillal	86.5	71.5	16
10	27-Oct-07	Zapotillal	85.0	83.5	39
11#	27-Oct-07	Zapotillal	----	----	11
12	27-Oct-07	Zapotillal	84.5	78.3	22
13	6-Nov-09	N. Jesús	84.4	82	12

Figures

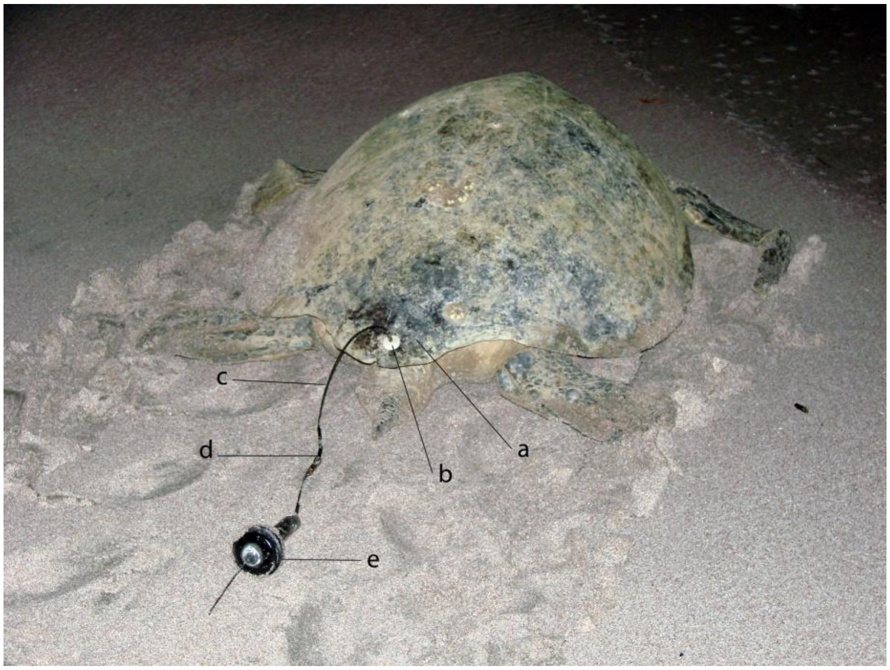


Figure 2.1: Satellite transmitter attachment to an East Pacific green turtle. a) posterior marginal scute. b) upper plastic button. c) flexible lanyard (400 lb monofilament fishing line). d) corrosive link with metallic crimps and swivel. e) Satellite transmitter (Mk 10 PAT tag, programmed for opportunistic transmissions)

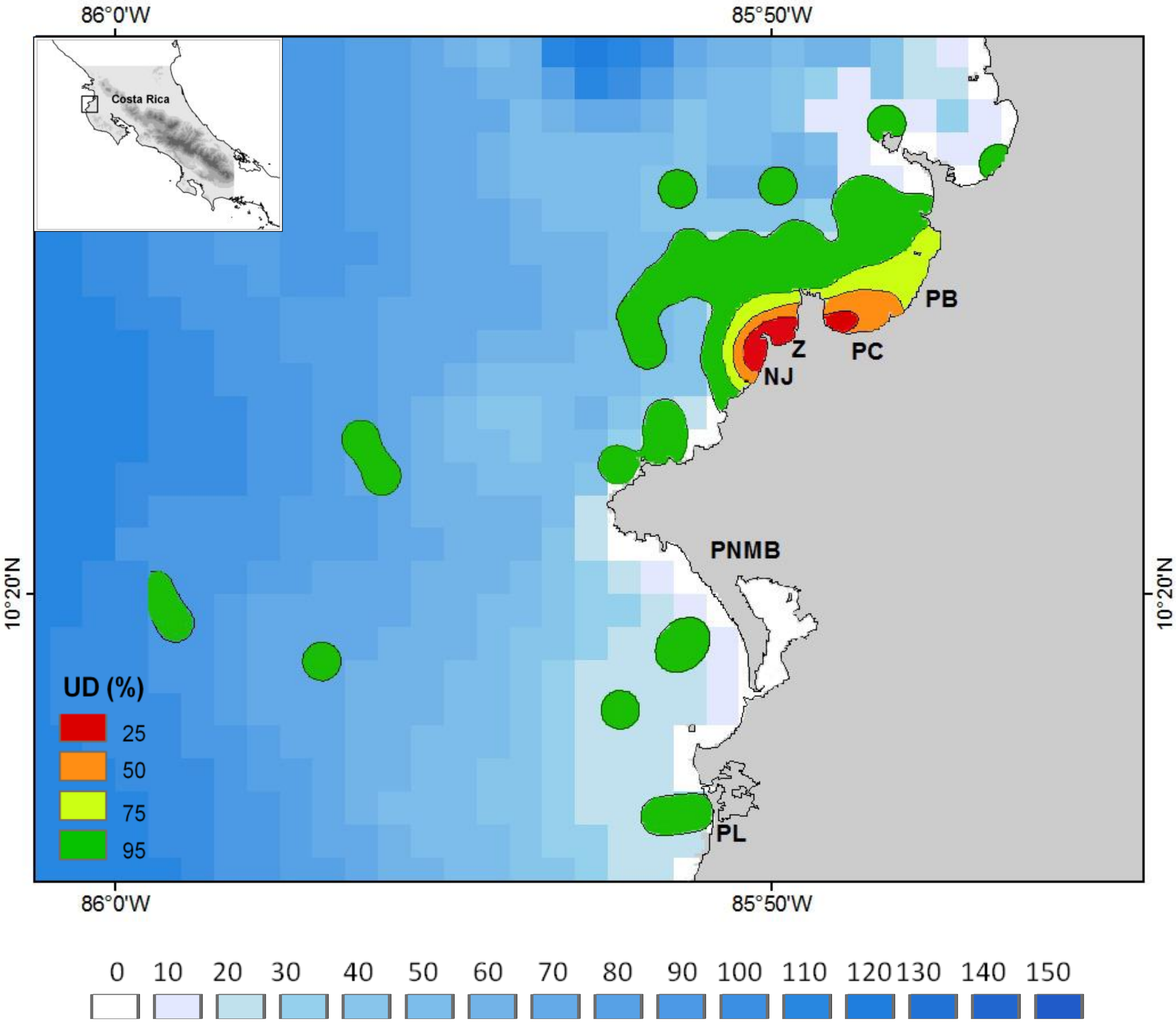


Figure 2.2: Fixed Kernel density analysis. Internesting areas occupied by East Pacific green turtles. Areas highly used are Nombre de Jesús (NJ), Zapotillal (Z), the Bay of Playa Brasilito (PB) and, Playa Conchal (PC). PNMB: Parque Nacional Marino las Baulas, PL: Playa Langosta. Utilization Distribution (UD) 25% = 1.57 (red), 50% = 4.5 (orange), 75% = 9.4 (light green) and 95% = 53.9 km^2 (dark green). Scale (from white to blue) represents depth (meters). Insert shows location on map of Costa Rica.

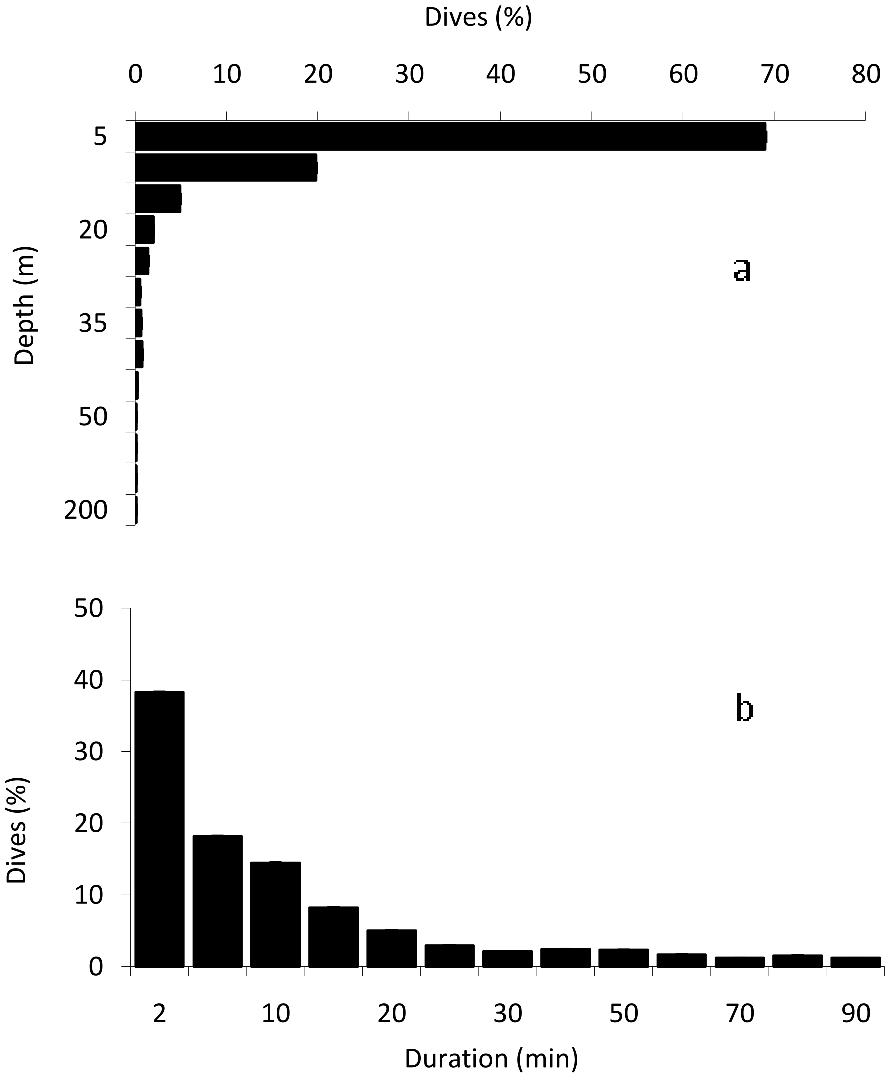


Figure 2.3: a) Percentage of dives culminating at specific depth intervals during internesting for 13 East Pacific green turtles from satellite data obtained through Argos and summarized in bins. We calculated the average at depth in relation to the total dives for each turtle. b) **Percentage of duration intervals of dives during internesting for 13 East Pacific green turtles** from satellite data obtained through Argos and summarized into bins. We calculated the average duration in relation to the total dives for each turtle.

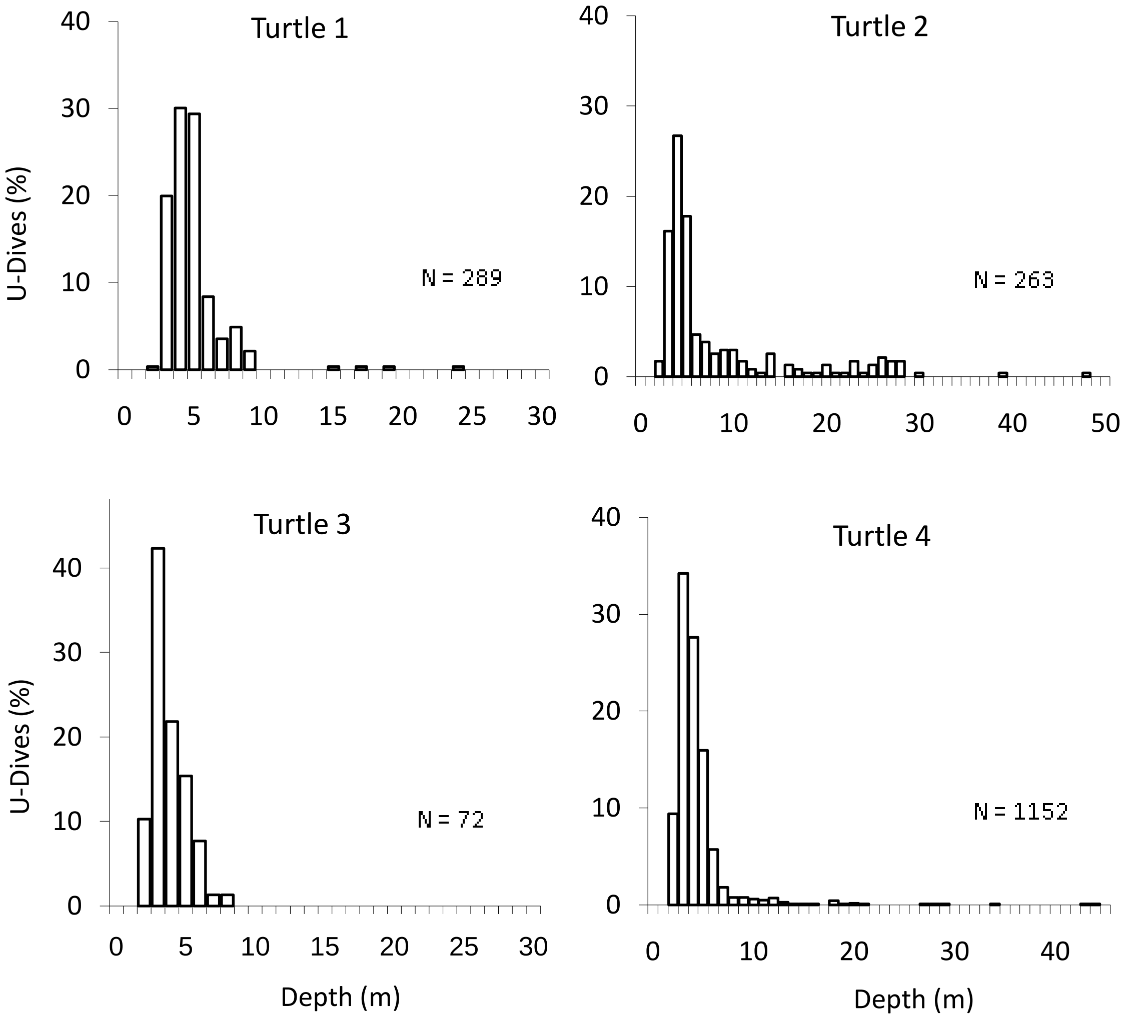


Figure 2.4: Percentage of U-dives of East Pacific green turtles ending at different depth intervals during internesting. The proportion of U-dives at depth was calculated in relation to the total U-dives for each turtle taken from data logged in the transmitter.

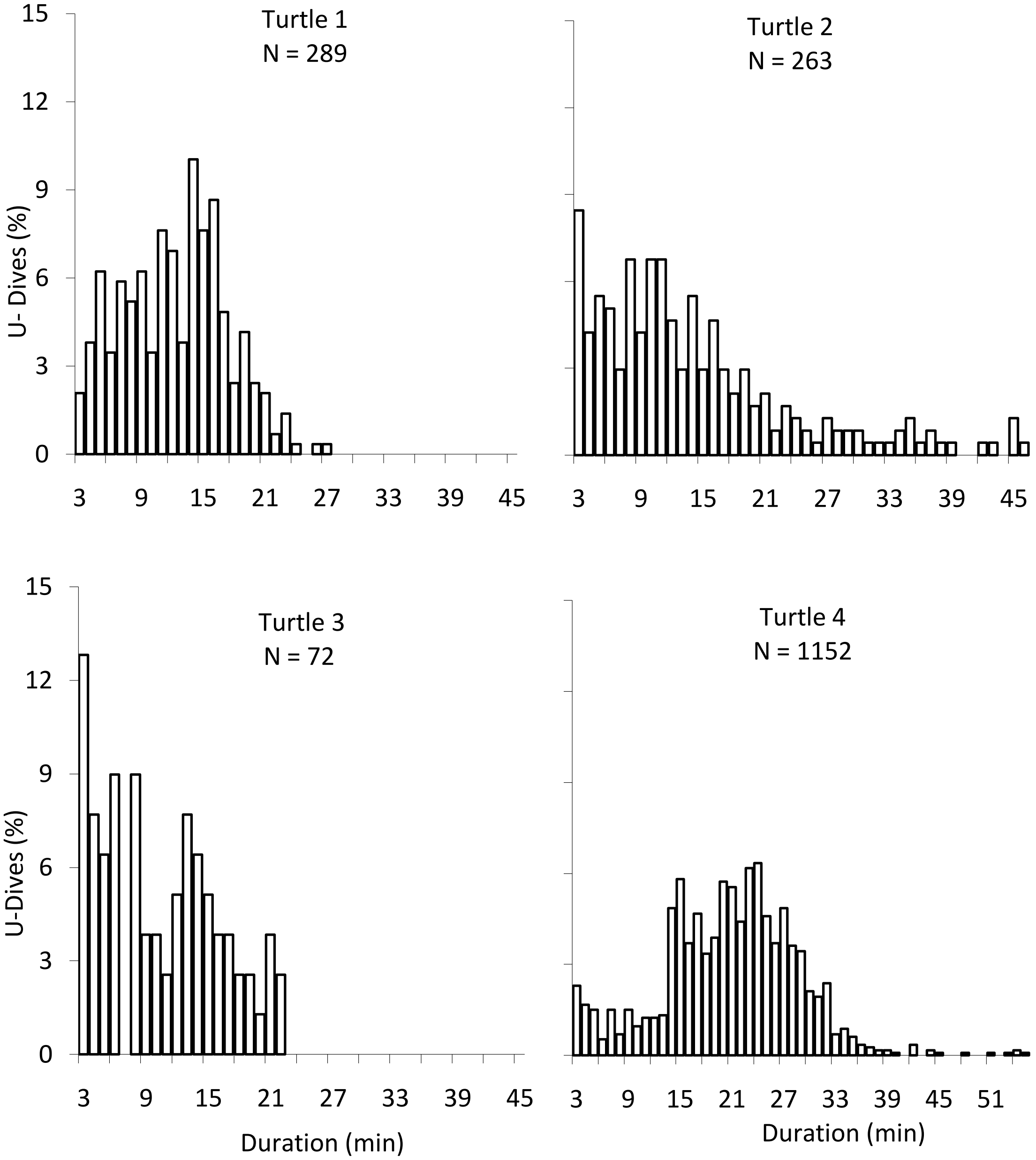


Figure 2.5: Duration intervals of U-dives of East Pacific green turtles during the internesting. The duration of U-dives was calculated in relation to the total number of U-dive for each turtle. Complete data were taken from satellite transmitters recovered.

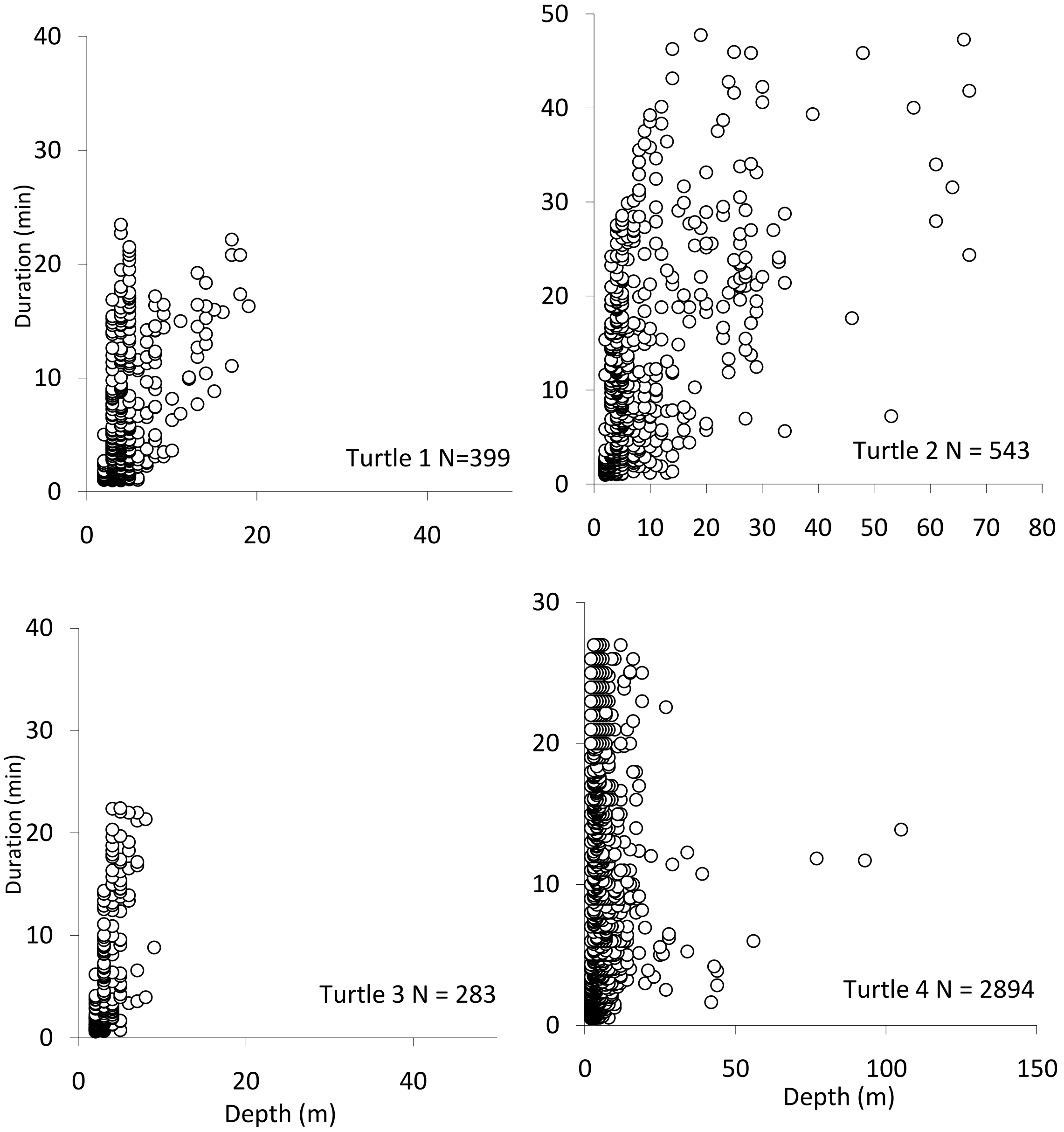


Figure 2.6: Regression of dive depth and dive duration including all dive types for East Pacific green turtles during internesting ($p < 0.01$). Turtle 1: $r^2= 0.215$, Turtle 2: $r^2= 0.213$, Turtle 3: $r^2 = 0.455$ and, Turtle 4: $r^2 = 0.01$. Data recovered from satellite transmitters.

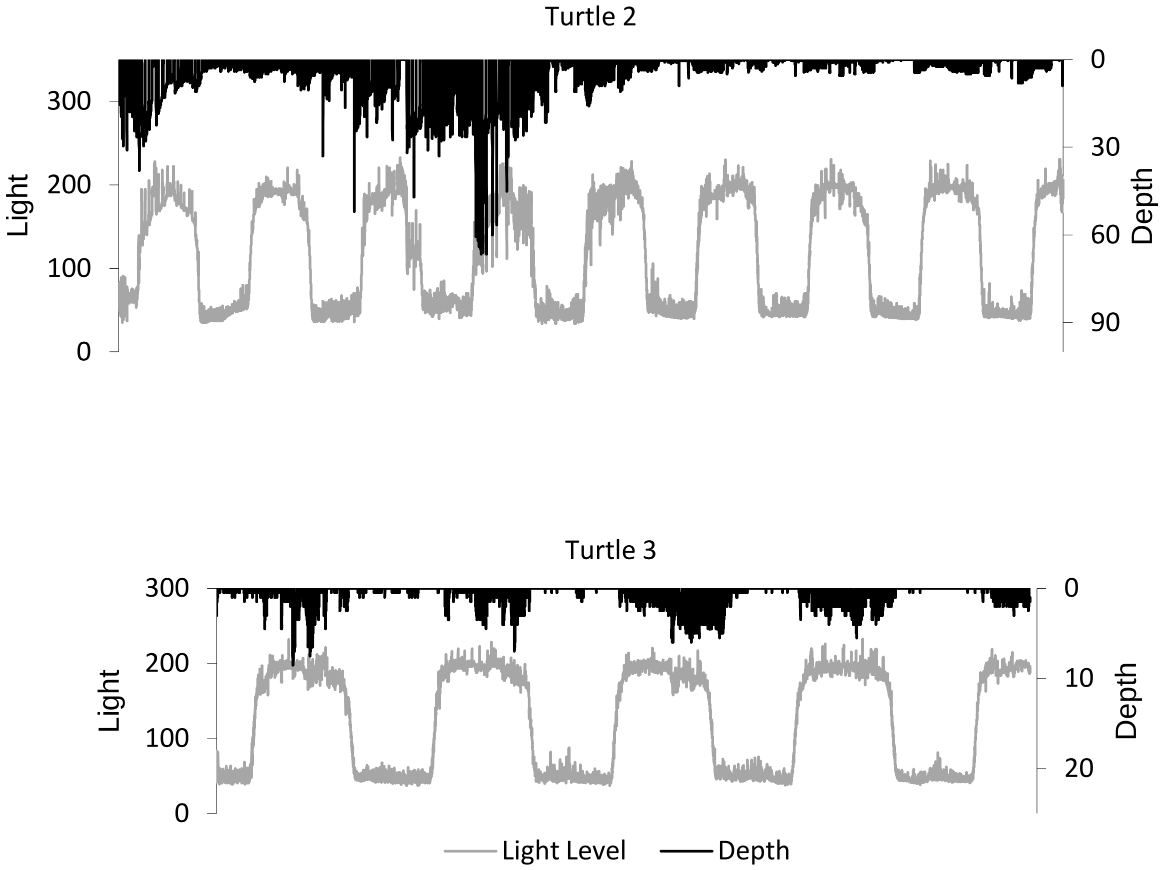


Figure 2.7: Dive profiles for East Pacific green turtles. Black lines represent depth and gray lines represent light levels. Elevated light levels represent daytime and low light levels represent nighttime. Turtle 2: Dives performed during day and night. Turtle 3: dives mainly performed during the day with prolonged time at surface during the night.

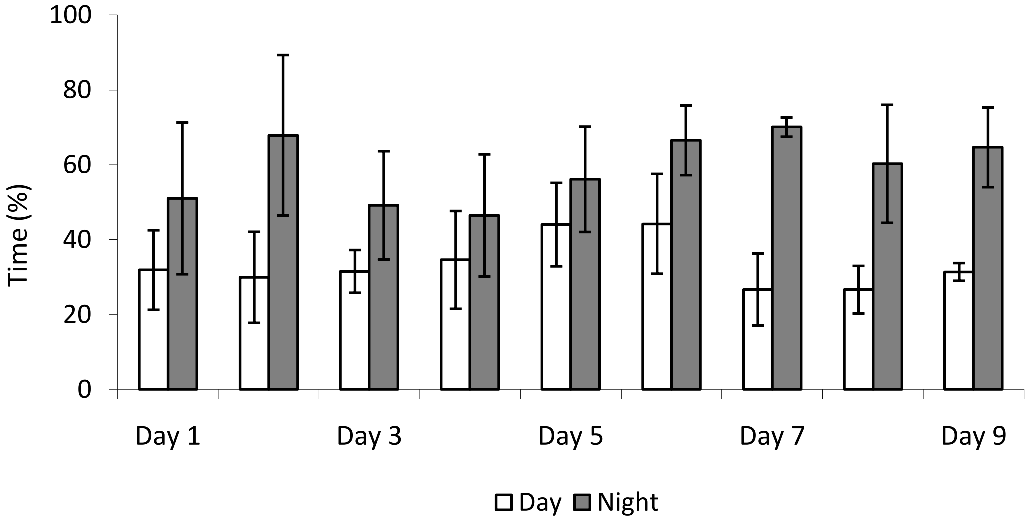
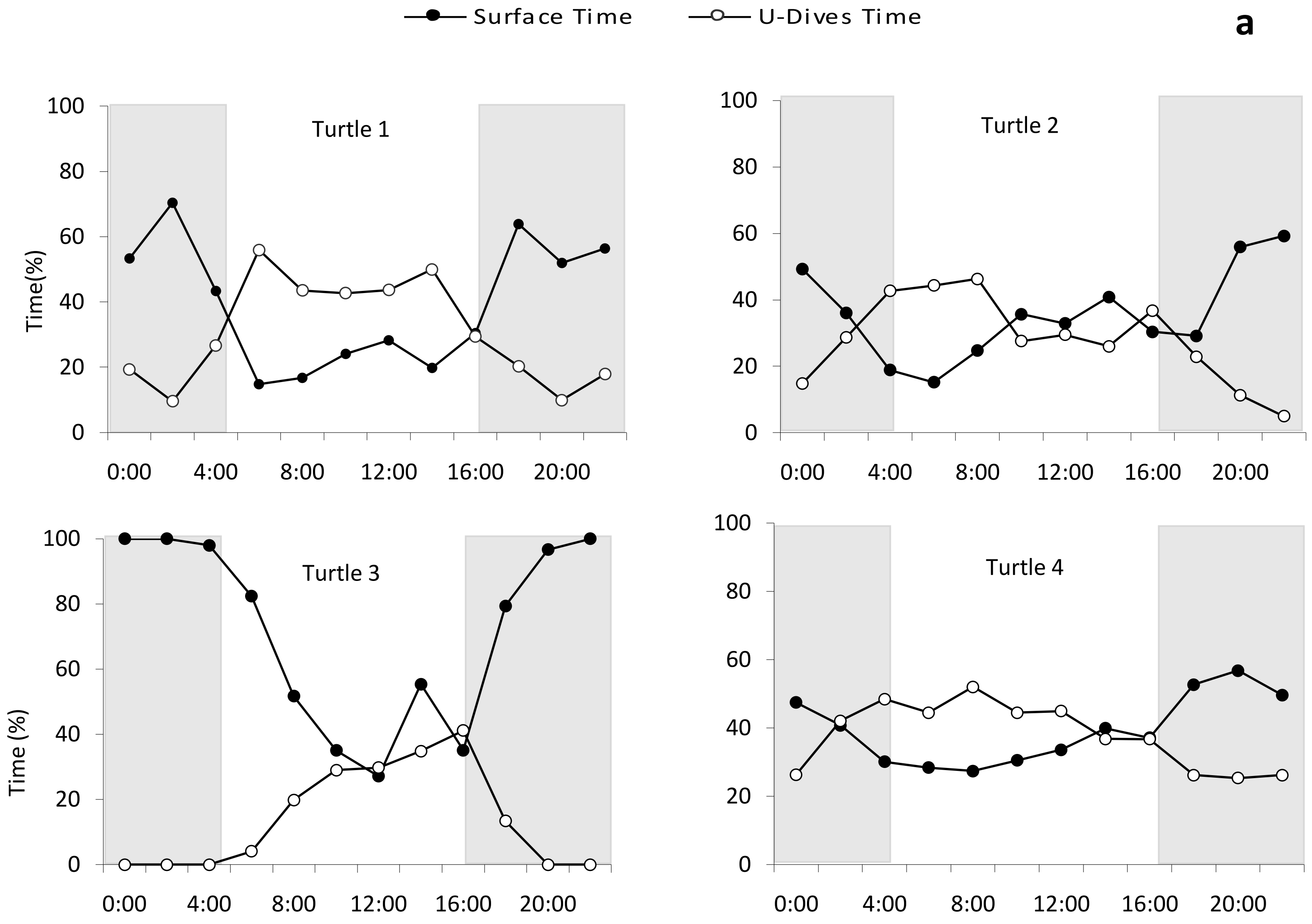


Figure 2.8: Difference between surface times of East Pacific green turtles during day and night. Day represents the 12 hours of light in the tropics. Days 1 to 4 includes 4 individuals; days 5 to 9 include 3 individuals. Day 1: first day after successful nesting (transmitter attachment). The percentage of time at the surface was calculated in relation to the total surface time during the 12 hour of light or darkness each day.


Surface Time
U-Dives Time
a
Turtle 1
Turtle 2
Turtle 3
Turtle 4
Time(%)
Time (%)
0
20
40
60
80
100
0:00
4:00
8:00
12:00
16:00
20:00

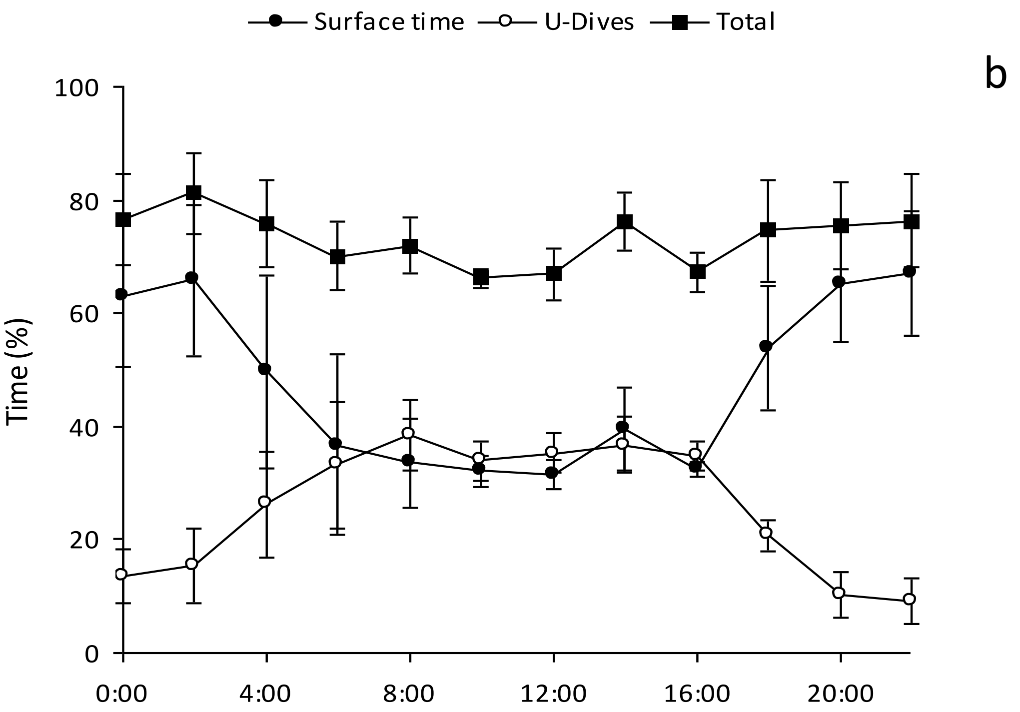


Figure 2.9: a) Surface time and U-dives during the internesting for 4 East Pacific green turtles. The shaded areas represent night (12 dark hours). Each data point represents an interval of 2 hours**. b) Proportion of time spent at the surface and u-dives performed at different times of the day for 4 East Pacific green turtles**. Total represents the sum of the proportion of time spent at surface and the proportion of U-dives performed by the turtles. Each data point represents an interval of 2 hours.

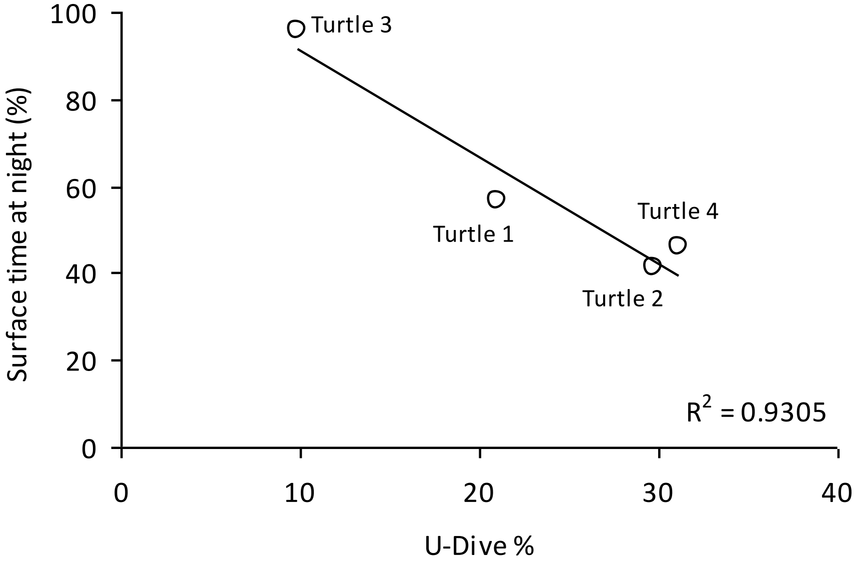


Figure 2.10: Correlation between the total time spent at the surface during the night and the total U-dives performed during the internesting by East Pacific green turtles ($p<0.05$, $r^2 = 0.930$). U-dives were calculated in relation to the total number of u- dives performed by each turtle during the internesting. Surface time was calculated in relation to the total time spent at the surface at night during the internesting.

Chapter 3: Reproductive Output and Ultrasonography of an Endangered Population of the East Pacific Green Turtle.

Abstract

Reproductive output is one of the most relevant aspects of life history; the lack of this information can hinder management plans and conservation efforts. The goal of this study was to analyze the reproductive output of the endangered East Pacific green turtle nesting on Nombre de Jesús in Costa Rica; supplementing beach patrols and estimation of clutch frequency with ultrasonography. Through the ultrasound scans we were able to classify the reproductive status of females based on the stage of their ovaries in: early stage (2 or more clutches), late stage (1 more clutch) and depleted ovaries (no more clutches). We also encountered turtles with shelled eggs returning to the water which coincided with disturbances on the beach such as egg collectors and/or tourists. We calculated the ECF (mean ± SD) 3.5 ± 1.8 (N=24) and added the information on the individual turtle ovaries to obtain the new ECF_U (mean ± SD) 5.2 SD = 1.3. This reproductive output is higher than previously described for East Pacific green turtles. Our study illustrated that the use of ultrasound as a non-invasive technique was an effective way to accurately determine the reproductive status and reproductive effort of green turtles. This key parameter provides knowledge on the number of females, annual fecundity, hatchling production and it can also influence male's breeding strategies. On one side, higher individual output could represent a healthier population; on the other hand it could decrease number of females previously estimated. Given the need for

accurate demographic data on sea turtle populations this technique should be used in nesting beaches studies. Our data along with the observations of egg poaching and uncontrolled tourism indicated that there is a great need to protect Nombre de Jesús because it hosts a high reproductive East Pacific green turtle population.

Introduction

Reproductive output is one of the most important aspects of life history; it is fundamental to understand the reproductive biology of a species, which is essential for developing effective conservation and management plans for individual populations. For sea turtles, many key aspects of reproduction have been difficult to study in the wild. As a result, little information is available regarding mating systems, lifetime reproductive output, and male and female reproductive strategies. This very lack of knowledge often hampers conservation efforts.

As a result of some thorough earlier studies, we do know some key steps in the reproductive biology of sea turtles. In general, mature female sea turtles have a pair of ovaries where follicles develop and become enlarged prior to mating (Owens 1980, Rostal et al. 1990). Usually sometime after mating, enlarged follicles are ovulated into the paired oviducts where they are fertilized and sheathed in albumen and shell material (Owens 1980). The ovaries and oviducts function synchronously during the reproductive season (Rostal et al. 2007), in which a single female will deposit anywhere from two to many clutches of eggs over a period of many weeks. Where and when the different steps in the female reproductive process occur has direct bearing on both female and male reproductive strategies. Undoubtedly, these strategies are directly relevant to conservation plans for individual species and populations of sea turtles; namely, where and when is it most effective to focus our energies.

For adult female sea turtles, all the energy needed for reproduction is accumulated in the foraging areas prior to migration. Eight to eleven months prior to the breeding season, they start a period of ovarian recrudescence where lipids are allocated and ovarian follicles start developing (Hamann et al. 2002). This is the process of vitellogenesis, which consists of the enlargement of ovaries and follicles before reproduction, and during which there is an incorporation of yolk proteins in the oocyte within the follicle (Rostal 2007). At this stage the females do not have fully mature follicles, but the ovary has several size classes of vitellogenic follicles that represent the number of clutches the turtle will lay during the season (Owens 1980, Etches and Petitte 1990, Rostal et al. 1998). These follicles continue to increase in size during pre-mating and mating periods (Rostal et al. 1990). For female turtles at the foraging grounds, a drop in estrogen and an increase in progesterone level may signal the beginning of the migration to distant nesting beaches (Owens 1997).

As female sea turtles get closer to the nesting season, they become receptive to the mating advances of males. At this stage the ovaries are completely developed (Rostal et al. 1998) and the final stages of follicular maturation begin (Owens 1980). Mating apparently occurs immediately prior to and at the beginning of the nesting season (Fitzsimmons 1998, Pearse and Avise 2001). It has been suggested that the first ovulation of the nesting season takes place several weeks after mating in loggerhead (*Caretta caretta*) and green turtles (*Chelonia mydas*) (Fitzsimmons 1998, Owens 1997). However, Manire et al. (2008) indicated that after successful intromission, ovulation may occur within a few days. It is the timing of the final stages of the female reproductive cycle and the mechanism of successful fertilization of the season’s eggs that will greatly influence the behavior and locations of male sea turtles in the population.

There is a possibility that free sperm in the oviducts from the male chelonids can contribute greatly to the female's next clutch (Pearse and Avis 2001). Such a mating system would favor a male that migrates to a nesting area to copulate with pre-ovulatory females (Owens 1980, Carr et al. 1974). However, many other systems could favor males that breed in foraging areas prior to female migration, or in courtship or staging areas along migratory routes, removed from the nesting and feeding areas (Miller 1997, Jessop et al. 1999; Schroeder et al. 2003, Bowen and Karl, 2007). It is common for chelonid females to store sperm in the oviducts, sometimes for extended periods (Gist and Congdon 1998, Fitzsimmons 1998, Uller and Olsson 2008). This mechanism of delayed fertilization could tip the scales in favor of early mating males, possibly those that breed prior to female migration. The benefits to early breeding males would be further enhanced with a mating system that favors the first male that copulates, which may be the case in sea turtles (Fitzsimmons 1998).

In addition to affecting mating strategy clutch frequency provides invaluable information for calculating population parameters, such as the number of females in a population, or estimates of annual reproductive output. Without such information, it is difficult to establish effective conservation strategies and management plans. Generally, sea turtles have high clutch frequencies and high seasonal reproductive output during the years when they nest. Leatherback turtles (*Dermochelys coriacea*) deposit approximately seven clutches in a nesting season (Reina et al. 2002), and for green turtles, clutch frequency in the Atlantic could be as high as six clutches per season (Bjorndal et al. 1999, Johnson and Ehrhart 1996). It is notable, however, that their conspecific, the East Pacific green turtle, is reported to have a clutch frequency of three or less for a nesting season

(Alvarado-Díaz et al. 2003). Even though there is clutch frequency information for all sea turtle species, complete information is limited because of incomplete coverage of nesting areas, loss of tags, loss of individual turtles, etc (Miller 1997). Additionally, for many of these reasons, the numbers of clutches laid per season may be underestimated for many populations. This may be the case for East Pacific green turtle populations, yet solid information on this important life history trait is still rare. Undoubtedly, such low numbers of clutches reported could help explain the extremely endangered status of these populations (Alvarado-Díaz et al. 2003), both as a function of low reproductive output, and as an influence on whether or not males of these populations are more driven to join females in their extensive breeding migrations.

Information on the reproductive cycle of turtles in the wild is difficult to obtain. Ultrasound imaging has been used to study reproductive cycles in tortoises (Robeck et al. 1990, Rostal et al. 1994, Casares et al. 1997) fresh water turtles (Kuchling 1989, Shelby et al. 2000) female sea turtles (Rostal et al. 1990, Rostal et al. 1996, Plotkin et al 1997, Rostal et al. 1998) and male sea turtles (Pease et al. 2010) and is especially useful to study the reproductive cycle and physiology of wild and captive animals. Ultrasoundography allows for the analysis of reptile reproductive status without the use of anesthesia or other invasive techniques (Rostal et al. 1990). This technique is an effective modality to repeatedly monitor follicular development and egg production (Robeck et al. 1990)

The objective of the current study was to analyze the reproductive output of the endangered East Pacific green turtles (*Chelonia mydas*) nesting at a beach complex in northwestern Costa Rica. To get accurate numbers, close observation of the entire nesting beach is needed for the entire season. Alternatively, on beaches where complete coverage is not possible, estimations can be made (Limpus et al. 2003). In our study we supplemented our beach patrols, tagging information, and seasonal clutch frequency calculations with ultrasonography of post-nesting females to enhance our estimates of seasonal reproductive output.

Study Area

The main nesting beach, Nombre de Jesús (10° 23’ 30” N; 85° 50’ 07” W) is a high energy sandy beach, approximately 1 km long located in the north of the Nicoya Peninsula, Guanacaste Province, Costa Rica. Along with its neighboring beach, Zapotillal, it hosts an important aggregation of nesting East Pacific green turtles, (also known as black turtles), with approximately 15 turtles per night during peak season.

Materials and Methods

We patrolled Nombre de Jesús from October 2008 to January 2009 and from July to November 2009 to intercept nesting female green turtles. After each turtle finished nesting we set up a portable real-time ultrasound scanner (Aloka SSD-500) behind the front flippers of the turtle. The scanner was plugged into a portable battery (Eliminator PowerBox 400 watt), and thus ran without any noise. The turtle was scanned while it was covering the nest. We used an electronic convex probe, 3.5 MHz, because low wave length penetrates deeper than 20 cm into tissue and is more effective in larger species of sea turtles (Rostal et al. 1990). The probe was coated with Acuasonic gel (Parker Laboratories), a coupling gel that enhances imaging. One ovary and oviduct at a time were scanned by placing the probe in the inguinal region above the hind flipper (Rostal et al. 1990); every scan was recorded using an attached printer (Sony video graphic printer). In addition to ultrasound scanning, each turtle was checked for PIT tags with a handheld PIT tag reader (AVID Identification System). If the turtle was untagged we applied a new PIT tag in the right front flipper for later identification. This study was approved by the Animal Care and Use Committee of Drexel University (Protocol 18466) and by the Ministry of Environment and Telecommunications (MINAET) in Costa Rica (ACT-PNMB-005-2007; ACT-SASP-PI-195; ACT-OR-D-050)

When turtles were observed during consecutive successful nesting events, we were able to calculate a mean observed internesting period (OIP), which was simply the interval in days between observed successful nesting events averaged among all turtles for which we had this type of data. Turtles observed after an interval greater than 20 days and less than 6 days were excluded from the analysis following protocol established by Reina et al. (2002). Similarly, we recorded observed clutch frequency (OCF) as the number of clutches actually observed during the sampling period for an individual. The OCF may underestimate the number of clutches per turtle (Frazer and Richardson, 1985, Steyermark et al. 1996) unless a turtle is seen every time it nests throughout the season, and therefore the mean OCF is undoubtedly an underestimate of this key population parameter. To approach a more realistic estimate, we calculated estimated clutch frequency (ECF) using the first and last date of observation of an individual turtle, dividing it by the OIP and adding 1 for the first oviposition (Reina et al. 2002, Limpus et al. 2003).

For turtles with complete information on the reproductive status from ultrasonography, we added 0, 1 or 2 clutches to their ECF based on the reproductive status they showed the last time they were seen on the beach. In this way we obtained an even more realistic ECF_U estimate (ECF + number of clutches remaining as observed in the last ultrasound).

To calculate OIP, OCF, ECF and ECF_U we used turtles encountered from July to November 2009 because the beach coverage was higher than in 2008. Although the beach was not completely covered for the entire season, the effort was high throughout the season, and there were enough consecutive encounters to provide a solid baseline for estimates of seasonal reproductive output.

As another benefit to the ultrasound technique, we also were able to calculate the percentage of turtles with late-stage or depleted ovaries to have a better idea of the timing of the end of the nesting season for this population, about which little was previously known. In this analysis we included all the turtles scanned in 2008 and 2009. This was supplemented with occasional surveys of the nesting beaches in March, April and June to verify the absence of tracks during those months.

Results

We encountered, and scanned with ultrasound, turtles 127 times (96 individuals) from October 2008 to November 2009. In 100% of the scans we were able to visualize the ovaries of the turtles. Scanning the ovaries, we were able to differentiate between an early preovulatory, late preovulatory and a depleted ovary (postovulatory) (Rostal et al. 1996). In the early stages (beginning of the nesting season) the ovaries were filled with vitellogenic follicles. In the late preovulatory stage we were able to distinguish only when one clutch was left, due to the presence of fewer follicles, coelomic space and atretic follicles in some cases. When the ovary was depleted, we observed atretic follicles and approximately less than 5 follicles, meaning that the clutch just laid was the last clutch of the season. An accurate estimation of the number of vitellogenic follicles using ultrasound was not possible; however, we could estimate the following: 1) Ovaries in early stage (Figure 3.1): turtles will lay at least two more clutches following the present nesting event, 2) Ovaries in late stage (Figure 3.2): turtles will lay one more clutch following the present nesting event, 3) Ovaries depleted (Figure 3.3): the turtle will not lay more clutches during the season.

In four cases we found shelled eggs (Figure 3.4) still in the oviduct when the turtle was covering the nest. These encounters coincided with the presence of poachers or tourists around the turtles. We observed that 90% of the eggs were taken on Nombre de Jesús by poachers except when researchers were on the beach and secretly relocated the eggs.

The OIP (mean ± SD) for this population was 12.0 ± 2.1 days (N = 37 individuals, 98 encounters). The OCF (mean ± SD) was 1.54 ± 0.79 (N = 24) and the ECF (mean ± SD) 3.53 ± 1.79 (N=24). The newly calculated ECF_U (mean ± SD) was 5.13 ± 1.32 (N = 24).

We also calculated the percentage of turtles seen with depleted and late staged ovaries during the months of August through February (Figure 3.5). There were two peaks where the greatest number of turtles left the nesting beaches, October-November and January. Occasional observations in March, April and June indicated the presence of nesting females on the nesting beaches in very low numbers

Discussion

Contrary to the findings of Cornelius (1976) on Playa Naranjo, Costa Rica and Alvarado-Díaz et al. (2003) that suggested the East Pacific green turtles nest an average of three times, our findings using regular tagging data and relocations on the beach indicated an ECF of 3.7 for this population. By adding the information obtained with the ultrasound, the new ECF_U increased 1.5 nests to 5 nests per season. This number is closer to the clutch frequency reported by Bjorndal et al. (1999) for green turtles in the Atlantic.

The difference in clutch frequency reported for different populations could be affected by loss of tags, beach coverage, time of the year, and beach fidelity. This includes tagging or recapturing turtles a fraction of the night instead of all dark hours or not covering the complete nesting season. By using the information provided by the ultrasound on the reproductive stage of the turtles through the season, we could estimate a more accurate clutch frequency for the Costa Rican population. The accuracy of this type of information, such as clutch frequency and internesting intervals, provides better knowledge of the number of females in a population, annual fecundity, hatchling production, etc (Miller 1997). The underestimation of these values could affect conservation strategies by overestimating the number of females in a population where number of females is estimated by number of nests. Alvarado-Díaz et al. (2003) calculated the number of females nesting per year based on OCF = 2.5 and compared it to the number of females nesting per year obtained by estimating it with ECF = 3.1; the annual numbers were reduced by 20%. Therefore the estimated number of females in the population is lower with a higher clutch frequency. If such a key parameter is incorrect it could lead to a misinterpretation of the status of a population.

The number of clutches a female produces in a single nesting season is also a key characteristic that could greatly influence a male sea turtle's breeding strategy (Gist and Congdon 1998). Stored sperm in the oviducts of chelonids may become much more advantageous after the first oviposition by a female. The passage of dozens of enlarged follicles and eggs can greatly distend the oviduct and sweep it clean of any existing free sperm. The subsequent clutches may then be fertilized mainly by sperm stored in the submucosal tubules high up in the oviduct. In fact, if mating does not occur shortly after egg laying, or later in the season, then stored sperm takes on a very important role and the payoffs for an early breeding male could be rather large, including a whole season's compliment of eggs (Fitzsimmons 1998). In conjunction with sperm storage, the number of clutches for a nesting female during a single season could dictate whether males were favored more heavily to stay in foraging areas or to migrate to breeding areas. With more clutches laid in a season, the genetic output of males is more important in the overall hatchling production of that given season. It is probably beneficial for a male to migrate to the nesting beaches because the concentration of females would be higher than in foraging areas. But also the migration and competition with other males for a female requires much energy. In addition, several questions still remain regarding the nature of sea turtle mating system. For example, if the first copulation yields a higher percentage of the clutches fertilized this would also favor the earliest breeding males. Indeed, mating at the foraging areas has been demonstrated through analysis of nDNA (Bowen and Karl 2007). Therefore, there is a possibility that the males that remain in a foraging area will also contribute to the production of the season by inseminating females before their migration. This would undoubtedly change the nature of assessment and conservation strategies.

During the course of this study we did not carry out surveys on the nesting beach all year around, although occasional observations in March, April and June indicated that the nesting season for East Pacific Costa Rican green turtles possibly extended all year around or at least 10 months as indicated by Cornelius (1976). There were two peaks for migrating turtles (turtles with depleted ovaries) in the months of October-November and January. Following our findings it appears that green turtles in Pacific Costa Rica take an average of two months to complete a nesting season. Therefore, turtles leaving the nesting grounds in October would have started nesting in August and turtles leaving in January would have started nesting in November. Based on our observations, there may be turtles arriving at the nesting beaches as early as June and turtles leaving the nesting grounds as late as April. However, in order to have a better understanding of the timing of the nesting season more observations throughout the year are necessary.

The use of ultrasound is a very successful methodology to understand the reproductive status of sea turtles. The scanner can be taken to the beach and the procedure does not require anesthesia or handling the animals and allows the acquisition of real time images which makes this methodology ideal for the study of wild animals (Rostal et al. 1990, Pease et al. 2010). The whole process can take between five to ten minutes. We conducted the scanning after the turtle laid the eggs. Although during the process the turtles were gently moving the rear flippers, there were times when they stopped and the scanning was performed with no inconvenience. Additionally the movement of the flippers allowed us to have a better vision of different portions of the ovary. Complete visualization of the ovary is not possible through ultrasound (Robeck et al. 1990) and at the beginning of the nesting season each ovary could have between 50 to more than 200 follicles (Rostal et al. 1990). That makes it impossible to estimate the number of eggs the turtle will lay during the season. However, this technique allowed us to identify the remaining reproductive output of every scanned turtle. At the beginning of the nesting season the ovaries of most green turtles displayed large quantities of preovulatory vitelogenic follicles. This characteristic also occurs in leatherback turtles showing that the reproductive cycle is common for different sea turtle species (Rostal et al. 1996). Even though the follicles have different sizes (Etches and Petitte 1990) it is difficult even to estimate the number of clutches the turtle will lay during the season. As the season progresses and the follicles were ovulated, the ovaries started showing fewer follicles and the presence of atretic follicles. Atretic follicles have an anechoic line surrounded by an echoic yolk (Rostal et al. 1990, Rostal 2007). The presence of these types of follicles is known for sea turtles (Rostal et al. 1990, Rostal et al. 1996, Rostal 2007) and tortoises (Robeck et al. 1990, Casares et al. 1997). Atretic follicles are the result of non-ovulated follicles during the nesting season. Casares et al. (1997) suggested that in Galapagos tortoises, the follicles go into atresia when conditions such as food availability and temperature are not favorable. Sea turtles potentially reuse the energy from the stored yolk by reabsorbing the yolk from the oocyte. The artretic follicle would be reduced in size leaving a scar (Rostal 2007). In our study turtles with one clutch left (post ovulatory stage) were followed until their last nesting event. The turtles with depleted ovaries were part of a different study in which we attached satellite transmitters to them and followed their migration; therefore we ascertained that the turtles had just one clutch left when she was scanned in her previous nesting event.

Our study illustrated that the use of ultrasound as a non-invasive technique was an effective way to accurately determine the reproductive status and reproductive effort of East Pacific green turtles. Given the need for more detailed demographic data to obtain a more complete understanding of the demographic status of sea turtle populations (Bjorndal et al. 2010) this technique should be used routinely in nesting beach studies.

Conservation Implications

The East Pacific green turtle is in danger of extinction (IUCN 2010). Our study indicated that there was a large and active breeding population on beaches without law enforcement along the Pacific coast of Costa Rica, where egg collection and unregulated fishing was a common activity. The poaching taking place on the nesting beaches was undoubtedly causing a decline in the population, as has been documented for leatherback turtles nearby (Santidrián Tomillo et al. 2007). We observed extensive poaching (90% of the clutches were taken) and uncontrolled tourism at night on Nombre de Jesús. We observed that turtles that were disturbed stopped laying eggs and walked away still carrying shelled eggs.

Even though the turtles are able to hold shelled eggs for long periods of time (Casares et al. 1997, Plotkin et al. 1997) they generally come back to the nesting beach, later that night or the following night, to lay the remaining eggs (personal observation). This caused the turtle to spend more energy than needed for a nesting season compared to a beach with no human interference. Indeed extra energy spent in unsuccessful nesting events could impact the overall number of clutches for that female in a season (Hamann et al. 2002). Additionally, the possibility of hatchlings emerging from very small nests is very low due to the lack of mutual stimulation and group activity displayed by the hatchlings digging upwards in the sand to get to the surface (Carr and Hirth 1961, Miller 1997). As a result, those eggs that were not deposited with the main clutch would probably be lost.

Reproductive output is one of the most important measures for population biology, conservation and management of sea turtle populations. The information obtained from this study showed a higher reproductive output than previously described for the East Pacific green turtle. On the positive side higher individual output could represent a healthy population with good resources available to foraging adults, which would allow them to produce more offspring. On the other hand, higher reproductive output could modify previous estimations in number of females in a population, decreasing numbers previously reported for this species.

Thus, the data collected in this study along with the observations of poaching activity and uncontrolled tourism indicate that there is a great need to protect Nombre de Jesús because it is one of the most important nesting beaches hosting a population with the highest reproductive output reported for East Pacific green turtles.

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Tables

Table 3.1: East Pacific green turtles selected from the database from which there was a complete record of their reproductive status through ultrasound; turtles were scanned every time they came to the beach during the period of study. ECF_U is the effective clutch frequency + the number of clutches left calculated from ultrasonography.

Turtle ID	First seen	Last seen	ECF	Clutches left	ECF_U
1	28-Jul-09	27-Oct-09	8.55	0	8.55
2	3-Aug-09	31-Aug-09	3.32	2	5.32
3	11-Aug-09	1-Sep-09	2.74	2	4.74
4	15-Aug-09	27-Aug-09	2.00	2	4.00
5	18-Aug-09	14-Sep-09	3.24	2	5.24
6	22-Aug-09	23-Oct-09	6.15	0	6.15
7	22-Aug-09	2-Nov-09	6.98	1	7.98
8	25-Aug-09	6-Sep-09	2.00	2	4.00
9	28-Aug-09	9-Oct-09	4.49	0	4.49
10	2-Sep-09	14-Sep-09	2.00	2	4.00
11	9-Sep-09	12-Oct-09	3.74	0	3.74
12	10-Sep-09	13-Nov-09	6.31	0	6.31
13	10-Sep-09	18-Oct-09	4.15	2	6.15
14	15-Sep-09	26-Oct-09	4.40	2	6.40
15	17-Sep-09	22-Oct-09	3.91	2	5.91
16	19-Sep-09	25-Oct-09	3.99	2	5.99
17	10-Oct-09	22-Oct-09	2.00	2	4.00
18	10-Oct-09	23-Oct-09	2.08	2	4.08
19	11-Oct-09	25-Oct-09	2.16	2	4.16
20	12-Oct-09	18-Nov-09	4.07	0	4.07
21	15-Oct-09	25-Oct-09	1.83	2	3.83
22	15-Oct-09	6-Nov-09	2.83	2	4.83
23	17-Oct-09	30-Oct-09	2.08	2	4.08
24	18-Oct-09	11-Nov-09	2.99	2	4.99
Mean			3.67		5.13
SD			1.79		1.32

Figures

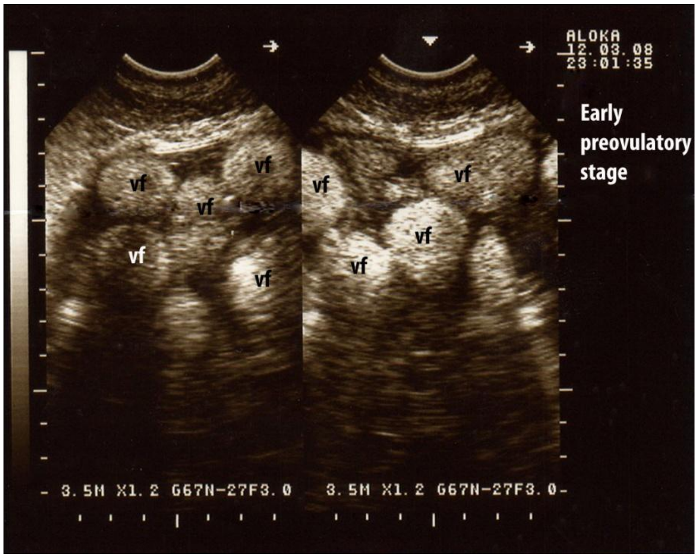

Figure 3.1: Ultrasonographic image of an ovary of an East Pacific green turtle (*Chelonia mydas*) after a successful nesting event. The ovary was filled with vitellogenic follicles (vf). The turtle had at least two more clutches to lay during the nesting season.

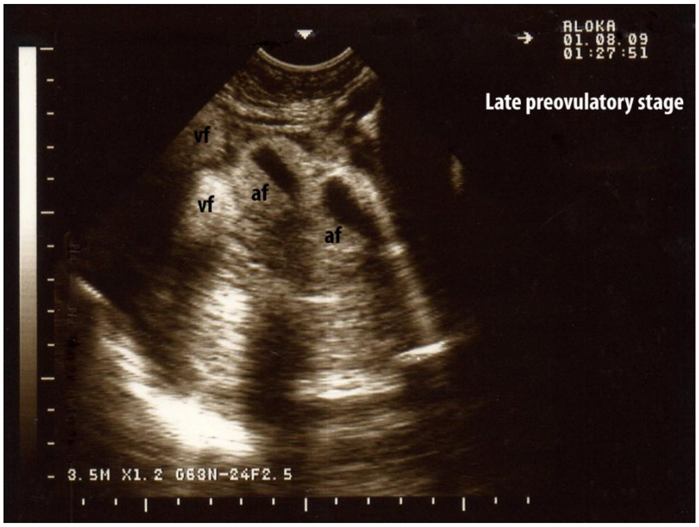

Figure 3.2: Ultrasonographic image of the ovary of an East Pacific green turtle (*Chelonia mydas*) after a successful nesting event. Ovary in late preovulatory stage. The turtle had one more clutch to lay during the nesting season. In this stage we observed vitellogenic follicles (vf), atretic follicles (af) and some coleomic (empty) space.

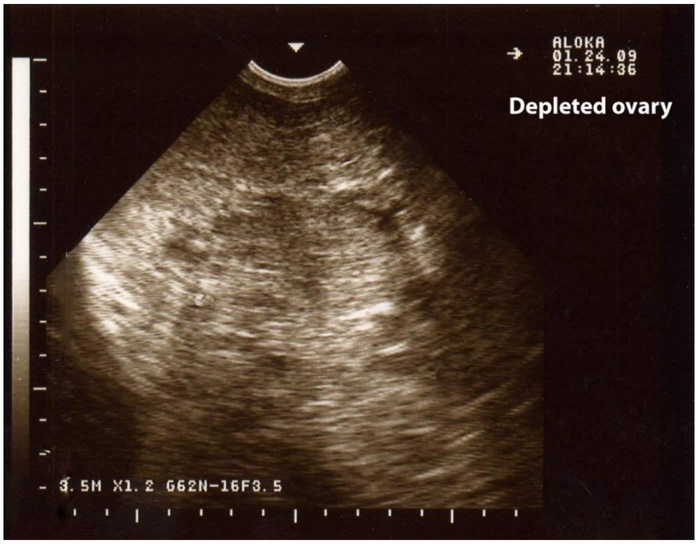

Figure 3.3: Ultrasonographic image of the ovary of an East Pacific green turtle (*Chelonia mydas*) after a successful nesting event. The depleted ovary indicated that the turtle had completed the nesting season and would start migrating. We considered an ovary depleted when we identified fewer than 5 vitellogenic follicles remaining (none in this picture).

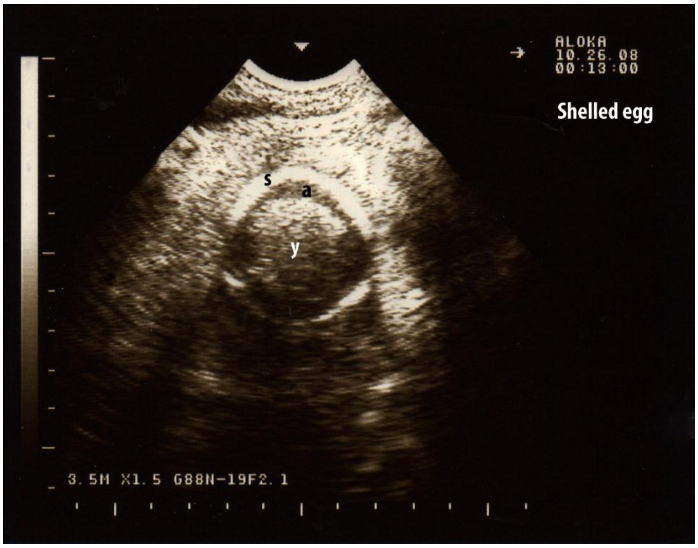

Figure 3.4: Ultrasonographic image of the oviduct of an East Pacific green turtle (*Chelonia mydas*) after a nesting event. The presence of the shelled egg after oviposition indicates that some kind of disturbance occurred during the nesting event causing the turtle to stop laying eggs and start covering the nest. s = shell, a = albumen, y = yolk.

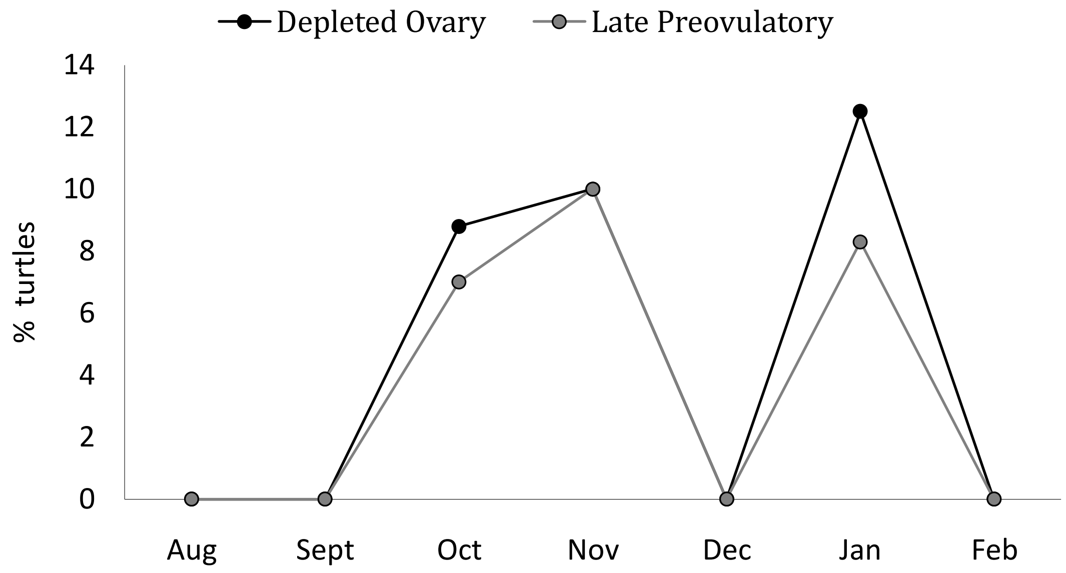

Figure 3.5: Percentage of East Pacific green turtles in Costa Rica with depleted ovaries and late preovulatory staged ovaries by month. The percentages were calculated in relation to the number of turtles scanned by ultrasound every month.

Chapter 4: Post-nesting Movements and Foraging Areas of East Pacific Green Turtles (*Chelonia mydas*) from Costa Rica

Abstract

We used satellite transmitters (Mk 10 Pat tags) to study the post-nesting movements, behavior and, foraging grounds of 10 East Pacific green turtles from Nombre de Jesús and Zapotillal beaches in Northwest Costa Rica. Some turtles were local residents in the Gulf of Papagayo; some moved an intermediate distance; and others moved to Panama or El Salvador. Total length of post-nesting migrations ranged from 5 to 1091 km, with a main daily speed of net travel of 37 km/day. Home range in the foraging areas varied from 265 km^2 to 18,260 km^2 (being one of the largest areas reported for this species). During migration turtles showed a bimodal distribution in duration of dives with majority of durations between 2-5 min and 40-60 min and dive depths mainly to 5 m or shallower. During foraging, distribution of dive duration was homogeneous, displaying all dive durations, while most of the dives were to 5-10 m depth. Sea surface currents did not influence preferred migration routes of the turtles. Nevertheless, some turtles seemed to benefit from currents by swimming in the same direction to reach the feeding grounds. The turtles in the present study did not exhibit patterns that would suggest that their behavior in the feeding grounds was influenced by variations in CHL or SST. However, all feeding grounds in this study had high primary productivity due to the oceanography of the area. The oceanic and bathymetric features could be influencing the general areas where the turtles are, but not their specific movements within the area. Our study indicated that green turtles that nest in Northwestern Costa Rica spend all their life

as adults in coastal areas of Central America. The coastal nature of their movements makes them vulnerable to many human coastal activities. With the new information provided by this study we suggest that there is a clear interaction between sea turtles and artisanal fisheries because they are occupying the same areas. The fact that the turtles are swimming through different countries makes management more complex and calls for agreements between nations. More information is needed in order to understand how severe the impact of coastal fisheries is on this population.

Introduction

Animals migrate in response to the need for resources that are not available at their present site. For example, red knots (*Calidris canutus*) travel from North America to winter areas in Argentina (Harrington et al. 1988) and the monarch butterfly (*Danaus plexippus)* migrates from eastern North America to over-wintering areas in central Mexico travelling 3600 km (Brower 1996). In general, whales also display a seasonal migration from high-latitude foraging areas to low-latitude reproductive grounds (Corkeron and Connor 1999). Migration is driven by balance of the cost of remaining at a given location, versus the benefit of moving (Morreale et al. 2007). In areas where food resources vary temporally or environmental conditions are not optimal all year, migratory behavior often evolves in the affected animals. For instance, if the conditions are optimal for adult populations but not for offspring development; the adults may undergo migrations to reproduce and ensure the survival of their offspring. This is common in animals such as whales and sea turtles.

Sea turtles are the only reptiles that exhibit long distance migrations (Plotkin 2003). Pacific Leatherback turtles nesting in Costa Rica migrate into the South Pacific off Chile and Peru (Morreale et al. 1996, Shillinger et al. 2008). Green turtles nesting on Ascension Island travel to feeding grounds along the coast of Brazil (Carr and Carr 1972, Hays et al. 2002). Olive ridley turtles nesting in northwestern Australia migrate between 180 and 1100 km to their feeding grounds (Whiting et al. 2007). Juvenile loggerheads transverse the entire Pacific Ocean during developmental migrations; traveling from nesting beaches in Japan and Australia to foraging areas in Baja California (Bowen et al.

1995); when they reach sexual maturity they return to the western Pacific where they remain the rest of their life (Nichols et al. 2000).

Sea turtles migrate in open ocean likely using a variety of cues. Hatchlings can follow light cues to get to the ocean, then orient into waves and also orient to the earth's magnetic field (Lohmann and Lohmann 1992). For adults orientation plays an important role because they show fidelity to a particular nesting beach and foraging area (Carr and Carr 1972, Nordmoe et al. 2004, Plotkin et al. 1996, Ireland et al. 2003). Adults appear to have the capability to migrate to a specific location possibly by using the inclination of the earth's magnetic field and by having a bicoordinate magnetic map (Lohmann and Lohmann 1996). Sea turtles also follow environmental features such as bathymetric contours or currents to help orientation (Morreale et al. 1996, Shillinger et al. 2008). Green turtles going from Ascension Island to Brazil may follow chemical cues, currents and magnetic cues collecting this information during the migration to adjust their course (Luschi et al. 1998).

East Pacific green turtles (*Chelonia mydas*) (also known as black turtles) belong to a distinct population of this endangered species inhabiting waters in tropical and sub tropical regions throughout the Eastern Pacific (Seminoff et al. 2002a). They range from Baja California to Chile and west to Galapagos Islands. The most important nesting grounds identified in the Pacific are found at Colola and Maruata in Michoacán (Mexico) (Alvarado and Figueroa 1992), and in the Galapagos Islands (Green 1984). Although green turtles are present along the Pacific coast of Central America (Cornelius 1979), limited information exists on populations nesting there (Richard and Hughes 1972, Cornelius 1976).

Turtles nesting in Michoacán move north and south along the Central American coast (Alvarado and Figueroa 1992). East Pacific green turtles that nest in the Galapagos show three different migratory strategies as indicated by flipper tag returns (Green 1984) and satellite telemetry (Seminoff et al. 2008). Some individual females swim through open ocean and reach the coast of central America (Green 1984, Seminoff et al. 2008); others reside among the Galapagos islands; and a third group moves to oceanic waters and feeds there (Seminoff et al. 2008). For green turtles that nest along the Central American coast it is not known where they migrate to reach their feeding grounds.

Juvenile and adult green turtles are known to forage in coastal areas, estuaries, lagoons (Seminoff et al. 2002a) and near shore insular habitats (Amorocho and Reina 2007). Even though it was believed that green turtles only foraged in coastal environments, recent studies demonstrated they also forage in open waters as adults (Quiñones et al. 2010). Their diet is mainly sea grass and red and green algae. However, they also eat invertebrates and gelatinous prey (Seminoff et al. 2002b, Seminoff et al. 2006a). Adult green turtles foraging off shore of Peru have a diet dominated by jelly fish, mollusks and crustaceans (Quiñones et al. 2010).

The eastern Tropical Pacific offers areas of high productivity as a result of its particular oceanic features. It is characterized by the presence of coastal and open ocean upwellings, fronts, eddies and meanders (Lavín et al. 2006). The convergence of the trade winds of the intertropical convergence zone (ITCZ) produces a low wind area off Central America where the SST (sea surface temperatures) is higher than elsewhere in the area. However, the wind blowing from land to sea produces the Tehuantepec, Papagayo and Panama jets causing eddies that generate productive areas exhibiting a decrease in SST and increase in chlorophyll levels and interrupting the warm low productivity “warm pool” (Palacios and Bograd 2005, Lavín et al. 2006). Within this region, the Costa Rican dome is another upwelling region in the eastern Pacific with high primary and secondary production (Lavín et al. 2006). Centered 300 km off the Gulf of Papagayo between Costa Rica and Nicaragua, it is produced by costal jets, eddies, the ITCZ and the geostrophic balance of the thermocline (Fiedler 2002).

In coastal areas, Costa Rica hosts an important population of the East Pacific green turtle along shore of Guanacaste on the Nicoya peninsula (Richard and Hughes 1972, Cornelius 1976). Little scientific data are available for this population and we do not know where their foraging grounds are, nor what routes they take to get to them. Anecdotal information suggests that these turtles are subjected to capture in longlines and gill nets and it is well known that poaching of eggs is rampant on many beaches in the area. In order to better protect this highly endangered population of green turtles from threats in the ocean we need to know their migration routes, foraging grounds and behavior at sea at the very least. The situation on the nesting beaches and during the internesting period was discussed in Chapter 2. Here we report the post-nesting movements, behavior and foraging grounds of green turtles that nest in Guanacaste and we discuss how they potentially respond to oceanographic conditions. We also discuss the conservation implications of these data.

Materials and Methods

We used satellite telemetry to study the post-nesting movements and behavior of East Pacific green turtles nesting on Nombre de Jesús (10° 23’ 30” N; 85° 50’ 07” W) in Guanacaste Province of Costa Rica. We patrolled the beach at night during the nesting season to intercept turtles during their last nesting event. We selected turtles with depleted ovaries for this study. To assess the reproductive status of each turtle and to verify that we were witnessing its last nest of the season we used an ultrasound instrument (Aloka SD 500) (Chapter 3). This ensured that the turtles would leave the area after nesting and not be subjected to poachers on the beach or fisherman near the beach. Satellite transmitters (Wildlife Computers Mk-10 PAT Pop up archival transmitting tag) were attached to 10 female green turtles, 1 in October 2006, 1 in August 2007, 2 in January 2009, 4 in October 2009 and 2 in November 2009 (Table 4.1).The transmitters were configured to transmit opportunistic transmissions so we could obtain real-time location data.

Satellite transmitter attachment

We followed a modified methodology used by Morreale et al. (1996) as described in Morreale (1999) to attach the satellite transmitters to the turtle. We measured the curved carapace length (CCL) of each turtle with a flexible measuring tape (± 0.5 cm). We cleaned the marginal posterior scute of the carapace with 70% alcohol and made a 3 mm diameter incision with a sterile electric drill bit (battery-powered electric drill). Immediately after the incision we applied lidocaine and inserted sterile surgical tubing. We positioned plastic buttons with Y holes above and below the carapace to avoid friction and consequent damage to the carapace. We connected the transmitter to the buttons on the carapace by a flexible lanyard (monofilament fishing line, 400 lb test) that passed through the holes and was secured to itself with a metal crimp. To avoid entanglement or long-term impediment of the turtles, we placed swivels and crimps which would break away with corrosion.

The attachment process took 7 to 10 min and was done when the turtle was covering the nest after laying eggs minimizing the impact on the turtle's natural behavior.

Satellite transmitters

We customized satellite tags with a buoyant case made out of syntactic foam. Satellite transmitters weighed ~115g (≈ 0.2 % of the turtle mass), had a hydrodynamic shape and trailed behind the turtle to minimize drag. The transmitter's positive buoyancy was 36g, enough to bring the antenna of the transmitter to the surface when the turtle breathed. We programmed the tags with duty cycles of 10h/24h (13:00-17:00hs and 18:00-00:00hs) to optimize battery life. The transmitter sampled and summarized data (dive depth, dive duration and time at depth) stored in categorized bins: Dive depth: 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 75, 100 and 200 m; Dive duration; 2, 5, 10, 20, 30, 40, 50, 60 and 90 min.

SSSM Method

We applied a Bayesian switching state-space model (SSSM) developed by Jonsen et al. (2007) to all of the raw Argos-acquired surface locations for each track (n = 10) resulting in daily position estimates. This model allowed location estimates to be inferred by coupling a statistical model of the observation method (measurement equation) with a model of the movement dynamics (transition equation) (Patterson et al, 2008)

The measurement equation accounted for errors in observed satellite locations and these were based on published estimates (Vincent et al. 2002). Similar priors were placed on model parameters as in Jonsen et al. (2007). When satellite positions were missing, linearly interpolated positions were used as initial values (Bailey et al. 2008).

The transition equation was based on a correlated random walk model and included a process model for each of two behavioral modes (Jonsen et al. 2005). Behavioral mode 1 was considered to represent transiting and behavioral mode 2 represented foraging (or area-restricted search behavior) (Bailey et al. 2010). Priors were specified assuming that during transiting turn angles should be closer to 0 and autocorrelation should be higher than when foraging (Jonsen et al. 2007).

The model was fitted using the R software package (R Development Core Team 2008) and WinBUGS software (Lunn et al. 2000). Two chains were run in parallel, each for a total of 30,000 Markov Chain Monte Carlo (MCMC) samples. The first 10,000 samples were discarded as a burn-in and the remaining samples were thinned, retaining every fifth sample to reduce autocorrelation. Thus, posterior distributions for parameter, state, and behavioral mode estimates were based on 4000 samples from each chain.

We plotted the migration routes on a map using ArcGIS version 9.3 geographic information system software (www.esri.com). Based on the daily locations obtained with the SSSM, we calculated distance traveled in one day and the total distance traveled. We included in this analysis the turtles from which migration was tracked for more than two days. We compared the size (CCL) of the turtles tagged with the total distance traveled and the daily movements. The longer tracks (> 100 km) were compared against geostrophic surface currents. Aviso geostrophic surface current (u and v vectors, cm/sec) were monthly composites, at a 0.5º spatial resolution (NOAA Ocean-Watch-LAS).

Diving behavior

We obtained dive depth and dive duration summarized in bins and transmitted through the Argos system. We separated dive data into migration and foraging based on the behavior mode determined with the SSSM model and calculated proportion of dives at depth and duration for each turtle. We calculated proportion and tested differences (one-way ANOVA) between depths of dives and duration of dives for all turtles during migration and foraging and during day and night. We also calculated and compared depth of dives for the turtles in different foraging areas. Each histogram was summarized in intervals of 4 hours, which allowed us to compare dive depth and dive duration for day and night. Statistical analyses were performed using SPSS Inc. Data were transformed when necessary before analysis to meet the assumption that data were normally distributed. Statistical significance was accepted at 0.05 level.

Foraging Areas

We estimated areas used for foraging for individual turtles using 100% Minimum Convex Polygons (MCP) to estimate their home range during foraging using the Hawths tools extension (Beyer 2004) for ArcGIS. Minimum convex polygon areas are based on minimum distance of outer locations for each turtle in foraging areas including all locations for duration of the transmission.

Based on differences in areas of polygons, we divided foraging time in weeks and preformed MCP calculations for turtles in which overall area of the polygons was higher than 10,000 km². To analyze use of foraging area in comparison with oceanic characteristics, we divided locations into months and created monthly MCPs. Oceanic variables analyzed were surface chlorophyll-a levels, geostrophic surface currents and sea surface temperatures (SST). These variables were obtained from NOAA OceanWatch-LAS and NOAA OceanWatch - Central Pacific (http://oceanwatch.pifsc.noaa.gov, http://las.pfeg.noaa.gov/oceanWatch/oceanwatch). The SST (ºC) grids were monthly composites with a spatial resolution of 0.1º and surface chlorophyll-a (mg/m^{-3}) grids were monthly composites, with a spatial resolution of 0.05º.

Results

Post-nesting movements

Through ultrasonography we identified turtles with depleted ovaries and all turtles with transmitters started post-nesting movements, without returning to the nesting beach.

The 10 satellite transmitters reported data for 25 to 102 days (mean ± SD = 62.2 ± 28 d). All turtles conducted post-nesting movements to neritic foraging grounds (Figure 4.1). Turtle 2 carried out the longest migration, approximately 1091 km southwards to the Gulf of Panama (Figure 4.1-d). Three turtles migrated (293, 410 and 425 km) northwards to the Gulf of Fonseca off El Salvador (Figure 4.1c). Four turtles carried out short migrations (24, 43, 71 and 152 km) to the Bay of Santa Elena in northern Costa Rica

(Figure 4.1 a-b). The last 2 turtles were local residents in the Gulf of Papagayo approximately 5 km north of the nesting beach. There was no correlation between the size of the turtles and the length of their tracks ($p = 0.614$, $N = 6$). The mean daily movement during the migration was 37.03 km ± 8.36 and it was not correlated to CCL ($p = 0.209$ $N = 6$).

Comparing post-nesting movements with geostrophic surface currents indicated that turtles migrating to the Gulf of Fonseca (Figure 4.2) swam in the same direction as the prevailing current, the Costa Rica Coastal Current (Kessler 2006). In contrast the turtle migrating to the Gulf of Panama swam both against and with the current.

Foraging Areas

We identified four coastal foraging areas for this population: Gulf of Fonseca, Gulf of Panama, Bay of Santa Elena and Gulf of Papagayo (Table 4.1). The daily movement during foraging was 12.8 ± 3.4 km and was not correlated with the turtle size ($p = 0.838$, $N = 9$). Even though turtles moved to the Gulf of Fonseca area, none of the turtles foraged inside the gulf. Behaving differently, the turtle that migrated to the Gulf of Panama resided for the duration of the transmitter life (44 tracking days in the foraging grounds) near shore in the Gulf of San Miguel. We calculated MCPs for each turtle including all the locations during foraging (Figure 4.3). Areas used during foraging for the individuals ranged from 265 to 18,260 km^2 (Table 4.2). Interestingly, there was no significant correlation ($p = 0.342$, $N = 9$) between the number of days of tracking and the area of the polygons. Also, we did not find a significant correlation ($p = 0.143$, $N = 9$) when we analyzed the relation between the foraging grounds and the area of the MCP.

Based on the differences in the areas of the MCP we divided the data to create weekly polygons. Only the turtles with the largest polygons (turtles 6 and 9) displayed notable shifts in their foraging areas with time (Figure 4.4).

Diving behavior

There were significant differences between the overall duration of dives (ANOVA) F = 3.125, df = 8, p = 0.003). Bonferroni post hoc multiple comparison test explained these differences by the difference between 2 and 90 and 40 and 90 min (p = 0.010 and p = 0.011 respectively). There were no significant differences (One-way ANOVA F = 1.218, df = 8, p = 0.295) between mean duration of dives during migration and foraging. However, the distribution of dive durations during foraging was more homogeneous with turtles performing 79% of the dives between 2 and 40 min. During migrations there was a bimodal distribution of dive duration; between 2 and 5 min (32 %) and between 40 and 60 min (46 %) (Figure 4.5). There were highly significant differences between the depth at which the dives were performed (ANOVA, F = 11.046, df = 12, p = 0.0001). These differences were explained by the difference between 5 m and all other depths (Bonferroni posthoc multiple comparison, p < 0.0001). Overall, the turtles carried out shallower dives (5 m) during both activities (migration mean ± SD 31.2% ± 5.7; foraging, mean ± SD 38.8 ± 5.6) (Figure 4.6).   There were no significant differences (ANOVA F = 1.23, df = 12, p = 0.273) between the depths of the dives during migration and foraging. Turtles used different depths even in the same foraging area (Figure 4.7). Turtles foraging in the Bay of Santa Elena dove to a predominant depth of 5 m (mean ± SD 51.5 ± 11.9%). Turtles foraging in the Gulf of Fonseca used different depths ranging from 5 to

80 m; while one turtle did not show a strong tendency to use a certain depth, the other turtle carried out 52 % of the dives in the first 5 m of the water column. The turtles foraging in the Gulf of Papagayo also used different depths. One turtle mainly used the first 15 m of the water column and the other turtle dove mainly to 70 m.

During migration and foraging turtles used similar depths during day and night (Figure 4.8) (5 and10 m, 49%, 42% respectively). There were no differences in dive duration between day and night during migration. During foraging there were two predominant durations of dives at night: short dives (2 min, 22%) and long dives (from 20-40 min, 49%), while during the day the duration of the dives varied widely from 5 to 40 min.

Oceanographic features

We divided all foraging locations monthly for each turtle and created monthly MCP. We also overlaid the monthly MCPs with SST (Figure 4.9) and chlorophyll-a for visual comparison (Figure 4.10). The SSTs ranged from 17 to 31 ºC. Turtles occupied areas ranging from 22 to 31 ºC during October, November, and December. In January the turtles stayed at temperatures higher than 24º C despite the fact that lower temperatures were available. Noticeably during January and February 2009, there was a drop in the SST reaching 22º C in the Gulf of Papagayo but a turtle foraging there did not respond to this drop and stayed in the same area. Overall, chlorophyll levels were higher closer to the coast but CHL variations occurred through the course of the study. Even though the turtles foraged close to the coast (where CHL concentrations were high), they did not apparently respond to variations. Turtles foraging in Santa Elena Bay experienced higher chlorophyll levels than the turtles foraging elsewhere. In January and February 2009 a bloom occurred in the areas off Costa Rica and Nicaragua affecting mainly the Gulf of Papagayo and the Bay of Santa Elena. None of the individuals foraging in those areas responded to these changes in productivity staying in the same areas. The turtles foraging near the Gulf of Fonseca did not select places with high primary productivity even though they were available closer to the Gulf in the period where the turtles were tracked.

Discussion

Post nesting movements

The satellite transmitters sent messages for 25 to 102 days. Even though battery life for some was less than expected, the short distances moved by the turtles allowed us to collect information on both post nesting movements and foraging areas for all turtles.

East Pacific green turtles moved between 5 and 1091 km after nesting. Some turtles were local residents in the Gulf of Papagayo, some moved an intermediate distance, and others moved to Panama and El Salvador. It appeared that Nombre de Jesús was an important nesting beach for turtles residing in waters throughout Central America. Turtles in this population did not undertake oceanic migrations reported for other sea turtles (Green 1984, Carr 1975, Plotkin et al. 1995, Seminoff et al. 2008). Rather they stayed within coastal areas even when migrating over 1000 km. Even though it may not be the shortest distance to the preferred foraging area, it appears that green turtles prefer to migrate along the coast in shallow waters. Green turtles from Wan- An Island migrate over the continental shelf to mainland China involving detours that increase the final migration distance (Cheng 2000). Commonly sea turtles from the same nesting area carry out post-nesting migrations using different routes (Plotkin et al. 1995, Seminoff et al. 2008, Hatase et al. 2006). Some olive ridely turtles nesting on Nancite beach (Gulf of Papagayo) migrate to coastal neritic environments (Honduras, El Salvador and Guatemala) whereas others move to oceanic areas in the Eastern Pacific (Plotkin et al. 1995). Green turtles nesting in Galápagos undertake coastal and oceanic migrations to reach different feeding grounds (Seminoff et al. 2008), as well as green turtles from the Ogasawara Island in Japan (Hatase et al. 2006). In the present study differences in migration routes were not related to the size of the turtles as occurred in green turtles from the Galápagos (Seminoff et al. 2008).

The turtle going to Panama exhibited the longest migration traveling 40 km/day and covering the distance in 25 days. This turtle migrated following the shoreline until it reached the Gulf of Panama, which it crossed straight to the Gulf of San Miguel along the coast.

Two turtles moved to the Gulf of Papagayo 5 km north of the nesting beach, where they resided for the rest of the tracking duration (25 and 63 days). Residency in green sea turtles also occurs in turtles nesting in Galápagos Islands. Contrary to the present study, resident Galapagos green turtles moved at least 75 km (Seminoff et al. 2008) from the nesting beach. Four green turtles moved to Santa Elena Bay; two of them completed their movement one day after laying the last clutch of the season and remained there for the rest of the tracking duration. Two turtles took longer (3 days) to reach the foraging area, the longer duration could be related to the turtles foraging on the way because they traveled across the Gulf of Papagayo where other turtles were foraging; or stayed after the last nest one or two days in the area close to the nesting beaches.

Of the three turtles that migrated to the Gulf of Fonseca, two moved along the coast. Turtle 1 was the only one to traverse deeper waters moving outside the continental shelf. And one turtle stopped north along the Santa Elena Peninsula before continuing the migration to the Gulf of Fonseca. These three turtles swam through suitable foraging areas (Gulf of Papagayo and Santa Elena Bay), where turtles from the same nesting beach were foraging, while continuing on to more distant foraging areas. Hawksbill, olive ridley and green turtles nesting at other locations stop and forage on the way to their final destination (Cheng 2000, Cuevas et al. 2008, Whiting et al. 2007) which may reduce the overall cost of migration (Godley et al. 2002).

Similar behavior occurs in the green turtles foraging along the coast of Brazil (Hays et al. 2002). The fact that turtles are swimming through zones that may offer the resources needed before they reach their final destination, raises the question of how the turtles select their foraging sites. Some discussion in the literature regarding this question arose when other populations displayed this pattern. The behavior was attributed to food resource limitation, proximity to over-wintering sites and territorial defense (Broderick et al. 2007). In the present study, we discard the possibility of the turtles being closer to overwintering sites for the obvious reason of inhabiting the tropics, we also discard the resource limitation because there are turtles foraging in all the areas. Additionally, the length of the migration and, as a result, the foraging sites are not related to turtle size. We suggest that as juveniles or sub-adults these turtles chose these foraging areas as a consequence of their early dispersal patterns as hatchlings, and as adults kept performing these migrations in response to fidelity to a specific foraging area (Broderick et al. 2007).

The mean daily speed of travel during migration for this population was approximately 37 km/day. East Pacific green turtles travelled slower than green turtles in the Caribbean of Costa Rica who travelled an average of 58 km/day to reach the foraging grounds (from 400 to 1090 km) north of the nesting beaches (Troëng et al. 2005). Also green turtles nesting in Taiwan move an average of 43 km/day to the continental shelf of China (Cheng 2000). These greater speeds of travel may reflect a lack of intervening foraging habitats or the need to travel greater distances.

Foraging areas

We identified 4 different foraging grounds: Gulf of Panama, Gulf of Papagayo, Bay of Santa Elena and Gulf of Fonseca. There were remarkable differences in how the turtles used these areas. Calculated foraging area home ranges varied from 265 km^2 to 18,260 km^2. Our findings differ from those for ridleys, loggerheads and other green sea turtles where the home ranges are smaller in general than the present study (Whiting et al. 2007, Makowski et al. 2006, Seminoff et al. 2002b). Olive ridleys in their foraging grounds of Australia use areas as large as 1260 km^2 (Whiting et al. 2007). Loggerheads in the Mediterranean use average home ranges of 305 km^2 ranging from 3.5 to 1,198 km^2 (Zbinden et al. 2008), while juvenile green turtles in Florida inhabit small reef systems using home ranges between 0.7 and 5 km^2 (Makowski et al. 2006). Seminoff et al (2002b) reported mean polygon areas of 16.6 km^2 for East Pacific green turtles foraging in Mexico. The two turtles that moved the most while foraging were turtle 6 in the Gulf of Fonseca and turtle 9 in Santa Elena Bay. Turtle 6 used a total area of 14,083 km², starting foraging in Nicaragua (south of the Gulf of Fonseca) and continuing until Guatemala. The weekly MCP showed that this turtle stopped at different places, probably exploring patchy food resources and was still moving at the end of transmission (80 days after leaving the beach). At least in two different weeks the turtle in Santa Elena Bay moved out to oceanic waters reaching areas with depths greater than 2000 meters covering an overall area of 18,260 km² during the duration of the tracking. In contrast, the turtle at Panama only foraged in the Gulf of San Miguel using 265 km² in 45 days. Whereas the turtle in Panama was probably feeding on sea grass and pastures related to estuarine environments, the turtle off Santa Elena may have been consuming macro algae and other components of the plankton like jellyfish (Quiñones et al. 2010). Turtles foraging in Santa Elena Bay displayed greater variations in the use of the area. Overall, differences in the uses of foraging areas can be due to different foraging strategies, food availability in each foraging site (Godley et al. 2003) and food availability in the different sites or within the same area (Seminoff et al. 2002b).

Sea grass and coral reefs provide foraging habitats for sea turtles (Chaloupka and Limpus 2001, Jackson et al. 2001). Coral reefs are present along the coasts of Guatemala, El Salvador and Nicaragua and Costa Rica. The coral reef located in the Gulf of Papagayo is dead and covered with filamentous algae (Glynn 2001). These patches of coral and their associated species of algae and invertebrates could explain the greater movements of the turtles foraging near the Gulf of Fonseca in contrast to the turtles foraging in the Gulf of Papagayo and Santa Elena Bay. In these regions macroalgae are present from 0.5 m until approximately 20 m depth (Bernecker and Wehrtmann 2009, Fernández and Alvarado 2008). The genus *Cladophora* and *Ulva* are the most common within the green algae populations in the eastern Pacific (Fernández and Alvarado 2008). Also species such as *Gracilaria spp, Gigartina spp* and *Codium spp.*are present along the Pacific coast of Costa Rica and are part of the diet of the green turtles in Gorgona (Amorocho and Reina 2007) and Gulf of California (Seminoff et al. 2002a). Sea grasses (*Ruppia maritima* and *Halophila baillonii)* were present in the Gulf of Papagayo but after a storm destroyed these pastures in 1996 no sea grass has been present along the Pacific coast of Costa Rica (Cortés 2001).

As a possible explanation for the short migrations of green turtles in the Caribbean it was proposed that this population spends less energy in migration and more in reproduction than green turtles elsewhere (Troëng et al. 2005). Our findings suggest that the East Pacific green turtles spend even less energy in migration reflected in the short distance traveled, and short distance covered in a day, but they used broader areas while foraging than many other populations and species. Along the coast of the Central America the food availably probably is wide spread causing the turtles to spend more energy in foraging (using larger areas to forage).

Diving behavior

During migration turtles showed a bimodal distribution in duration of dives with major durations between 2-5 min and 40-60 min. The shorter intervals were associated with shallow dives and the longer intervals with deeper dives. Depth most used during migration was 5m. These short shallow dives allow the turtles to swim more efficiently by reducing drag which increases at the surface and decreases when the depth is 2-3 times the body thickness (Hays et al. 2001). It has been reported that shallow dives are mainly found during movement of turtles when they are swimming towards a specific destination (Rice and Balazs 2008). During migration the turtles also dived deeper than during foraging with a mean depth of 40 m and long submergences ranging from 40 to 60 min. The deeper dives during migration may be related to resting behavior (Rice and Balazs 2008) and avoiding predation (Hays et al. 2001). Also turtles are known to forage during migration (Cheng 2000, Cuevas et al. 2008, Whiting et al. 2007) and in this study the coastal movements showed that they swim through other suitable foraging areas suggesting that these deeper and longer dives are related to foraging on the way to their final destination.

During foraging the distribution of the dive duration was homogeneous displaying all dive durations. On the other hand, most of them were performed at 5-10 m depth. In foraging areas the turtles display different behaviors probably associated with different foraging strategies. Besides foraging, the turtles are carrying out other activities for example: resting, moving from patch to patch, exploring the area (Seminoff et al. 2006b) or even performing self cleaning behavior (Heithaus et al. 2002). It is difficult to determine what type of behavior the turtle is undertaking when submerging to a certain depth. Most of their behavior is related to the environmental characteristics of the specific foraging area and to the food available at the site. In general, green turtles can forage in benthic environments (3-32 m) or the mid water column (3-5 m) (Seminoff et al. 2006b). In our study the four turtles foraging in the Gulf of Santa Elena foraged mainly in the first 5 m of the water column. Those shallow dives may be related to the turtles foraging at the bottom of the coastal environment. However, two of the turtles foraging in that area made excursions to deep water environments suggesting they were also foraging on animals or floating algae associated with drifting material such as trees or other floatsom. The variation in the depths used may be associated with the feeding preferences of the individual turtles. Turtles foraging in the same area commonly show different depths depending on whether they are planktivores or herbivores (Hatase et al. 2006). Green turtles inhabit both shallow water and offshore deeper water where they could be resting or foraging on deep water invertebrates (Seminoff et al. 2006b). In some populations turtles avoid waters deeper than 10 m due to the lack of food availability and to avoid predation by sharks (Senko et al. 2010). The turtles foraging in the Gulf of Papagayo used different depths suggesting they may be using different resources in the same area. One of the turtles used almost exclusively the first 20 m of the water column while the other showed a peak at 70 m and the rest of the dives were distributed between 25 and 50 m. Turtles foraging in the Gulf of Fonseca also used different depths with one individual diving from 15 to 75 m, and the other mainly diving in the upper 5 m of the water column and at 70 and 100 m. The turtles swimming to 70 m depth were probably swimming to the ocean floor because that was the depth in the areas where this behavior occurred.

This population did not use extensively the 20 m depth that was suggested as neutral buoyancy for green turtles (Hays et al. 2000) and the average depth where green turtles may rest (Hays et al. 2001). However, buoyancy control may not be a unique strategy for resting sea turtles (Seminoff et al. 2006b). We did not find differences when we compared depths and durations during day and night during migration. During foraging there was a peak at 5 m depth during the night with duration of 2 and 20 – 40 min dives. The significant proportion of shallow and short dives during the night indicated that these turtles were not achieving neutral buoyancy to rest but were resting very close to or at the surface. As indicated for this population during internesting, the turtles may float at the surface as a resting strategy (Chapter 2). The long duration of night dives could also be related to vertical migration performed by plankton at night and the turtles foraging on it as described for green turtles in Japan (Hatase et al. 2006).

Oceanic features

Effect of currents on turtle migrations

Ocean currents may influence differently sea turtle migration. Three turtles moved in the same direction as the Costa Rica coastal current (CRCC) while migrating to the Gulf of Foncesca. Sea turtles use currents to minimize energy costs while migrating (Luschi et al. 2003a), their migratory routes drift as a result of prevailing currents causing them to deviate from their original trajectory (Luschi et al. 2003b, Shillinger et al. 2008) and their movements are influenced by oceanographic features like eddies or fronts because of an increase in food availability (Seminoff et al. 2008). The CRCC is the east edge of the CRD and continues along the coast until the Gulf of Tehuantepec in Mexico where it gets cut off and turns offshore feeding the North Equatorial Current (Kessler 2006). Probably the three turtles migrating to the Gulf of Fonseca benefited from this current while going from the nesting beach to the foraging area. However, the coastal nature of two of these turtles indicated that they were following the coast independently of the current. One of the turtles moving north swam farther from the coast suggesting that the original route may have drifted due to the speed of the current. If these individuals were taking advantage of the CRCC to reach the foraging area they would have to swim against this prevalent current (that is present all year around) when they returned to the nesting beach using the same migratory path. As for the turtle migrating to the Panama Gulf, she swam with and against the prevalent current. The area is affected by the north equatorial counter current which produces southern flow of the current until the Gulf where the combination of trade winds and the north flow along the Colombian coast causes the current to circulate north (Kessler 2006). In general, we suggest the surface currents did not have an influence on the preferred migration routes of the turtles. Nevertheless, some turtles may be benefiting from currents by swimming in the same direction to reach the feeding grounds. The CRCC could have drifted the original trajectory of one of the turtles.

Effect of currents, SST and CHL in foraging grounds

The turtles in the present study did not exhibit patterns that would suggest that their behavior in the feeding grounds was influenced by variations in CHL or SST. The eastern Tropical Pacific is characterized by coastal and open ocean upwellings, fronts and eddies (Lavín et al. 2006). One of the most important oceanic features of the eastern Pacific is the Costa Rican Dome (CRD), located off the Coast of Central America and centered 300 km off the Gulf of Papagayo between Costa Rica and Nicaragua (Fiedler 2002). These characteristics may explain the importance of the Gulf of Papagayo, Bay of Santa Elena and Gulf of Fonseca as foraging areas for the east Pacific green turtles. Even though the data did not indicate that the turtles selected the sites with higher CHL; all the feeding grounds described in this study had high primary productivity due to the oceanography of the area. This could be influencing the general areas where the turtles are, but not their specific movements within the area. The CHL levels do influence movements of Galapagos green turtles (Seminoff et al. 2008) and loggerheads foraging in the transition zone of the North Pacific (Polovina et al. 2001).

The turtles in our study used SSTs ranging from 22 to 31ºC. Even in the Papagayo and Santa Elena region there was a decrease in the temperature produced by the Papagayo winds, the turtles during these months did not show variation in their movements. Although it was suggested that migrating turtles reach a threshold at 25 ºC (Seminoff et al. 2008) it may be possible that during foraging they could support lower temperatures.

During January and February 2009 there was an unusual drop in the SST and an increase in the chlorophyll levels produced by the Papagayo winds. The temperatures decreased considerably along the coast reaching 22 ºC. This unusual phenomenon did not produce a change in the foraging area for the turtles which continued in the Papagayo Gulf.

Conservation implications

The East Pacific green turtle is in danger of extinction (IUCN, 2010). Our study indicated that green turtles that nest in Northwestern Costa Rica spend all their life as adults in coastal areas of Central America (Panama, Costa Rica, Nicaragua, Honduras, El Salvador and Guatemala). The coastal nature of their movements makes them vulnerable to human activities in those countries. Small and large scale artisanal and commercial fisheries in Central America use principally longlines, gillnets and trawling nets as fishing gear, that are sources of high bycatch for sea turtle populations (Lewison et al. 2007) . Commercial fisheries target mainly yellowfin tuna, swordfish, dolphin fish and marlin. Whereas artisanal fisheries in Costa Rica target species like flounder, grouper, croaker and snapper among others (Obtained from Manual de Especies Comerciales de Costa Rica).

Different populations of sea turtles had been reported to decline due to bycatch by fisheries (Lewison et al. 2004, Spotila et al. 2000, Troëng et al. 2004). Based on our results the East Pacific green turtles are mainly exposed to artisanal fisheries operating in Central America. Small-scale fisheries have been overlooked over the past years as researchers focused primarily on commercial large-scale fisheries that affect principally highly migratory species (Peckham et al. 2007). There is a lack of information about artisanal fisheries because they operate mainly without management, and their landings are mostly unreported, as a consequence there is no information on their interaction with turtles. During the course of this study we observed longlines and gill nets set in the waters close to the nesting beach, and observed the capture of East Pacific green turtles and ridley turtles in the Gulf of Papagayo. With the new information provided by this study we suggest that there is a clear interaction between sea turtles and artisanal fisheries because they are occupying the same areas. The fact that the turtles are swimming through different countries makes management more complex and calls for agreements between nations. More information is needed in order to understand how severe the impact of coastal fisheries is on this population, which is extremely important to the species (Chapter 3).

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Tables

Table 4.1 Post-nesting movements of East Pacific green turtles (*Chelonia mydas*) with satellite transmitters attached from Nombre de Jesús, Costa Rica. Track length is total distance moved of the turtle during migration. Length of migration is the calculated number of days the turtles took to reach the foraging areas. Total tracking includes the total duration of the satellite transmitters.

Turtle ID	Attachment Date	CCL (cm)	Total Tracking (days)	Foraging grounds	Length of Migration (days)	Track length (km)
1	17-Oct-06	77.50	29	Fonseca Gulf	29	430
2	24-Aug-07	91.40	70	Panama Gulf	26	1086
3	16-Jan-09	78.10	54	Fonseca Gulf	17	390
4	24-Jan-09	84.00	63	Papagayo Gulf	0	0
5	9-Oct-09	87.70	89	Santa Elena Bay	3	66
6	23-Oct-09	88.00	80	Fonseca Gulf	10	270
7	25-Oct-09	81.40	25	Papagayo Gulf	0	0
8	27-Oct-09	86.00	26	Santa Elena Bay	3	98
9	13-Nov-09	82.50	84	Santa Elena Bay	1	77.5
10	18-Nov-09	84.40	102	Santa Elena Bay	1	62.5

Table 4.2 MCPs of East Pacific green turtles (*Chelonia mydas*) on the foraging grounds. The MCPs were created based on all locations of the turtles in the foraging areas. Foraging (tracking days) refers to the time spent on the foraging grounds.

Turtle ID	Foraging ground	Foraging (tracking days)	Polygon area (km²)	Polygon perimeter (km)
2	Panama Gulf	45	265.07	75.24
3	Fonseca Gulf	33	4817.38	353.50
4	Papagayo Gulf	58	1071.60	138.83
5	Santa Elena Bay	84	1168.70	145.54
6	Fonseca Gulf	71	14083.71	823.00
7	Papagayo Gulf	18	602.68	94.40
8	Santa Elena Bay	18	2976.47	241.42
9	Santa Elena Bay	77	18260.10	631.56
10	Santa Elena Bay	89	2472.40	197.04

Figures

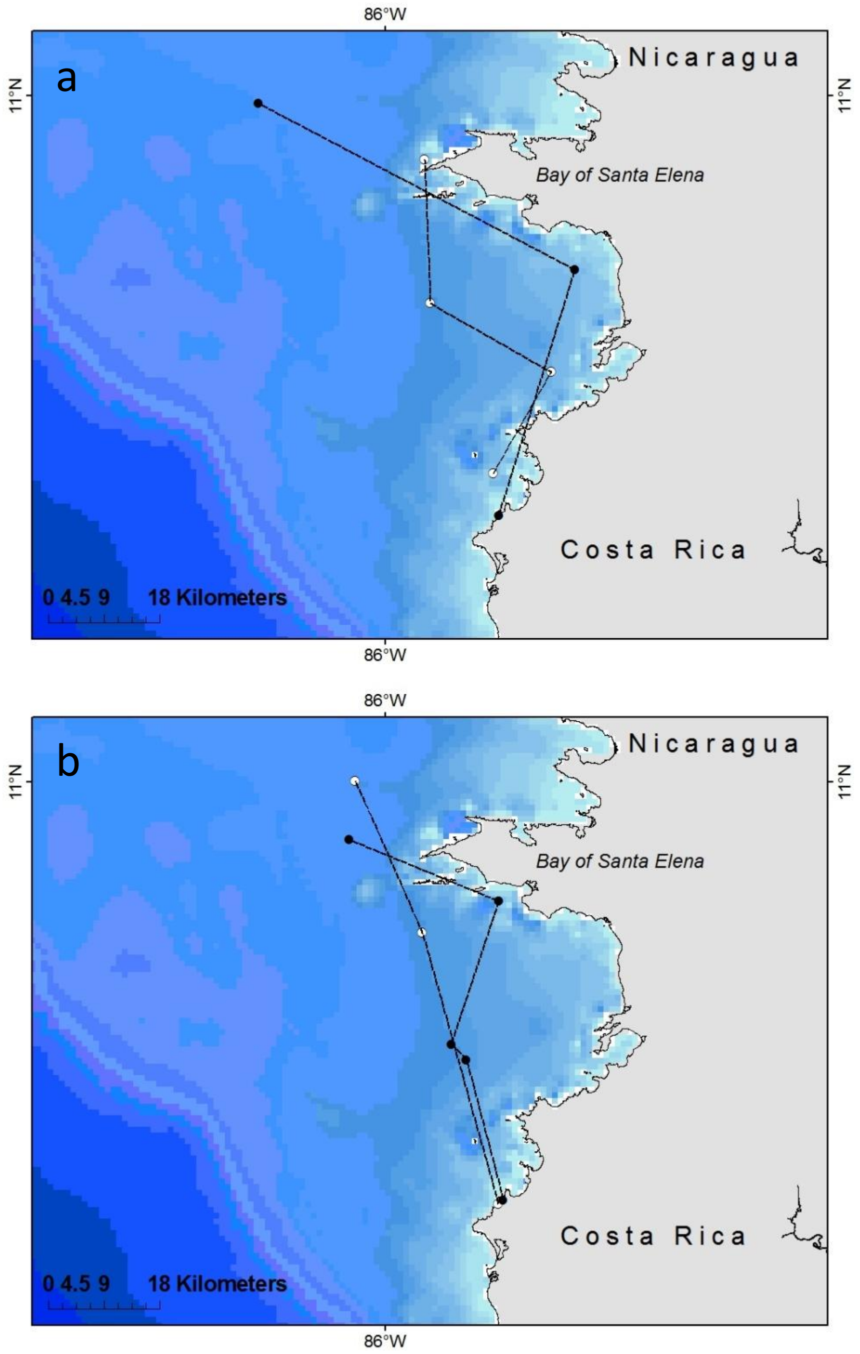


Figure 4.1: Post-nesting movements of east Pacific green turtles nesting on Nombre de Jesús, Costa Rica that migrated to the area of Santa Elena Bay(a, b), within the area of Gulf of Fonseca(c) and to the Gulf of Panama (d).

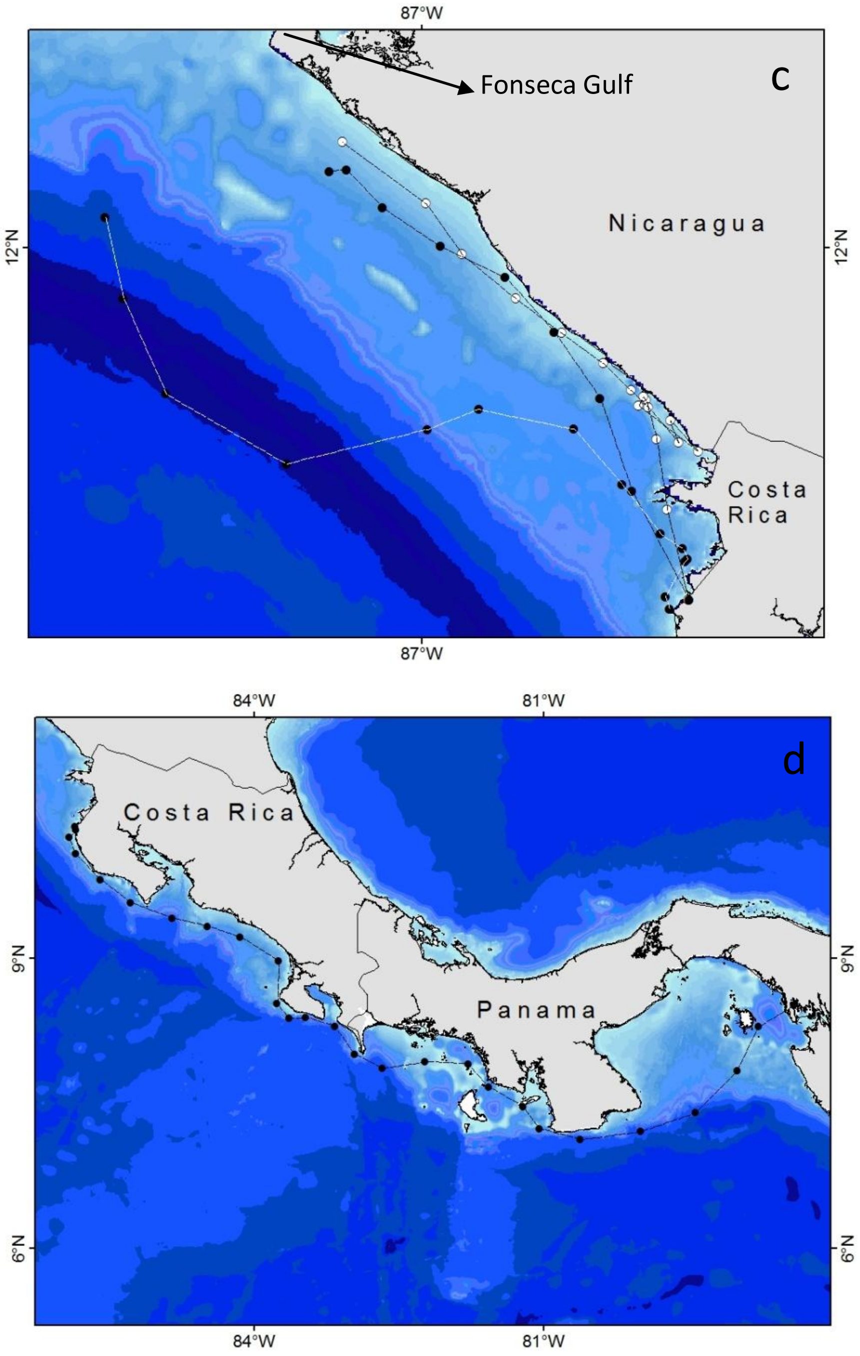


Figure 4.1: Continued

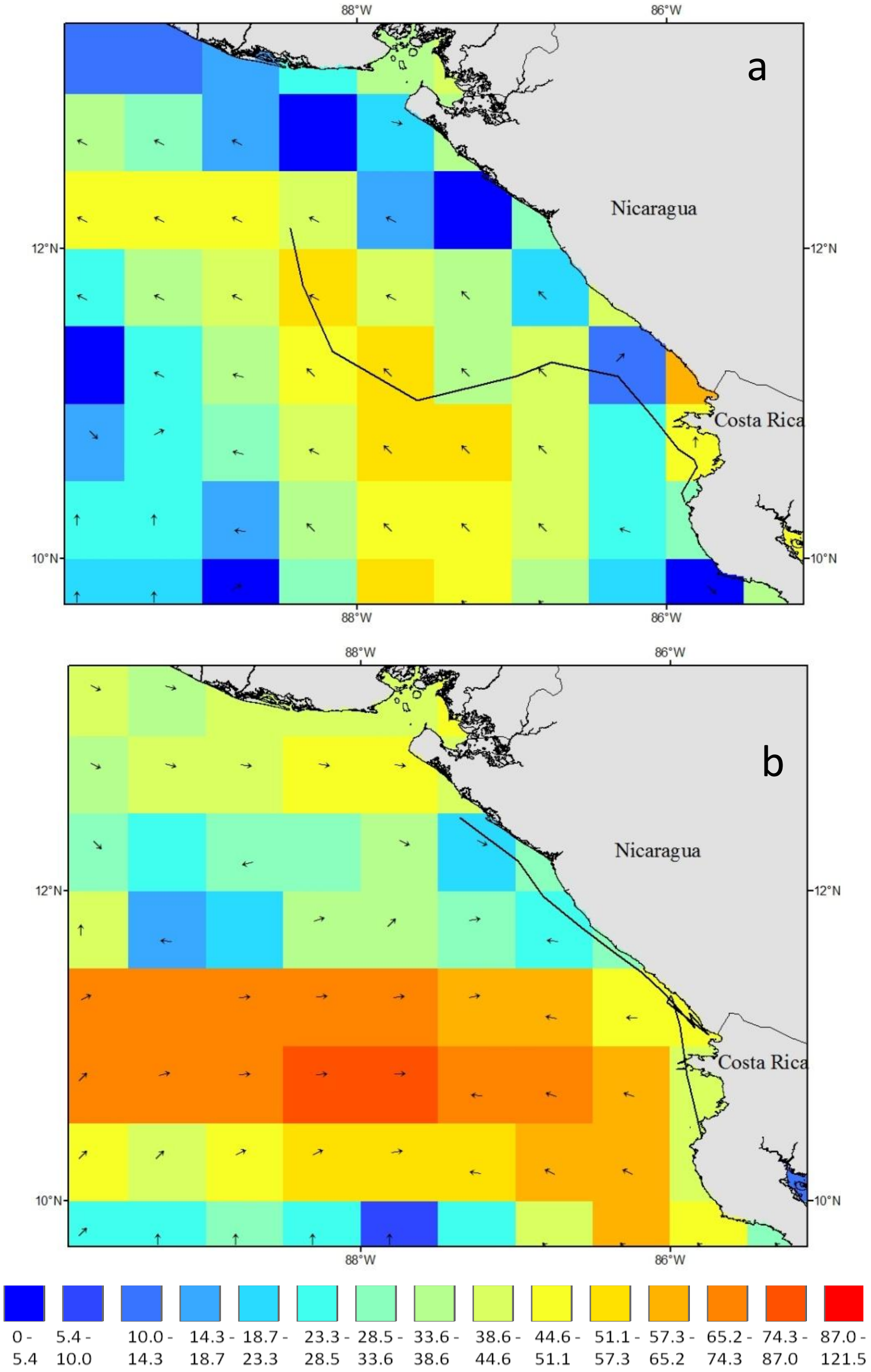


Figure 4.2: Migration routes in relation to geostrophic surface currents (0.5º spatial grid, monthly composites) of East Pacific green turtles from Nombre de Jesús that migrated to the area of the Gulf of Fonseca (a, b, c) and to the Gulf of Panama (d). Scale represents magnitude of currents (cm/sec).

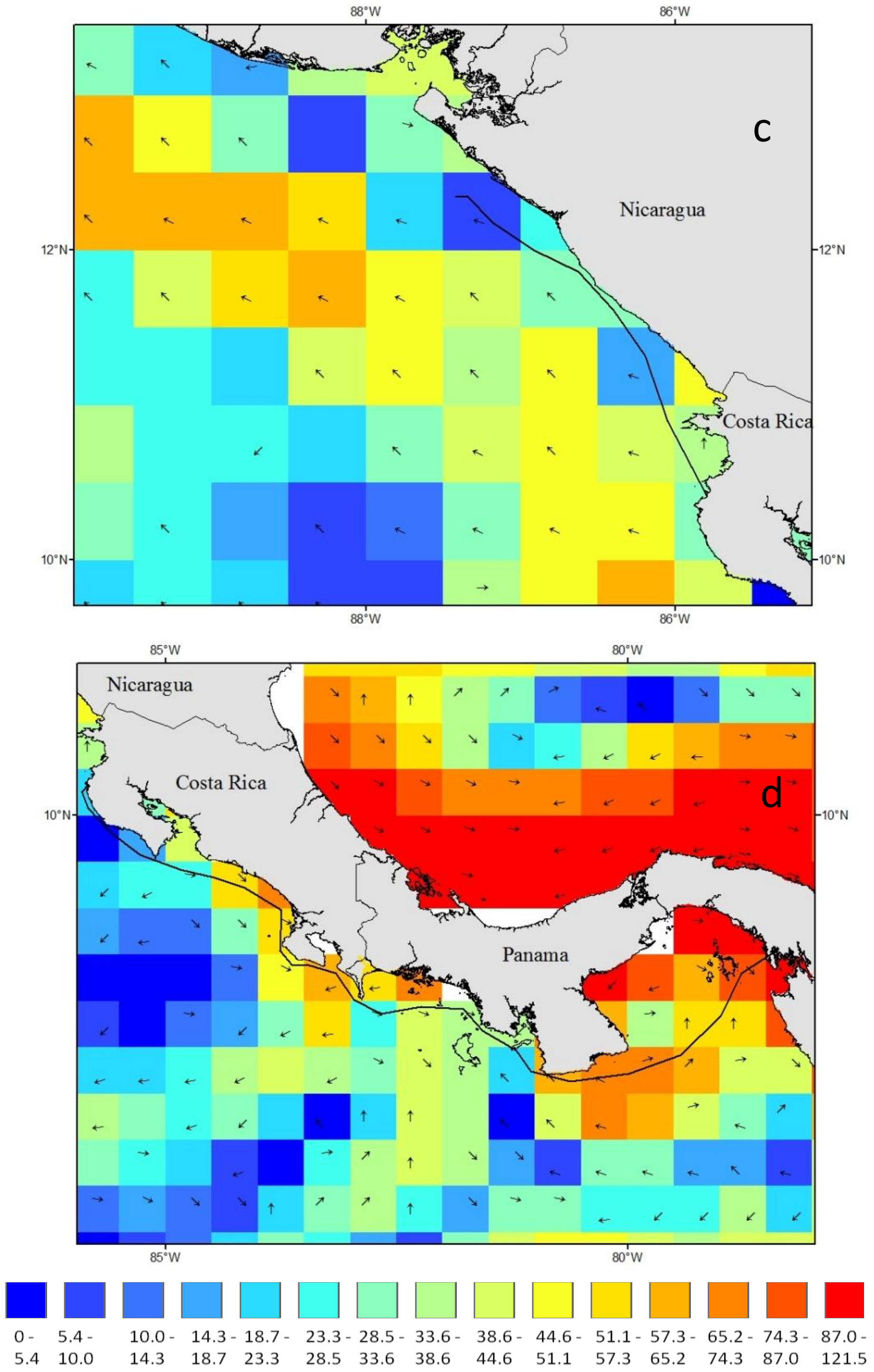


Figure 4.2: Continued

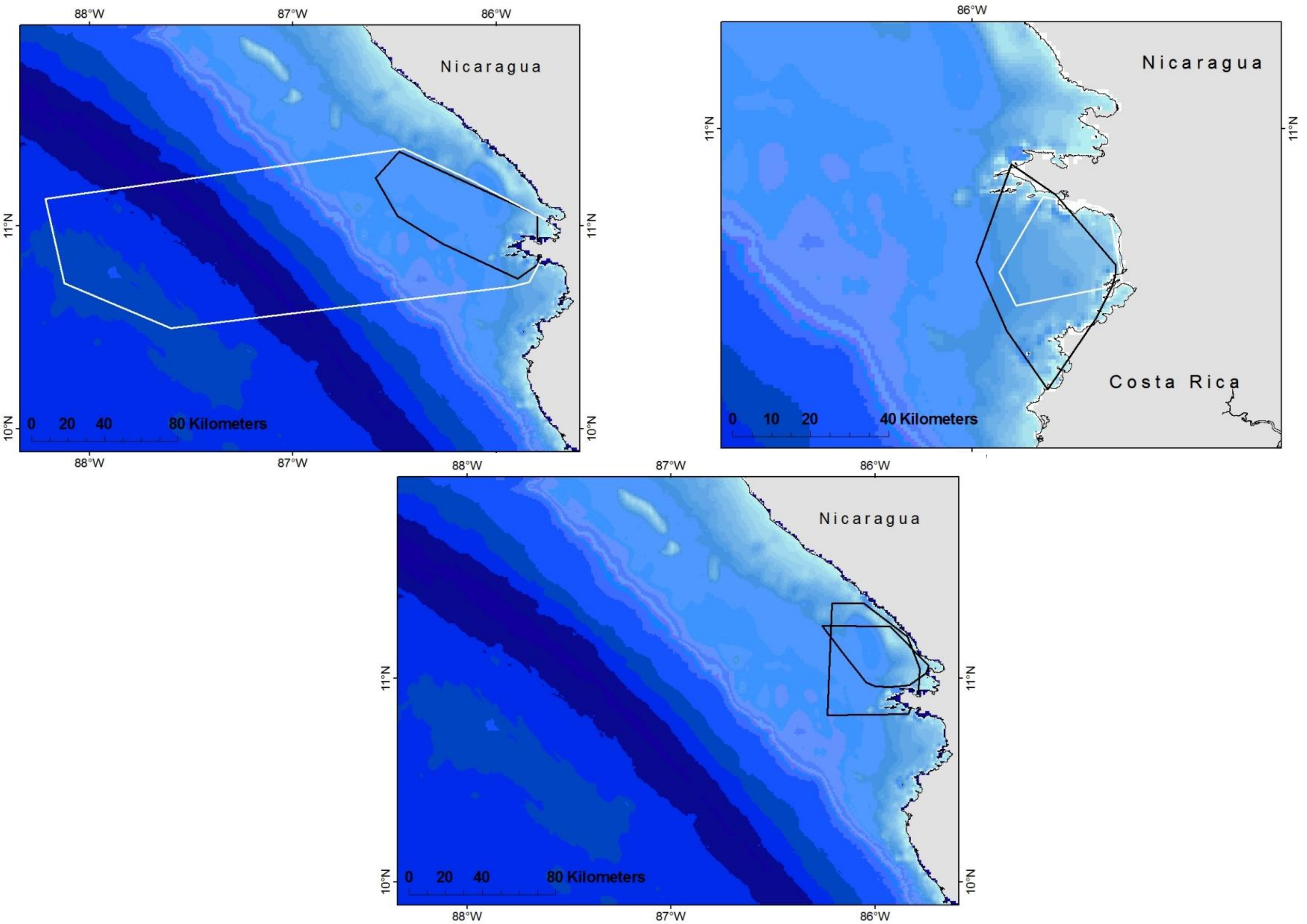


Figure 4.3: Foraging areas of East Pacific green turtles represented by 100% MCP. Each polygon includes all the locations for the individual turtles during foraging.

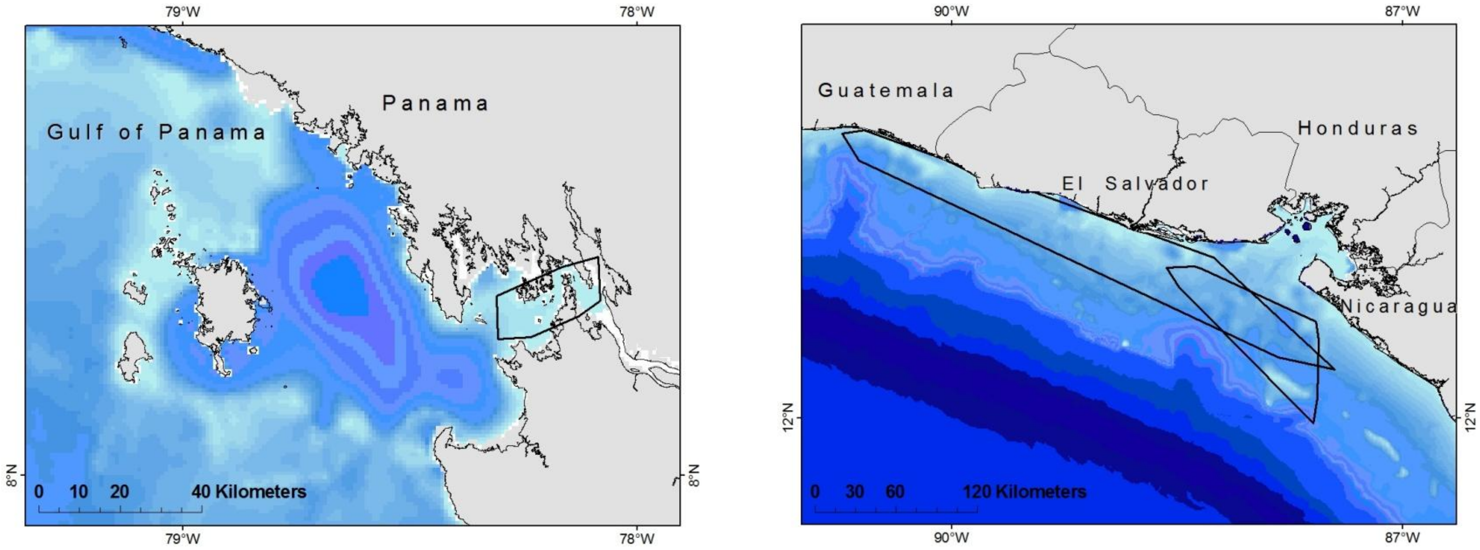


Figure 4.3: Continued

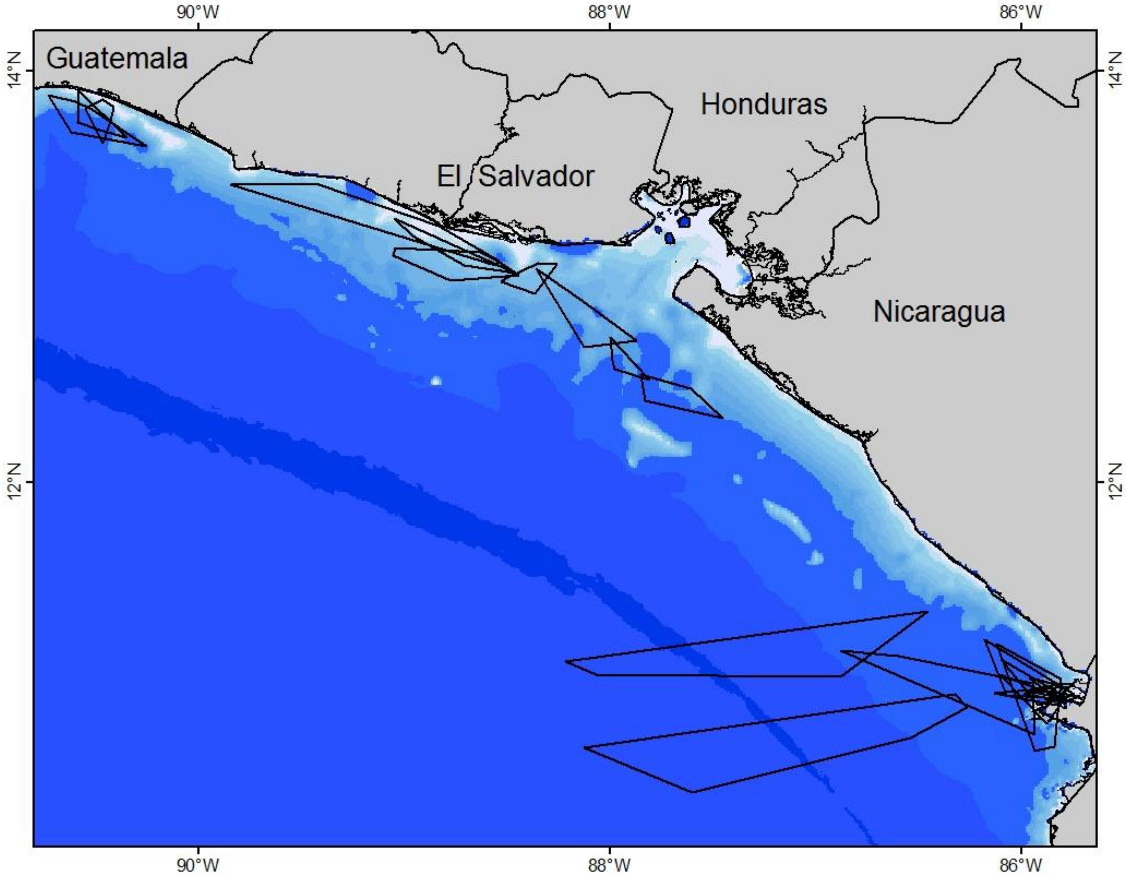


Figure 4.4: MCP per week of two east Pacific green turtles whose MCP areas were higher than 10,000 km^2. Each polygon includes locations for 7 days in the foraging areas.

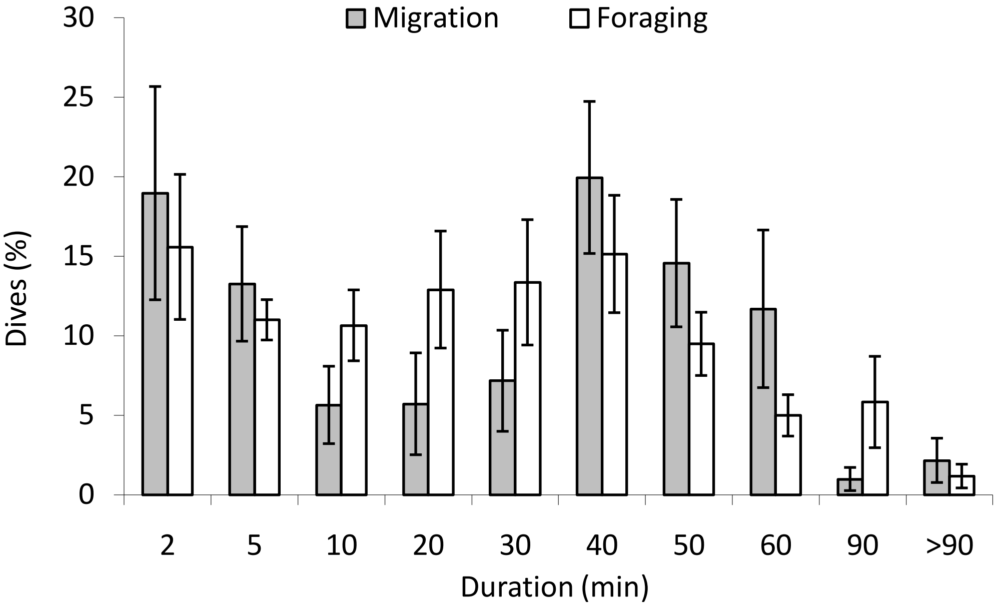


Figure 4.5: Percentage of dives of different durations performed by east Pacific green turtles during migration and foraging. Migration = 8 turtles, foraging = 9 turtles

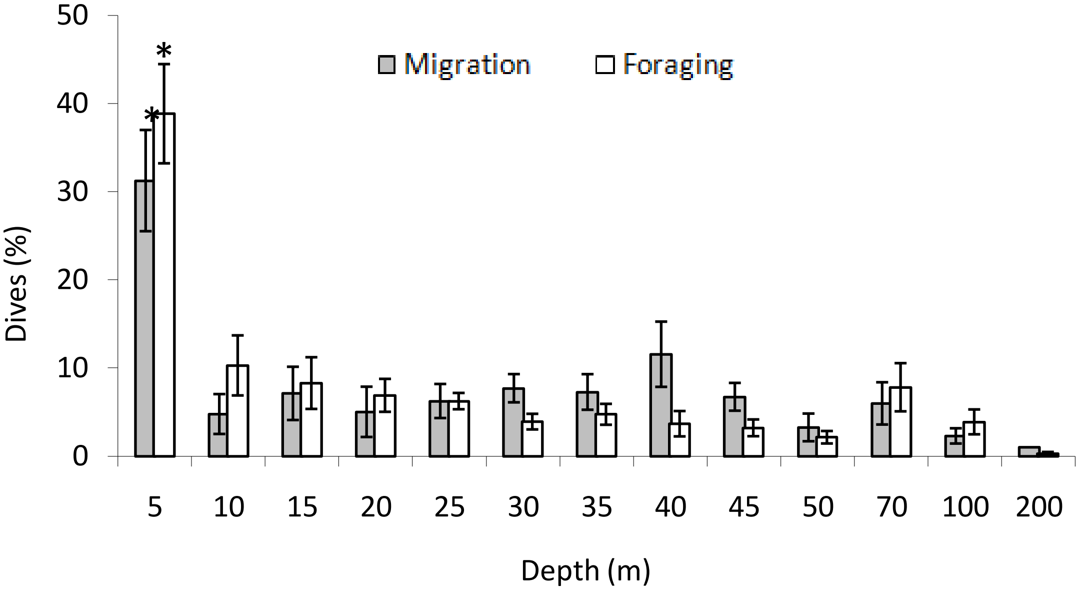


Figure 4.6: Percentage of dives at different depths performed by east Pacific green turtles during migration and foraging. Migration = 8 turtles, foraging = 9 turtles. *Indicates significant differences (ANOVA, $p < 0.05$) between 5 m and other depths.

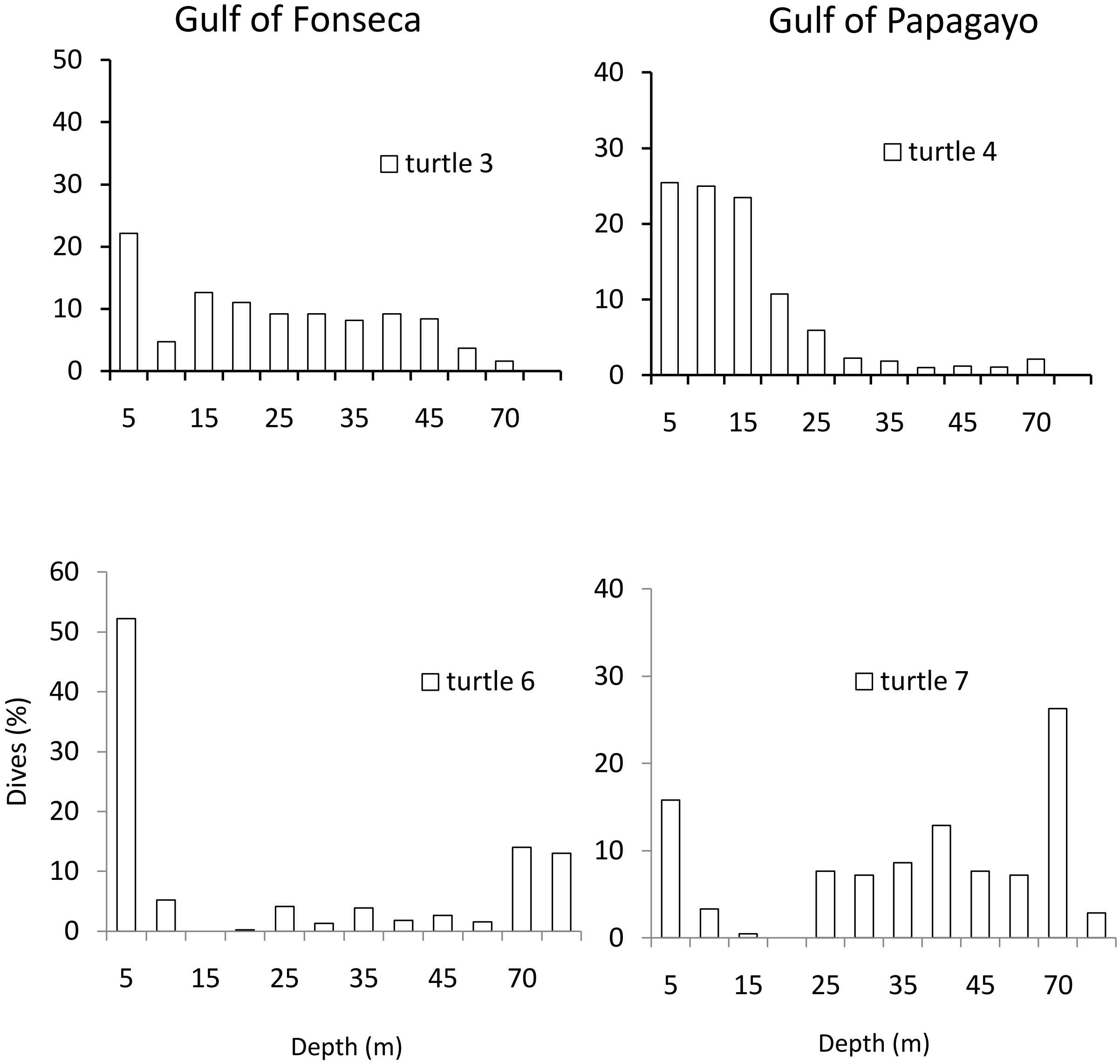


Figure 4.7: Percentage of dives at different depths performed by East Pacific green turtles in the foraging areas. Santa Elena bay includes 4 turtles because of the small variation between individuals (bars represent SD)

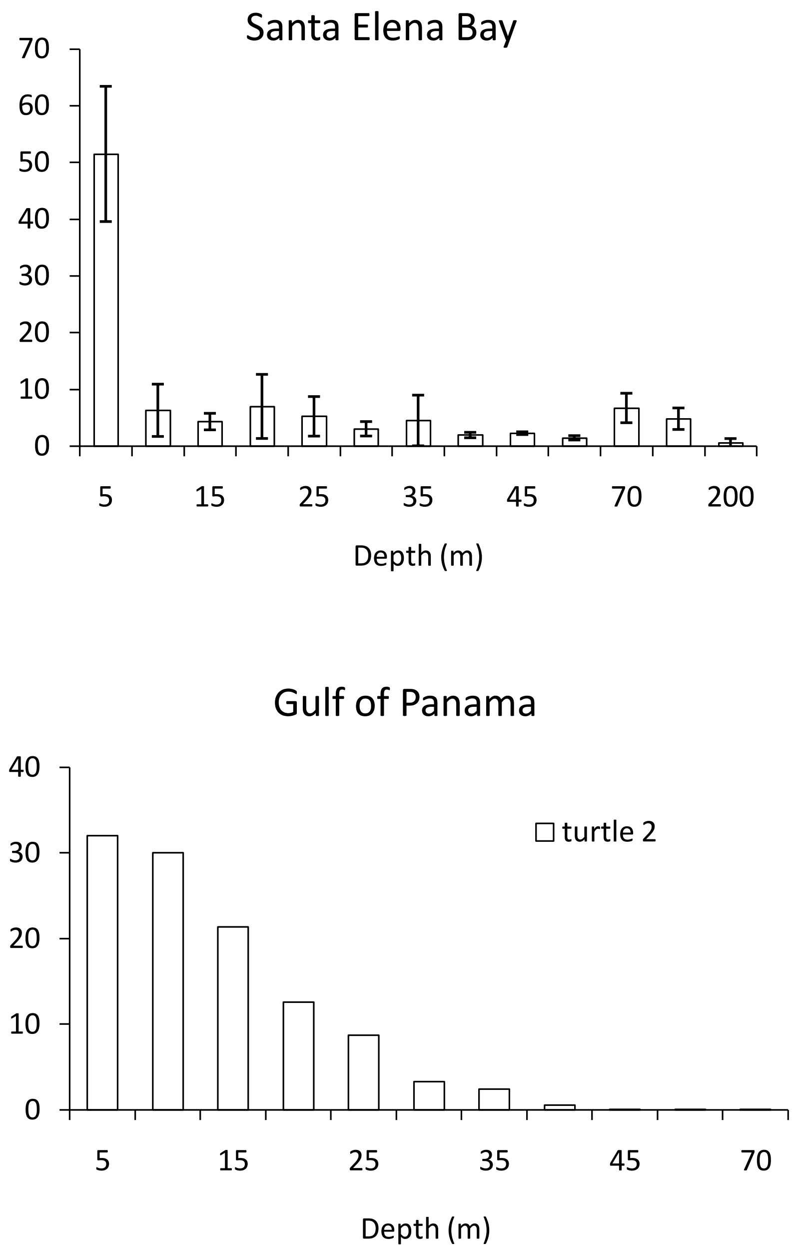


Figure 4.7: Continued

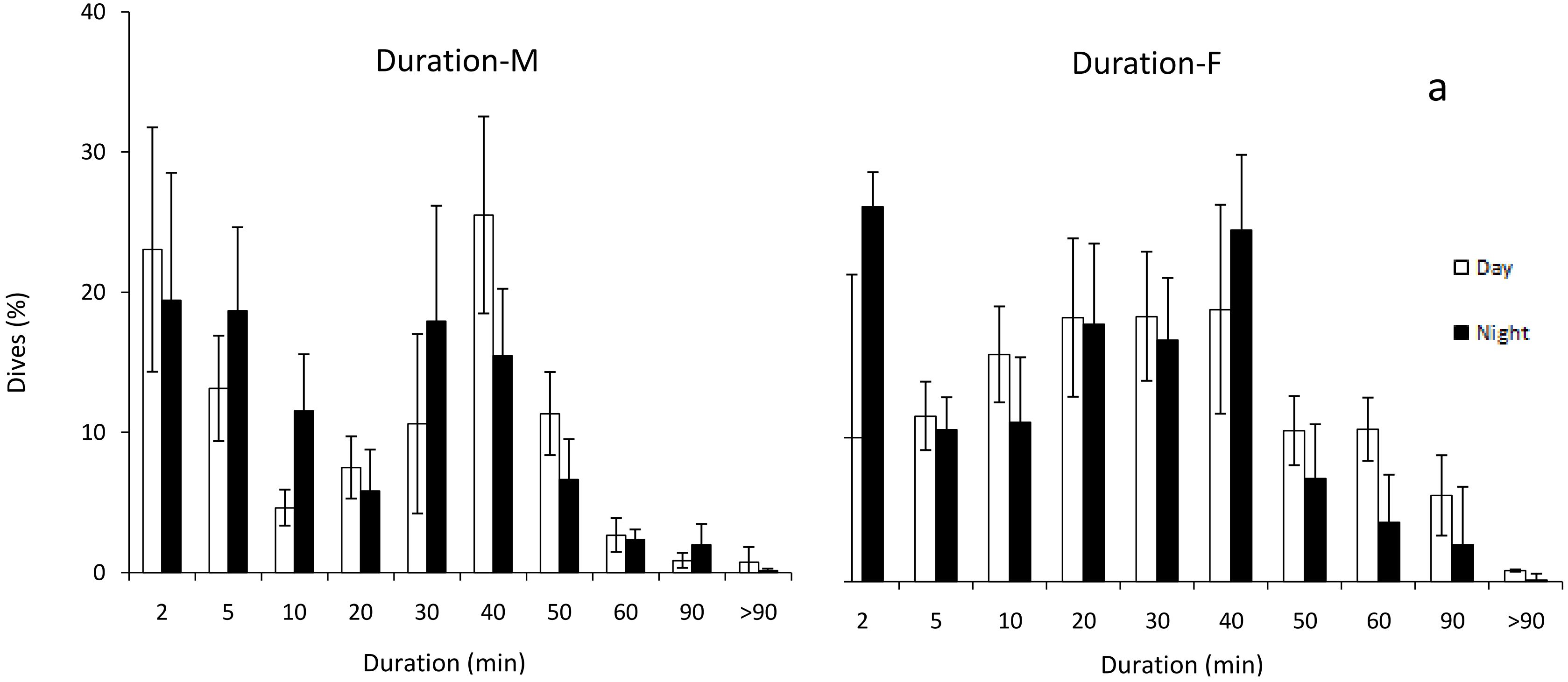
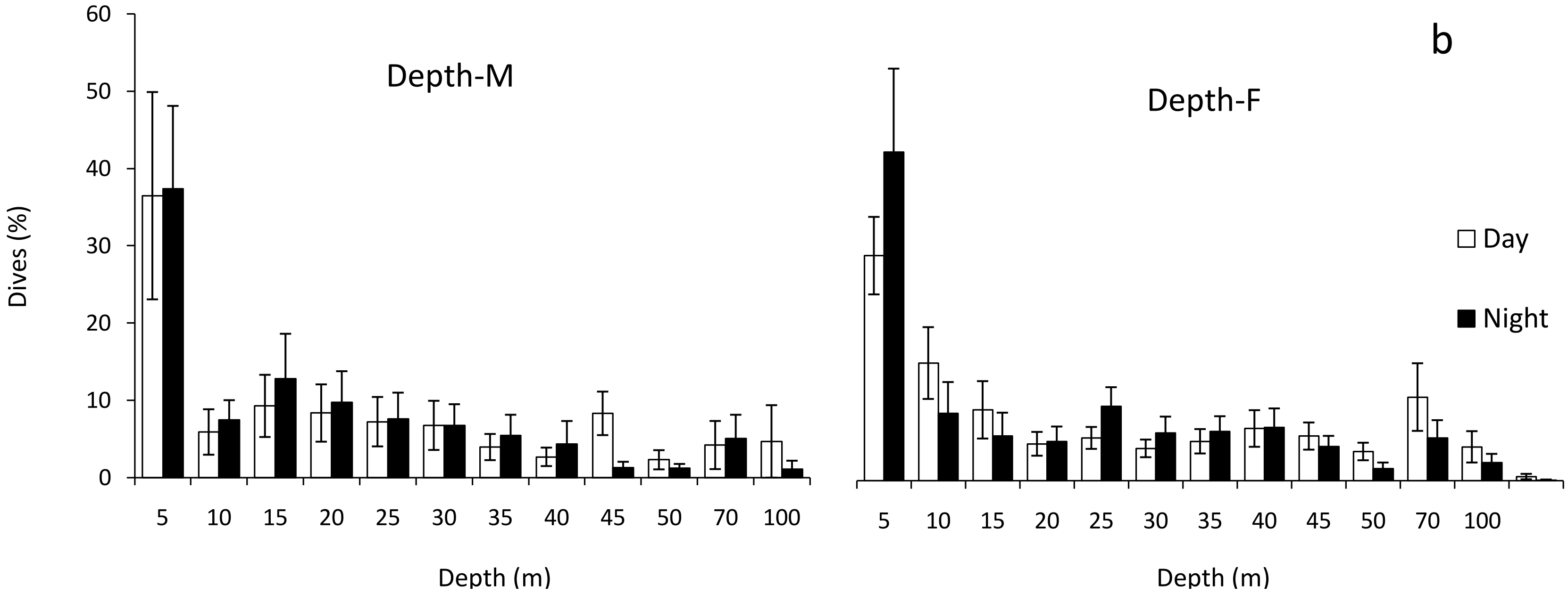


Figure 4.8: Percentage of durations (a) and depths of dives (b) during migration and foraging of East Pacific green turtles. Each graph includes percentages corresponding to day (white bars) and night (black bars). M: migration, F: foraging. Migration = 8 turtles, foraging = 9 turtles.



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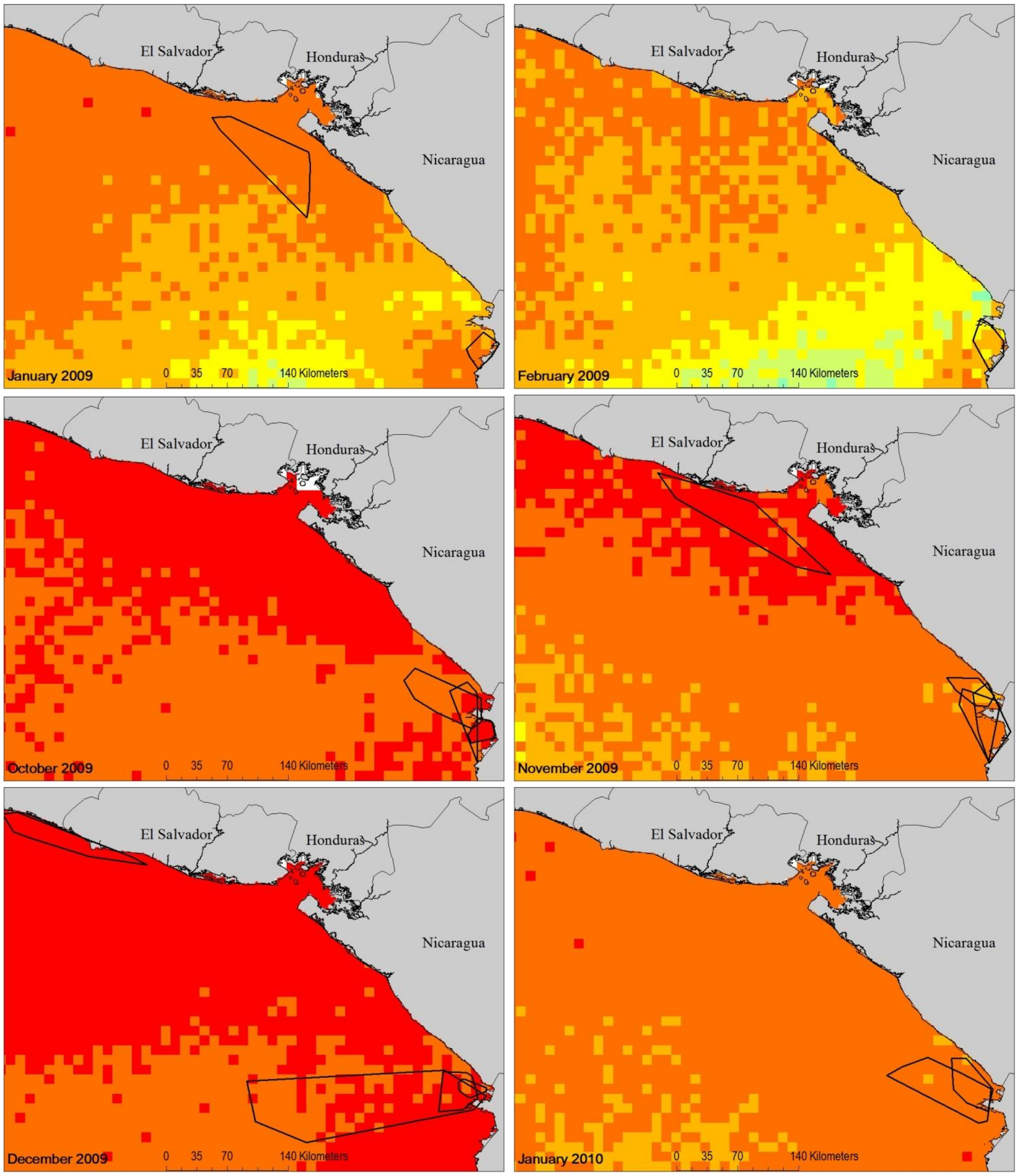

Figure 4.9: **Monthly MCP in relation to Sea Surface Temperature (SST)**. SST (0.1° spatial grid, monthly composites) for each month of study. MCPs correspond to all locations in a month for each turtle in the foraging area.

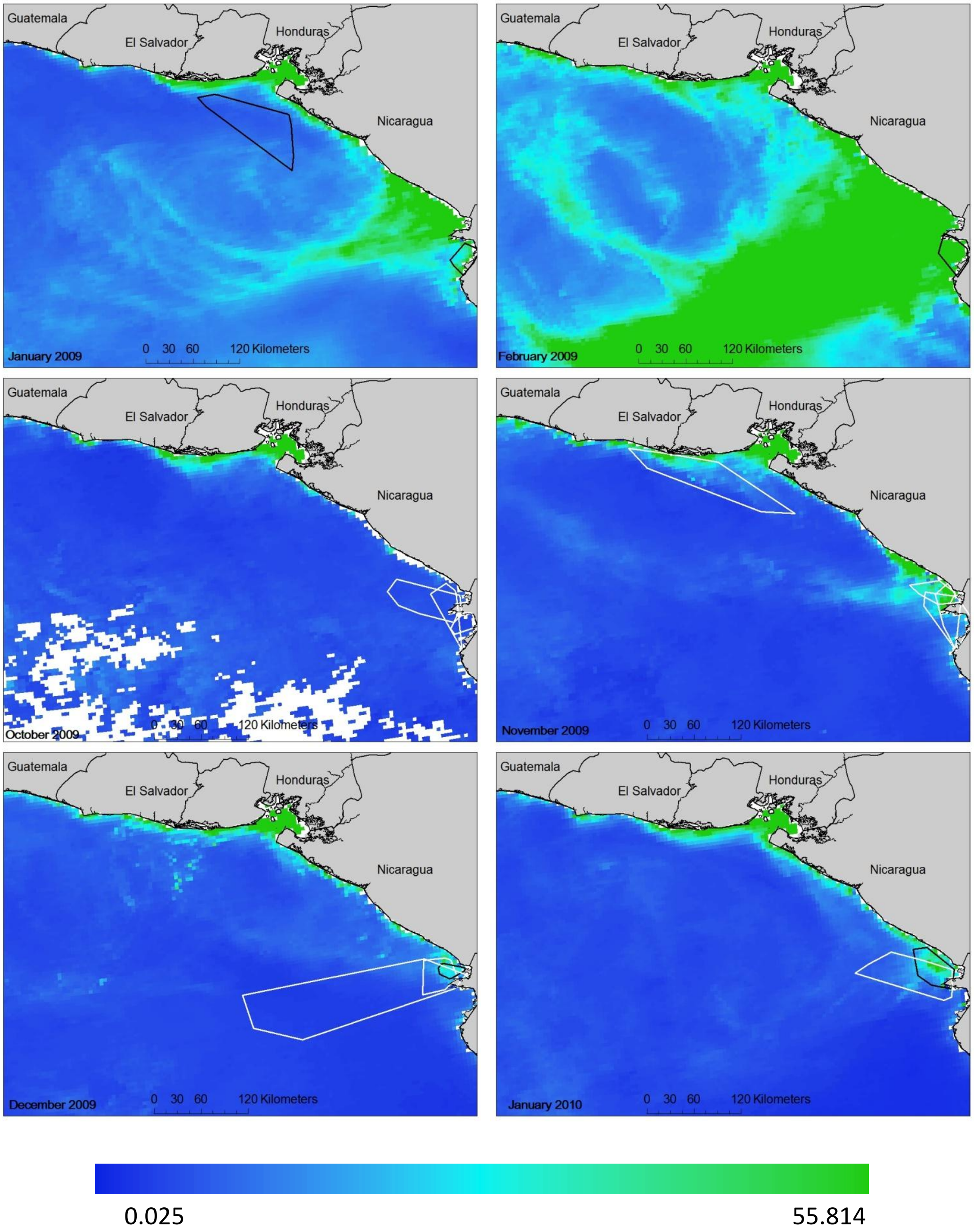

Figure 4.10: Monthly MCP in relation to Chlorophyll-a (CHL). CHL (0.05° spatial grid, monthly composites) for each month of study. MCPs correspond to all locations in a month for individual turtles in the foraging areas.

Chapter 5: Dispersion of East Pacific green turtle hatchlings emerging from Nombre de Jesús, Costa Rica.

Abstract

We designed and developed a program to estimate the dispersion of East Pacific green turtle hatchlings emerging on Nombre de Jesús, Costa Rica. First we created a DOS program using FWTools and phyton script, then passed the output to a spatially explicit model we created using ArcInfo Workstation to simulate the trajectory produced by oceanic surface currents on an ideal planktonic particle. The model simulates a hatchling drifting with the currents in the uppermost layer of the water column. We tested three scenarios releasing the hatchling 10 km off: 1-Nombre de Jesús in peak hatchling season (1st week of December), 2- Nombre de Jesús in non hatchling season (1st week of June) and 3-same latitude as the nesting beach, but in the southern hemisphere. Simulated hatchlings showed a broad dispersion from Nombre de Jesús with the southernmost location 1º 35’ S off Ecuador, the northernmost location 14º 30’ N off southern Mexico and 115ºW in the Pacific Ocean. We found three different scenarios in which hatchlings could be dispersed depending upon the year of emergence. 1- modeled hatchlings were transported to oceanic waters and after three months were pushed back closer to the coast 2- hatchlings were transported north or south remaining close to the coast for the whole year and 3- hatchlings were transported to waters off the coast for the whole year but still within the Eastern Tropical Pacific (ETP). Areas with concentrations of hatchlings concur with adult foraging areas suggesting that adult feeding grounds are in locations where hatchlings are naturally deposited by the currents. The magnitude of currents in the

southern hemisphere was significantly lower than those near Nombre de Jesús suggesting that the oceanography in the ETP provides a unique area for hatchling development. The main oceanic characteristics related to the hatchling dispersal were the Costa Rican Dome (CRD) associated with the eddies produced by the Tehuantepec, Papagayo and Panama jets. The eddies and the CRD have associated with them high biological productivity which would provide hatchlings with the necessary resources for development. This model was the first attempt to simulate the hatchling dispersion from Pacific Costa Rica and provided insights into the possible early life stage of the East Pacific green turtles.

Introduction

Sea turtles go through different ontogenetic stages in which they inhabit different habitats. Generally adult foraging areas are neritic environments for all sea turtles species except leatherbacks (*Dermochelys corieacea*), which forage in pelagic environments (Shillinger et al. 2008). From the feeding grounds sea turtles migrate to nesting beaches to lay eggs. Once these eggs hatch, hatchlings move into the ocean currents, entering early juvenile nursery areas in oceanic environments (Musick and Limpus 1997). This is also called the oceanic post-hatchling phase (Carr 1987). After this dispersion phase turtles move to the later juvenile developmental habitats which commonly are neritic environments (Musick and Limpus 1997). The flatback turtle (*Natator depressus*) is the only sea turtle species that lacks an oceanic phase in its life cycle (Walker and Parmenter 1990).

Sea turtle neonates emerge from the nest, crawl immediately to the ocean and swim away from shore hyperactively (Musick and Limpus 1997). This active swimming is called the hatchling frenzy characterized by hatchlings swimming almost continuously for a period of approximately 24 hours or more (Wyneken and Salmon 1992). This “frenzy” is crucial for their survival because they swim away from shore where predators are more abundant (Salmon and Wyneken 1987) and hatchlings also move to the main offshore currents (Bolten 2003). Post-frenzy activity is the phase where hatchlings swim during daylight hours and rest by floating at the surface during dark hours (Wyneken and Salmon, 1992). Hatchlings initially orientate through visual cues following the brighter oceanic horizon when they are on the beach crawling to sea, then they orient into waves as they swim away from the beach and after that they orient using the earth's magnetic field as a cue (Lohmann and Lohmann 1992). During the post hatchling transitional stage the young turtles start to feed while still in neritic zones and it is at this stage that they reach the oceanic zone.

East Pacific green turtles (*Chelonia mydas*) nest in Costa Rica (Cornelius 1979) with a peak nesting time in October (Chapter 3). Considering that mean incubation period for green turtles is approximately two months (Fowler 1979), the peak hatchling season for the turtles nesting on the Pacific coast of Costa Rica occurs at the beginning of December. The offshore waters of the Eastern Tropical Pacific (ETP) offer unique characteristics for hatchling dispersal and development.

Some of the most productive waters of the world exist in the ETP (Fiedler et al. 1991). The ETP is located between the subtropical gyres in the North and South Pacific at 23.5º N and S and 140º W. The eastern boundary is the California Current flowing from the north and the Peru Current flowing from the South, and it is also constrained by the impact of two equatorial currents (Fiedler and Talley 2006, Pennington et al. 2006). The ETP is characterized by the presence of coastal and open ocean upwellings, fronts, eddies and meanders (Lavín et al. 2006). The convergence of the trade winds in the intertropical convergence zone (ITCZ) produces a low wind area off Central America where the sea surface temperatures (SST) are higher than elsewhere in the area leaving a "warm pool" (> 27.5 ºC) west of Mexico and Central America (Lavín et al. 2006, Fielder and Talley 2006). However, the wind blowing from the land to sea produces the Tehuantepec, Papagayo and Panama jets causing eddies (upwellings) that generate productive areas (with a decrease in SST and increase in chlorophyll levels) interrupting the warm low productivity “warm pool” (Palacios and Bograd 2005). All the gulf regional winds enhance euphotic nutrient supply and biological productivity. The jets are highly seasonal, being stronger from December through April and decreasing or disappearing after May (Pennington et al. 2006). Another characteristic present in the ETP is the equatorial cold tongue (centered south of the equator) that is produced by the Peru Current and equatorial upwelling which extends to 120ºW (Fielder and Talley 2006).

The Tehuantepec bowl (13N, 105W) is a shallow upwelling feature delimited in the south by the Costa Rican Coastal Current which flows continuously from Costa Rica to the Gulf of Tehuantepec (Kessler 2006). The Costa Rican dome (CRD) is the biggest upwelling region of the ETP with high primary and secondary production (Lavín et al. 2006). The CRD is a shoaling of the thermocline of the ETP where the top of the thermocline is 15 m deep at the dome at the center of the dome and 30 to 40m to the north and south (Fiedler 2002). The CRD is centered 300 km off the Gulf of Papagayo between Costa Rica and Nicaragua (9N, 90W); it is associated with the equatorial current system and with the costal jets, eddies, the ITCZ and the geostrophic balance that occurs in the thermocline (Fiedler 2002, Fiedler and Talley 2006). The CRD varies in size and location through the year. In January the dome is far from the coast, there is a shoaling of the thermocline at the coast (next to the Papagayo Gulf) that increases through March and during this time the dome remains connected to the coast. During May and June it is separated from the coast and from July to October the dome increases in size and extending to the Gulf of Tehuantepec in November, and then decreases in size in December (Fiedler 2002).

All these oceanographic characteristics make the ETP suitable for species that congregate in this area. For example 29 species of cetaceans (Wade and Gerrodette 1993), 4 sea turtle species (Spotila 2004), numerous sea birds and fish (Greenblat 1979, Au and Pitman 1986) among many other species inhabiting the ETP.

In this study, we estimated the dispersion of east Pacific green turtle neonates after hatching on Nombre de Jesús beach on the Nicoya Peninsula of Northwest Costa Rica in their post-hatchling stage following the currents in the area. The oceanographic characteristics in the region were assumed to dominate dispersal and determine where hatchlings would eventually reside and ultimately determine their return to the coast.

Materials and Methods

We designed and developed a model to simulate the dispersion produced by oceanic surface currents for an ideal planktonic hatchling released from different locations in the ETP. Sea turtle hatchlings are carried by ocean currents and act as passive dispersers, like plankton. A similar approach was used to simulate the dispersal of loggerhead hatchlings in Greece (Hays et al. 2010).

The currents included in the model were the Aviso geostrophic surface current (u and v vectors, cm/sec) from years 1992 to 2009 and obtained from NOAA OceanWatch-LAS (http://oceanwatch.pifsc.noaa.gov/las/servlets/dataset). Aviso was calculated with the sea surface height anomaly data, merged with sea-surface height climatology and then converted to current (Niiler et al. 2003). The Grids were netcdf files composited during a 7 day period, 0.5º spatial grid.

First we created a DOS program that used FW (Frank Warmerdam, http://fwtools.maptools.org/) tools, phyton script and the GDAL (Geospatial Data Abstraction Library, Geospatial Foundation) subpackage to read and convert netcdf files to u and v layers in ASCII format readable by ArcInfo. Then we wrote a program in ArcInfo Workstation (http://www.esri.com/software/arcgis/arcinfo) that took the present grid with magnitude of the current and a model hatchling (assumed as ideal planktonic) and made it travel along with the speed of the surface current (magnitude and direction) for a 7 day period. Next the model hatchling moved to the next grid for the following week and repeated the process for the amount of time indicated. We set the program to run for every week starting with the first week of December or June until the last week of November or May of the following year depending upon the conditions simulated.

The initial release point for the model hatchling was situated 10 km off the coast which accounted for the first day of the frenzy where hatchlings swim away from shore and would reach and be exposed to the main offshore currents (Bolten, 2003). We ran the model in three different scenarios extended over 17 separate years 1992-2009 from which oceanic data was available. First, we set the release point 10 km off Nombre de Jesús (10° 23’ 30” N; 85° 50’ 07” W), Costa Rica during the first week of December simulating the peak of hatchling emergence season for East Pacific green turtles and we modeled it for one year with corresponding oceanography. Second, the release point was 10 km off the nesting beach starting the first week of June simulating the non hatchling emergence season and we modeled the dispersal for one year. Lastly we ran the model from an initial release point 10 km off the coast of South America at 10° 23’ 30” S (a mirror image from the latitude of the nesting beach) to simulate the dispersion in the southern hemisphere.

The model produced possible outputs of latitude and longitude, magnitude of currents and date for each location where the model hatchling was transported for one year. This allowed us to statistically compare the magnitude of the current to which particles were exposed during different years and different months, with differences in magnitudes between hatchling emergence season and no emergence season incorporating differences between the currents at the nesting beach as well as differences in the southern hemisphere.

Based on this information we generated maps using ArcGis version 9.3 geographic information system (GIS) software (www.esri.com/software/ArcGIS) for visual interpretation. First we plotted the location of the hatchlings for each year, and then we divided the locations into 3 months periods, overlapping them with the magnitude of the current in the first week for each period. We also mapped speed and direction of the currents to analyze oceanic characteristics present during dispersion and visualized how they varied in the season.

Statistical analyses were performed using SPSS Inc. Statistical significance was accepted at 0.05 level.

Results

Modeled hatchlings transported from Nombre de Jesús showed a broad dispersion with the southernmost location 1º 35’ S in Ecuador, the northernmost location 14º 30’ N in the south of Mexico and the westernmost location at 115ºW in the Pacific (Figure 5.1). There were significant differences (ANOVA, F = 27.72, df = 15, $p < 0.001$) between the magnitude of the currents to which the hatchlings were exposed during different years (Table 5.1). The highest speed was in 1997 (65.86 cm/sec) and the lowest speed was in 2005 (19.36 cm/sec). We mapped the magnitude and direction of the currents in the first week of December, March, June and September (Figure 5.2 shows one year as an example). Even though there were no significant differences in overall speeds between months (ANOVA, F = 1.728, df = 11, p = 0.63) there were obvious differences in speed of currents in particular locations in the ocean during different months. March was the month with highest current speeds, followed by December, June and September (mean = 32.99, 30.6, 30.4, 23.8 cm/sec respectively for all years). There was considerable variation between years resulting in high variance and a lack of overall statistical significance in the months

Although there were no significant differences in the current speed in which the hatchlings were transported during emergence season (1st week of December) versus the non hatchling season (1st week of June), there was a strong trend for hatchlings released during emergence season to experience higher speeds (Hatchling season, Mean ± SD = 29.16 ± 20.0 cm/sec; Non hatchling season, Mean ± SD = 27.4 ± 20.3 cm/sec) (t-test, t = 1.720 df = 823, p = 0.086). The high variance from year to year reduced the overall statistical significance of the differences. There were significant differences between the current speeds experienced by the hatchlings released during emergence season from Nombre de Jesús and the current speeds experienced by the hatchlings released from the equivalent latitude to Nombre de Jesús in the southern hemisphere (12.51 ± 7.289) (t-test, $t = 21.559$, $df = 823$, $p<0.001$). Currents near Nombre de Jesús were almost three times faster than in the southern hemisphere.

In 10 of the 16 years analyzed, we found a similar trajectory for the first month after the model hatchling was released. Approximately in week 5 hatchlings reached between 95º and 100ºW and would then be transported to areas closer to the coast (Figure 5.3). Years 1994 and 2000 displayed a different dispersion pattern where the model hatchlings were transported north staying for the full year south of the Gulf of Fonseca in Nicaragua (Figure 5.3). In 2005 and 2008, on the other hand, model hatchlings were transported to the west reaching longitudes between 110º and 115º W (Figure 5.3). These two years had the lowest mean magnitude in current speeds. In 7 of the modeled years, towards the end of the year, the model hatchlings transported to the coast of Colombia and Panama.

The comparison between the geostrophic currents and how the model hatchlings were transported (Figure 5.4) indicated that there were predominant features controlling the model hatchling drifting in the ETP. The main characteristic was related to the CRD which caused the model hatchlings to move to oceanic waters in December and January and come closer to the coast in March. Also the jets produced by the trade winds transported hatchlings north and south.

Discussion

The “post hatchling transitional stage” refers to the phase when the turtles start foraging while they are still within the neritic zone and ends when the turtles enter the oceanic zone initiating the “oceanic juvenile stage” (Bolten 2003). During both these stages turtles mainly drift with the ocean currents (Carr 1987, Bolten 2003, Musik and Limpus 1997). For this reason we suggest that the model estimating the movement of a model hatchling that is being transported by a current represents the movements of green turtle hatchlings emerging from Nombre de Jesús.

Overall the hatchlings occupied a broad area of the ETP for all years. Main concentrations were found along the coast of Nicaragua and the coast of Colombia and Ecuador. There was also an important aggregation of hatchlings along the coast of Costa Rica. The area in Nicaragua (near the Gulf of Fonseca) is highly used by East Pacific green turtles as a foraging ground (Chapter 4), which suggests that the location of adult feeding grounds are the direct result of hatchling dispersion. Contrary to our results Atlantic loggerhead post-hatchlings are commonly found in the edge of the Gulf Stream and the loggerheads hatching in Japan transverse the entire Pacific to the coast of California (Bowen et al. 2005) travelling extensively through the ocean. Our model suggested that hatchlings emerging in the Pacific coast of Costa Rica may be transported by currents and “captured” in the oceanographic system of the ETP.

There were statistical differences between the magnitudes of the current between the years. Even small variations in the characteristics of currents could lead to different distributions of hatchlings (Collard and Ogren 1990). Based on the results of the model, hatchlings emerging from Nombre de Jesús could disperse following three different scenarios. The most common trajectory observed in most of the years studied had turtles leaving the nesting beach with model hatchlings transported to waters off the coast. The main oceanic feature influencing the dispersion of hatchlings was the Costa Rican Dome (CRD) which increased in size and was closer to the coast from January through March (Fiedler 2002). After three months the model hatchling was transported back closer to the coast, where in some cases it remained in coastal areas and in other simulations it was transported back to oceanic areas off Panama.

The second scenario that resulted from the simulation had the model hatchling being transported north or south but, remaining close to the coast for the entire year. This simulation resulted in hatchlings spending their first year of life in neritic environments along the coast of Central America north and south from the natal beach (Figure 5.2 years 1994, 1997, 2000, 2007). If the currents are drifting the hatchlings into coastal areas then (depending on the year of emergence) these turtles may not have an oceanic phase. Even though in these particular simulations post-hatchlings may be associated with neritic coastal environments they still inhabit the surface; therefore this hatchling stage is different than the neritic juvenile stage where juveniles forage on the sea floor (Musick and Limpus 1997). In the third model scenario hatchlings were transported to the west at about 10° N, off the coast for the first year in which case the hatchlings would be in areas of low productivity but still within the ETP (Fiedler et al. 1991).

The magnitude of the currents in the southern hemisphere was significantly lower than the currents near Nombre de Jesús which suggests that the oceanography in the ETP makes it a unique area for hatchling development. Hatchlings emerging from hypothetical nesting beaches along the shore of Ecuador, which is 10° S of the equator and a southern mirror image of the Costa Rican beaches, would not have the same opportunities for dispersal as do hatchlings from Costa Rica. The simulation and models revealed two main oceanic features that may be related to hatchling dispersion. First the CRD is surrounded by currents flowing cyclonically (Fiedler 2002) and even though in December the dome is separated from the coast, the current off the Nicoya Peninsula transported model hatchlings towards the dome. The model suggested that the Tehuantepec, Papagayo and Panama eddies played an important role transporting hatchlings. These eddies are produced by the winds blowing from land, which intensify during the dry season (November to April) (Willet et al. 2006). The Tehuantepec and Papagayo eddies are important transporters of nutrients from the continent to the ocean and cause upwellings, which also bring nutrients to the surface waters (Palacios and Bograd 2005). The currents related to these eddies may be the main factor transporting hatchlings to the ocean. Carr (1987) found post-hatchling turtles associated with floating material and Witherington (2002) found loggerhead post- hatchlings associated with debris and other biota in the edge of the Gulf Stream.

The most important characteristic associated with eddies and the dome is their high biological productivity. The cyclonic circulation associated with the CRD combined with the strong and shallow thermocline produce an upwelling which makes the CRD a distinct biological habitat (Ballance et al. 2006). In addition, the Tehuantepec and Papagayo eddies transport coastal waters (nutrient rich) to the ocean interior that combine with the process of downwelling during intensification and upwelling as they decay resulting in a high primary and secondary productivity area (Palacios and Bograd 2005). These high productivity areas should provide the necessary nutrients to produce food for the hatchlings so that they can develop into juveniles.

The duration of the oceanic stage for Atlantic green turtles is between 2.8-4.6 years (Reich et al. 2007), for Hawaiian green turtles it extends to 6 years (Zug et al. 2002) and for Atlantic loggerheads as much as 7 years (Bjorndal et al. 2003). The variations in the duration of the oceanic stage may depend upon the available resources in the locations where the turtles spend this stage (Bolten 2003). During all these years the turtles also move actively and considering that turtles are approximately 15-20 cm at one year of age (Bjorndal et al. 2003, Zug et al. 2002) they may be able to swim and select places to forage within the same general area. After one year the juvenile turtles from Costa Rica could be actively swimming in the same oceanic features where they developed because of the important biological productivity of the Eastern Tropical Pacific.

This model simulated the drift of a particle based on ocean currents and was an estimation of the dispersal of sea turtle hatchlings. This model provided insights into the early life stage of East Pacific green turtles and indicated that they would disperse throughout the region as currents shifted from year to year. However, the predominant locations where hatchlings would congregate would be along the Costa Rican coast, off Panama and Colombia and off Nicaragua. These are some of the same areas to which adult females migrate after nesting on Nombre de Jesús (Chapter 3), although we did not find any turtles migrating to Colombia. The model indicated that the driving forces for hatchling dispersal were a unique set of currents, upwellings and other oceanographic features in the Eastern Tropical Pacific Ocean. This first attempt to simulate green turtle hatchling dispersion from Costa Rica demonstrates that one of the important reasons for successful green turtle nesting in Costa Rica is that the oceanic features nearby ensure a wide dispersion of hatchlings into productive waters where they will thrive and grow to become juvenile turtles that can navigate and move about by active swimming. By the time they have entered the free swimming juvenile stage turtles will have experienced a wide area of the Eastern Pacific Ocean and have a map and memory of conditions in the region. Considering that the oceanic phase is the least understood in sea turtle life history (Witherington 2002) more research needs to be focused in this direction. More detailed modeling coupled with oceanic sampling will refine the initial estimates we derived from this model. This research also raises a conservation issue. Since oceanic debris and trash also drift with currents and are influenced by oceanic features such as upwellings and convergence zones, we can expect that plastics and other waste from human civilization along the Central American coast accumulate in the same places as the green turtle hatchlings and are a potential source of mortality for those turtles (McCauley and Bjorndal 1999).

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Tables

Table 5.1 Mean magnitude (cm/sec) of currents in the eastern Tropical Pacific Ocean that transported a model hatchling for one year for all years analyzed.

Year	Magnitude (Mean)	SD
1992	18.25	16.404
1993	38.12	21.691
1994	28.58	7.545
1995	21.48	13.419
1996	21.13	13.943
1997	65.86	25.787
1998	22.27	16.839
1999	42.73	21.091
2000	26.06	5.867
2001	22.46	14.803
2002	26.64	13.017
2003	24.73	21.712
2004	25.49	19.020
2005	19.36	10.403
2006	22.13	14.082
2007	34.00	18.021
2008	20.05	12.118

Figures

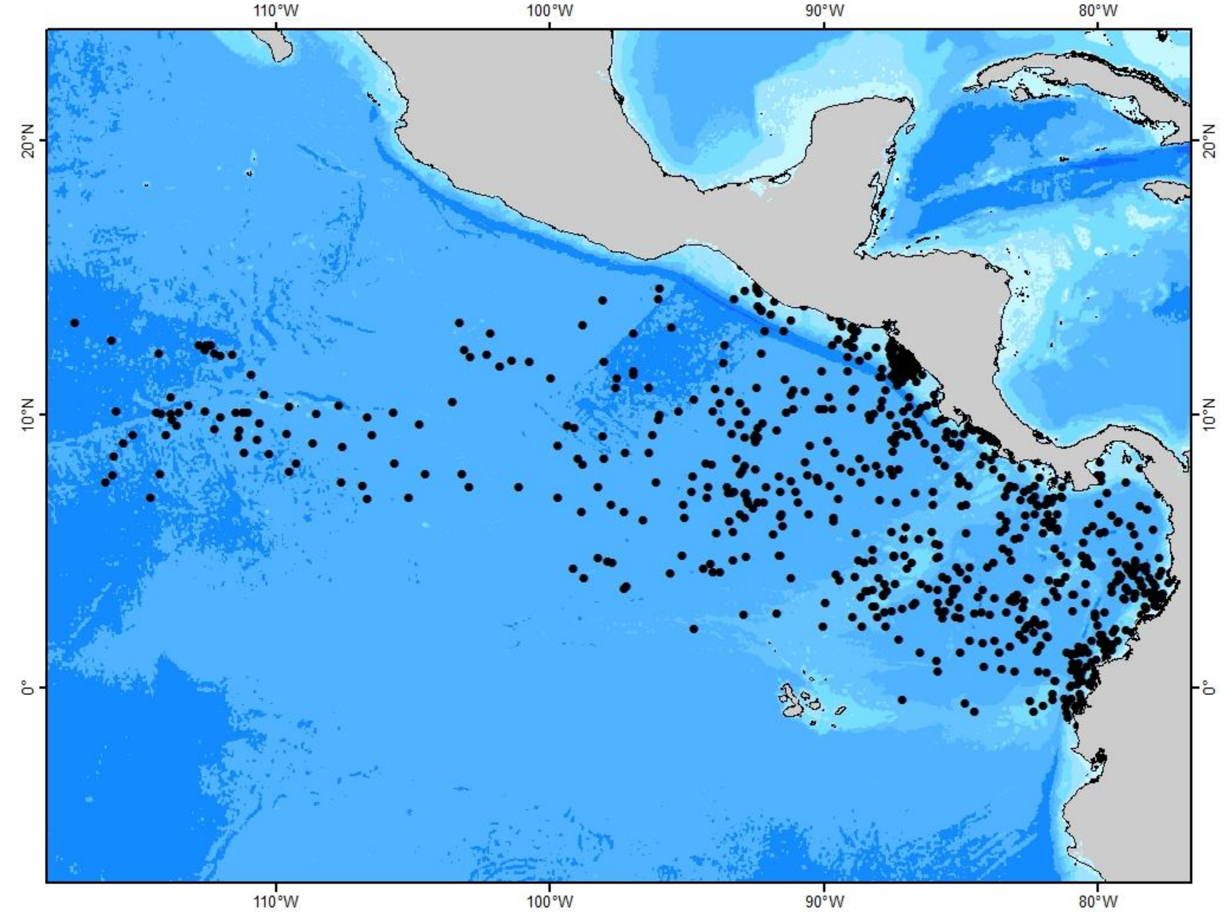


Figure 5.1: **Location of model hatchlings released 10 km off the coast of Nombre de Jesús** in northwest Costa Rica as calculated by the model every week for all analyzed years (1992-2009). Each dot represents the new position of the model hatchling after being transported by a current for a period of 7 days.

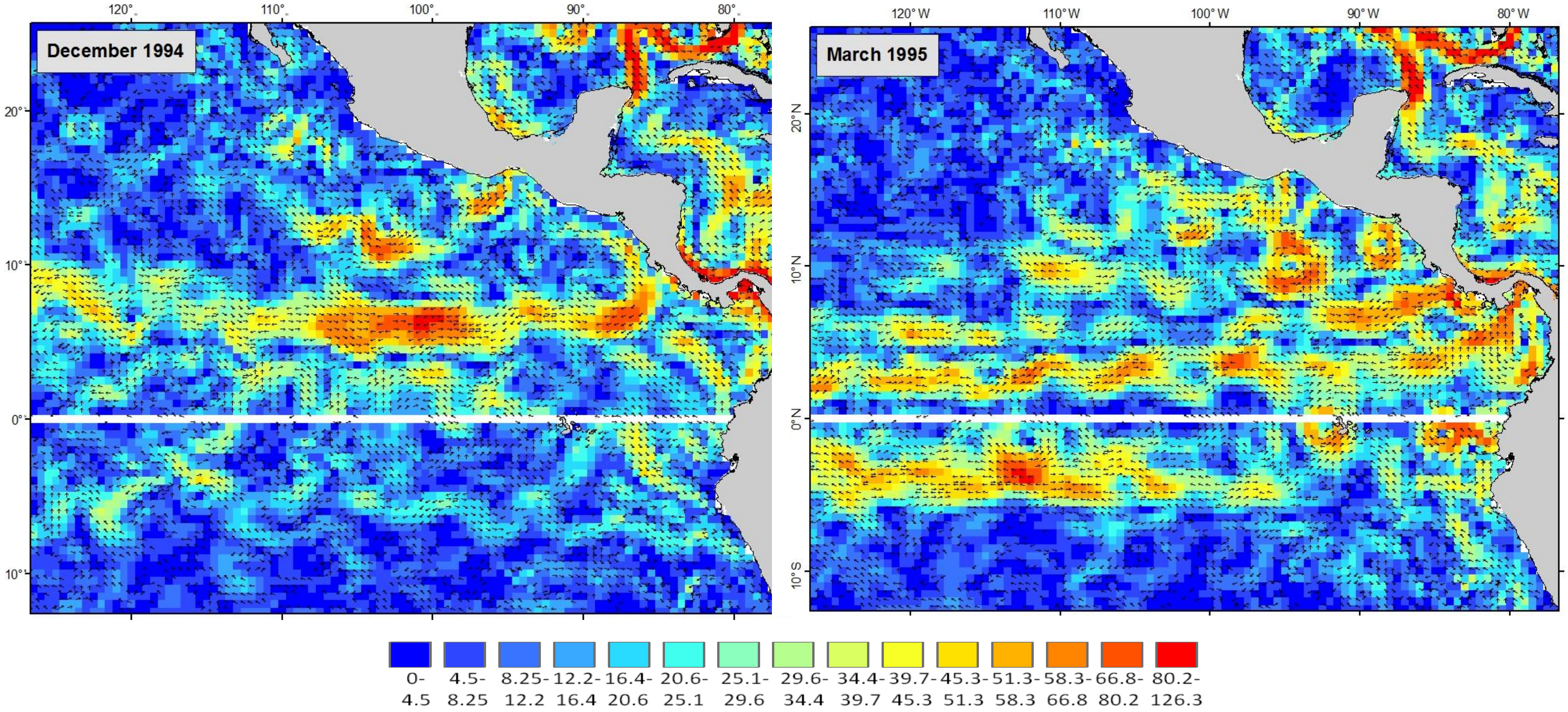


Figure 5.2: Circulation of currents in the Eastern Pacific Ocean at different times of the year. Colors represent magnitude (cm/sec) and arrows represent direction of the currents. Each picture represents the first week of the months referred to in the legend. We obtained data from NOAA OceanWatch-LAS. The grids were composited in a 7 day period with 0.5º spatial resolution. Scale represents magnitude of the currents (cm/sec)

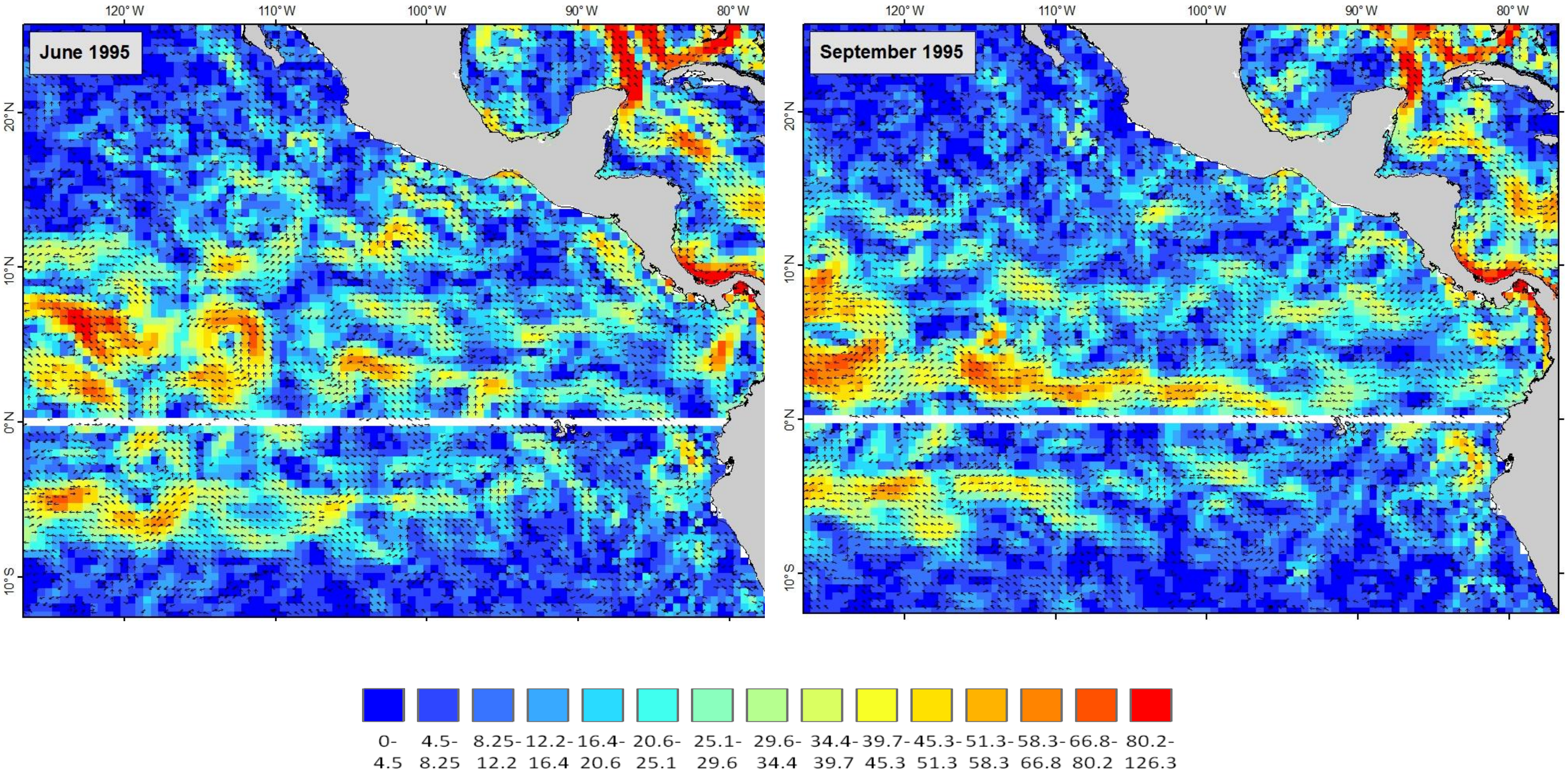


Figure 5.2: Continued

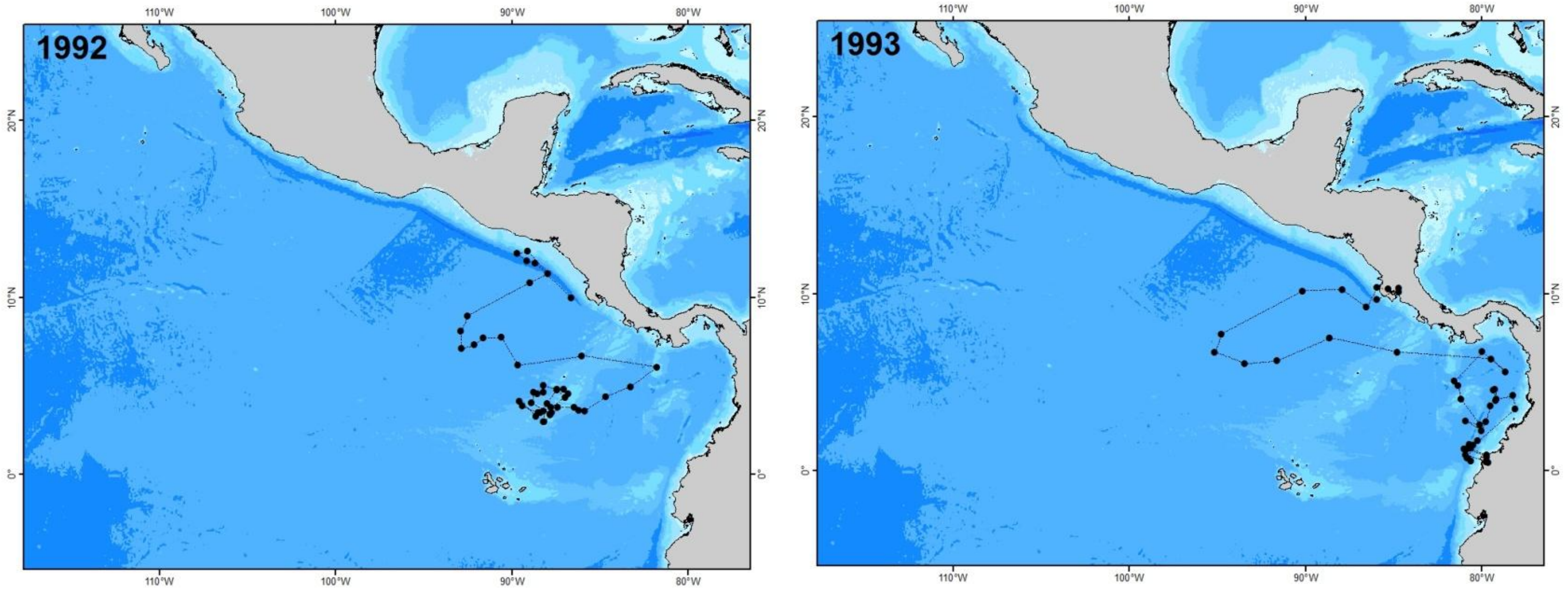


Figure 5.3: Movement of model hatchlings released 10 km off the coast of Nombre de Jesús in northwest Costa Rica as calculated by the model for each year from 1992 to 2008. Each dot represents the new position of the model hatchling after being transported by a current for a period of 7 days. Lines connecting points represent probable trajectories from one week to the next.

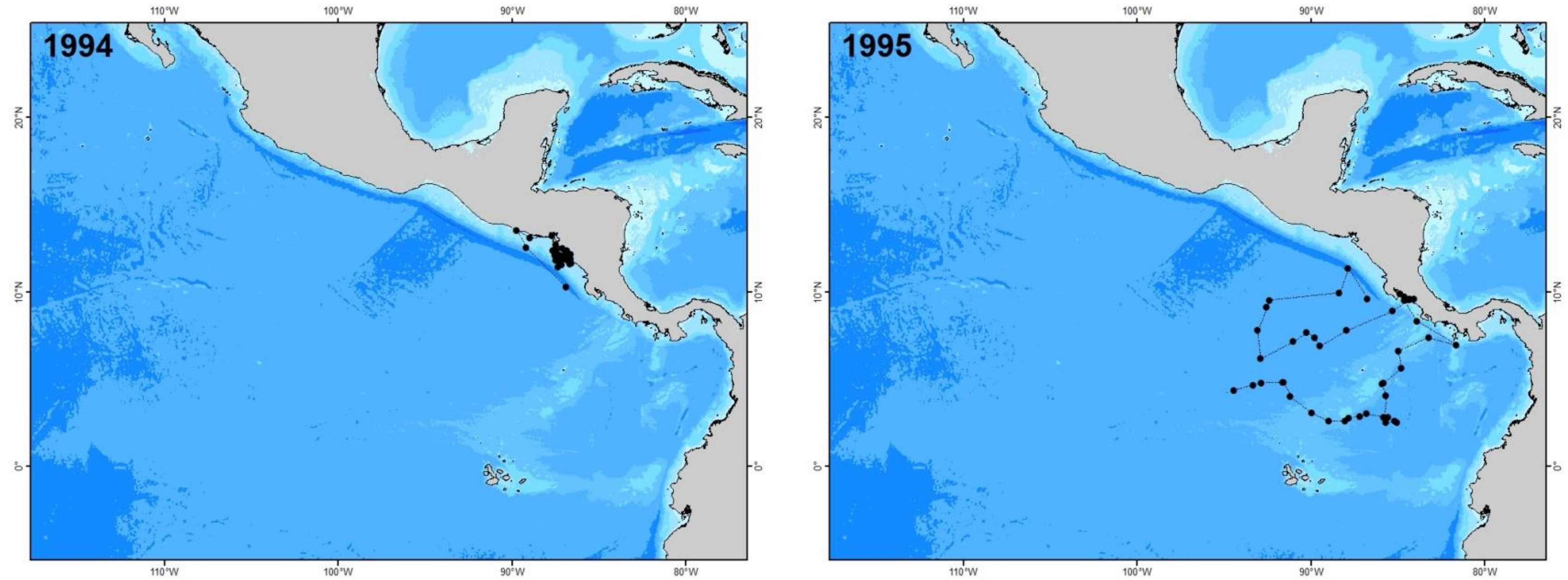


Figure 5.3: Continued

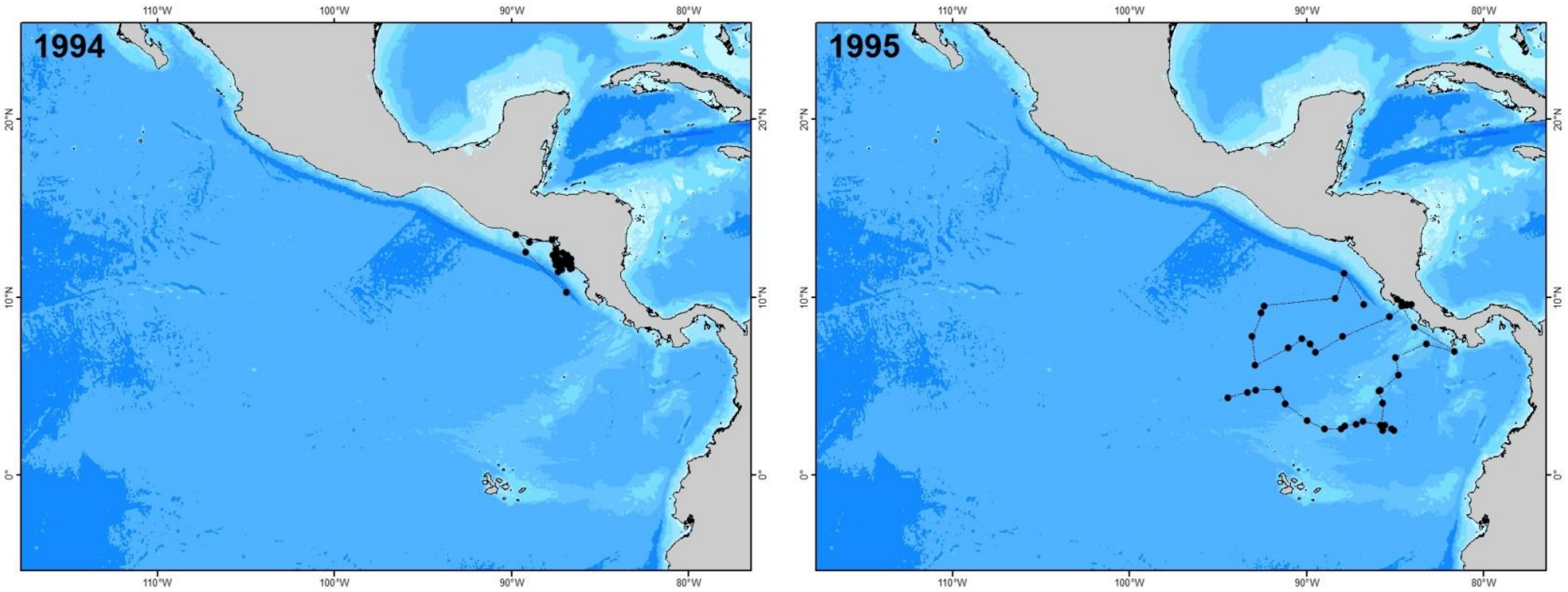


Figure 5.3: Continued

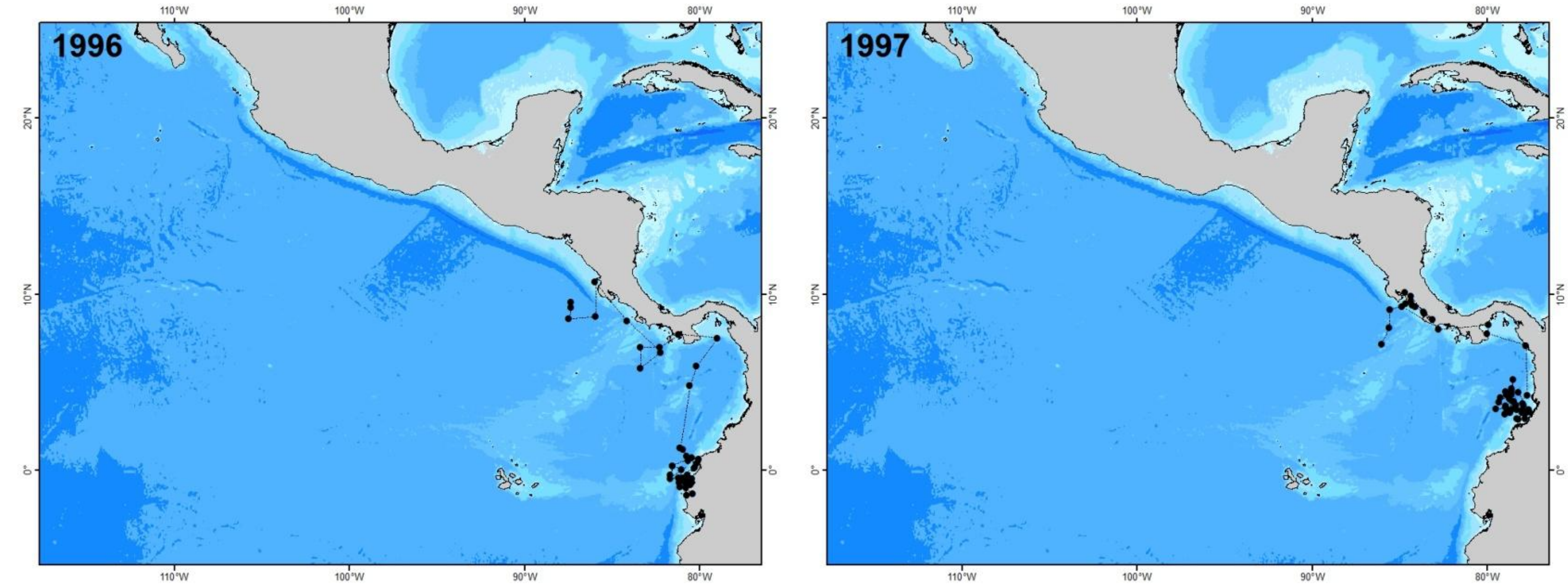


Figure 5.3: Continued

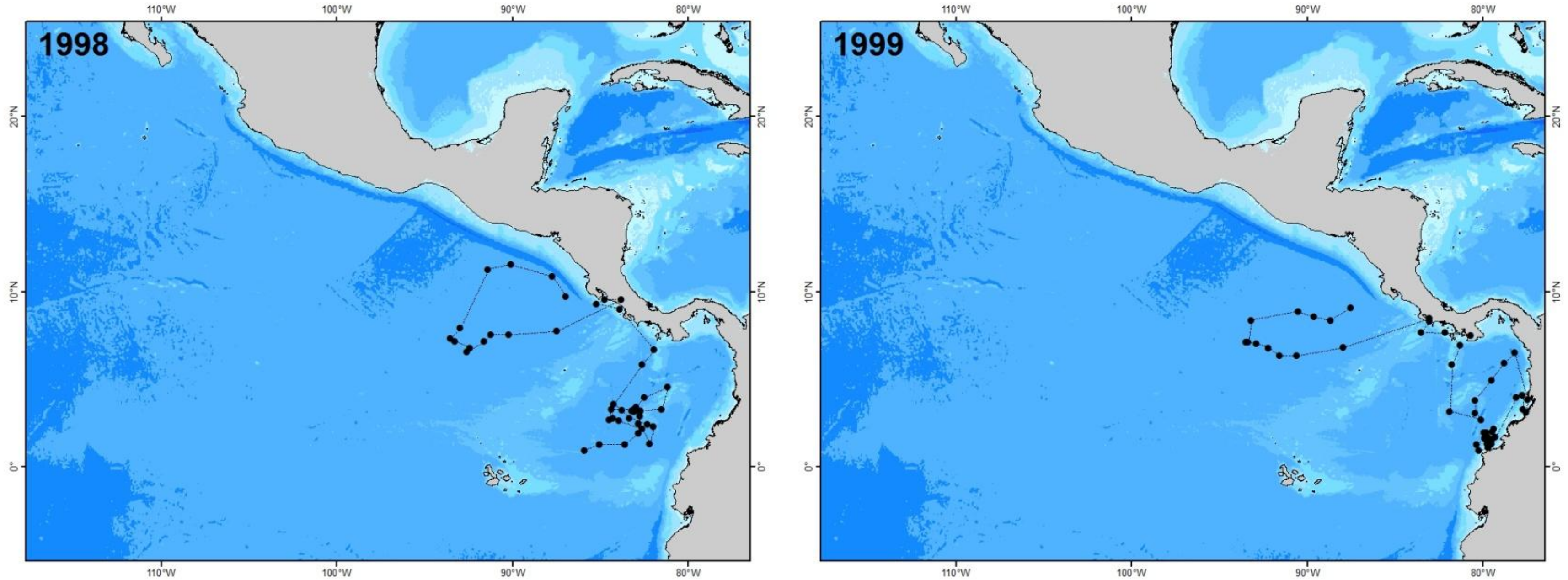
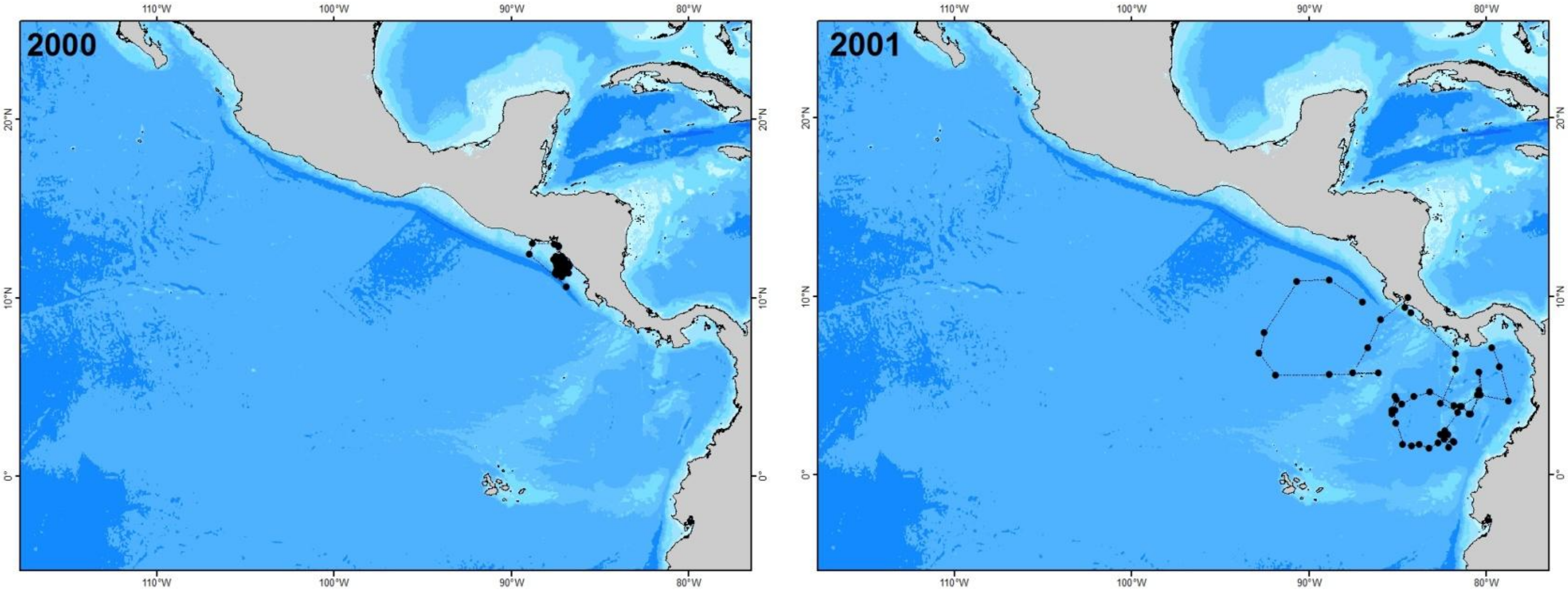


Figure 5.3: Continued



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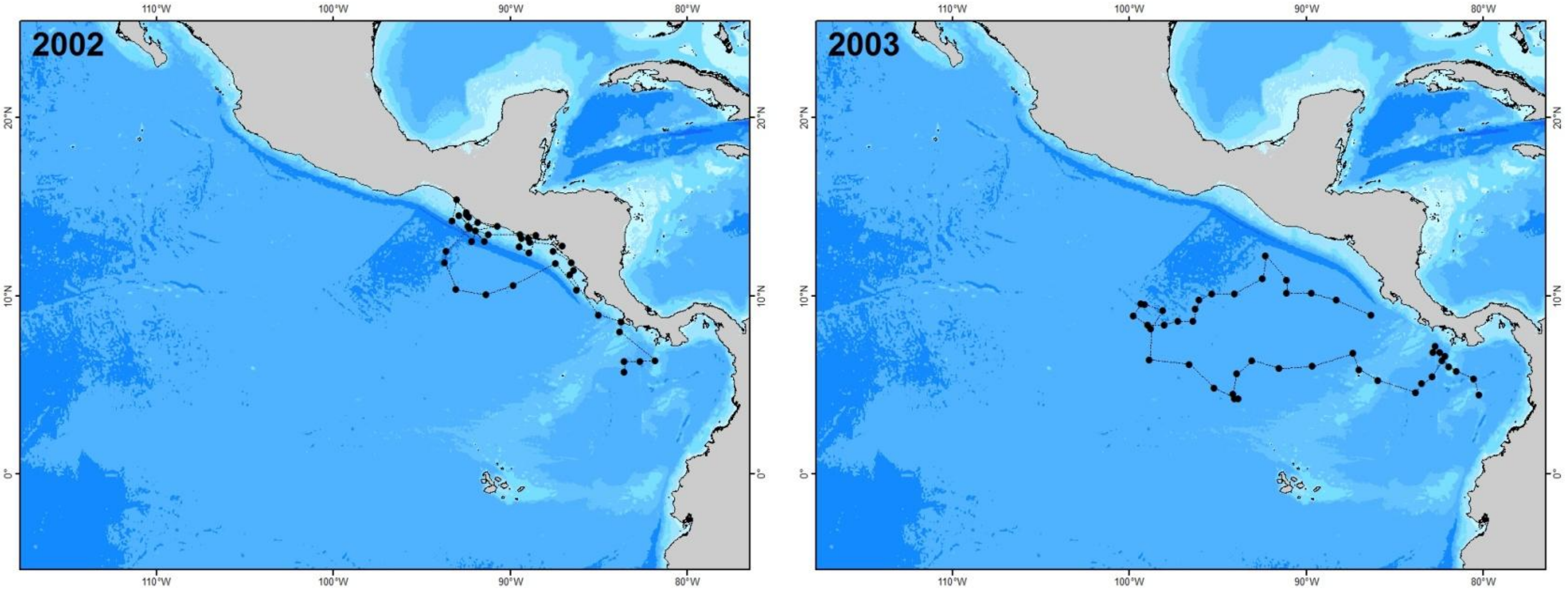

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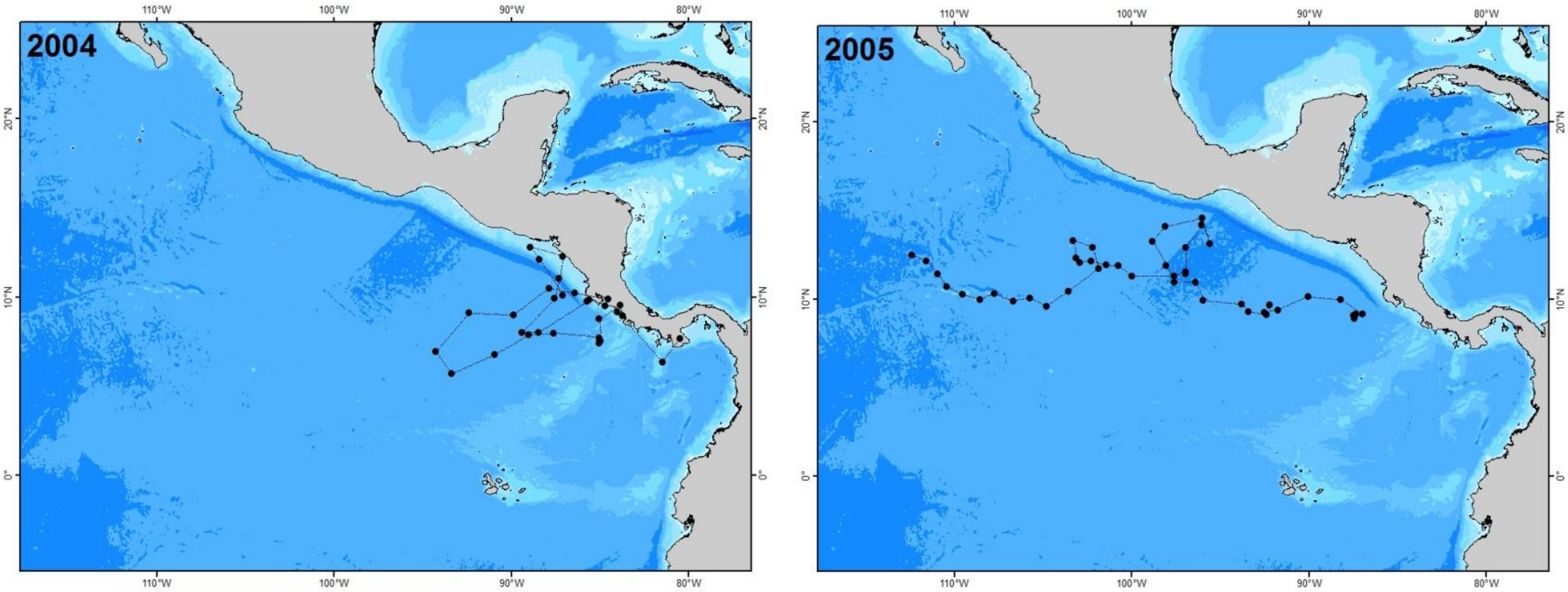

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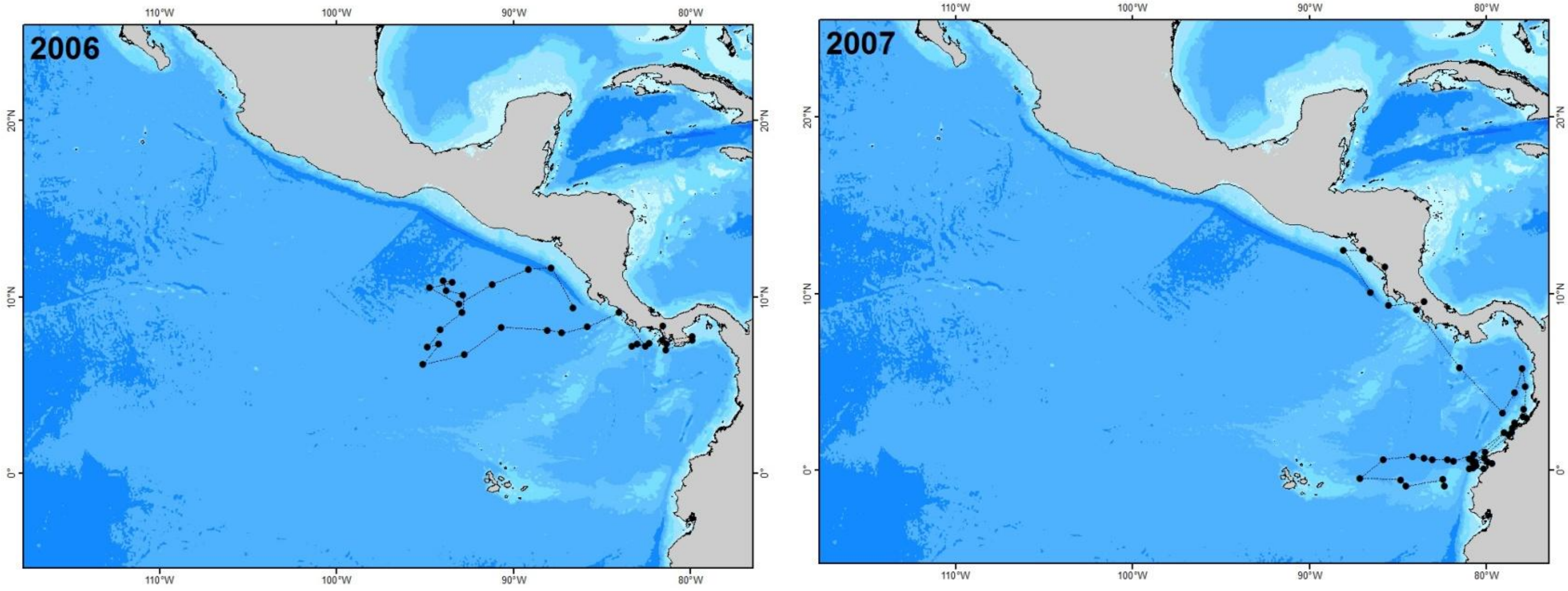

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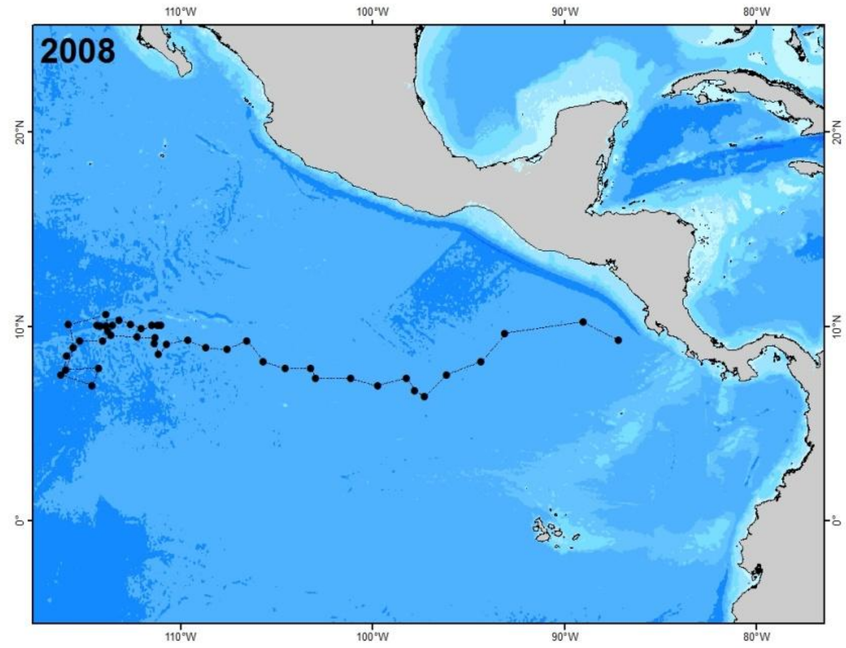

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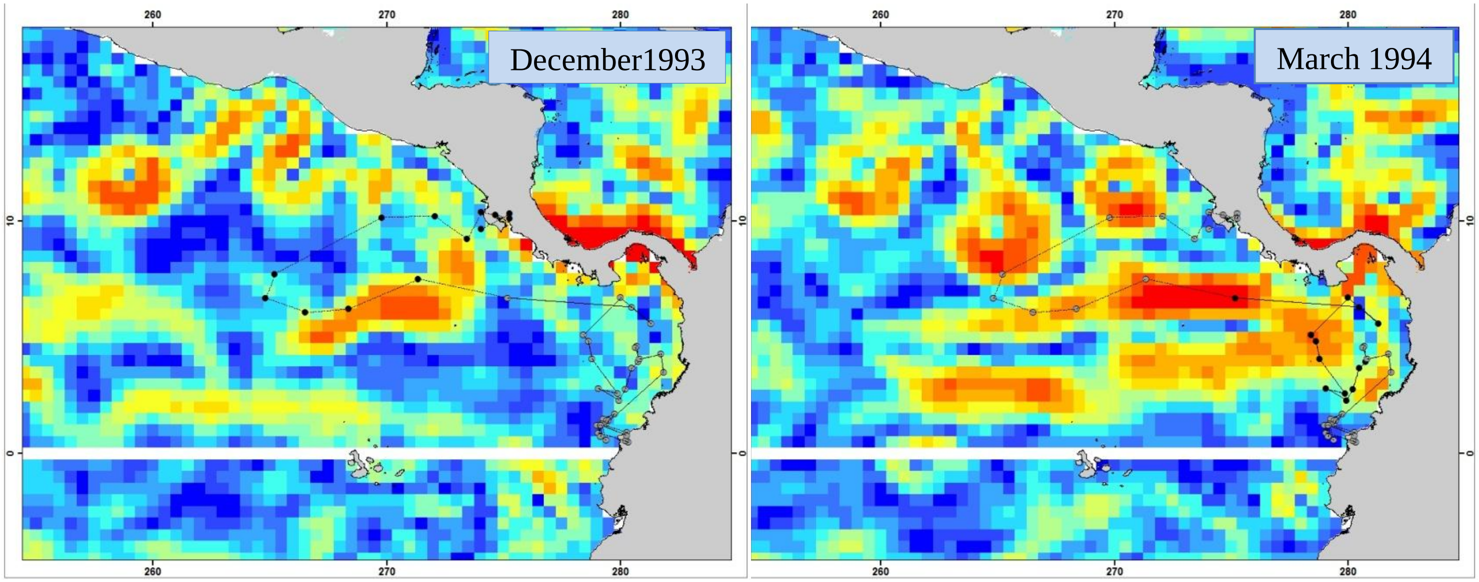


Figure 5.4: Movement of model hatchlings released 10 km off the coast of Nombre de Jesús in northwest Costa Rica in comparison with ocean currents as calculated by the model for each year from 1992 to 2008. Each dot represents the new position of the model hatchling after being transported by a current for a period of 7 days. Black dots represent a three month period starting the same week as the period of the background current image. Grey dots represent the rest of the locations for the year. Background color represents the magnitude of the currents (cm/sec) for the first week of the month referred to in the map. Scale represents magnitude of the current (cm/sec)

Color reference	0-4.5	4.5-8.25	8.25-12.2	12.2-16.4	16.4-20.6	20.6-25.1	25.1-29.6	29.6-34.4	34.4-39.7	39.7-45.3	45.3-51.3	51.3-58.3	58.3-66.8	66.8-80.2	80.2-126.3
	🟦	🟦	🟦	🟦	🟦	🟦	🟩	🟩	🟨	🟨	🟨	🟧	🟧	🟥	🟥

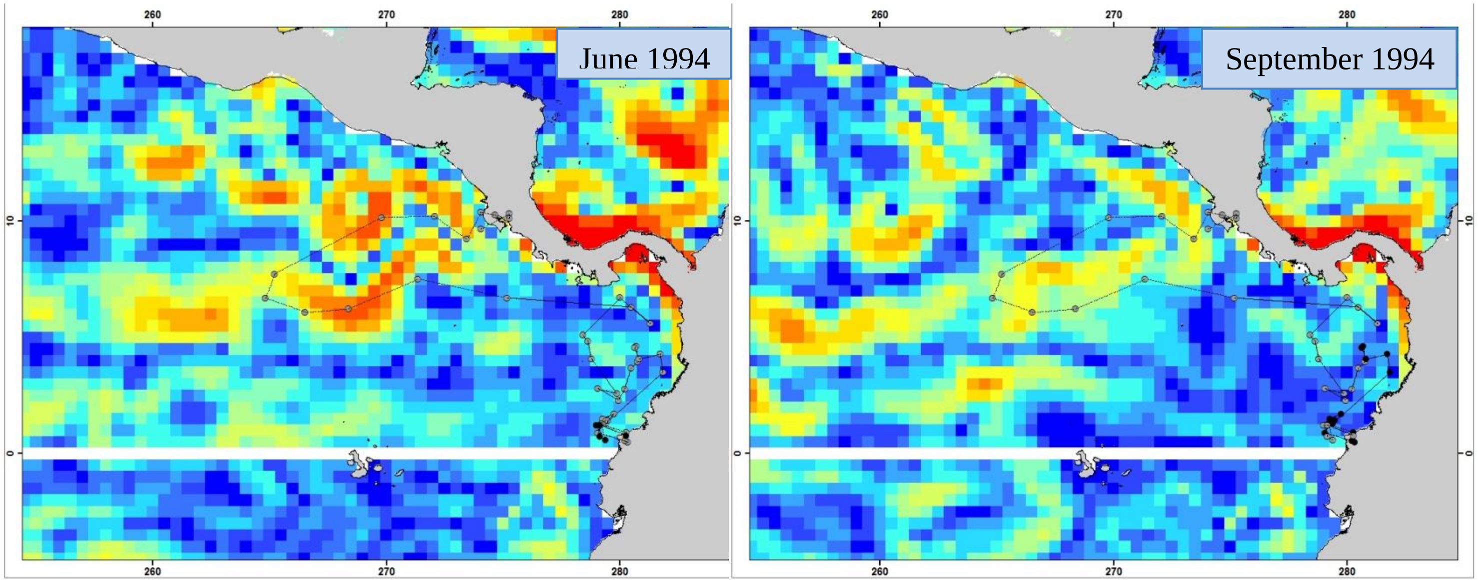
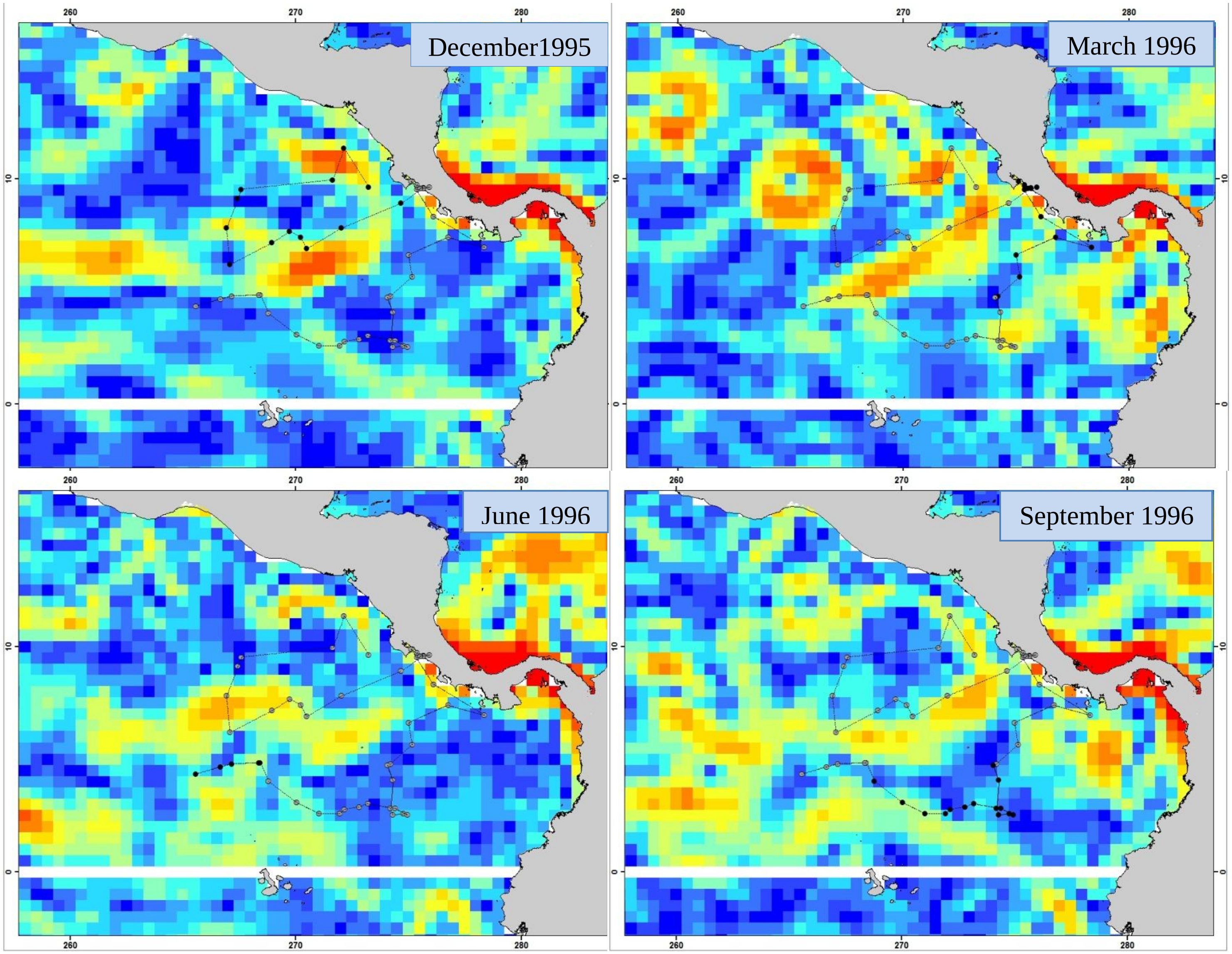


Figure 5.4: Continued



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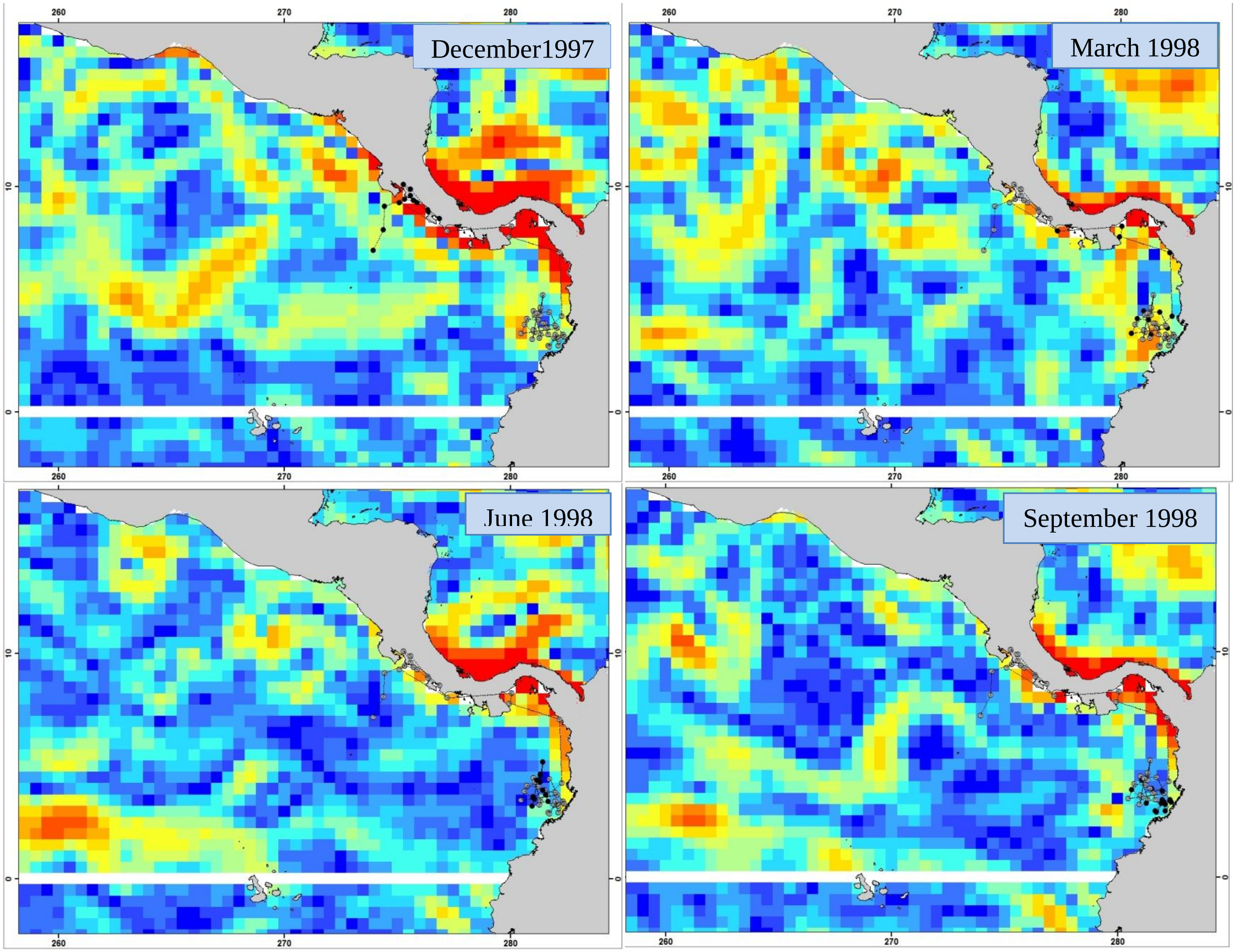


Figure 5.4: Continued

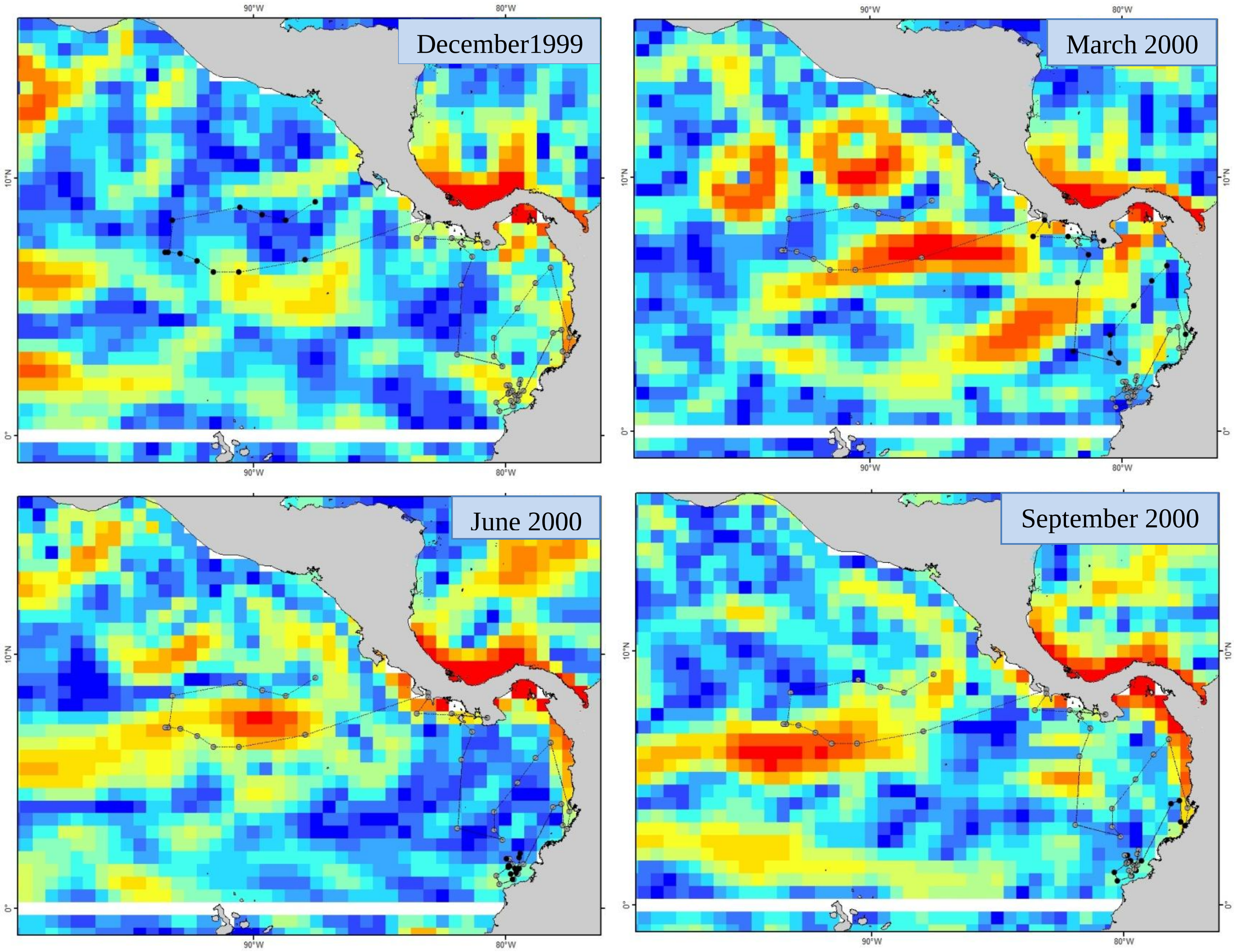
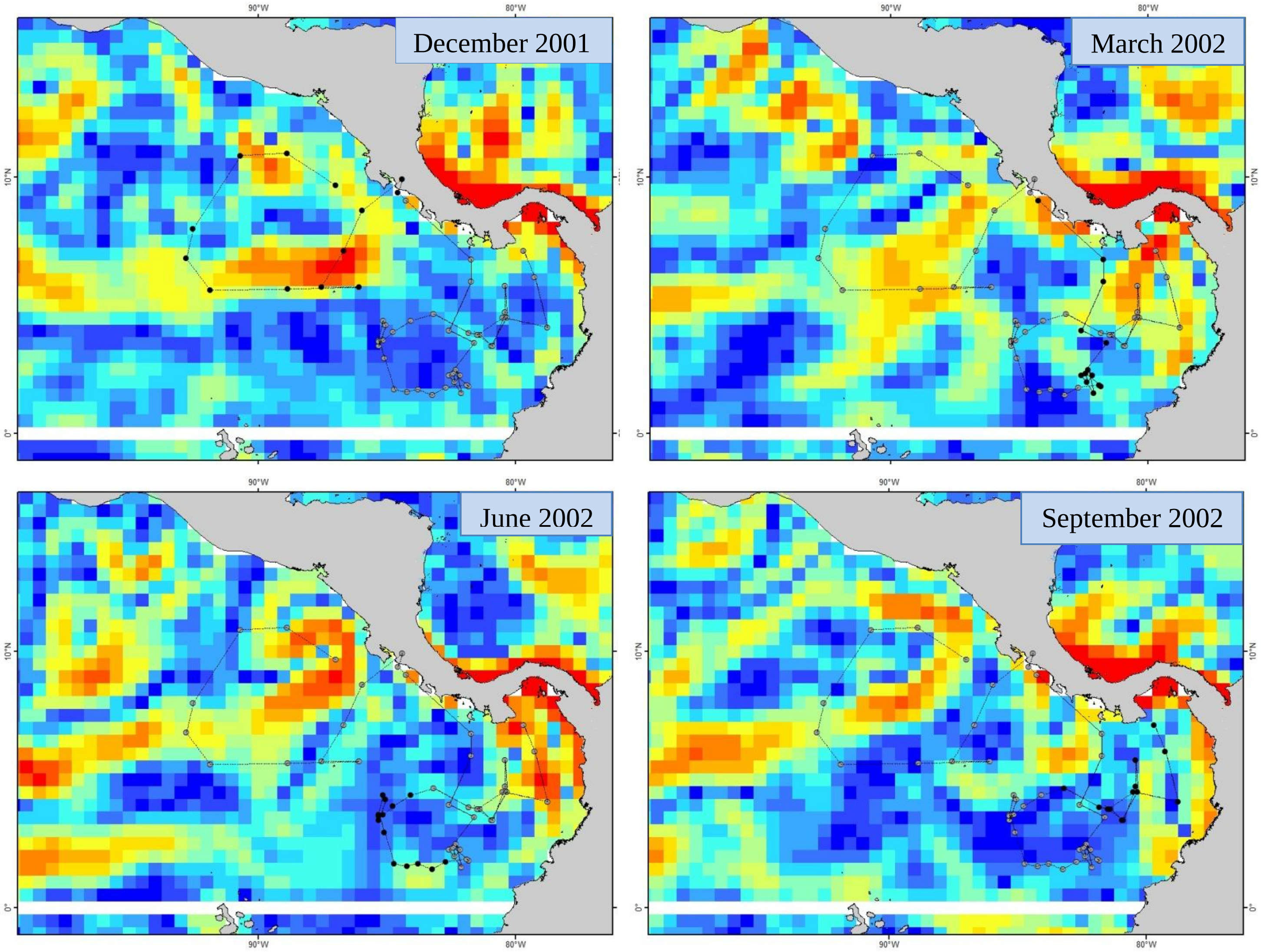


Figure 5.4: Continued



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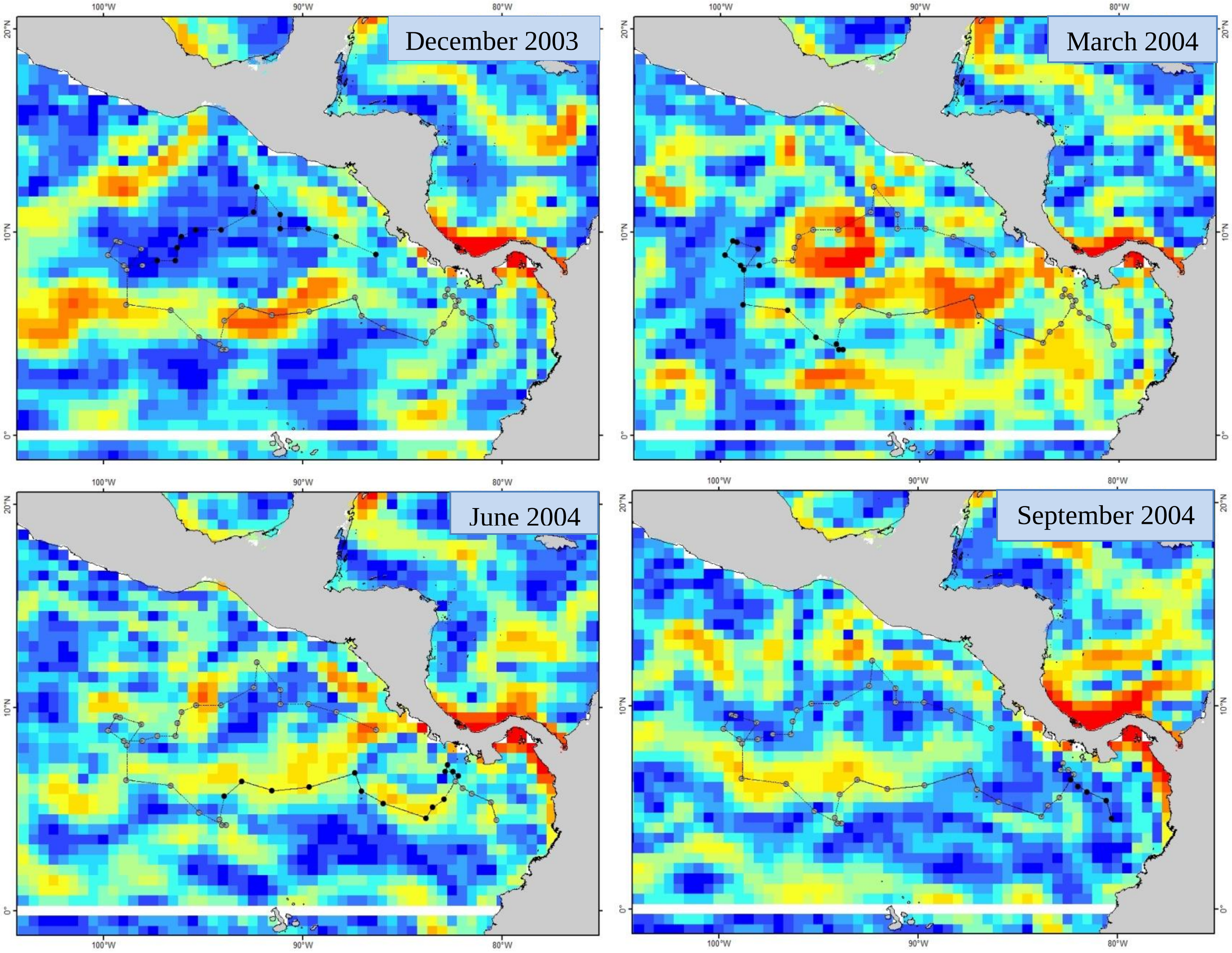

December 2003

March 2004

June 2004

September 2004

Figure 5.4: Continued

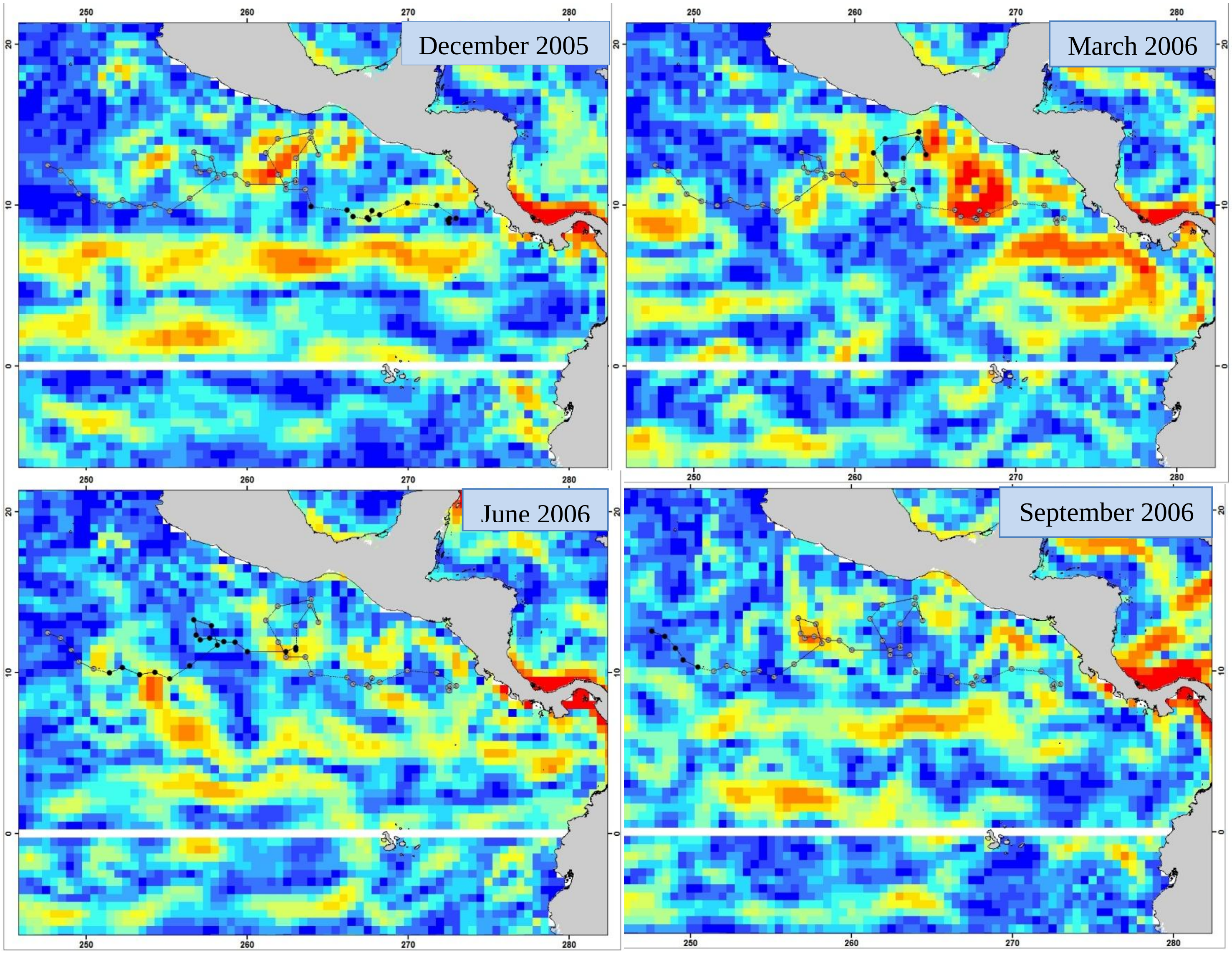

Figure 5.4: Continued

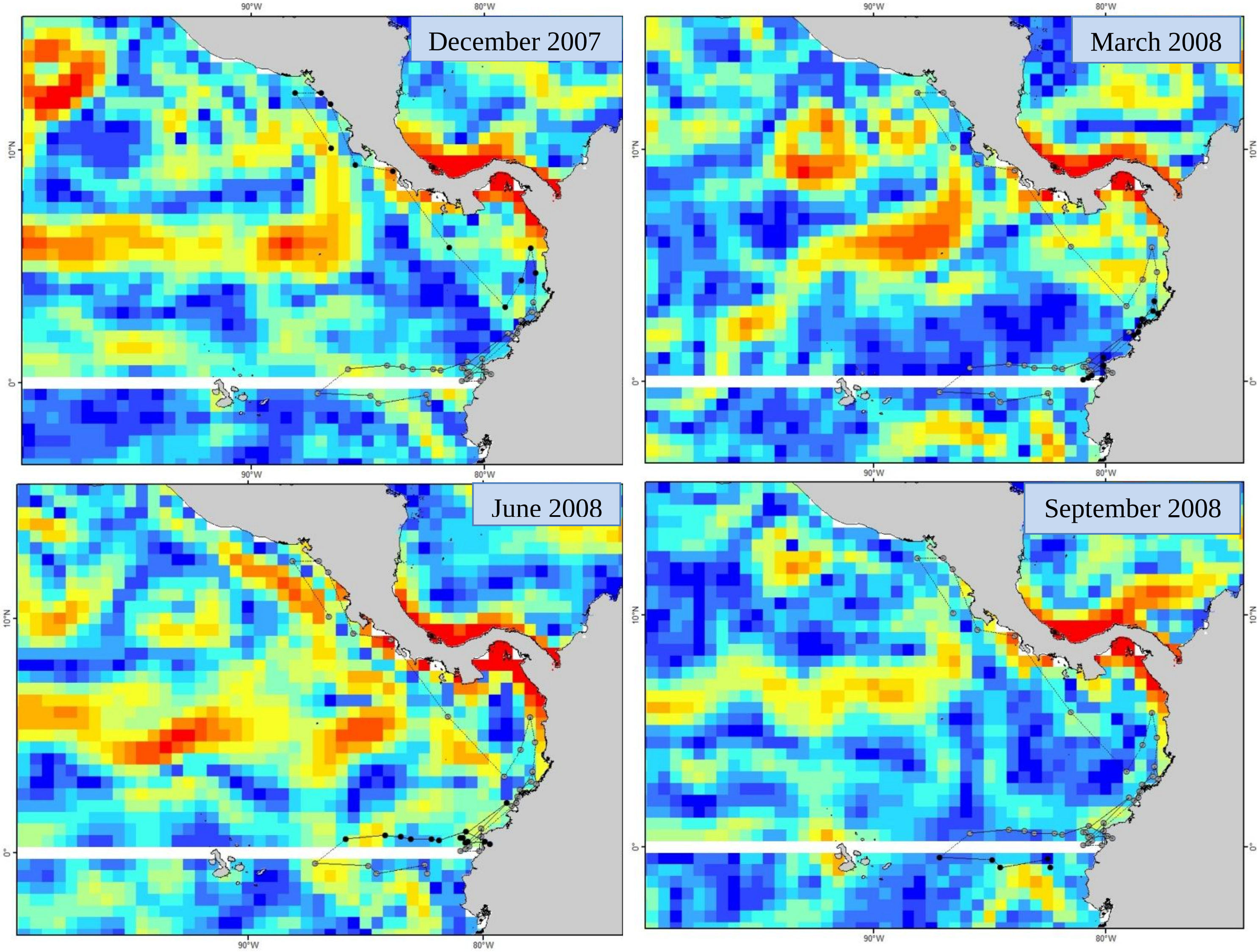

Figure 5.4: Continued

Chapter 6: Conclusions

The East Pacific green turtle nests in high concentrations on Nombre de Jesús and Zapotillal. These two beaches represent the most important nesting site for this species in Northwestern Costa Rica. By using the information obtained with ultrasound scans we could estimate a more accurate clutch frequency. Turtles nested 5 times in a season, the highest number reported for green turtles in the Eastern Pacific Ocean. The accuracy of this information is crucial to calculate population parameters, such as the number of females in a population, or estimates of annual reproductive output. Also it can give us insights into mating strategies. Without such information, it is difficult to establish effective conservation strategies and management plans. During the nesting season, this population spent the time between clutches in a small area in front of the nesting beach diving to the bottom, thus using the complete water column, demonstrating the importance not just of the nesting beach but also of the waters surrounding it for the conservation of green turtles. During the internesting, the turtles spent most of their time resting. The strong diel pattern in their diving behavior demonstrated that during the day the turtles rest by performing U-dives but during the night the turtles float at the surface. We could estimate through modeling currents and simulating the transport of hatchlings that once the eggs hatch, the neonates coming from Nombre de Jesús would disperse in different ways depending on the year. The hatchlings could be transported to the area of the Costa Rican Dome (CRD) ~300km off the Papagayo Gulf; they could be transported north and south along the coast and less common they could be transported to waters off the coast still within the Eastern Tropical Pacific Ocean. Interestingly, hatchlings may be foraging during their oceanic stage in areas close to the adult foraging areas where females go immediately after the nesting season. Adult foraging areas were in the Gulf of Papagayo, where turtles demonstrated to be resident of the area, the Bay of Santa Elena, the Gulf of Fonseca and the Gulf of Panama. All the post nesting movements were coastal. During migration the turtles used mainly the first 5 meters of the water column, performing short dives (2 min) and long dives (40 min). During foraging the turtles dove mainly between 5-10 meters, showing variability between foraging areas and between individuals. The fact that the Pacific green turtle is spending its entire life cycle in the Eastern Tropical Pacific reveals the unique characteristics that this oceanic region offers for hatchlings and adults. Despite the fact that adult females did not follow currents to migrate; seasonal oceanic features make the area rich in nutrients. The main features affecting the turtles are the CRD and eddies produced by the trade winds blowing from the Gulf of Papagayo, Panama and Tehuantepec. These produce upwelling areas which are rich in primary and secondary productivity. The foraging areas in Papagayo and Santa Elena and Gulf of Fonseca are directly affected by the CRD and by the Papagayo and Tehuantepec eddies.

The findings of this project have major implications for conservation. First, number of females nesting per night added to their high reproductive output may indicate this is a population with good resource availability. Because historic records for this population do not exist we could not estimate if the intense egg poaching taking place on the nesting beaches is already affecting these numbers. Urgent action must take place to protect beaches because this activity is detrimental for sea turtle populations. The habit of staying within 5 km of the nesting beach during internesting and the consequent presence of males in the area makes the waters off Nombre de Jesús a hot spot for conservation of this species. The coastal habit of these turtles and the fact they are travelling through waters of Panama, Costa Rica, Nicaragua, Honduras, El Salvador and Guatemala makes them vulnerable to the human activities in the region. Artisanal fisheries are one of the mortality sources for sea turtles due to by catch, activity which is common in Central America. Therefore, it is essential that enhanced protection be provided both on the beaches and in the waters of Northwestern Costa Rica if the east Pacific green turtle is to be protected from extinction over the next few years.

Curriculum Vita
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EDUCATION

Ph.D., 2005-present: Drexel University, Philadelphia PA. Dissertation Research: “Movements and Behavior of the East Pacific Green Turtle (*Chelonia mydas*) from Costa Rica”. **Defense date**: October 2010.
***Licenciatura* in Biological Sciences, 2005**: Universidad Nacional de la Patagonia, SJB, Comodoro Rivadavia, Argentina. Thesis Research: Uso de la Ría Deseado por parte de la Tonina Overa (*Cephalorhynchus commersonii*): Pautas para el manejo y conservación de la especie.

RESEARCH EXPERIENCE

2006- 2010. Principal Investigator. Migration and Behavior of Eastern Pacific green turtles.
2007-2009. Co-Principal Investigator and Field Manager. Leatherback Turtle Project, Playa Grande, Costa Rica. Earthwatch Institute. Drexel University/Indiana-Purdue University Fort Wayne.
2006. Research Assistant. Population studies of red-bellied turtles. Drexel University, Philadelphia, Pennsylvania

TEACHING EXPERIENCE

2006. Teaching Assistant. Cells and Genetics. Bioscience and Biotechnology. Drexel University.
2006. Teaching Assistant. Microbiology. Bioscience and Biotechnology. Drexel University.
2005. Teaching Assistant. Molecular Biology. Bioscience and Biotechnology. Drexel University.

OUTREACH/ INFORMAL TEACHING ACTIVITIES

2008 - Primary schools in Guanacaste, Costa Rica.
2007-2009–Visiting Universities and volunteers. Parque Nacional Marino Las Baulas, and Goldring Marine Biology Station, Playa Grande, Costa Rica.

PUBLICATIONS

Santidrián Tomillo, M.P.; Suss, J.; Wallace, B. P.; Magrini, K; **Blanco, G.**; Paladino, F.V.; and Spotila J. R. 2009. Influence of emergence success on the annual reproductive output of leatherback turtles. *Marine Biology* 156: 2021-2031.

Blanco G. S., Morreale, S. J., Vélez, E., Piedra, R., Paladino, F. V. and Spotila, J. R. Reproductive output and ultrasonography of an endangered population of east Pacific green turtles. Submitted to Journal of Wildlife Management.

PRESENTATIONS AT SYMPOSIA: 6 presentations at scientific meetings

GRANTS AND AWARDS

2009 Research Fellow Grant. Wildlife Conservation Society.
2010 Travel Grant Biology Department, Drexel University.
2007-2010 Research Fellow. Betz Chair of Environmental Science.