

ABSTRACT

Title of Thesis: LEATHERBACK TURTLE MOVEMENT
AND DISPERSAL FROM NESTING
BEACHES IN COSTA RICA WITH
IMPLICATIONS FOR MANAGEMENT AND
CONSERVATION

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Marine Estuarine Environmental Sciences

Electronic tagging permits movement and distribution studies of sea turtles as they traverse large distances through a dynamic ocean environment. However, little is known about the movements of early life stages at sea, a period termed the 'lost years'. I developed and tested a method for attaching an acoustic tag suitable for use on leatherback turtles that was then applied to hatchlings in Costa Rica to obtain measures of speed and directionality. This was compared with ocean currents and revealed that the hatchlings actively swam against nearshore currents, although they were still advected by them. Finally, a Poisson generalized linear model in a continuous-time Markov chain model framework was used to predict adult, post-nesting Eastern Pacific leatherback movement based on environmental drivers, such as sea surface temperature. Monthly, near real-time predictions of leatherback

movement were estimated using the most recent satellite-derived environmental information to help inform conservation management strategies.

LEATHERBACK TURTLE MOVEMENT AND DISPERSAL FROM NESTING
BEACHES IN COSTA RICA WITH IMPLICATIONS FOR MANAGEMENT
AND CONSERVATION

by

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Chapter 1: Introduction

Movement is fundamentally a change in location over time, a process altered by an organism's internal factors and interactions with its environment (Nathan et al. 2008). Many factors influence the movements of individuals. Organisms move to forage, reproduce, avoid predation, reduce competition, find suitable habitats for exploitation of new resources, or gain benefits of genetic dispersal and increased fitness (see Dingle and Drake 2007). A conceptual framework for understanding the processes of movement is defined by Nathan et al. (2008), including external drivers (e.g. population density, abiotic conditions, and food availability) and internal motivations such as maturation and physiology (Secor 2015). Given this complexity of processes underlying movement at many levels, movement ecology, which focuses on the individual's ability to move (Secor 2015), is often interpreted to define population movements.

Insight into ecological and biological conditions encountered by the organisms can reveal complex relationships between individual, population, and species-wide movements. The rapid rise of technology, such as acoustic and satellite tags, is increasing our understanding of the movement and behaviour of previously unknown and difficult to study highly migratory species (e.g. Block et al. 2011). Acoustic telemetry provides further-reaching observations than traditional, resource-intensive visual techniques, and larger satellite tags expand upon the capabilities of acoustic tags, providing ocean-wide, extensive monitoring (Cooke et al. 2004, Hussey et al. 2015). These data can be combined with environmental data to identify habitat

preferences and developed into decision support tools for management as illustrated with blue whales (Hazen et al. 2016), bluefin tuna (Hobday & Hartmann 2006, Hartog et al. 2011, Hobday et al. 2011), and sea turtles (Howell et al. 2008, 2015). Appropriate conservation efforts for species rely on understanding their distribution and movement to effectively prevent negative consequences of anthropogenic and other disturbances (Bauer et al. 2009). The need for such tools is likely to increase as the consequences of climate change materializes (Hamann et al. 2010, Lewison et al. 2015, Willis-Norton et al. 2015). Since many migratory species move seasonally in response to dynamic changes in the ocean conditions, telemetry technology and habitat-based models can be used in the development of dynamic management for highly migratory species, such as sea turtles capable of traversing ocean basins, producing management schemes that change through space and time with conditions (Hays & Scott 2013).

Conservation planning and management can be strengthened through resolution of unknown movements across size, age classes, and species of sea turtles (Scott et al. 2012a, Hays & Scott 2013, Lascelles et al. 2016). The large distances over ocean basins and the unknown movements of the youngest stages of sea turtles present challenges to both current and future management of these vulnerable species (Lascelles et al. 2014). Juvenile sea turtles can migrate long distances (~12,000 km) exceeding those of marine mammals and fishes of the same size class (Hays & Scott 2013), while distances and movement patterns of recently hatched sea turtles remain unknown.

Sea turtle movements

Sea turtles are reptiles that have undergone 110 million years of evolution (Hirayama 1998), and their spatiotemporal movements throughout life stages are influenced by many factors. They are air breathers, are constrained spatially by the water temperature due to their inability to produce metabolic heat, and are internal fertilizers, requiring a land nesting stage for final egg development (Eckert et al. 2012). These changing spatial demands, temperatures, and energy requirements throughout life have different roles in growth and development, which can result in ontogenetic habitat shifts across thousands of kilometres of open ocean and international boundaries (Bolten 2003a). Sea turtles are part of the superfamily Chelonioidae with late-maturing, long-lived life histories that make them vulnerable to a range of predators and anthropogenic impacts on land and sea.

Little is known about sea turtles between the time they leave the nesting beach as hatchlings until the time reproductively active females return to the beach to nest. This cryptic period is often termed the 'lost years' (Carr 1986). Although much research has gone into tracking the movements throughout life stages of sea turtles, there are many gaps remaining in their ontogenetic habitat use, such as moving from oceanic to nearshore foraging grounds, which varies among species (Fig. 1.1) (Musick & Limpus 1997, Meylan et al. 2011). Sea turtles spend the majority of their life at sea, generally only on land to hatch or nest, and undertake ontogenetic and reproductive migrations to diverse habitats. Life at sea begins with the dispersal of hatchlings from the nesting beach to oceanic waters. This dispersal is the start of the 'lost years' of sea turtles, more recently termed the 'epipelagic stage' (Meylan et al.

2011). This highly individualized, less directed movement (Liedvogel et al. 2011) towards the epipelagic zone leads them to nursery habitats that are poorly known, rendering sea turtle populations during their early life stages problematic to predict and manage.

The 'lost years'

Developmental stages of sea turtles differ among families and species, complicating our understanding of sea turtle population dynamics and management abilities. There is a general process after egg growth, hatching, and natal beach departure. This process includes juvenile movement into little-known oceanic, epipelagic waters for years, succeeded by a subadult benthic phase before maturation (Fig. 1.2) (Carr 1986, Bolten 2003a, Bowen & Karl 2007, Godley et al. 2010, Meylan et al. 2011).

Besides the Australian flatback (*Natator depressus*) (Bolten 2003a) and at least partially, Pacific hawksbills (*Eretmochelys imbricata*) (Van Houtan et al. 2016), juveniles spend time in oceanic surface waters foraging far from shore (Meylan et al. 2011). These early epipelagic years can include long migrations (Bolten 2003b, Shillinger et al. 2012a, Hays & Scott 2013). For example, Bowen and Karl (2007) review the use of the Kuroshio Current by juvenile Western Pacific loggerheads (*Caretta caretta*) to travel from Japan to foraging grounds in Baja California (Bowen et al. 1995, Polovina et al. 2000) and then actively migrate back to Japan as adults (Nichols et al. 2000). Western Atlantic juvenile loggerheads that forage in the distant Mediterranean Sea (Laurent et al. 1998) return to the western basin before the subadult phase (Maffucci et al. 2006).

At the larger subadult stage, most Cheloniids show juvenile homing (e.g. Avens et al. 2003, Bowen et al. 2004) by shifting to neritic waters near their natal beach to forage on benthic algae, macroinvertebrates, and sea grasses (Meylan et al. 2011). This return may be a result of reduced nearshore, size-related predation risks and increased access to food resources (Luschi et al. 2003, Wyneken et al. 2013). This separate juvenile period of benthic habitat use prior to maturation is most evident in greens (*Chelonia mydas*), Kemp's ridleys (*Lepidochelys kempii*), and hawksbills (Meylan et al. 2011).

The onset of maturation likely causes a migration from developmental habitat to adult foraging grounds (Meylan et al. 2011). In comparison to the other species of sea turtles, leatherbacks (*Dermochelys coriacea*), the only surviving species in the family Dermochelyidae, have largely unknown movements during these young life stages (Bowen & Karl 2007). The divergent habitat preferences of sea turtles, as well as separations in thermal tolerances between size classes and species, result in differing geographical and ecological niches. These factors minimize overlap of habitats and resource utilization of sea turtles, but also complicate management strategies (Bowen & Karl 2007).

All mature Cheloniids, with the exception of olive ridleys, spend their lives in coastal foraging habitats, while leatherbacks mainly forage in pelagic waters (Fig. 1.2) (Bolten 2003a). Periodic migrations are undertaken from feeding grounds to the neritic zone to reproduce in the internesting and breeding habitat (Wyneken et al. 2013). Returning to nest near the beach sea turtles departed as hatchlings is called natal homing or philopatry (Wyneken et al. 2013).

Long migrations undertaken throughout life stages and natal homing are two reasons why the navigational ability of sea turtles is well known. However, as sea turtle research advances, this generalized model of sea turtle movement and habitat utilization has shifted to adult habitat “polymorphism” (Wyneken et al. 2013), where subsets of populations exhibit opposing foraging strategies. This is similar to the notion of partial migrations, which are exhibited by many species (Chapman et al. 2011). Meylan et al. (2011) further reviewed the complexities of ontogenetic shifts and the developmental habitat hypothesis, as overlap or partial overlap may occur across life stages for different populations of sea turtles. The developmental habitat hypothesis posits that some species have a geographically separate developmental habitat from that of the pelagic ‘lost years’ habitat and the adult foraging and breeding areas (Carr et al. 1978, Meylan et al. 2011). However, this assumption of exclusive developmental habitat phases has been challenged and still presents unknown questions (Meylan et al. 2011). Understanding these complex movements of different age classes will improve our ability to describe how sea turtles are utilizing their environment, which will inform management efforts for these threatened highly migratory species (see Bowen and Karl 2007).

Habitat utilization and movement throughout life must be understood to properly manage highly migratory marine species, particularly those that are threatened and endangered (Hays & Scott 2013). Sea turtles represent the most vulnerable group of migratory marine species according to the International Union for the Conservation of Nature (IUCN) (Lascelles et al. 2014). The poorly understood ‘lost years’ of sea turtles hinder management efforts as habitats cannot be predicted or

protected. Research has begun to confirm the oceanic to neritic ontogenetic shift for juvenile Cheloniids (Reich et al. 2007), but large knowledge gaps remain (Hamann et al. 2010), especially for leatherback turtles. Resilient management and conservation strategies to prevent declines in sea turtle populations require this missing ‘lost years’ information, which is beginning emerge through such technology as biologging advancements (Rutz & Hays 2009, Hazen et al. 2012, Shillinger et al. 2012a).

Sea Turtles of Costa Rica

Costa Rica, with nesting beaches along both the Caribbean and Pacific basins, is an important nesting area for many sea turtle species. Guanacaste, Costa Rica includes the nesting beaches of Playa Grande, Playa Cabuyal, and Playa Ostional. Playa Grande is a critical nesting area for Eastern Pacific leatherback turtles, one of the last remaining nesting sites contributing to the continuation of this population (Fig. 1.3) (Shillinger et al. 2012b), but the secondary leatherback nesting beaches of Playa Cabuyal and Playa Ostional are also important nesting areas for olive ridley and green sea turtles. However, small numbers of nesting female leatherbacks have been recorded in Playa Grande in recent years (< 30 per year) (G. Shillinger, personal communication).

The Pacific Costa Rican breeding population of olive ridley sea turtles is classified as threatened by IUCN (Abreu-Grobois & Plotkin 2008), and there is still limited knowledge on their hatchling dispersal and survivorship. The green sea turtle population is endangered (Seminoff 2004), and the leatherback population is critically endangered (Wallace et al. 2013). These listings signify the need for proper management of Costa Rican sea turtles. Guanacaste is managed under two

conservation zones by the Ministry of Environment and Energy, the Tempisque Conservation Area and the Guanacaste Conservation Area, with varying protection levels at each beach. Playa Cabuyal lacks official protection (Santidrián Tomillo et al. 2015), and Playa Ostional is designated protected as a national wildlife refuge (Alvarado et al. 2012). The main marine conservation area is the no-take Parque Nacional Marino Las Baulas (PNMB) that Playa Grande falls within, but these static zones do not protect interesting and migrating turtles outside their borders, reducing their efficacy at minimizing human interactions (Shillinger et al. 2010, Roe et al. 2014).

The Caribbean coast of Costa Rica is a continuous stretch of nesting beaches that extends north into Nicaragua and south into Panama. This extended stretch of nesting beach has been estimated at approximately 1,000 - 2,500 nesting leatherback females each year, making it an important rookery (Troëng et al. 2004). Pacuare Nature Reserve in the Limón Province is a small stretch of beach near the middle of this international rookery and has approximately 100 to 250 nesting females per year (estimation of 5 clutches per female as in Spotila et al. 1996) (Troëng et al. 2004), much higher than those nesting in Guanacaste. This same area is also well-known for green sea turtles as one of the largest worldwide rookeries (Troëng & Rankin 2005), as well as the critically endangered hawksbill (Troëng et al. 2005, Mortimer et al. 2008). The regular utilization of this beach by multiple species, similar to the beaches of Guanacaste, highlights the need for scientific data to inform management and policy along this international nesting beach and its accompanying waters.

Leatherback turtles

With a carapace of skin and flesh over small, bony plates, leatherback turtles are the only extant member of the family Dermochelyidae, separate from the other six sea turtle species (Cheloniidae) (Dutton et al. 1999). At 1.2 - 2.4 m, leatherbacks can range in weight from 250 - 1000 kg (Paladino et al. 1990, Tiwari et al. 2013), reach estimated maturity around 9 - 15 years (Zug & Parham 1996, Jones et al. 2011), and are distributed from breeding grounds in the tropics nearly into the Arctic Circle (Goff and Lien 1988, Hays et al. 2004, Benson et al. 2007, 2011). Their lifespan is not known, with the oldest female aged estimated at 43 through skeletochronology (Avens et al. 2009, Eckert et al. 2012).

Leatherbacks are separated into seven populations throughout the ocean defined by their migratory movements (Dingle & Drake 2007, Wallace et al. 2013) based on natal homing behaviours, which have created genetically distinct nesting populations (Dutton et al. 1999). Major worldwide population declines have been estimated in the past 30 years due to cumulative effects of adult and egg harvest, incidental fisheries catch, coastal development, pollution, and changes in prey abundance (Chan & Liew 1996, Sarti et al. 1996, Spotila et al. 2000, Alfaro-Shigueto et al. 2007, 2011, Lewison & Crowder 2007, Sarti Martínez et al. 2007, Troëng et al. 2007, Santidrián Tomillo et al. 2008, Žydelis et al. 2009).

The Northwest Atlantic population has begun to rebound and is classified as least concern under IUCN (Tiwari et al. 2013), but there are declining trends in leatherback nesting abundance from the Costa Rican rookery (Troëng et al. 2004, 2007). The Caribbean nesting beaches, which include Pacuare Nature Reserve,

contributing to the Northwest Atlantic population are not experiencing the recovery evident in the overall population (Troëng et al. 2007). Fisheries bycatch of these Costa Rican-origin leatherbacks in the Gulf of Mexico may be preventing recovery of this rookery (Stewart et al. 2016), but unknown habitat utilization throughout life stages has complicated the understanding of this rookery's population dynamics.

The Eastern Pacific leatherback has declined nearly 98% since the 1980s with unknown numbers prior (Sarti et al. 1997, Spotila et al. 2000). The population is at risk of regional extinction (Wallace et al. 2013) and is susceptible to threats with this greatly reduced population size (Saba et al. 2008b, Wallace and Saba 2009). They historically nested in Mexico and Costa Rica, and losses from fisheries bycatch and egg poaching are the major reasons for their decline (Sarti et al. 1996, Spotila et al. 2000, Sarti Martínez et al. 2007, Santidrián Tomillo et al. 2008, Wallace et al. 2010). Despite conservation efforts and a large reduction in egg poaching, the population has neither recovered nor stabilized due to high levels of at-sea mortality, particularly affecting older age classes (Kaplan 2005, Lewison & Crowder 2007, Santidrián Tomillo et al. 2007, 2008). Their limited foraging grounds may be less consistently productive than foraging habitats of other populations (Saba et al. 2008b, Bailey et al. 2012a, 2012b), especially during El Niño years (Saba et al. 2008a), prioritizing the need to reduce negative anthropogenic impacts.

Current beach conservation efforts must expand beyond the terrestrial stage to oceanic waters to reduce turtle mortality from bycatch, as adults of long-lived species can be sensitive to losses at older ages (Heppell et al. 1996). In addition, management requires national and international regulations as political boundaries are crossed by

the highly mobile species capable of traveling 35 km/day and 10,000 km a year (Hays et al. 2006, Shillinger et al. 2008, Hays & Scott 2013, Lascelles et al. 2014). Unlike other sea turtles, leatherbacks can keep their body temperature above the water temperature, extending seasonal horizontal and vertical movements into colder waters and thus, expanding their range beyond other species' (Paladino et al. 1990, Southwood et al. 2005, Shillinger et al. 2011). Focusing on the habitat utilized by this Eastern Pacific leatherback population and expanding to include habitat changes from climate shifts are instrumental steps in reducing fisheries bycatch and managing the population in the oceanic zone (Sarti et al. 1997, Spotila et al. 2000, Roe et al. 2014, Willis-Norton et al. 2015).

Objectives

The primary purpose of my thesis research is to develop techniques to understand the distribution and movements of hatchling and adult leatherback turtles. In Chapter 2, I examined the effects of acoustic tag attachment on the speed of young sea turtles to comprehend how the use of tag nanotechnology may influence scientific results. In the third chapter of my thesis, I examined dispersal of hatchling leatherback turtles to begin to resolve some of the unknown movements of this species to better inform management efforts. The final chapter of my thesis is the creation of a habitat-based model using satellite telemetry data to dynamically predict adult leatherback turtle distribution to inform managers and other stakeholders to help reduce fisheries bycatch for the Eastern Pacific leatherback subpopulation.

Objective 1 (Chapter 2)

To examine whether miniature acoustic tags alter the speed of young sea turtles, I ran trials on post-hatchling green sea turtles because captive young leatherback turtles were not readily available, and green turtles were most similar in size. Vemco V5 acoustic tags were used because they were the smallest acoustic tags available at the time and likely to be used by scientists worldwide. Individuals were separately placed in a tank under each of three treatments for 25 minutes apiece. The three treatments were a control with no alteration to the turtle, a Velcro® attachment using Vetbond on the carapace, and a harness attachment wrapping around their shoulder girdle. Attachments consisted of a braided monofilament line with 2 floats in parallel with the acoustic tag hanging at the end to provide visual and acoustic points of contact (Gearheart et al. 2011). Cameras overhead and underwater recorded behaviour. Trials were run over a two-week period. Video analysis was completed with the Tracker Video Analysis and Modeling Tool program (Brown 2014). I ran a within-subjects repeated measures ANOVA to test the hypothesis that the speed of post-hatchling green sea turtles would not be altered by an attachment method compared to the control.

Objective 2 (Chapter 3)

After testing methods of acoustic tagging in Chapter 2, I implemented the procedures in field trials in Guanacaste and Limón Provinces, Costa Rica to obtain estimates on hatchling sea turtle speed and directionality. Hatchling turtles were obtained from nesting beaches after emerging from nests. Acoustic tag attachments were attached via Vetbond. Hatchlings were released outside the surf zone with these

attachments and followed in a boat using both visual tracking and a Vemco directional hydrophone. In Guanacaste, olive ridley hatchlings ($n = 2$) were tagged with Vemco V5 acoustic tags because no leatherback hatchlings were available as a result of the strong El Niño conditions. This provided field-testing and refining of the methodology, as well as the applicability of the tracking methods to smaller Cheloniid hatchlings. On the Caribbean coast of Costa Rica, leatherback hatchlings ($n = 43$) from the Northwest Atlantic nesting population were tagged and followed using the same methods. Surface drifters were released to obtain surface current estimates and to test the hypothesis that hatchlings are passive drifters in the ocean currents. Over-ground and in-water swimming speed estimates were determined from positions obtained from the surface drifter positions and hatchling turtle trajectories obtained via the acoustic receiver.

Objective 3 (Chapter 4)

To create monthly predictive estimates of Eastern Pacific leatherback turtle distribution, I obtained satellite telemetry and fisheries observations positions of these leatherbacks between 1992 and 2015. A Bayesian switching state-space model was applied to the raw satellite tracks to obtain daily positions. Environmental covariates throughout this time period were obtained for both the individual positions of leatherbacks and as monthly rasters. Multiple models, including a Random Forest and Generalized Additive Mixed Model were explored to describe habitat-use throughout the South Pacific. However, in order to account for the spatiotemporally auto-correlated, unbalanced, and presence-only telemetry observations of leatherbacks, a novel modeling approach was applied in this analysis. We used a Poisson generalized

linear model in a continuous-time discrete-space Markov chain Monte Carlo model framework (Hooten et al. 2010, 2016, Hanks et al. 2015) for the telemetry data to predict individual, post-nesting leatherback movement throughout the South Pacific based on environmental drivers. Sea surface temperature and bathymetry were the environmental covariates included in the model as they span the time period. A generalized linear model with Poisson regression provided estimates for use in a population-level hierarchical Bayesian model. Posterior distributions from the population-level approach provided predictions for monthly leatherback distribution estimates.

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Figures

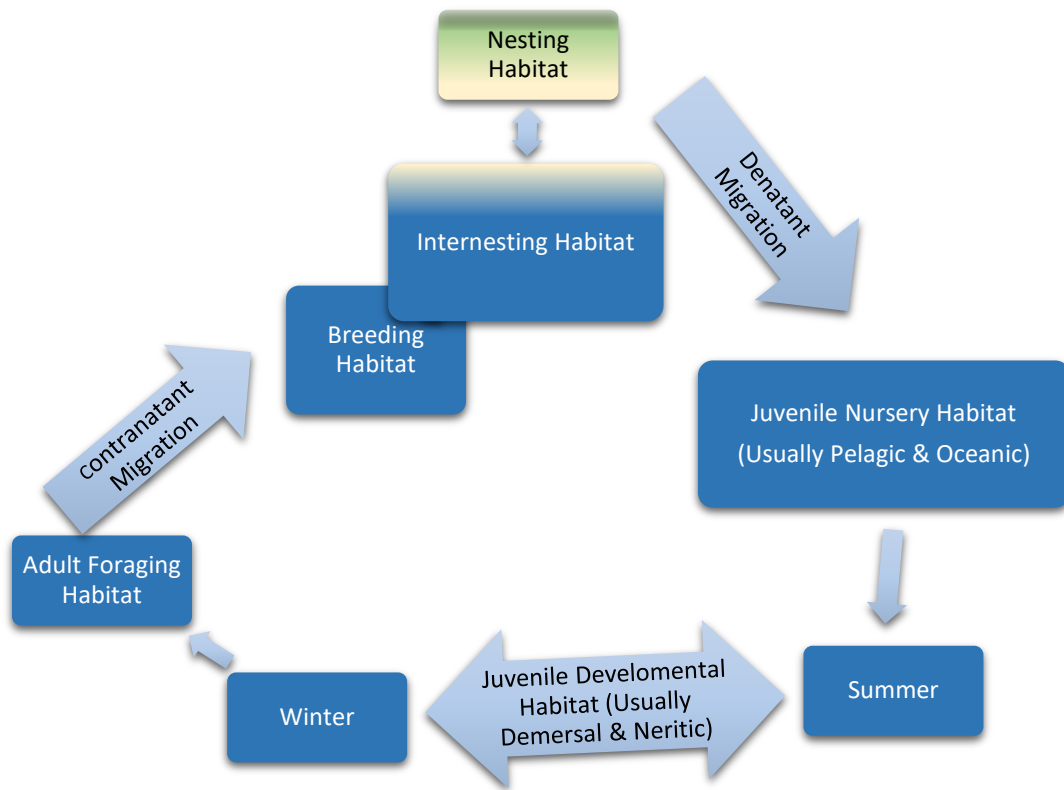


Figure 3.1. Generalized life history model from Musick and Limpus (1997) depicting sea turtle habitat utilization and movements.

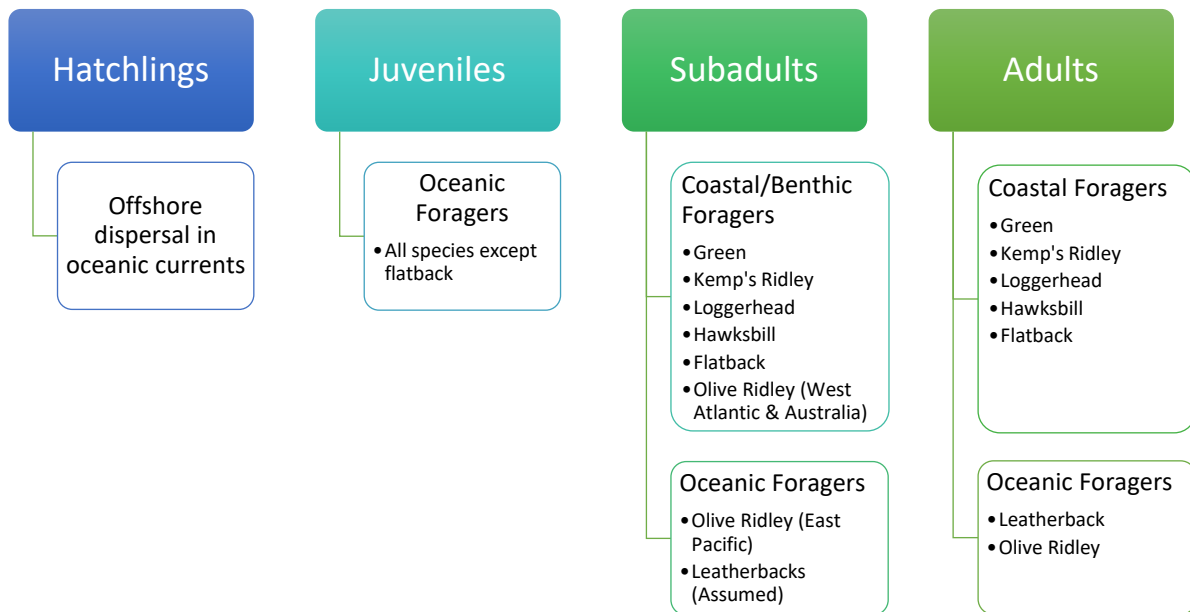


Figure 1.4. Sea turtle ontogenetic habitat utilization by species during developmental migrations adapted from Bowen and Karl (2007) (Bolten 2003a, Meylan et al. 2011). The heterogeneous spatiotemporal distribution and individualized responses to a dynamic ocean environment increase the challenge of isolating and defining habitat utilization across both age classes and species (Hamann et al. 2010).

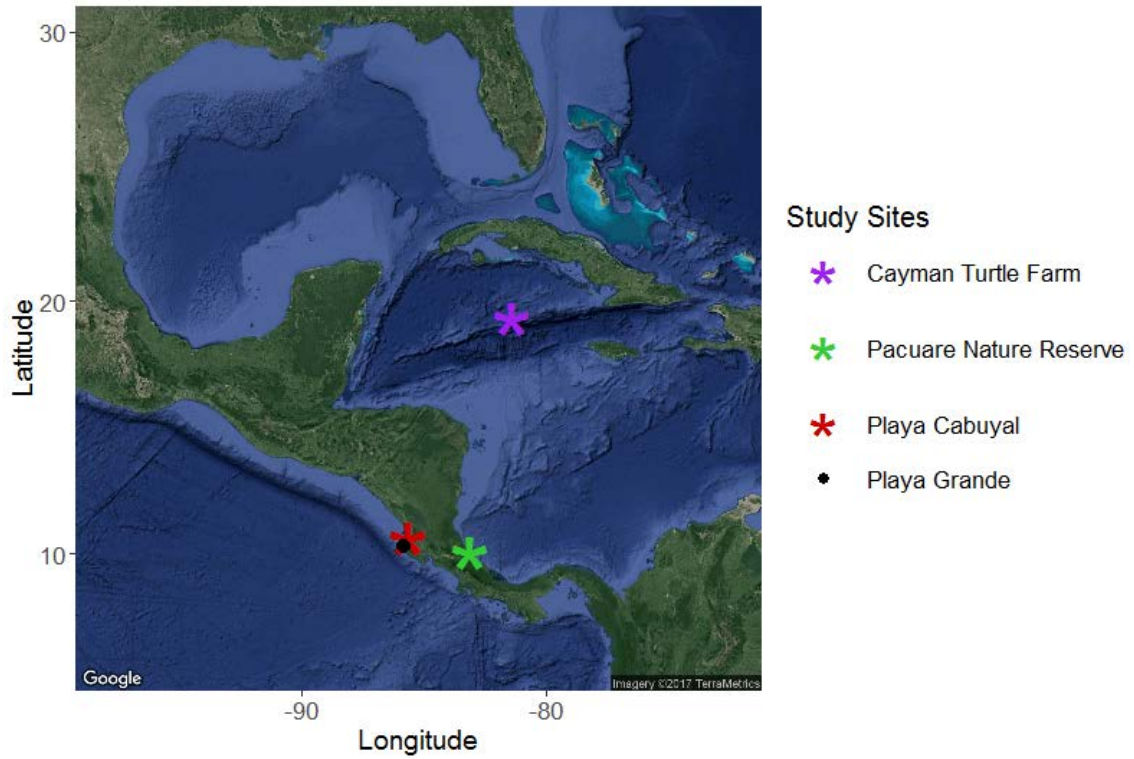


Figure 1.3. Map of study locations. These include Playa Grande and Playa Cabuyal on Costa Rica’s Pacific Coast, Pacuare Nature Reserve on the Atlantic Coast, and the Cayman Turtle Farm in the Caribbean. Playa Grande serves as the only remaining nesting beach for the Eastern Pacific leatherback, and the nesting beach at Pacuare contributes to the Northwest Atlantic population. Map was generated using ‘ggmap’ in R (Kahle & Wickham 2013).

Chapter 2: Identification of acoustic tag attachments suitable for mobile tracking of hatchling leatherback turtles

Introduction

Effective conservation efforts for marine species are hindered by a lack of knowledge regarding movements and habitat utilization (Bowen & Karl 2007). Highly migratory marine species, such as sea turtles, pose additional complexities for management as they traverse large distances and cross international boundaries throughout their life history (Hays & Scott 2013). Early life stages, notoriously difficult to track, can even undergo these long migrations (Bolten 2003b, Hazen et al. 2012, Shillinger et al. 2012a). The ‘lost years’ of sea turtles are an enigmatic period of unknown distribution and developmental habitat after hatchlings leave natal beaches. This period has been increasingly studied as conservation efforts expand beyond terrestrial zones and investigations of at-sea movements during early stages are made possible by advances in biologging technology (e.g. Mansfield et al. 2014, Scott et al. 2014a, Thums et al. 2016). Threatened and endangered species with unknown life history patterns, including highly vulnerable sea turtles (Lascelles et al. 2014), have been a research focus to advance management strategies under such legislation as the Endangered Species Act (Hays & Scott 2013).

Information about sea turtle dispersal and behaviour during the ‘lost years’ has been gained through modelling approaches (Hays et al. 2010, Shillinger et al. 2012b, Putman et al. 2013, Casale & Mariani 2014), telemetry (Nagelkerken et al. 2003, Witherington et al. 2012, Mansfield et al. 2014, Scott et al. 2014a), and other emerging technologies, such as stable isotopes (Bowen & Karl 2007, Reich et al.

2007, Snover et al. 2010, López-Castro et al. 2014). Due to a lack of information on active dispersal capacity, modelling efforts heavily rely on classifying young turtles as “passive drifters”, with little influence on their movement and surroundings (Hays et al. 2010, Shillinger et al. 2012b, Gaspar et al. 2012, Putman & Mansfield 2015). Biophysical models can be strengthened and verified by incorporating behavioural data, such as swim speed and orientation (Putman et al. 2012a, 2013, Kobayashi et al. 2014, Briscoe et al. 2016), as both swim behaviour and ocean currents control young sea turtles’ directionality and influence dispersal outcomes (Gaspar et al. 2012, Putman & Mansfield 2015, Briscoe et al. 2016). Behavioural data can be collected by deploying instruments to track turtle movements (Putman et al. 2012a, Thums et al. 2013, Mansfield et al. 2014, Scott et al. 2014a).

Reduction or elimination of tag effects when examining sea turtle early life stages is of high importance in order to maximize field data integrity and minimize negative impacts on tagged individuals (Jones et al. 2013). Acoustic tags are lighter and smaller than satellite tags, but appropriate methods of attaching these tags to turtle hatchlings are still under development and lacking for many species (Hazen et al. 2012, Shillinger et al. 2012a). Small turtles experience a higher drag ratio compared to larger, more frequently tracked adult turtles, resulting in higher bioenergetic transport costs of attachments. Impacts on turtle movements and behaviour are often presumed to be negligible when below the colloquial 2-3% tag-to-body-weight threshold (e.g. Murphy et al. 1996, Vandenabeele et al. 2012). Hatchling sea turtles tagged with miniature acoustic tags generally meet this requirement (Thums et al. 2013, 2016, Scott et al. 2014a), but the influence of tag attachments on animal

behaviour should still be carefully considered prior to field studies on threatened and endangered species (Jepsen et al. 2005, Vandenabeele et al. 2012). An examination of movement metrics, such as speed and diving depth, should be undertaken prior to deploying transmitters on wild turtles to ensure that the tracking process is unlikely to decrease fitness or survival, whilst providing biologically representative information (Casper 2009, Mansfield et al. 2012, Jones et al. 2013).

A direct attachment method on the plastron has been developed for flatback, green, and loggerhead hatchlings (Thums et al. 2013, 2016, Scott et al. 2014a). However, we sought a design that would be suitable for leatherback turtles, which have a unique oily skin, and that would detach easily during recovery to ensure the tags were guaranteed to be recovered and removed from a critically endangered sea turtle population in field studies. The direct attachment method would also make it difficult to maintain visual contact with the small, dark bodies of hatchling turtles during mobile active tracking in the open ocean. The existing direct plastron attachment method utilized in other studies (Thums et al. 2013, 2016, Scott et al. 2014a) was therefore not suitable and an alternative attachment design required.

In this study, we examined methods for monitoring in-water movements of post-hatchling sea turtles and tested the assumption that attaching Vemco V5 acoustic tags would not affect post-hatchling movements. We sought an attachment design to allow for multiple means of observation to increase the likelihood of maintaining contact in field studies using mobile tracking and detach easily during recovery from these at-risk species. To evaluate potential effects, this study was undertaken with hatchery-reared post-hatchling stage green sea turtles in Grand Cayman serving as a

conservative proxy for leatherbacks. Due to a low drag coefficient combined with a small frontal area, young green sea turtles (*Chelonia mydas*) may encounter greater drag costs than other sea turtle species (Jones et al. 2013). The objectives of this study were to 1) develop a protocol for attaching miniature acoustic transmitters to hatchling sea turtles suitable for mobile tracking of hatchling leatherbacks in the open ocean and 2) quantify the effects of tag and attachment materials on young sea turtle swim speed and dive behaviour.

Methods

Tag attachment protocol

We conducted experiments with twelve 8-week-old hatchery-reared green sea turtles (*Chelonia mydas*) at the Cayman Turtle Farm on Grand Cayman in December 2014. The sample size ($n = 12$) reflects the number of post-hatchlings available from the hatchery at the time of the study. The turtles remained out of public view prior to experiments. The mean weight of the turtles was 59.9 g (range = 38.3 - 74.3 g), and the mean straight carapace length notch-to-tip was 73.5 mm (range = 64.0 - 78.5 mm). All weights were recorded in-air.

We tested two alternative methods for attaching Vemco V5-180 kHz acoustic transmitters (0.65 g) (Vemco Ltd, Halifax, Canada) to hatchling turtles. For both turtle attachment methods, tags were affixed to a tether in a similar arrangement to Gearheart et al. (2011). Attachments had braided monofilament line (1.75 m) suspending two painted floats (4.4 cm by 1.9 cm) behind the turtles (Fig. 2.1). The monofilament line was doubled onto itself to mimic the weight of an anticipated longer

fieldwork attachment due to restrictions encountered by the size of the tank. The acoustic tag was suspended 0.25 m from the second float, and the combined weight of the line, floats, and tag was 7.5 g. There were two attachment mechanisms tested in this experiment. The line-float-transmitter assembly was affixed to the turtles' carapace by one of two methods. For the Velcro® treatment, a 1 cm² Velcro® square (1.71 g) was directly bonded to the carapace with several drops of Vetbond™ (Jones et al. 2000, Salmon et al. 2004, Thums et al. 2013, Scott et al. 2014a) and linked to a sister piece of Velcro® on the line-float-transmitter assembly. Initial testing of Vetbond™ used for the Velcro® treatment was conducted with naturally deceased hatchlings to ensure the bonding agent would dissolve and separate from hatchlings. The Velcro® attachment could be removed easily with a slight pull within a few days, suggesting the attachment material would be shed easily under natural conditions. For the harness treatment, the line-float-transmitter assembly was linked to a harness (0.47 g) made from 3M™ Coban™, a self-sticking latex/spandex/polyethylene compound. The harness attachment consisted of the same braided monofilament line and float setup, slipped over the head, and wrapped around the widest part of the turtle (Fig. 2.2). Trials with the Velcro® treatment, harness treatment, and a control treatment with no attachment were conducted with each turtle in a randomized fashion.

We conducted trials to monitor for behavioural responses of turtles to each treatment in a 12.25 m² hexagonal tank filled with seawater to 0.6 m depth with a flow rate of 60 litres per minute (Fig. 2.3). A 25 cm by 25 cm grid was placed over the tank to track distance travelled by each turtle for speed calculations. Vertical distance was labelled by a pole with centimetre intervals in the middle of the tank. Every turtle

was observed individually for 25 minutes under each of three treatment scenarios: control, Velcro®, and harness. Turtles were randomly selected for each treatment and given a minimum period of two days between treatments over the two week study period. Movements were recorded using two GoPro HERO 4 cameras (GoPro, Inc., San Mateo, CA), one placed underwater near a corner of the tank and one hoisted 5.1 m centred overhead.

Our aim was to choose the least intrusive methods of attachment to address potential concerns for animal welfare. Initial testing of the bonding agent was completed on naturally deceased turtles to minimize handling of live turtles. To ensure the bonding agent would dissolve and separate from neonate turtles, we monitored the attachment point dissolution time. Attachments removed with a slight pull within a few days, suggesting a short duration in the absence of removal. There were no evident injuries from the Velcro® or harness attachments. Permission for all procedures was obtained prior to the experiment from the University of Maryland Center for Environmental Science's Institutional Animal Care and Use Committee (Research Protocol No. S-CBL-14-14). The research was conducted under approval of scientific study from the Cayman Islands' Department of Environment.

Horizontal movement analysis

Video was compiled with Adobe Creative Premiere Pro CC (Adobe Systems, Inc., San Jose, CA), and turtle movements were analysed using the Tracker Video Analysis and Modeling Tool program, an Open Source Physics Java framework (Brown 2014). Horizontal swim speed was calculated within the program as a function of movement in the x- and y-directions. Speed was estimated every second

and averaged at 10 second intervals for each 25 minute trial. This 10 second interval provided a fine-scale measure of the variability in speed without oversampling. Time was then split into 5 minute blocks, producing five time periods over each 25 minute trial to allow us to investigate changes in the response across a time scale more appropriate to field conditions. Analyses were run in the R statistical software environment (R Core Team 2016).

A within-subjects repeated measures ANOVA with a block on each post-hatchling was conducted to test differences in speed using the R package ‘nlme’ (Pinheiro et al. 2016). The response variable of speed was square-root transformed based on results of a Box-Cox transformation to meet model assumptions (package ‘MASS’) (Venables & Ripley 2002). Variation in turtles’ speed was investigated using explanatory categorical factors of treatment (control, harness, and Velcro®), time period (five minute blocks), and the interaction of these variables. The best error structure fit with restricted maximum likelihood was a lag 1 autoregressive structure combined with a nested random effects structure of random intercepts among treatments for individual turtles. The autoregressive process of order 1 error structure suggests there is a dependency in the errors between the current value and the previous value, adjusting for correlations among repeated measures. The appropriate fixed effects structure was determined to be the interaction of treatment with time using maximum likelihood. The final model was refit using restricted maximum likelihood. The appropriate ANOVA model was chosen by the Akaike information criterion at each step (*e.g.* “drop1” in R software). The Tukey’s honest significant

difference test from the package ‘multcomp’ was used in post-hoc analysis (Hothorn et al. 2008).

Vertical movement analysis

To determine if diving behaviour was affected by transmitter attachments, an underwater camera captured each turtle’s movement over time for each treatment. The camera was physically moved side to side as turtles moved throughout the tank to ensure all turtle movements were captured. A depth threshold of 15 cm was set to delineate time spent at the surface versus time spent diving. For these trials, this resulted in the surface classified as the upper quarter of the water column where swimming was underneath the air-water interface in contrast to definitive diving behaviour. Diving behaviour was measured this way because a true dive depth could not be measured within the available tank. Only a field experiment with a depth recorder could provide this level of estimation without potential tank interference. This classification was a compromise to generically categorize whether having an attachment altered vertical movements through the water column. Water column depth was estimated every second, and these counts of being at the surface or below were compiled every 10 seconds. This provided a proportion interval similar to the horizontal analysis. Time spent below 15 cm versus time spent at the surface could then be compared amongst treatments. In a similar manner to speed, data were separated into five minute blocks across the 25 minute recording time. A generalized linear mixed model with a binomial error distribution and logit link function was applied to the response variable of the proportion of time below 15 cm within each 10 second period (package ‘lme4’) (Bates et al. 2015). The categorical explanatory

variables were treatment, time in the form of five minute periods, and their interaction. Using Akaike information criterion, the best random effects structure was initially found to be a random intercept varying among turtles and among treatments for each turtle (Zuur et al. 2009). To account for model overdispersion, one random effect level for each observation (e.g. record number) was included in the model (Browne et al. 2005). The interaction of treatment and time was significant for the best fixed effects structure. Therefore, the final model was the interaction of treatment and time with 3 random effects: among turtles, among treatments for individuals, and an unstructured error. Model contrasts against the control treatment were completed for each time period to provide a post-hoc test for appropriate significance values across these levels and treatments of the linear model.

Results

Horizontal movement analysis

There was a statistically significant interaction between treatment and time on turtle speed (Table 2.1, Fig. 2.4A). Swim speed was not significantly different for the Velcro® treatment compared to the control for any time periods (Tukey's; $\alpha = 0.05$). Swim speed was significantly reduced with the harness attachment compared to the control during the middle 5-20 minutes of the trial, time-steps 2-4 (Tukey's; $p < 0.01$; $p = 0.026$; $p < 0.01$, respectively).

Vertical movement analysis

Turtles spent 36% of trial time below the surface 15 cm of the tank (Figs. 2.4B and 2.5). The generalized linear mixed model (GLMM) did not find significant

differences in the proportion of time at the surface amongst treatments at each of the five minute time periods ($\alpha = 0.05$; Table 2.2). There is no evidence to suggest diving behaviour was different between treatments.

Discussion

We tested miniature acoustic transmitter attachment protocols for efficient tagging of leatherback turtles, using green turtles as a proxy, to minimize impediment of swimming and diving of small sea turtles, while still providing a means of visual contact with diving turtles. Our study suggests outfitting young sea turtles with Vemco V5 acoustic tags will not significantly alter their swim speed or dive behaviour with a Velcro® attachment configuration to the carapace, at least in controlled lab conditions. The Velcro® attachment approach did not result in a significant change in the swim speed or dive behaviour of the turtles at any point during the trials. The Velcro® attachment was ultimately more suitable than the harness attachment, which significantly decreased swim speeds during the middle 15 minutes of the trial.

Our visual observations suggest that the harness disrupted turtle behaviour compared to the control, possibly from constriction of the shoulder girdle, thus reducing swimming speed. We observed that turtles with harness attachments initially spent time at the surface attempting to remove the harness, then conducted a series of rapid dives, whereas the control treatments generally had smooth transitions between the surface and depth separations within the water column. Irritation caused by the harness attachments make this approach less desirable for field experiments and could alter interpretations of past studies that utilized harness methodologies on young sea

turtles over short time frames. Based on our results, an experiment utilizing harness attachments should allow for an acclimation period of at least 20 minutes, while the Velcro® attachment method does not require acclimation. This study can help inform tagging procedures for field studies examining movement of free-ranging hatchling sea turtles.

There are limitations to studies such as this because gaining access to endangered species is difficult. The inability to access at-risk sea turtles resulted in a low sample size. Mansfield et al. (2012) utilized an ANOVA framework with smaller sample sizes on sea turtles, and our sample size is within the generally accepted size for this statistical test. While a larger sample size could theoretically increase statistical robustness, this was not feasible given available turtles at the time, and data corrections were applied to meet all model assumptions. Speed is highly variable and individualistic, inconsequential of sample size. Therefore, the sample size may be low, but a larger sample size would not guarantee more power in the statistical tests given the high variability inherent in the measured parameter.

Our approach of using a line-float-transmitter attachment was chosen over a direct tag attachment to the plastron at the cost of increased drag because it allows for visual tracking in the water during mobile tracking and should prevent signal dampening or distortion during future field experiments (Thums et al. 2013). This will also help field studies better interpret sources of signal loss at a given location, from occurrences such as predation, tag malfunction, wave interference, or departure from the study site (Thums et al. 2013). Mobile acoustic tracking is very difficult when trying to obtain fine-scale movements through an area. Visual contact with the

tracked organism provides the means of fully tracking an organism during a given time period. Although the tag to body weight ratio increases with the Velcro® attachment, there were no significant differences from the control in the metrics we measured. Overall, both attachments allow for a safe, full removal from actively tracked turtles, reducing experimental exposure time for wild turtles.

Organisms are adapted to live in particular environments; thus, any object placed on an organism may affect its natural behaviours and increase its energetic costs. Consequently, an objective of this methodology was to provide appropriate consideration to the development of tag attachments for leatherback turtles that minimize these negative effects and extend beyond controlled tank environments (Mansfield et al. 2012, Jones et al. 2013). Given the oily, rubbery skin of leatherbacks, which could reduce adherence, we wanted multiple modes of attachment in field trials. A vertically attached tag to the plastron, as used by Thums et al. (2016), would not allow for maintained visual contact with deep-diving leatherback hatchlings, and it would only provide a very small attachment site on oily skin that has the potential to react differently to Vetbond™. Therefore, methods that would allow for both visual and acoustic contact to be maintained were considered most effective for actively tracking critically endangered leatherback turtles.

Although there was no significant difference between the control and harness for the proportion of time spent below the surface, this may have resulted from individuals generally spending greater amounts of time at the surface during the control because behavioural reactions to the attachment generally occurred within the surface layer. Any tag attached to an organism should theoretically increase drag, and

it is possible the turtles increased power output (e.g. swam harder) to overcome this additional drag, something a longer temporal study might determine (Jones et al. 2013). Limitations in both vertical and horizontal movements may have resulted from the experimental tank design. However, visual observation indicated the turtles moved vertically throughout the tank in a similar manner across all treatments, which was supported by the results of the GLMM. Edge effects of the tank could alter turtle behaviour through more frequent changes in direction or by seeking shelter, for example, and the depth of the tank may have changed diving patterns. Although the tank was shallower than the length of the attachment, time spent at depth was usually sustained swimming around the circumference of the tank. Therefore, it adequately provides information on whether the attachment changed their vertical movements.

We did not provide direct estimates of swimming speed as we recognize that the tank will potentially limit the speed capacity of the turtles, and it would be an inappropriate comparison to other studies of this species. The repeated measures ANOVA appropriately examined changes in speed within individuals, which was the goal of the analysis. Given these turtles generally swam in continuous circles during the study period, we believe any changes in drag which turtles experienced as they moved throughout the tank (e.g. if the line went slack upon changing course) was properly accounted for in our models. A few turtles became entangled in the gear, and untangled themselves. This was an artefact of multiple factors: the size and shape of the tank, as well as the age and behaviour of the turtles. In the open ocean, for which this method was developed, this is not an anticipated concern if turtles are in a frenzied state where swimming will be directed and continuous (Wyneken & Salmon

1992). Further, the short duration and controlled design did not consider wind drift effects, which have the potential to impact movement during longer studies utilizing these methods (Jones et al. 2013).

Sea turtle early life histories are poorly understood, and lack of knowledge regarding movements and developmental habitat may impede conservation efforts. Advancement of appropriate management strategies requires an understanding of movement and dispersal beyond the adult stage. The 'lost years' paradigm begins upon natal dispersal of hatchlings in a neritic-to-oceanic migration to unknown or unclearly defined nursery habitats. Combining miniaturized electronic tag technology and physical modelling efforts enables much-needed characterization of movement, habitat utilization, behaviour, and life strategies of young sea turtles throughout these cryptic years (Briscoe et al. 2016). As habitats are drastically changed by anthropogenic forces, migrations of many species may be shorter or migratory routes may shift from recorded patterns (Brower & Malcolm 1991, Wilcove & Wikelski 2008). Understanding the mechanisms underlying these movements will improve our ability to describe sea turtle environmental utilization, predict population dynamics, and manage species internationally under changing conditions (Nathan et al. 2008, Bauer et al. 2009). The challenge thus remains to decipher movements among ontogenetic habitats within and across species and understand how to manage these highly migratory species throughout multiple life stages.

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Tables

Table 2.1. Repeated measures ANOVA results examining square-root transformed speed (cm s^{-1}) as a function of the interaction of treatment and time as five minute periods. numDF represents the degrees of freedom of the numerator for the F statistic, and denDF is the degrees of freedom of the denominator. Statistical significance is denoted by an asterisk at $p < 0.05$.

| Factors | numDF | denDF | F-value | p-value |
|----------------|-------|-------|---------|---------|
| Intercept | 1 | 4727 | 512.416 | <0.001* |
| Treatment | 2 | 22 | 9.440 | 0.001* |
| Time | 4 | 4727 | 3.185 | 0.013* |
| Treatment:Time | 8 | 4727 | 5.949 | <0.001* |

Table 2.2. The generalized linear mixed model with a binomial error and logit link function results for the proportion of time spent below 15 cm in relation to the interaction of treatment and time. Model contrasts were completed at each five minute period. The estimate, standard error, and p-value are reported. Minutes comprising each period in the stepwise comparison are 1 = (0-5 min), 2 = (5-10 min), 3 = (10-15 min), 4 = (15-20 min), 5 = (20-25 min). Statistical significance is denoted by an asterisk at $p < 0.05$.

| Factors | Estimate; SE; p-value | | |
|--------------------|-----------------------|--------------------|-------------------|
| | Intercept | Velcro® | Harness |
| Time 1 (0-5 min) | -1.82; 1.06; 0.085 | 0.63; 1.07; 0.56 | -0.71; 1.08; 0.51 |
| Time 2 (5-10 min) | -2.57; 1.06; 0.015* | 0.41; 1.08; 0.71 | -0.82; 1.08; 0.45 |
| Time 3 (10-15 min) | -2.38; 1.06; 0.025* | 0.20; 1.08; 0.86 | -0.15; 1.08; 0.89 |
| Time 4 (15-20 min) | -2.46; 1.07; 0.17 | -1.95; 1.08; 0.072 | -2.10; 1.09; 0.31 |
| Time 5 (20-25 min) | -1.97; 1.06; 0.064 | -1.01; 1.09; 0.35 | -0.73; 1.09; 0.50 |

note: the control treatment is the reference level.

Figures

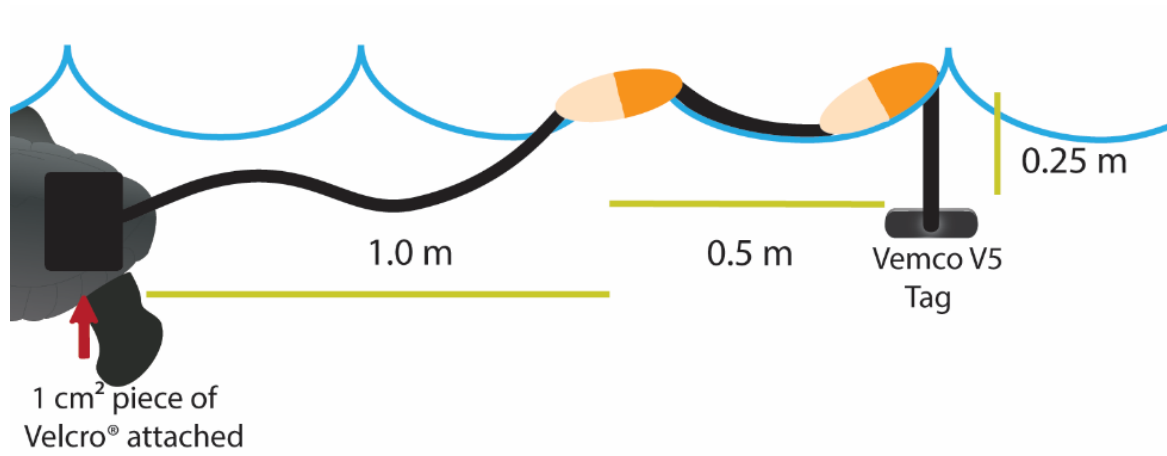


Figure 2.1. Acoustic transmitter Velcro® attachment method modified from Gearheart et al. (2011). Symbols are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).



Figure 2.2. Images of the harness design and application on *Chelonia mydas* hatchlings. Footage from an underwater GoPro camera.



Figure 2.3. Scale of the tank experiment at the Cayman Turtle Farm. The GoPro camera hoisted 5.1 m above the hexagonal tank filmed each turtle for 25 minutes per treatment. Each square is 25 cm by 25 cm to serve as a distance reference.

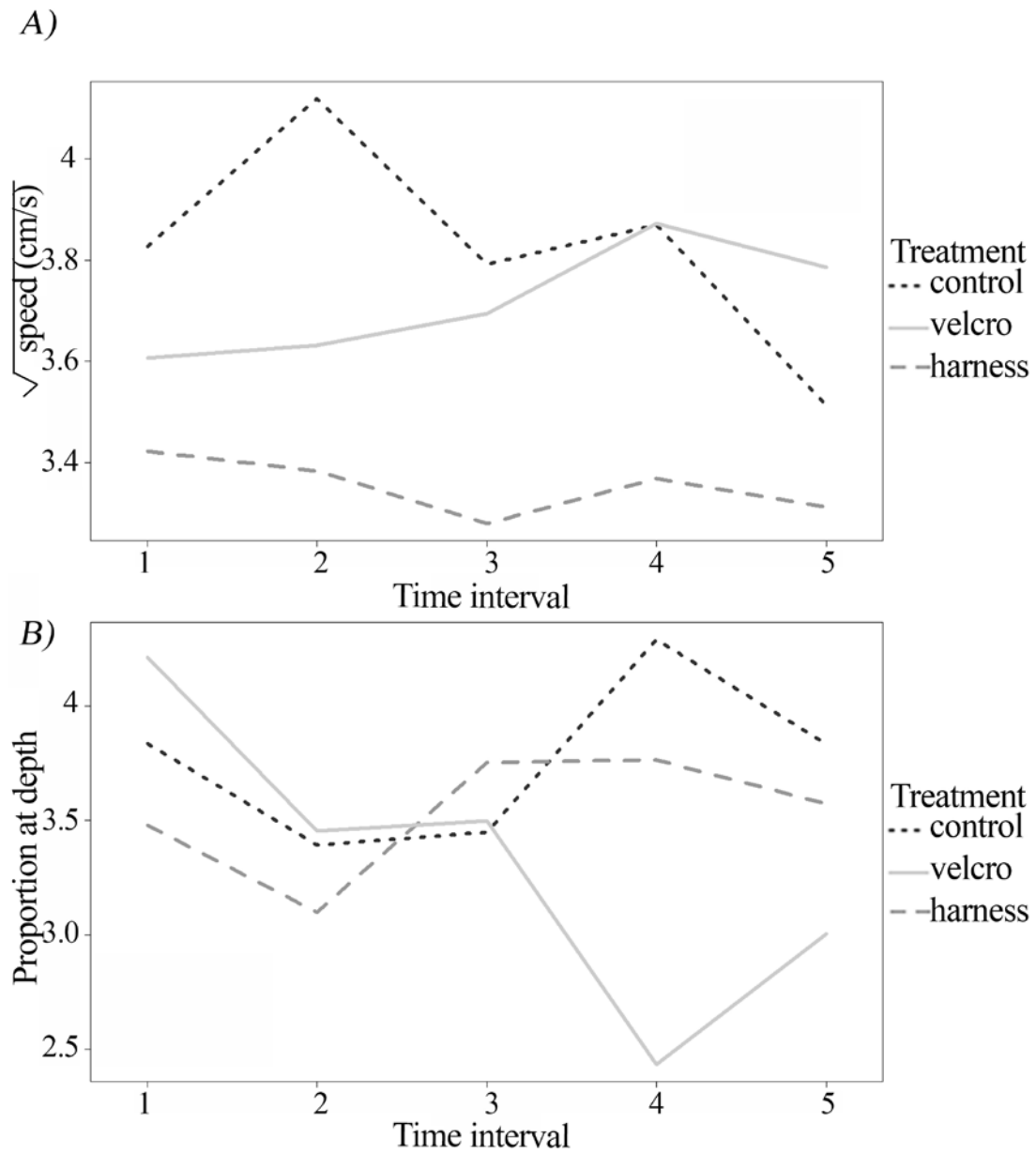


Figure 2.4. A) Interaction plot of the square-root transformed speed (cm s^{-1}) as a function of time for each treatment. B) Interaction plot of the proportion of time spent below 15 cm as a function of time for each treatment. Minutes comprising the time periods are 1 = (0-5 min), 2 = (5-10 min), 3 = (10-15 min), 4 = (15-20 min), 5 = (20-25 min).

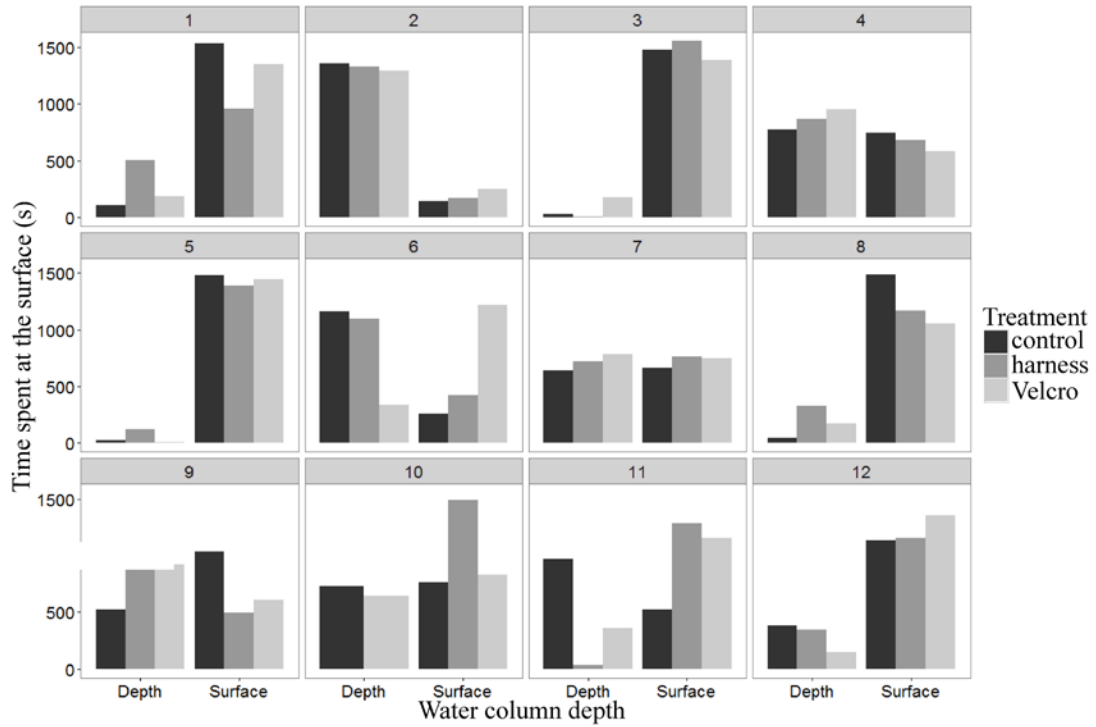


Figure 2.5. Barplots of time spent below 15 cm (“Depth”) and at the surface (“Surface”) by subject and treatment over the study period. Water column depth was measured every second over the 25 minute study period. Each subject is indicated by the number in the grey box.

Chapter 3: Neonate dispersal of Atlantic Leatherback turtles (*Dermochelys coriacea*) from a non-recovering subpopulation

Introduction

Highly migratory marine species have complex conservation needs and pose management challenges (Hays & Scott 2013, Lascelles et al. 2014). The large area of the ocean, dynamic ocean conditions, and observational challenges of this three-dimensional environment result in the unknown spatiotemporal distributions of many species (Cooke et al. 2004), including sea turtles that undergo long distance oceanic migrations (Hamann et al. 2010, Hazen et al. 2012, Shillinger et al. 2012a).

Management is complicated by their little known ‘lost years’, the time after which hatchlings depart from the nesting beaches, develop in undetermined habitats, and eventually return at maturation to breed (Carr 1986, Bolten 2003a, Shillinger et al. 2012a). Adult leatherback turtles (*Dermochelys coriacea*) have the widest reptilian distribution (Goff & Lien 1988, Hays et al. 2004, Benson et al. 2007b, 2011) but have largely unknown movements and nursery habitats during young life stages (Bowen & Karl 2007).

Leatherbacks are the largest and oldest lineage of the marine turtles, and some populations have experienced dramatic declines in the last decades (Troëng et al. 2007, Tiwari et al. 2013). These substantial losses are often attributed to fisheries bycatch, pollution, climate change, nesting beach degradation, and poaching of eggs and adults (Sarti et al. 1996, Sarti Martínez et al. 2007, Santidrián Tomillo et al. 2008). To prevent extirpation of declining populations and ensure the future of stable

populations, modelling efforts on the dispersal and habitat utilization throughout life stages aim to increase understanding of population distributions. These biophysical models are based on the historical premise of denatant dispersal, where the young of species passively drift with winds and currents from hatching to nursery areas (Jeffers 1939, Harden Jones 1968) and regularly do not include behavioural information, such as orientation and speed of hatchling turtles (Shillinger et al. 2012b, Scott et al. 2014a, Thums et al. 2016). However, both swimming and currents influence the ultimate dispersal outcome of hatchlings (Putman et al. 2012a, 2013, Gaspar et al. 2012, Putman & Mansfield 2015, Briscoe et al. 2016), and research has recently taken place to understand the active movements of sea turtles during the ‘lost years’ period (e.g. Mansfield et al. 2014, Briscoe et al. 2016, Christiansen et al. 2016).

It is becoming apparent that dispersal outcomes for hatchlings can be greatly influenced by even slight active movement in strong currents, and these outcomes influence population dynamics (Putman et al. 2012a, 2012b, Scott et al. 2012b, 2014b). While the surface current plays a role in the dispersal of hatchlings, their speed and direction will give greater insight into predictive model parameters (Shillinger et al. 2012b, Scott et al. 2014a, Putman & Mansfield 2015). Knowledge gaps on this role of active movement still persist, especially for leatherback turtles during their most vulnerable hatchling stage (Hazen et al. 2012).

Dispersal during the hatchling frenzy period, a period of continuous swimming (Deraniyagala 1930), must be efficient and directed to prevent predation and entrainment in coastal waters (Wyneken & Salmon 1992, Okuyama et al. 2009), and dispersal outcomes can be influenced by minor alterations of position within

moving water masses (Putman et al. 2012a, Scott et al. 2012b, Christiansen et al. 2016). Hatchlings' active movements can change the distance and direction ultimately travelled to developmental habitats (Hein et al. 2012, Scott et al. 2014a, Christiansen et al. 2016). The inherent small size of hatchling turtles increases the difficulty of obtaining long-term observations because technology commonly deployed in movement studies, such as satellite tags, are still too large for these small individuals to carry. Therefore, direct field observations and short-term experiments remain the best method for attaining these data.

In this chapter, I focus on the distinct leatherback turtle population of the Northwest Atlantic, which is classified as endangered on the U.S. Endangered Species Act and of least concern on the IUCN Red List (Tiwari et al. 2013). The Costa Rican rookery of this population has not experienced the recovery documented in other nesting locations (Troëng et al. 2007), and disproportionately high fisheries bycatch in the Gulf of Mexico may be one source of this downward trend (Stewart et al. 2016). This chapter assesses hatchling dispersal of the nesting population of leatherback turtles at Pacuare Reserve, Costa Rica using active acoustic tracking to determine their transport from the natal beach. I undertook field experiments to obtain *in-situ* observations of individual hatchling Atlantic leatherback movements using acoustic tracking to improve our knowledge of their behaviour and dispersal. Acoustic telemetry has been successfully employed to track other hatchling sea turtle species (Thums et al. 2013, 2016, Scott et al. 2014a), but only short trials have been attempted on leatherback turtles (Gearheart et al. 2011).

The goal of this chapter is to characterize the directionality of leatherback hatchling movements leaving Costa Rica to test the hypothesis that hatchlings passively drift in the ocean currents. The specific objectives were to 1) test whether the attachment protocol and acoustic tracking methods could be used for tracking hatchling leatherbacks at sea, 2) acoustically track individual hatchling leatherbacks for insight into initial movements after natal beach departure, a novel approach for leatherbacks, and 3) deploy drifters throughout the study to provide a short-term understanding of local oceanic conditions encountered by this nesting population and how it influences the dispersal of leatherback turtle hatchlings.

Methods

Fieldwork

Hatchling tracking

To examine *in-situ* factors of turtle dispersal into the offshore environment, I tagged hatchlings with coded acoustic transmitters after emergence. The first part of this research was undertaken at Playa Cabuyal in Guanacaste, Costa Rica, in March 2016 to test the attachment and tracking method in the field (Fig. 3.1). Turtles were taken from the nesting beach following a morning emergence. Attachments were joined to the carapace with Vetbond™. The Vemco V5-180kHz transmitter was tethered to the turtle via line and Vetbond™ in a similar method to Gearheart et al. (2011) (Fig. 3.2) and based on the results of Chapter 2 (Fig. 2.1). The line was sewn to a 1 cm² piece of Velcro® with its sister piece bonded to the carapace (Jones et al. 2000). This small attachment area reduced the likelihood of damage or interference

on the swimming hatchling. The brightly coloured floats allowed for visual tracking in the water (Fig. 3.3). Tracking was completed using a portable acoustic receiver and directional hydrophone. Each turtle was followed at a distance of 10 - 20 meters in a small boat using a Vemco VR100 acoustic receiver and VH180-D-10M directional hydrophone (Thums et al. 2013). The VR100 detected the signal emitted by the V5 tag, and the directional hydrophone was used to determine the direction of the turtle for tracking. The V5 tag detections extended to approximately 200 m. The VR100 receiver stored the detections, and the data were downloaded to reconstruct hatchling movement paths. The mobile acoustic receiver allowed tracking of the turtles' movements for a longer period and over a broader area than visual tracking alone because there is a limited ability to visually track hatchlings in open waters. Hatchlings were tracked only during daylight hours. Although hatchlings generally emerge during cooler, evening hours of the day in Costa Rica, no effect on movement is anticipated (Frick 1976, Okuyama et al. 2009). Turtles were tracked for approximately 90 minutes, with a minimal track length of 30 minutes required for inclusion in my analyses.

The second portion of fieldwork was undertaken in August and September 2016 in Pacuare Nature Reserve, Limón Province, Costa Rica. This area has a much larger number of nesting females ($n > 200$ nesting leatherbacks per season) on the Caribbean coast of Costa Rica. Hatchlings were obtained from hatchery-reared ($n = 22$), incubator-reared ($n = 15$), or relocated ($n = 6$) nests, for a total of ($n = 43$). The hatchery nests were reburied in protected areas along the nesting beach to secure and monitor the nests. Incubator-reared turtles were raised under experimental protocol of

doctoral student Sean Williamson, and his methods can be obtained from Monash University's Protocol No. BSCI/2016/13. Turtles held overnight post-emergence were kept in moistened, sand-lined incubators at approximately 30°C to reduce energy expenditure prior to trial release and prevent potential decreases in swimming performance (Pilcher & Enderby 2001). To minimize the influence of genetic relatedness, hatchlings were taken from all available nests ($n = 9$) at the time of the study. Turtles were weighed and measured prior to trials. To prevent overheating on the boat, turtles were transported in a bucket covered by a wet towel with a moistened cloth inside.

Turtles were tracked in the same manner as in Guanacaste, Costa Rica. Tracking began outside the surf zone along the nesting beach, approximately 0.4 km from shore. The experimental release location was the designated midpoint of the two hatcheries where hatchlings were collected. Turtles were tracked individually from a small boat. Tracking occurred during daylight hours over the course of 3 weeks given hatchling and boat availability. Track duration was a trade-off between obtaining a large sample of tracks to account for individual variability, while providing robust speed and orientation information. Turtles were tracked for approximately 90 minutes, but some hatchlings were tracked for 120 minutes when time and conditions permitted longer tracks. Compass headings were taken for each hatchling using both a compass and a phone application. Deviation from true heading cannot be determined for this experiment, and differences should be insignificant as the boat was fibreglass. Hatchlings were expected to be within their frenzy state during this study. This frenzy state is a period of continuous, active swimming that results in a rapid retreat away

from nearshore waters (Deraniyagala 1930, Carr 1962). Given the different developmental conditions encountered by turtles reared in incubators, this could not be conclusively determined. At the end of each track, the turtle was recovered, the attachment was completely removed, and the turtle was released at the recovery location. The Velcro® piece easily removed from the carapace, and there were no evident damages, marks, or lesions from this attachment method on the leatherback hatchlings.

Handling was kept to a minimum to reduce any unnecessary stress on the turtles. All procedures for fieldwork in Pacuare Nature Reserve followed approved protocol under Monash University's School of Biological Sciences Animal Ethics Committee (Protocol No. BSCI/2016/13), the University of Maryland Center for Environmental Sciences' Institutional Animal Care and Use Committee (IACUC) (Research Protocol No. S-CBL-16-11), and the Costa Rican Ministerio Del Ambiente y Energia, Sistema Nacional de Áreas de Conservación (SINAC), Área de Conservación La Amistad Caribe (ACLAC) (RESOLUCIÓN SINAC-ACLAC-PIME-VS-R-022-2016; RESOLUCIÓN SINAC-ACLAC-PIME-VS-R-025-2016). Permission for the procedures for the fieldwork in Guanacaste, Costa Rica was also provided by UMCES IACUC (Research Protocol No. S-CBL-16-01) and SINAC, ACLAC (RESOLUCIÓN SINAC-ACT-OR-DR-015-16).

Surface current trajectories

Two drifters were used during the study at Pacuare Nature Reserve to obtain data on sea surface currents. By estimating the surface currents, a better understanding of actual hatchling behaviour and trajectory can be estimated (Putman

et al. 2016). A Pacific Gyre Microstar™ drifter was deployed at the beginning of the turtle tracking (Fig. 3.4A). The drifter's surface float was equipped with a GPS unit that used the iridium short burst data service to broadcast location coordinates every five minutes. A flag was attached to the surface float for increased visibility. To provide estimates of surface flow, the drifter's drogue was composed of a radar reflector with its centre at a depth of 1 m in the water column. Sea surface temperature was also recorded by the drifter with a Pacific Gyre probe of 0.1°C accuracy. The position and temperature data of each drifter release were retrieved from the Pacific Gyre website (www.pacificgyre.com). One of these drifter tracks was removed from analysis because it entered the surf zone and did not represent nearshore surface currents.

A second drifter was launched when feasible at the approximate halfway point during tracking of a turtle. This was done to estimate shifts in the nearshore currents as the turtles headed offshore compared to the initial hatchling and Microstar™ drifter release site. The Microstar™ drifter launched at the start of each track and each turtle's path seemingly diverged quickly near the beginning of the study, and this secondary drifter was a means of obtaining current information closer to the hatchling. If the starting surface flow was different than the flow near the end of the 90 minute tracking period, this midpoint release was a compromise to obtain a mean estimate given available equipment. This second drifter was constructed using a Davis Instruments aluminium radar reflector with 80 cm of parachute cord attached to a 20.3 cm diameter Panther Plast trawl float (Fig. 3.4B). The centre of the drogue sat 1 m from the water's surface, similar to the Microstar™ drifter. A piece of wood

affixed to the top of the float had a Samsung Galaxy Core Prime mobile phone attached in a waterproof bag. A GPS application was started with each drifter release to provide locations. This did not require an internet connection, making it an inexpensive, practicable drifter option as currents moved it offshore, away from cellular networks. Foam tubing zip-tied around the middle of the trawl float prevented the float from flipping and submerging the GPS unit. The float also had a flag attached for visibility on the water. Positions were stored on the phone and downloaded upon retrieval of the drifter. Both drifters were recovered at the completion of every trial.

Analyses

Intervals greater than 5 minutes between recorded hatchling positions were removed to prevent erroneous calculations, 0.03% of recorded positions. These time lapses occurred when the boat actively searched for lost turtles, and the GPS location obtained after relocating a turtle may not accurately reflect its position relative to the previously recorded location due to a major repositioning of the boat. Maintaining visual and acoustic contact with turtles was difficult even in calm waters with the combination of surface floats and the directional hydrophone. Distances resulting in speeds greater than 0.75 m/s (0.02% of positions) were removed as spurious positions because they were extreme outliers and inconsistent with adjacent values. These values were greater than all but the largest recorded hatchling sea turtle speeds (Ireland et al. 1978, Salmon & Wyneken 1987, Wyneken 1997, Thums et al. 2016). To correct for boat movement as it changed position relative to the hatchling in order to maintain a 10 - 20 m distance, mean latitude and longitude values were calculated

for 5-minute time periods. This provided a regularized track representative of hatchling movement throughout the study period from which distances and speeds were calculated. Drifter distances were calculated using the GPS locations from the Microstar™ surface float GPS and the mobile phone GPS. The phone GPS was averaged into 5 minute intervals to match both the averaged hatchling locations and the GPS output of the Microstar™ GPS. After converting these distances to speed, seven values exceeding 1.0 m/s were removed as it represented the majority of the outliers. The ‘argosfilter’ package in the R statistical software was used in all distance and bearing calculations (Freitas 2012). Over-ground speed of hatchlings was calculated based on the total distance over the recorded time period of each hatchling trial. This over-ground speed is the apparent speed of the turtle moving through the water, which includes the turtle’s movements and the drift of the surface water. The speed of the drifter was calculated in the same manner.

To obtain a value for the true swimming speed component of a hatchling turtle, the surface water flow in which they are swimming must be removed from the measured speed of the turtle (Gaspar et al. 2006). In-water swimming speed accounts for the velocity of the current in which the turtle is swimming and estimates the turtle’s true speed (Fossette et al. 2010). This is the difference of the over-ground velocity and the velocity of the surface currents, estimated by the drifters. Over-ground speed of hatchlings and drifters was broken into velocity components using equations similar to that in Bailey et al. (2010), which accounted for each turtle’s speed and bearing to obtain east-west (u) and north-south (v) components. The nearest five-minute intervals of each hatchling were matched with the corresponding

drifter released. Some hatchlings did not have drifters deployed with them due to equipment issues. For turtles with two drifters launched during the trial, one in the beginning and one in the middle, the second drifter data were used once the record started because this provided surface current values closer to that directly experienced by the hatchlings at each given time period. The drifter's u and v -velocity components were differenced from each hatchling's corresponding over-ground speed components. The in-water speed of the hatchlings was then defined as the square-root of the summed squared u - and squared v -components of speed. All analyses were done in the R environment (R Core Team 2016).

Results

In the first part of the study at Playa Cabuyal, I was only able to track two hatchling olive ridley turtles because egg development and hatching success of sea turtles were extremely poor due to high temperatures associated with strong El Niño conditions, and no leatherback turtle hatchlings were available for the project (Figs. 3.3 and 3.5) (Saba et al. 2007, 2008b, Santidrián Tomillo et al. 2012). Olive ridleys are much smaller than leatherback hatchlings and may be a third of the size (Jones et al. 2007). However, the olive ridley hatchlings successfully carried the tracking attachment, even given their small body size. They travelled 0.84 km over 105 min and 0.39 km over 75 min, producing over-ground swimming speeds of 0.13 m/s and 0.09 m/s, respectively (mean = 0.11 m/s; Fig. 3.5). The mean bearings for each turtle were $29.62^\circ (\pm 22.02 \text{ SD})$, a northeast trajectory and $240.98^\circ (\pm 39.42 \text{ SD})$, an approximately southwest trajectory, respectively. The second turtle was released after south-southwesterly winds increased within the bay. While the turtle oriented

northward along the shoreline, it was unable to overcome the current as seen in its movement path (Fig. 3.5).

In the second part of the study at the Pacuare Nature Reserve, the mean weight of the leatherback turtles tagged was 42.5 g (± 3.5 g SD) with a mean standard carapace width of 41.8 mm (± 1.6 mm SD), mean standard carapace length of 60.4 mm (± 3.6 mm SD), and 17.8 mm (± 0.6 mm SD) head width. I had an approximately 98% success rate for my tracking study, with only one track out of 43 interrupted within the starting 30 minute window set for inclusion in the analysis. The tag attachment always remained behind swimming hatchlings. Tracking required both a combination of visual and acoustic, as it was difficult to pinpoint the exact location solely using the directional hydrophone given the wide swath created by a 200 m detection radius and reflections from the boat hull. The hydrophone provided a reduced search area, but it was not suitable alone as a comprehensive tracking mechanism. Periodically, spotting of a lost turtle would occur via the head surfacing, but in the great majority of instances, visual recovery relied on the trailing painted floats. The floats were particularly necessary on rougher days (Beaufort sea state 4 or higher) when it was difficult to maintain the boat position relative to hatchling movement, although the low platform height in the small boat also made visual tracking challenging.

Predation was of high concern given previous hatchling studies (Thums et al. 2013, Scott et al. 2014a). However, only one hatchling was predated by a tarpon at 85 minutes. The attachment on this predated turtle was rejected by the tarpon and recovered. Another turtle was attacked by a frigate bird prior to reaching the 30

minute minimum track length, excluding it from all analyses. The turtle was recovered, the attachment was removed, and it was released without apparent injuries. A total of 42 turtle tracks were obtained during this trial, with only 3 of these tracks under 90 minutes (minimum: 80 min).

Overall, hatchlings were actively tracked for a mean of 94 minutes. An average hatchling compass heading of 45.8° was recorded, a north-east trajectory. Distances travelled were 0.75 - 3.85 km for hatchlings, 0.11 - 2.76 km for the MicrostarTM drifter, and 0.40 - 2.01 km for the mobile phone drifter (Table 3.1). Mean over-ground swimming speed of hatchlings was 0.39 m/s (± 0.14 m/s SD) (Fig. 3.6). This is equivalent to approximately 6.46 body lengths per second. The mean hatchling bearing was 108.17° ($\pm 18.95^\circ$ SD) (Fig. 3.7A). Mean current speeds were determined from the drifters and used to compare hatchling movements from tracks during the lowest, middle, and highest flow periods from the study. The mean current speed was 0.114 m/s during the low flow period, 0.275 m/s during the medium flow period, and 0.469 m/s during the high flow period (Table 3.2). The u and v components of over-ground swimming speed and in-water swimming speed were calculated for these low, medium, and high surface current flow periods, as determined by the speed and distance travelled by the drifters (Table 3.2). Percent differences for in-water swimming speed of 131% and 147% in the u and v components, respectively, were found when comparing the high and low surface current days.

The Pacific Gyre MicrostarTM drifter was deployed at the beginning of tracking 31 of the turtles. The mean MicrostarTM drifter bearing was 147.16° (\pm

39.05° SD) with an average speed of 0.27 m/s (± 0.17 m/s SD), and the mean phone drifter bearing of 152.91° ($\pm 16.58^\circ$ SD) with a mean speed of 0.33 m/s (± 0.21 m/s SD) (Table 3.1; Fig. 3.7B). Over-ground swimming speed for the subsample of turtles ($n = 31$) that had drifters deployed during their trials was similarly 0.39 m/s (± 0.15 m/s SD) (Fig. 3.8). The mean in-water swimming speed of these leatherback hatchlings was 0.48 m/s (± 0.20 m/s SD). The mean water temperature recorded from the Microstar™ drifter was 29.8°C ($\pm 0.8^\circ\text{C}$ SD).

Discussion

Estimates of leatherback hatchling speed are rare, making estimating the active component of turtle swimming in biophysical models difficult. This study allowed us to assess the effectiveness of the mobile acoustic tracking technique on hatchling leatherback turtles, as well as provide speed estimates that will serve as a foundation for other models. Our mean measured over-ground swimming speed and estimated in-water speed of leatherbacks were higher compared to the previous estimate of 0.91 km/h (0.25 m/s) (Wyneken 1997). The observed mean over-ground swimming speed was 0.39 m/s, whereas the mean in-water swimming speed was 0.48 m/s. The faster in-water speed suggests the hatchlings were actively swimming against the currents in the nearshore zone, although their overall movements were strongly influenced by the currents.

This active swimming will be more energetically costly to the hatchlings than passive drifting. The hatchlings ultimately had insufficient in-water swimming speed to move in their north-easterly compass heading and fully overcome advection by the nearshore currents. This swimming to overcome stronger currents could have

implications for the distance from shore while within the frenzy state and the amount of time hatchlings can swim on their yolk reserves, the critical energy source for initial dispersal, before obtaining an external energy source (Jones et al. 2007). The amount of energy required to avoid entrapment in strong nearshore currents could have implications on reaching productive offshore eddies. Hatchlings in high currents had higher in-water swimming speeds and greater differences between over-ground and in-water speeds than hatchlings in lower currents, suggesting hatchlings in high-flow surface waters were swimming harder and exerting more energy (Table 3.2).

In previous studies, a small sample of unharnessed loggerhead hatchlings were recorded at 1.1 - 1.4 km/h (0.31 - 0.39 m/s) (Salmon & Wyneken 1987), and green turtle hatchlings were recorded at 0.8 - 3.2 km/h (0.22 - 0.88 m/s) (Ireland et al. 1978). The mean mass of the leatherback hatchlings (42.5 g) was within the higher range recorded in prior studies of Atlantic and Pacific hatchlings (Jones et al. 2000, 2007). This increased size could potentially result in greater speed during the frenzy period as size may influence the locomotive capabilities of turtles (Sim et al. 2015), although this is confounded by many factors with smaller animals swimming faster in some trials (Burgess et al. 2006). As reptiles, water temperature will affect the body temperature of hatchlings turtles, which also plays a role in their movement performance (Booth & Evans 2011). The mean recorded water temperature was within a relatively small range ($29.8 \pm 0.8^{\circ}\text{C}$) and should not have affected hatchlings differentially. However, factors I did not measure, such as incubation temperature, can also influence swimming capabilities (e.g. Burgess et al. 2006).

The stronger the nearshore currents, as indicated by the distance and speed the drifters travelled and the strength of the u - and v - components, the greater the surface water influenced hatchling movement, such as during tracking on August 25th and September 2nd (high surface current flow; 0.506 m/s and 0.469 m/s, respectively) (Table 3.2; Fig. 3.8). The hatchlings generally moved the farthest when the nearshore current was strong, but they moved in a more southerly direction due to its influence. When the current was weaker, the turtles moved more easterly and farther offshore, and travelled a greater distance compared to the drifters. During tracking in slower currents, the components of over-ground swimming speed and in-water swimming speed were similar. As the currents increased, changes in the components between the two swimming speeds increased. This suggests that the hatchlings could detect the currents and/or that they were being advected and would swim more vigorously to compensate.

The active movement of the hatchlings can have an important role in their dispersal patterns (Fig. 3.8). Over large distances, small changes in directionality influenced by the strength of the currents could have large influences on the ultimate destination of the hatchlings. The strength of the currents will be affected by the tidal cycle and lunar cycle. As in Putman et al.'s (2016) models, release of young turtles only a day apart could have major impacts on the environment encountered and dispersal of individuals. Hatchlings emerging on different days and different times of the day could result in different dispersal outcomes and final developmental habitat if suitable areas are reached. Under normal swimming conditions, leatherback hatchlings have sufficient yolk reserves to sustain continuous swimming for nearly

three weeks before foraging is necessary (Jones et al. 2007). Therefore, while actively swimming and orienting themselves to prevent nearshore entrainment, timing of departure from the natal beach could be a critical determinant of hatchling dispersal outcomes and entrance into optimal developmental habitat.

Hatchlings were able to dive deeper than 1.5 meters and pulled the attached floats underwater. Some turtles dove well below 2 meters throughout the trial, and a longer attachment would be suggested to allow full dives to occur. However, while young leatherbacks have the capability of diving deeply (Salmon et al. 2004), there is a trade-off in increased drag and difficulty in personnel handling the excess line compared to the advantage of decreased inhibition on diving and forward underwater movement. Given younger leatherback hatchlings have been observed making few U-dives compared to larger, older conspecifics that are foraging for prey, it seems unlikely a short tether greatly reduced their forward progress during dives (Salmon et al. 2004).

Some hatchlings did not dive and steadily surface swam with a persistent heading, consistent with previous observations of hatchlings (Salmon et al. 2004). Therefore, we observed behaviour seen in previous studies, where individuals exhibit different swimming strategies regardless of the presence of the attachment. Compass headings taken during the trials suggested nearly all turtles targeted a north-easterly offshore retreat from the nesting beach. When they veered from this north-eastward trajectory after surfacing from a dive, they redirected themselves. Overall, the tracking method performed effectively for leatherback hatchlings, and attachment removal was easy, immediate, and non-damaging.

Fine-scale, nearshore current data is difficult to obtain from satellites. Therefore, I utilized drifters during this experiment to account for the influence of currents on hatchling movement. The drifters generally moved south-southeasterly, suggesting a dominant along-shore current. Further work would benefit from more detailed measurements of the coastal currents, for example, using an acoustic Doppler current profiler to provide current flow data within the precise area of the hatchlings. While the mobile phone drifter did not have a temperature sensor or live GPS feed, additional components could be easily and inexpensively added. The overall cost was very low (~\$120), and I did not observe any difference in movement between the two drifters.

The small size and lack of defences of hatchling sea turtles increase predator vulnerability, producing low survival likelihoods (Mazaris et al. 2005), particularly until they enter deeper oceanic waters (Bolten 2003a). Whether our method actually deterred predation or not (given only a single observed predation event), I was able to witness near attacks that did not ultimately result in predation. I observed what seemed to be typical predators, e.g. seabirds and large piscivorous fishes, avoid an attack when, seemingly, the line of the attachment was detected on the approach. The floats appeared to deter predators as they veered from the attack on many occasions, both in our Atlantic and Pacific trials. In Limón Province, there is heavy sportsfishing in the area; tarpon, the target of fishers, and seabirds that follow these fishing boats for scraps, may be accustomed to avoiding fishing line and bobbers. Prior to the experiment, there was concern that the attachment and tracking method could increase their vulnerability to predation. The methods may have functioned as a very

short-term head-start, potentially increasing the survival likelihood by avoiding the high nearshore predation (Bolten 2003a, Nagelkerken et al. 2003, Wyneken et al. 2008, Santidrián Tomillo et al. 2010). Observations of hatchlings avoiding nearby fishes suggests they were still able to overcome possible predation with their attachment. Whether predation was prevented due to these evasive behaviours or the deterrent of the attachment is unclear, but the tracking method did not appear to increase the predation risk or mortality rate.

Hatchlings were difficult to obtain during the first part of the study for a number of reasons. In Guanacaste, 2015/early 2016 was a very strong El Niño year, which created poor hatching conditions along nesting beaches (Saba et al. 2007, 2008b, Santidrián Tomillo et al. 2012). In the Eastern Pacific population, El Niño conditions reduce the remigration probability of females, reducing the overall number of nests laid along beaches in this critically endangered population (Saba et al. 2008b). For those females that do remigrate, El Niño creates dry, hot conditions resulting in egg mortality and reduced emergence success (Santidrián Tomillo et al. 2012, 2014). The reproductive output (eggs laid per clutch) of Eastern Pacific leatherbacks is already low relative to other populations, worsening the impacts of El Niño on the availability of hatchlings for scientific study (Saba et al. 2008b). Further, we also witnessed the highest tides seen in 10 years at Cabuyal, Guanacaste, which destroyed nests relocated to “safe” areas along the beach (P. Santidrián Tomillo, personal communication). Bacterial or fungal pathogens within nests on Pacuare on the Caribbean side resulted in egg mortality and loss of entire nests prior to our arrival (Rosado-Rodríguez & Maldonado-Ramírez 2016). All these factors

compounded to limit the number of nests available for our study, reducing hatchling availability. The effects of El Niño not only challenged our attempt to understand dispersal of hatchlings, but these effects could have implications on population dynamics in subsequent years given reduced hatchling production.

This study applied methods on short-term tracking techniques for hatchling leatherback turtles, as well as provided speed estimates and movements relative to ocean currents that serve as a foundation for dispersal models for this and other populations. These data will be incorporated into a biophysical model to understand early dispersal movements, behaviour, and survival of *D. coriacea* hatchlings for the Northwest Atlantic population. The information collected can help predict entrance into offshore eddies of advantageous foraging habitats and temperature ranges, and ultimately, estimate adult habitat selection, survivorship, and overall population dynamics (Putman et al. 2012a, Scott et al. 2012b, 2014a, 2014b, Shillinger et al. 2012b). The data characterize the directionality of the hatchlings' movement as they leave the beach and swim offshore, which can be used in determining the influence of environmental factors on behaviour, and can be included in dispersal models for both the Caribbean and Pacific Costa Rican populations. Longer tracking of hatchlings in different surface current conditions would provide valuable data on the degree of influence of these nearshore currents. Future tracking studies at other rookeries could utilize these methods to understand implications of natal beach dispersal on leatherback population dynamics. Furthermore, this study can inform the design of fixed acoustic arrays near the nesting beaches.

Comprehension of dispersal components, both active and passive, of young sea turtles extends the understanding of all sea turtle life stages, from developmental habitats to adult foraging ground selection and ultimate survivorship of a population (Hays et al. 2010, Scott et al. 2014a, Stewart et al. 2016). These data are pivotal in developing knowledge of this threatened species during their most vulnerable time, providing key data for accurate development of biophysical dispersal models and quantifying natural and anthropogenic forces acting on swimming behaviour and orientation of hatchlings. Data from the towed attachment method used in our study can inform dispersal models to provide critical information on the spatial distribution of the earliest life stages of vulnerable marine turtles. Further, the modelled data can be coordinated with future head-starting efforts to understand appropriate oceanic release locations throughout early life development of leatherbacks and incorporated into multiple studies in both the Atlantic and Pacific basins. Neritic swimming speeds can provide an estimate of where these hatchlings will be relative to the nesting beach when the dispersal swimming frenzy and yolk reserves run out, an important aspect to understand with transforming ocean conditions under a changing climate. Leatherback turtles are facing unprecedented population declines, and this information can be used to build knowledge and strengthen conservation efforts vital to preventing extirpation and, ultimately, extinction of this species.

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Tables

Table 3.1. Distances travelled (km) and speed (m/s) of leatherback hatchlings and drifters deployed from Pacuare Nature Reserve, Costa Rica. Mean times are provided in minutes, along with the mean, standard deviation, and median distances travelled. Dist stands for distance, Min for minimum, Max for maximum, and SD stands for standard deviation.

| | Min Dist (km) | Max Dist (km) | Mean Dist (km) | Dist SD (km) | Median Dist (km) | Mean Time (s) | Mean Speed (m/s) | Speed SD (m/s) |
|-----------------------|---------------|---------------|----------------|--------------|------------------|---------------|------------------|----------------|
| Leatherback Hatchling | 0.75 | 3.85 | 2.17 | 0.77 | 2.08 | 5621 | 0.39 | 0.14 |
| Microstar™ Drifter | 0.11 | 2.76 | 1.29 | 0.77 | 1.27 | 4870 | 0.27 | 0.17 |
| Phone Drifter | 0.40 | 2.01 | 1.00 | 0.61 | 0.91 | 3324 | 0.33 | 0.22 |

Table 3.2. East-west (u) and north-south (v) components of both over-ground and in-water hatchling speed (m/s) in low, medium, and high surface current flows during the study period. Absolute values are given. Daily mean distance (m) per day of hatchlings and drifters are provided, as well as mean daily speed of drifters (m/s).

| | Low | Middle | High |
|---|-----------|-----------|-----------|
| Date of release | 8/23/2016 | 9/03/2016 | 9/02/2016 |
| East-west (u) over-ground | 0.199 | 0.195 | 0.378 |
| North-south (v) over-ground | 0.198 | 0.214 | 0.326 |
| East-west (u) in-water | 0.224 | 0.226 | 0.494 |
| North-south (v) in-water | 0.213 | 0.277 | 0.425 |
| In-water u and over-ground u difference | 0.025 | 0.031 | 0.115 |
| In-water v and over-ground v difference | 0.015 | 0.062 | 0.099 |
| Mean distance (m) hatchlings | 1651.28 | 1714.15 | 2854.14 |
| Mean distance (m) drifter | 634.13 | 1593.28 | 2534.38 |
| Mean daily speed of drifter (m/s) | 0.114 | 0.275 | 0.469 |

Figures



Figure 3.1. Map of hatchling acoustic tracking studies from Costa Rica. These include Playa Cabuyal on Costa Rica’s Pacific Coast and Pacuare Nature Reserve on the Atlantic Coast. Pacuare Nature Reserve is part of a continuous string of nesting beaches for Northwest Atlantic leatherbacks. Playa Cabuyal is a subsidiary nesting beach to Playa Grande for Eastern Pacific leatherbacks. Map was generated using ‘ggmap’ in R (Kahle & Wickham 2013).

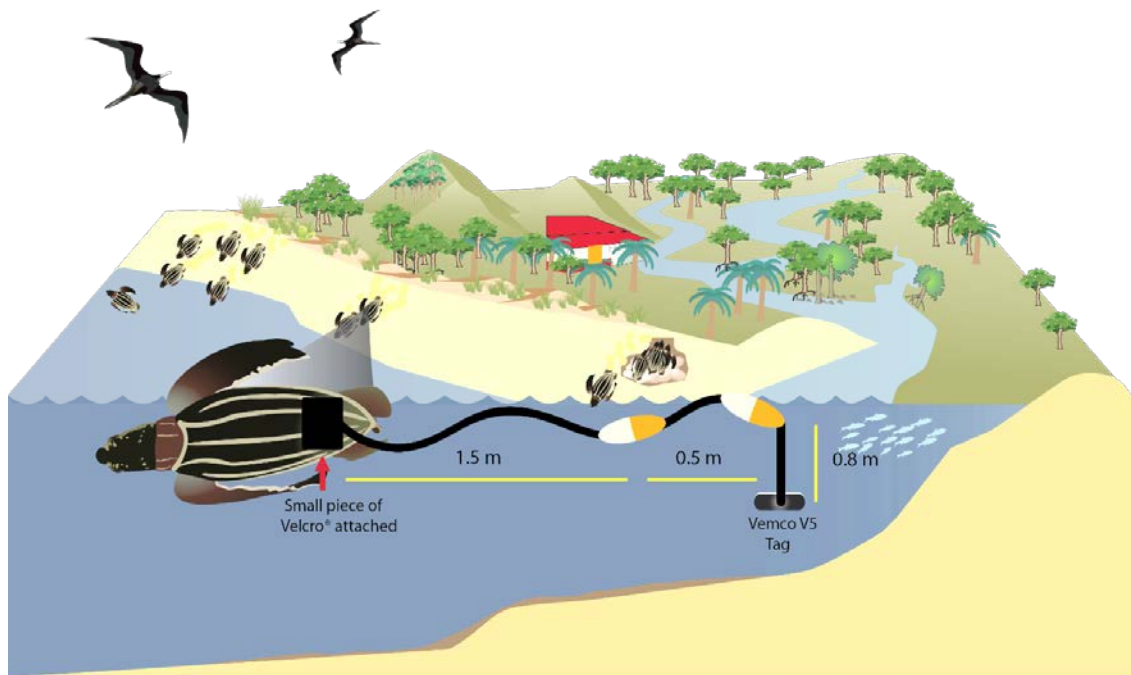


Figure 3.2. Acoustic transmitter attachment method on a leatherback hatchling modified from Gearheart et al. (2011). The main predators visible in Pacuare Nature Reserve, Costa Rica were tarpon and frigate birds. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).



Figure 3.3. Tracking of an olive ridley turtle in March 2016 in Cabuyal, Costa Rica. A) The turtle (i.) was tracked using floats (ii.) and acoustically with a hydrophone and receiver detecting the Vemco V5 tag (iii.) seen underwater and B) visually at the surface with these floats. Photos courtesy of Lauren Cruz.

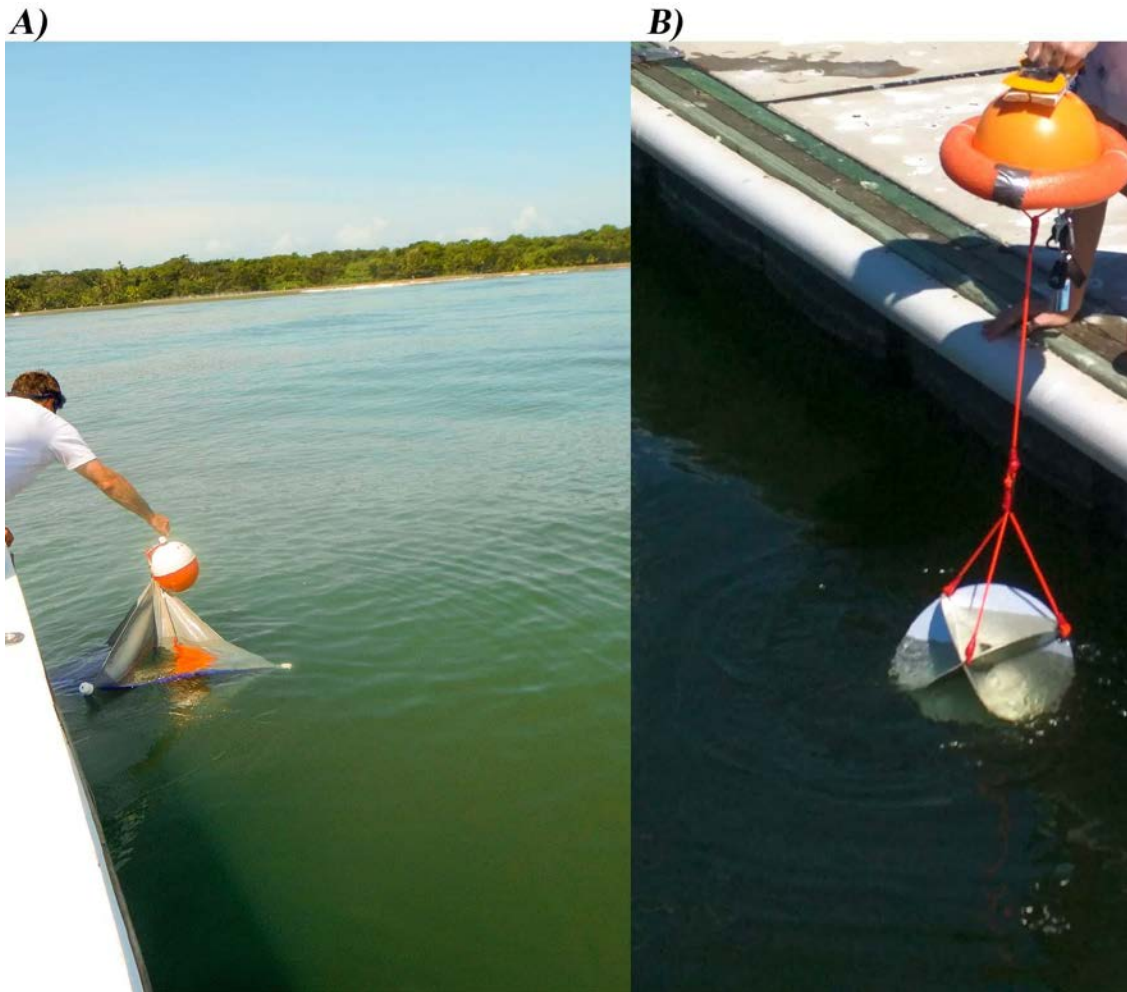


Figure 3.4. A) The Pacific Gyre Microstar™ drifter launched nearshore Pacuare Nature Reserve, Costa Rica prior to starting a hatchling track. B) The surface drifter design with a mobile phone to record GPS locations launched at the midpoint of hatchling tracks.

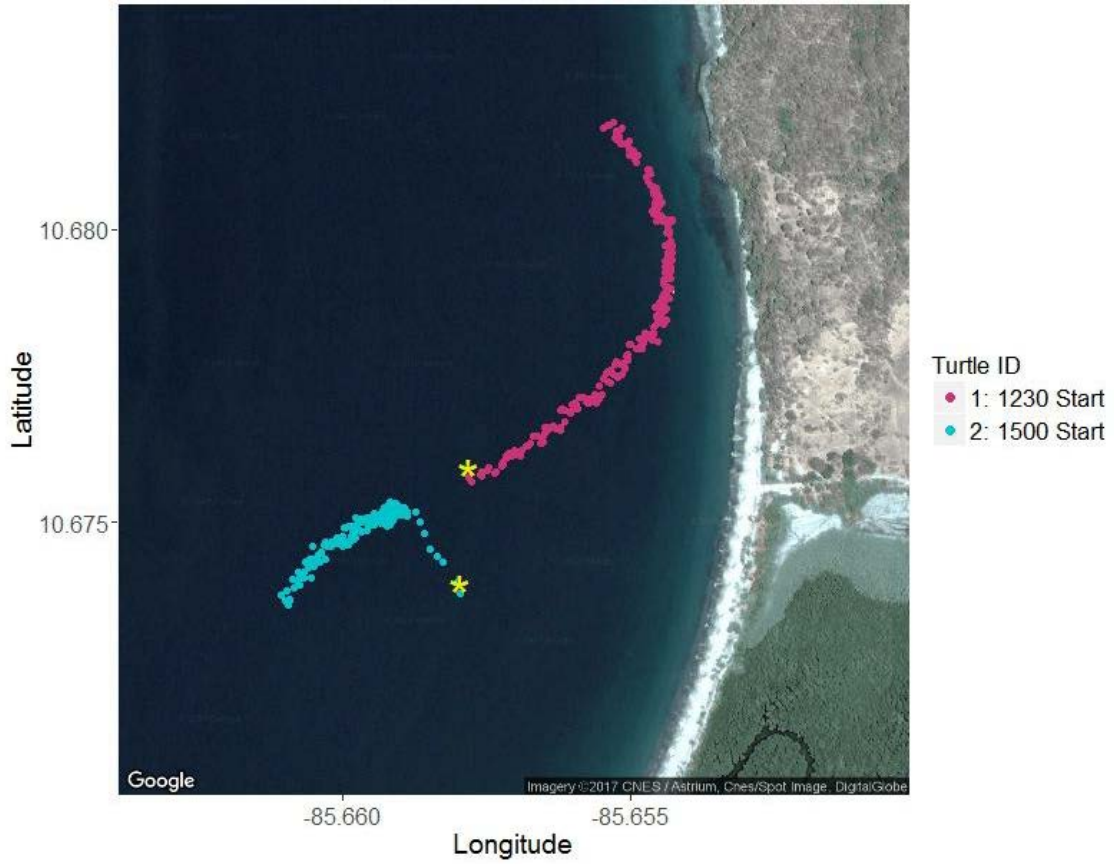


Figure 3.5. Tracks of two frenzied hatchling olive ridley turtles at Playa Cabuyal, Costa Rica in March 2016. The first turtle was released at approximately 1230, and the second turtle was released at approximately 1500. The start of each track is marked with a yellow asterisk. South-southwesterly winds were much stronger during the second release, likely altering the movement path of the second olive ridley. Both oriented in the same direction (northward coastally) during the tracking period. Map was generated using ‘ggmap’ in R (Kahle & Wickham 2013).

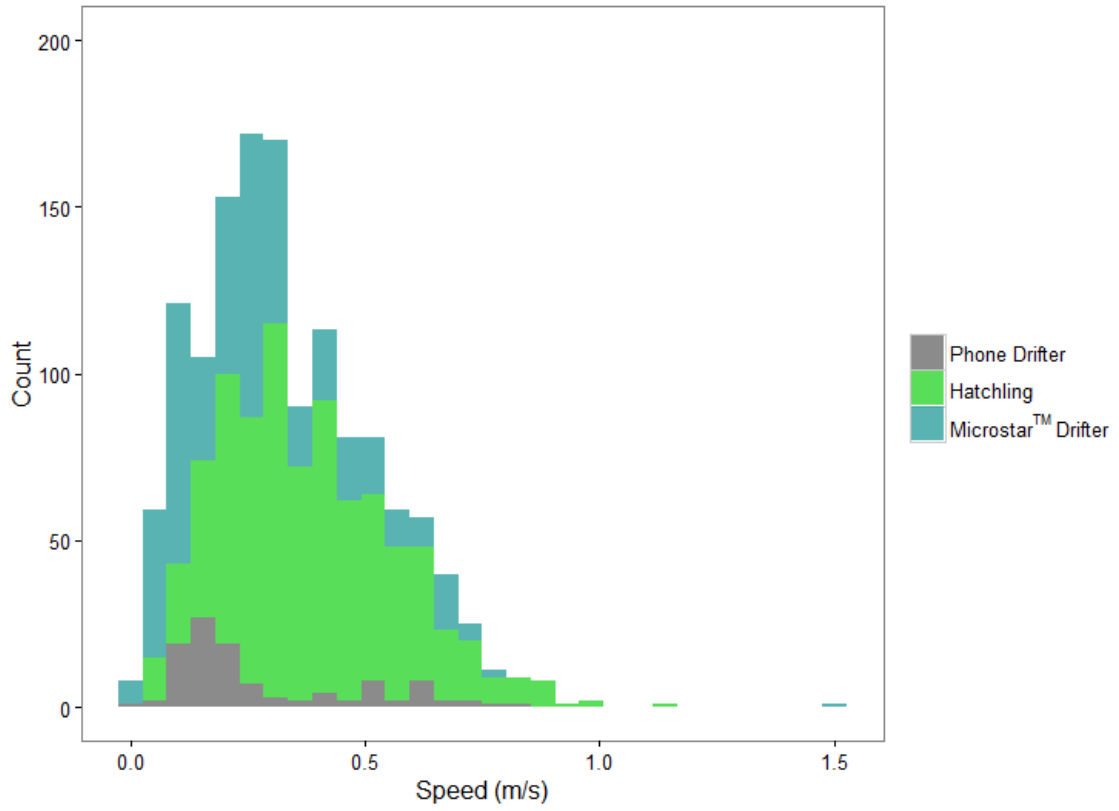


Figure 3.6. Histogram of speed values averaged for five minute periods for the hatching leatherbacks and Microstar™ and phone drifters.

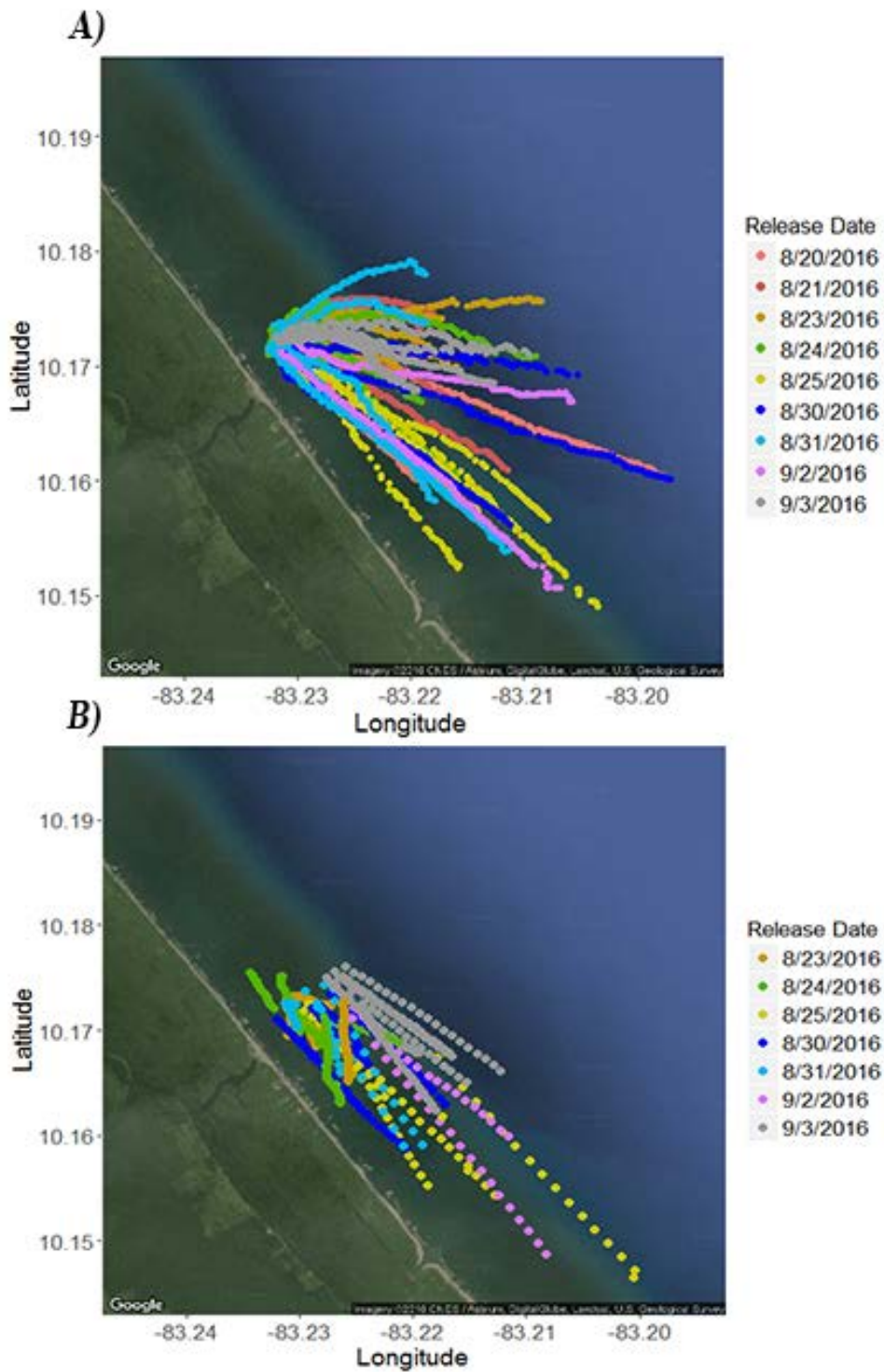


Figure 3.7. Trajectories of A) hatchlings and B) surface drifters released outside the surf zone near Pacuare Nature Reserve, Costa Rica in August and September 2016. Maps were generated using ‘ggmap’ in R (Kahle & Wickham 2013).

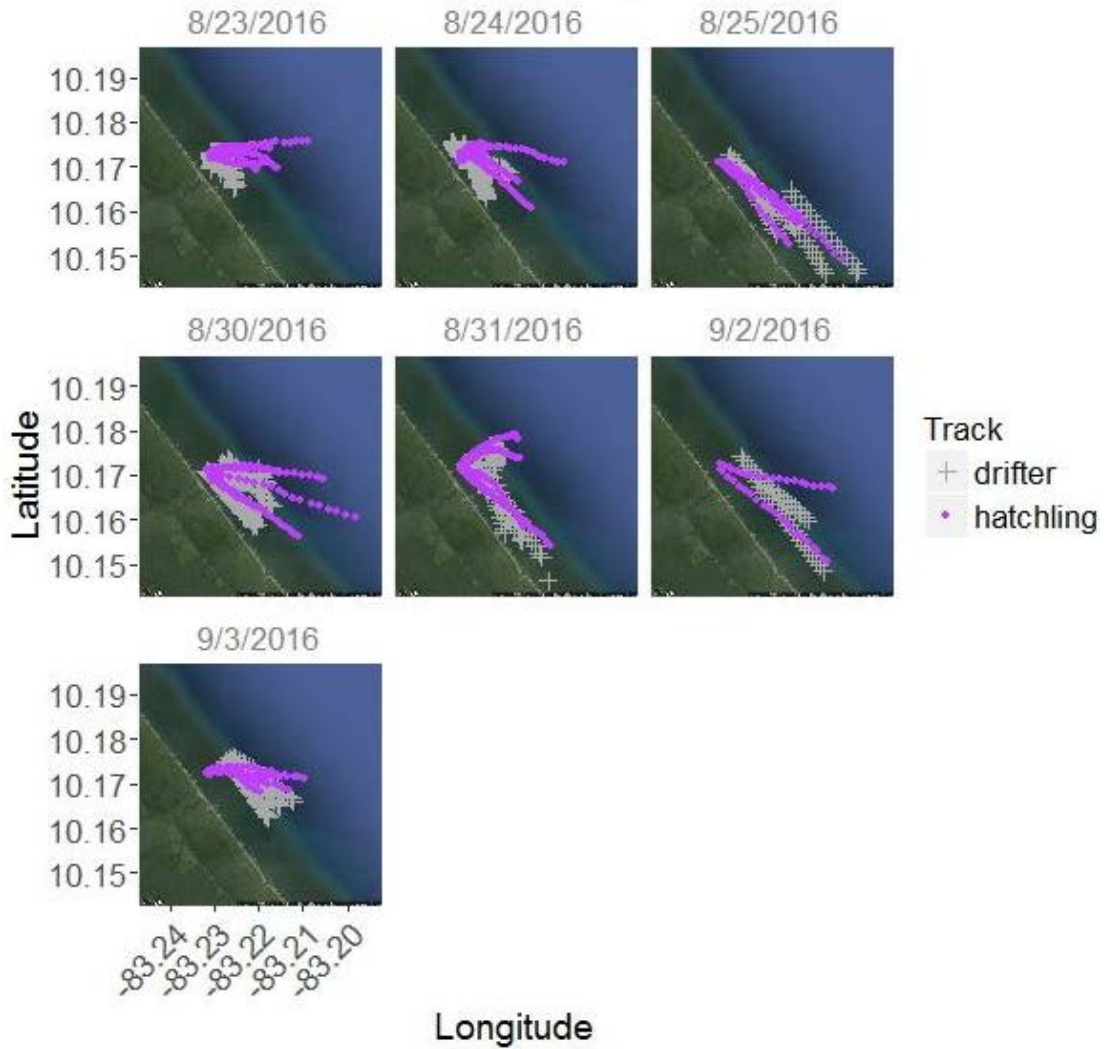


Figure 3.8. Tracks of drifters and hatchlings by the date of release near Pacuare Nature Reserve, Costa Rica. The movement of the drifters represented the nearshore surface drift encountered by the hatchlings. Maps were generated using ‘ggmap’ in R (Kahle & Wickham 2013).

Chapter 4: South Pacific TurtleWatch: Development of a novel approach for modelling the movement of Eastern Pacific leatherback turtles for use as a dynamic management tool

Introduction

Highly migratory marine species cross jurisdictional boundaries as they traverse thousands of kilometres of ocean. Traditional management methods, such as static area closures (e.g. Marine Protected Areas) and global legislation like the Convention on Fishing and Conservation of Living Resources, are valuable management tools, but do not always meet the needs to appropriately protect these species (Crowder & Norse 2008, Brown et al. 2015). Management of highly migratory marine species requires national and international cooperation, sound, consistent scientific data on movement and behaviour, and a clear understanding of the shared water resources of humans and animals. Dynamic ocean management is defined as management that changes spatiotemporally based on the incorporation of near real-time data to manage commercial and environmental resource utilization (Lewison et al. 2015). It is therefore capable of responding to a changing ocean by adapting across space and time given near-real time data integration (Hobday et al. 2014, Lewison et al. 2015, Maxwell et al. 2015). This can serve as the necessary flexible approach to meet different objectives, while maintaining ecosystem functions (see Lewison et al. 2015).

Focused management areas can be planned, implemented, and evaluated with knowledge gained from tagging studies, allowing for dynamic, real-time changes to be employed to reduce bycatch of protected species (Howell et al. 2008, 2015, Block

et al. 2011, Scott et al. 2012a). Dynamic spatial management can be compulsory, as with the southern bluefin tuna limits in the eastern Australian longline fishery (Hobday & Hartmann 2006, Hobday et al. 2011) or voluntary, as with loggerhead sea turtles in the Hawaiian longline fisheries (Howell et al. 2008, 2015). However, lack of incentives may present a challenge to implementation (Senko et al. 2011), and mandatory requirements can have unintended political pushback and economic consequences, creating international disincentives to implementation (Senko et al. 2017). Variability in the environment drives the movement and behaviour of leatherback turtles (*Dermochelys coriacea*) (e.g. Bailey et al. 2012a), requiring a management scheme that follows these changing conditions. In addition to these dynamic oceanic conditions already present, changes in global climate have the potential to increase interactions outside of static protected areas as both the highly mobile fisheries and sea turtles move to new areas (Fuentes and Cinner 2010, Hazen et al. 2013, Willis-Norton et al. 2015).

Leatherback populations have faced great declines in recent decades (Spotila et al. 1996, 2000, Tapilatu et al. 2013). Bycatch is one of the threats preventing leatherback populations from recovering (Chan & Liew 1996, Spotila et al. 1996, 2000, Lewison et al. 2004, Kaplan 2005, Santidrián Tomillo et al. 2008, Stewart et al. 2016). The IUCN Red List places ‘fishing and harvesting of aquatic resources’ as the top threat encountered by sea turtles (Lascelles et al. 2014) and has listed the Eastern Pacific leatherback as critically endangered (Wallace et al. 2013). Preventing regional extinction of the Eastern Pacific leatherback by reducing fisheries bycatch both nearshore and offshore (Kaplan 2005, Lewison & Crowder 2007, Wallace et al.

2010) is a global effort as they migrate long distances across transboundary waters and provide vital ecosystem services (Shillinger et al. 2008). Long distance movements of leatherbacks may increase the potential for interactions with international fisheries both nearshore and offshore (e.g. Hays et al. 2003, Benson et al. 2011, Bailey et al. 2012b). Population stability and growth should be achievable through reduction in adult mortality due to fisheries bycatch because current land conservation efforts have failed to stop their decline (Spotila et al. 2000, Hays et al. 2003, Lewison et al. 2004, Santidrián Tomillo et al. 2007, Wallace et al. 2010).

The large size of adult leatherbacks enables them to tolerate larger satellite tags that provide greater spatial coverage than acoustic tags. Satellite telemetry allows for remote tracking of individuals for an extended period, providing tracking data to relate movement and behaviour to satellite-derived environmental data such as ocean currents and sea surface temperature to identify key habitats (Godley et al. 2008, Hazen et al. 2013, Mansfield et al. 2014, Howell et al. 2015). Temperature is a driver of leatherback movement across age classes, with the minimum temperature threshold of leatherback decreasing with size, which results in changing movements based on the ability to withstand low temperatures. While adult leatherbacks are able to maintain their body temperature over 8°C warmer in cold waters (James & Mrosovsky 2004) and subcarapace temperatures 4°C warmer in warm waters (Southwood et al. 2005), they actively move away from areas of temperature stress (Shillinger et al. 2010). Leatherbacks with a curved carapace length (CCL) of <1 m generally stay in waters warmer than 26°C (Eckert 2002).

During interesting periods, which generally occurs during October-March in the Eastern Pacific, leatherbacks are in surface waters of approximately 27.5°C and below 31°C (Shillinger et al. 2011). They will target cooler waters during the interesting period if the water temperatures near the nesting beach are too warm (Shillinger et al. 2011). Post-nesting adults have been recorded in temperatures ranging from 3.6 - 34.4°C (Shillinger et al. 2011), with an estimated lower temperature threshold of surface waters between 10 - 15°C (McMahon & Hays 2006, Witt et al. 2007, Shillinger et al. 2011, Gaspar et al. 2012). As they migrate from nesting beaches, Eastern Pacific leatherback turtles tend to occupy waters of approximately 26°C until they reach the foraging grounds with average temperatures of about 19°C (Shillinger et al. 2011). These differences in temperature zones occupied across movement phases are important to understand how temperature can influence the movements of Eastern Pacific leatherbacks.

In this chapter, satellite tracking data and satellite-derived environmental data are integrated to develop a habitat-based model of leatherback turtle occurrence in the Eastern Tropical and South Pacific Ocean. Temperature has been implemented as a single proxy for physical oceanographic processes that shapes sea turtle distribution, based on its past use in habitat models (Howell et al. 2008, 2015, Shillinger et al. 2010, 2011). Both juvenile and adult Eastern Pacific leatherbacks interact with fisheries (IATTC sightings; Alfaro-Shigueto et al. 2007, 2011, Donoso & Dutton 2010). Bycatch assessment and mitigation is a major challenge encountered worldwide, and this near real-time product will predict the habitat of these leatherbacks, suggesting dynamic areas to avoid throughout the year to minimize

interactions threatening the population. This dynamic management tool can assist with efforts to decrease adult mortality on Eastern Pacific leatherbacks.

Methods

Leatherback turtle data

The satellite telemetry data included multiple tagging locations over a 20 year period (Fig. 4.1). Adult females were tagged with Argos satellite transmitters throughout nesting beaches of Mexico (1993 - 2003) and Costa Rica (1992 - 1995; 2004 - 2008) (n=80; Shillinger et al. 2008, 2010, Bailey et al. 2012b). Four leatherbacks caught in the Peruvian driftnet fishery were released with Argos tags (2014 - 2015). Sightings were also provided by the Inter-American Tropical Tuna Commission's (IATTC, courtesy of Martin Hall) fisheries observers (1990-2012) (Table 4.1). The telemetry data were all from adult leatherbacks (up to 165 cm CCL), whereas the fishery observations included a range of sizes from 10 cm to 180 cm CCL.

Mean daily location and behavioural mode estimates (classified as foraging or transiting) were obtained for satellite telemetry positions of leatherback tracks from those in Bailey et al. (2012a), and those not previously analysed similarly had a Bayesian switching state-space model (SSSM) applied using the R package 'bsam' (Jonsen et al. 2005, 2013, Jonsen 2016). The SSSM is composed of an observation process and a movement model. The observation process is the tracking location plus its error. The movement model utilized a first order correlated random walk model, which describes the mean turning angle and autocorrelation in speed and direction of

the leatherback's movement that is used to estimate the behavioural mode. The inclusion of the observation process plus the movement model results in improved location estimates with behavioural mode predictions. For each position, the SSSM uses the last location as a prior and the current observation with a known error distribution, to provide a best estimate of location. Two Monte-Carlo Markov Chains (MCMC) were run with 30,000 samples, a burn-in of 20,000 burn-in, and thinning of 10. SSSM-derived position estimates on land were corrected to the nearest plausible location at sea. All analysis was conducted using the R statistical computing environment (R Core Team 2016).

Environmental data

Environmental data corresponding to the time and location of each leatherback turtle position were extracted from the ERDDAP server at the NOAA/NMFS Southwest Fisheries Science Center, Environmental Research Division (Simons 2016). These data were extracted within an area corresponding to the 95% credible limits around each turtle position estimated by the SSSM (with a maximum radius set as the upper quartile of these limits). Multiple sensors were required for some of the environmental variables extracted due to the long time period of the turtle data. Sea surface temperature (SST) data were obtained from NOAA's Advanced Resolution Radiometer Pathfinder (AVHRR) and NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) (Table 4.2). The SST values for the period when the sensors overlapped (2003 - 2007) were compared and analysed in a linear regression model to determine if a correction factor was needed for transitioning from Pathfinder to MODIS data. Frontal probability index, Ekman upwelling, sea surface

height anomaly (SSHa), and bathymetry were also extracted for each turtle position. Bathymetry values were obtained from NASA's Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER). NASA's SeaWinds scatterometer and NOAA/NESDIS's Advanced Scatterometer (ASCAT) provided Ekman upwelling data. Sea surface height anomaly was available from merged radar altimetry products. NOAA's Geostationary-orbiting Operational Environmental Spacecraft (GOES) Imager provided frontal probability index values.

Continuous-time Markov chain models

Model description

Previous studies to analyse species distributions and create near real-time tools, for example, used kernel density approaches (Howell et al. 2008, 2015) and generalized additive mixed models (e.g. Hazen et al. 2016) based on the movements of a relatively small number of individuals to create population-level predictions. Preliminary analyses of our data set using these previous methods did not adequately describe or predict seasonal movements of leatherback turtles (see Appendix for details). In this study, we sought a model with the power to make robust population predictions given the available data. In order to account for the spatiotemporally auto-correlated, unbalanced, and presence-only telemetry observations of leatherbacks, a novel modelling approach was therefore applied. To quantitatively describe how these individuals move (or do not move) throughout their heterogeneous oceanic environment, we used a continuous-time Markov chain (CTMC) model proposed in Hanks et al. (2015) and Hooten et al. (2016) built upon the individual continuous-

time discrete-space (CTDS) movement model from Hooten et al. (2010). Only post-nesting portions of the leatherback tracks were used because these models are unable to run with missing values, and the nearshore satellite-derived environmental data in the inter-nesting region had many missing values. Post-nesting was determined for the animals tagged on the nesting beaches by removing the initial part of the track that was indicative of inter-nesting behaviour as in Bailey et al. (2008, 2012a). One turtle was removed from the analysis because the track only had one post-nesting location. Tracks with gaps too large for the SSSM to accurately interpolate across (≥ 20 days) were split into track sections. Overall, there were 88 post-nesting tracks from 74 individual turtles, totalling 12338 daily positions and spanning January 1992 through January 2015 (Table 4.1).

Our model aimed to understand resource selection given the environmental covariates presented to the individual, as well as account for uncertainty in the movement path (Hooten et al. 2010), and scale that to describe the population (Hanks et al. 2015, Hooten et al. 2016). The Lagrangian, or individual-based, model describes whether an individual stays or moves and the direction it proceeds given environmental drivers (Schick et al. 2013). Telemetry data provide continuous, high-resolution information, while environmental covariates are gridded over a discrete resolution. Individual resource selection and movement must therefore be studied at a resolution of the environmental variables available. This model framework utilized here has the capability to account for the temporal dependence of the data (Hooten et al. 2016). A Bayesian approach was utilized because it better quantifies and accounts for uncertainty given observations of a

particular system through its use of a prior distribution that is updated with the data using Bayes' theorem to obtain a posterior distribution. Bayesian analysis allows utilization of a classic frequentist model, for example, a generalized linear model, and incorporates a Bayesian framework to account for uncertainties and create a more accurate model. The ability to use both frequentist and Bayesian approaches can lead to more informative data interpretation, and this approach was favoured in our analysis.

A two-stage procedure was applied to create our model following Hooten et al. (2016) (Lunn et al. 2013). The CTMC was represented as a generalized linear model (GLM) with a Poisson regression, which is simpler for a computer to process given the large quantities of data input (Hanks et al. 2015). GLMs are commonly used in telemetry analyses (e.g. Bailey et al. 2012a, Scott et al. 2012a, Thums et al. 2016), and this method provides a more cohesive approach across studies. Understanding the drivers of these behaviours is an important component to describing population movement. The CTMC model framework accounts for environmental parameters that may be driving such behaviour.

Environmental covariates

Environmental covariates with potential to include in this model were sea surface temperature, bathymetry, sea surface height anomaly, frontal probability index, and Ekman upwelling (Table 4.2). Monthly values of environmental (spatial) covariates were obtained from the NOAA/NMFS ERDDAP server within a latitudinal range of -30° to 30° N and longitude from -175° to -75° E (Table 4.2). These were downloaded in netcdf format for all available periods at their given resolution. All

covariates were aligned to these coordinates by reformatting those in a different coordinate system. We chose a 0.5° grid cell over which to build the model to provide a cell size which leatherbacks have the potential to move through within one day given transiting speed estimates (Bailey et al. 2012b), but as large as possible to reduce computational intensity given the large prediction area. To create these lower resolution monthly rasters, we applied a median filter to the data with missing values removed from calculations. The number of cells contributing to the median values was dependent on the resolution of the original data. To equalize extents across all covariates, a fine-scale bilinear resampling was applied. This was chosen over nearest-neighbour sampling to create higher spatial accuracy within the resampling area, though extreme values may have been smoothed. Resampling put all variables and months to the same resolution for calculations to be completed across rasters. Erroneous land values were removed at 0.5° using the R ‘mask’ function (Hijmans 2015).

Environmental variables that did not cover the entire time period from January 1992 - January 2015 had empty rasters created to fill any gaps for the model to run. 277 rasters per environmental condition were stacked together to form a total of 554 snapshots of environmental conditions. This created a large set of data files for every step of the model. High computational power was necessary to handle this amount of data to create the baseline model. Rasters were scaled to reduce variability within and across the different covariates that prevented the model iterations from converging. The mean and standard deviation of SST were the centre and standard deviation used for scaling, respectively. This is similar to creating z-scores for each

variable. When scaling the environmental covariates, all rasters for each environmental covariate, including the raster over which predictions were to be made, had to be scaled to avoid bias. For example, to obtain estimates for December 2016, the scaled SST rasters were monthly values during January 1992 through January 2015, in addition to December 2016 from -175° to -75° E longitude and -30° to 30° N latitude. Bathymetry was only scaled on one raster, as it is invariant through time.

Model application

This first phase of the CTMC model provides the response of the leatherback to each environmental condition. Code derived from the R package ‘ctmcmove’ was primarily used in this analysis (Hooten et al. 2010, Hanks et al. 2011, 2015, Hanks 2016). We input the monthly environmental conditions as raster layers along with the latitude and longitude of each leatherback position at its given time. We fit a quasi-continuous path model to the telemetry data through space and time to provide a joint model for drivers of leatherback movement (Hanks et al. 2015). We used the daily SSSM-derived leatherback positions as the quasi-continuous path model within this analysis. This provided a regular temporal resolution for the track observations. A discrete-space path was created from these tracks (code written by Dong Liang). The model then derived parameters from each environmental layer corresponding to every location’s time. The R package ‘ctmcmove’ used the continuous-time Markov chain to produce the output (Hanks 2016). The continuous-time Markov chain framework (CTMC) takes environmental covariates stacked as rasters representing monthly data for our model and describes movement based on these environmental conditions during each month. It outputs a binary response with

1 representing each cell occupied by every track location and 0 for each of the surrounding grid cells, along with predictor variables and the Poisson GLM log-link offset, τ . These conditional response variables of movement can then be utilized to build a discretized path throughout the environment using a Poisson regression. This model phase couples movement and environmental conditions to allow for fitting of a Poisson GLM. It was repeated for every monthly layer and environmental condition within each leatherback's track. Grid cells containing "0" or missing values were removed from analysis. We did not create multiple paths for all tracks because we used the posterior mean from the SSSM, and no false-absences were created because they are unnecessary in the CTMC approach. Instead, we used the posterior means from this first stage. The benefits of this are that it reduces the computational power needed to run the model and reduces possible loss of accuracy at the population-level.

Poisson GLM

Parallel processing was used to independently fit the individual-level models to spatial covariates (Hooten et al. 2016) using the 'parallel' package (R Core Team 2016). This model is only computationally feasible through the use of parallel processing given the vast amounts of input. An automated MCMC algorithm (Gelfand & Smith 1990) was used with the package 'RStan' (Stan Development Team 2016) and function 'poisson.stan' (Carpenter et al. 2016). The model is fit independently using an adaptive MCMC with a Gibbs sampler (Hooten et al. 2016). The stacked binary response, correlated random walk component, imputed path and its offset, τ , and the covariates were input into a Poisson GLM. The correlated random walk component takes into account the persistence of animal

motion, where the next movement is dependent upon the previous movement. This ability to model auto-correlated, presence-only data is advantageous over the classical method. Gradual movement changes occur in organisms, not random motion, and this parameter describes the autocorrelation between movements. Parallel processing was used to complete the Poisson GLM (R package 'doParallel'; Revolution Analytics & Weston 2015). The covariates were run as 'location-based' or 'static' drivers of movement (Hanks et al. 2015, Hooten et al. 2016), which explain movement given the environmental conditions alone and does not explain biases possible within this movement (e.g. predator-prey interactions or directional seasonal migrations, termed 'directional drivers'). All tracks included the environmental variables sea surface temperature and bathymetry (Dodge et al. 2014). SST was a primary covariate to incorporate as it spans the entire time period of the tracks, and bathymetry remained constant. This ensured all steps of the model would process without missing data throughout months. Some environmental covariates did not span the entire period of the tracks, making them a challenge to incorporate into this framework.

The response was run as a Poisson distribution with log-link function. The response variable was the binomial response of a leatherback entering or not entering a grid cell surrounding the actual location. The predictor variables were the sum of SST, bathymetry, and the correlated random walk (CRW) component. Therefore, it is a prediction of leatherback movement as a function of three factors. This was run over subsets of individuals to reduce computer processing, which is an additional benefit of this approach and not feasible in some other model frameworks. An offset

of $(\tau + 0.001)$ was applied to obtain the proper response variance from parameterizing the CTMC model as a Poisson GLM. This is used in Poisson regression because the regression requires a predictor variable with a coefficient of 1 to obtain a rate of events. No additional weighted values were included. Because the Poisson GLM can be run independently for each leatherback, individual iterations on tracks were run given the covariates available during each track's time period. The GLM output provides a separate regression coefficient, beta, associated with each predictor. This resulted in two Betas: SST and bathymetry. These regression coefficients are the estimates for the change in the log odds for a unit change in the predictor variable adjusted for other environmental factors, which is the motility of an individual. Motility can also be described as the transition of a leatherback per unit time or a description of whether a leatherback will 'stay or move' within a given grid cell. These data represent a reciprocal resource selection, where the resources input are more likely to be utilized when negative values are obtained and less likely to be utilized when positive values are present. However, we sought to understand the movements of the population, not individuals. Therefore, a hierarchical Bayesian model was utilized.

To account for satellite tag attrition that results in more leatherback locations recorded in warmer temperatures as they leave tropical nesting beaches, a second GLM was run with an additional variable of distance from release site determined using the 'argosfilter' package (Freitas 2012). A subset with leatherback locations only below the equator, to better represent the foraging period, was run as a third GLM with predictor variables of SST, bathymetry, and CRW. This was tested to

examine whether these positions in the southern hemisphere better predicted temperature as a driver of leatherback movement during other life phases, which are difficult to obtain from satellite tagging adult females on the nesting beaches. Models were compared using AIC.

Hierarchical model and predictions

The second phase of the movement model proposed in Hooten et al. (2016) was completed to obtain population-level predictions of leatherback movements given environmental conditions specified within the model. Estimated coefficients can be used within predictions with future environmental conditions to create a near real-time tool to inform managers and other stakeholders. A hierarchical Bayesian model provides a method of describing movement in addition to obtaining the importance of environmental covariates to the individuals. Population-level inference is then possible using this approach (Hooten et al. 2016). This MCMC had 20,000 iterations with a burn-in of 10,000 and a thinning of 2. We defined a multivariate Normal prior of $N(0,100)$ for population level motility coefficients (Hanks et al. 2015). We used a Wishart prior for the corresponding population level precision matrix. The individual-level model was resampled in parallel in this second MCMC model to obtain estimates on the population (Hooten et al. 2016). The resulting posterior predictive distribution describes the probability of an individual using a particular area, upon which environmental selection can be determined (Hooten et al. 2010, 2016). The further from 0 in either direction the posterior distribution is, the greater the influence an environmental covariate has on movement, either positive or negative. A positive coefficient is indicative of a

leatherback quickly moving away from the given space, and a negative coefficient is the opposite, with leatherbacks more likely to stay in a space. The posterior distribution was then used to obtain the predictive values given regridded, scaled rasters of SST and bathymetry using the scaling method described previously to prevent biased estimates. As the log-link function is used in binary regressions to quantify log odds, the prediction of leatherback movement was made on the exponential values of the posterior distribution. We did not include a correlated random walk component into the predictive phase because we assumed the previous direction of movement was perpendicular to the current direction, eliminating the beta coefficient describing directional persistence.

Results

Leatherback turtle positions

The daily SSSM-derived leatherback turtle positions spanned from the nesting beaches in Mexico and Costa Rica to the South Pacific Ocean, and fisheries sightings were recorded along the coasts of Central and South America (Fig. 4.1). We analysed the monthly distributions of leatherback turtles and the associated SST (Fig. 4.2). Based on the linear regression model between Pathfinder and MODIS SST, the intercept value as a correction factor of 0.32°C was added to the Pathfinder SST values for the regression models and GAMMs (see Appendix).

CTMC movement models

The model framework is described in Fig. 4.3. The best GLM was chosen through AIC. This was determined to be the initial model of SST, bathymetry, and

CRW as predictor variables with all post-nesting leatherback locations. Motility estimates were obtained from the response binary variable of ‘stay or move’, and predictions were calculated for June and December 2016 (Table 4.3; Fig. 4.4). The population-level 95% confidence interval for each environmental covariate predicted spanned 0 indicating a strong linear association between SST, bathymetry, and motility was not predicted given these results. The maps in Fig. 4.4 describe the SST temperature recorded and the motility estimates or reciprocal resource selection by Eastern Pacific leatherbacks based on the model. In general, high values indicate leatherbacks do not stay in a given area and move quickly away. Low values mean they move slowly in the area because there are desirable landscape characteristics, and these areas can be considered potential leatherback hot-spots. June (Fig. 4.4A) has a wider distribution of warmer water temperatures than December (Fig. 4.4C), particularly extending from the nesting beaches westward across the equatorial region. Given this large warm water mass throughout most of the South Pacific in June, the expectation would be leatherback movement to the south and southeast portion of the study area. This would create a higher expected likelihood of movement to cooler areas off the western coasts of South America. A comparison between the two monthly predictive outputs, indicates leatherback movements in December 2016 were more likely to be away from the shore compared to the June 2016 estimates. Leatherbacks in June and December 2016 were likely to move more slowly through the waters west of Peru and Chile as expected given the distribution of observations.

Discussion

Turtles tagged during nesting in January and February began their post-nesting migration southwards through the eastern tropical Pacific in February to May. In the South Pacific Ocean there is a seasonal pattern with turtles moving south to the South Pacific Subtropical Convergence (Saba et al. 2008a) in the austral summer (December to April) when temperatures are higher at these temperate latitudes (approximately 30-40°S) and returning north to warmer, tropical waters (approximately 0-20°S) in the winter (May to November). There are also movements along the coast of South America, which are emphasized by the inclusion of fisheries observations from IATTC and leatherback interactions with the Peruvian driftnet fishery. The bimodal SST distribution observed in our dataset is due to nesting leatherbacks entering warmer waters in the tropics to breed when all available leatherback data is included, while those not breeding, post-nesting leatherbacks, were within cooler temperate waters.

Using the CTMC modelling framework, I aimed to predict the probability of leatherback turtle movement during two months in 2016 (Fig. 4.4). The warm water present west of the nesting beaches during June and December should cause leatherbacks to move away from shore if they are not breeding. We would expect higher nearshore values near nesting areas in December, as expected given leatherbacks are breeding at the nesting beaches during this time (October-March; Piedra et al. 2007). Overall, movement estimates should predict leatherbacks leaving warm coastal waters as only post-nesting behaviour was included in the analysis. We would also expect a larger area outside of the immediate coastline with high values

indicating movement from this warmer area based on the distribution of observations. While some females quickly depart these coastal areas post-nesting, other females may remain while they complete their nesting cycle. Further, as high temperatures off the nesting beaches were recorded in December (Fig. 4.4A), we would expect large areas of offshore movement. Additionally, December had very warm waters in the southwest part of the study area, and leatherbacks would be predicted to transition quickly away from that area (Shillinger et al. 2011). These results may be due to the scaling parameter used, which may be reducing seasonal variability. Higher latitudes in the South Pacific are more productive, but temperature is ultimately expected to be a proxy for predicting prey abundance (gelatinous zooplankton), the driver of leatherback movement (Heaslip et al. 2012, Jones et al. 2012). Leatherbacks avoid cooler water farther south where they forage around 19°C and generally avoid warmer water (> 31°C) when breeding (Shillinger et al. 2010, 2011). This provides the expectation of a higher probability in the north during austral winter months and a higher probability in the south during these summer months, completing a north-south seasonal cycle throughout the South Pacific.

We assumed within the GLM that the association between the leatherback movement and environmental variables was linear. However, this assumption was found to be inappropriate (Table 4.3), and a GAMM may be a more suitable model to include in the framework in this case. This is supported by the high adjusted r-squared value obtained (0.723) in the non-Bayesian utilization of a GAMM (see Appendix). The model framework can easily be modified to include a GAMM, and a time-varying component could be added to improve the representation of seasonal

movements. This would be a similar model to that of Willis-Norton et al. (2015), with a Bayesian CTMC framework and incorporation of hierarchical analysis to create population-level inference of leatherback movement as our response variable.

Weighted values may need to be incorporated into the framework to account for the changes in the availability of tracking information as leatherbacks move from tropical nesting areas into the South Pacific Gyre. There are challenges in completing this due to missing values that need to be incorporated into the predictive component of the model, as well as computational power necessary to complete the Poisson GLMs (or GAMMs) and MCMCs for each track. While the movement model is much more computationally efficient than prior models (Hanks et al. 2015), there is still a large demand from the model.

Benefits of applying the Hooten et al. (2010, 2016) approaches are that they are robust, applicable across situations, automated, parallelizable, incorporates multiple types of data (e.g. locational and environmental satellite data), can be extended to population-level inference, provide information on resource selection, and are relatively easy to interpret compared to solely relying upon GAMMs (Hooten et al. 2010). Data can be irregularly spaced to start, and the model will modify it appropriately. Organismal movement is often highly complex, not simply a straight path from a beginning point to an end, and this framework is able to accommodate environmental selection by individuals. Hanks et al. (2015) expand upon this framework to create a much more computationally efficient model. Further, the individual model allows for separation of individuals when run in parallel, as had to be completed for our model. While the separation indicates the

necessity of high computing power, the ability of the model to run separately or independently of one another is advantageous to this type of telemetry modelling (Hooten et al. 2016). A Gibbs Sampler method was utilized, which is automatic and easy for users to implement within the MCMC framework (Hooten et al. 2016). This is an iterative approach used for simulation-based inference. By doing this, repeated models can be run quickly, even as the complexity of the model increases. The dependence structures within the data can be determined without over-simplifying the model for a computer to execute it. MCMC approaches also allow the same samples to be used repeatedly to draw inferences on different parameters of interest. Joint inferences can be made among parameters as well (Hooten et al. 2016).

The hierarchical modelling approach is a higher-level estimation of persistent, predictable behaviour across a population, which is particularly relevant to understanding the movements given environmental cues encountered by Eastern Pacific leatherbacks. The CTMC model framework does not require the creation of false-absences of pseudo-tracks commonly used in GAMM analyses of telemetry data (e.g. Willis-Norton et al. 2015, Hazen et al. 2016). CTMC models are capable of efficiently modelling auto-correlated presence-only data with environmental covariates. Different data sources are key to robust dynamic management models, but they are difficult to incorporate given inherent differences in errors, among other things. These models provide a means of including multiple data sources, which strengthens their capabilities for modelling available data and maximizing sample sizes. Bayesian analyses have been shown to have stronger predictive power, especially as model complexity increases because all known sources of variation can

be incorporated. The Bayesian approach is flexible, particularly in that it can be adapted around the same framework indeterminate of the model used. There is also the ability to change the prior distribution to include additional known information at any time to strengthen the model as new information becomes available. This CTMC approach provides population-level inference estimates that are rigorous through MCMC resampling.

Our approach had a number of benefits, but there are also limitations and complexities to the modelling. Issues with our scaling parameter may be causing unexpected occurrences in warmer waters, or the grid-cell of 0.5° may be detrimentally smoothing data. Overall, the model may be relying too greatly on bathymetry values and not predicting the behavioural response to the degree expected as the estimates of leatherback motility visually mimic bathymetry contours. If the regression coefficients, beta, are small at the individual-level predictions, consistent patterns across population-level inferences will not be observed. The lack of linear association between leatherback movements and the environmental covariates included in this model resulted in the low variation in the prediction maps. Low individual level variation can propagate into the model and result in even smaller variation seen in the population-level prediction maps (Figs. 4.6B and 4.6D). This further suggests it is important to appropriately propagate errors to the population level within a model framework.

Minor adjustments in the model may strengthen the distribution predictions, such as altering this scaling parameter, changing the offset, or adding a weighting scheme. Estimating the appropriate prior distribution can be difficult, and there is a

level of subjective interpretation in doing this. True model testing of the prior is not possible, enhancing the difficulty inherent in choosing a prior. Vague priors were used to drive inference given the data available to prevent negatively influencing the model. Priors could be modified with additional information to try to increase predictive power, another benefit of using this Bayesian approach. No model selection tool is readily available for the population-level models, making it difficult to evaluate the predictive power given different predictor variables. MCMCs can have approximation errors, and they must converge, although we do not believe this was an issue in our model. Samples obtained through MCMCs are also not independent of each other and must be handled appropriately. We thinned the samples to reduce the autocorrelation inherent in the MCMC method. The Gibbs Sampler can slow computing speeds if there are dependent covariates, and we aimed to create a model that was computationally feasible. Within a MCMC, the early samples drawn are strongly influenced by the initial distribution of the model. To remove these values unrepresentative of the steady state of the MCMC, we discarded a burn-in. Overall, we addressed many of the challenges of this approach and believe the Bayesian framework provides more robust, population-level inferences than other approaches commonly utilized.

Different sex and age classes were represented within our data, with telemetry predominantly representing mature females, whilst the fisheries sightings included adults and juveniles. The distribution of immature leatherback turtles is therefore likely under-represented and is generally unknown. Each data source also has different errors associated with it that had to be considered and accounted for in

modelling habitat utilization. The location errors in the satellite telemetry were accounted for through the use of the switching state-space model. Given the differing lengths of leatherback tracks, there is inherent bias at the tagging location because there are a greater number of observations. Also, mainly mature females were tagged and the track durations were not sufficient (Table 4.1) to encompass the entire remigration interval of approximately 4 years (Reina et al. 2002). It is unknown whether males may be responding differently in this population. Block et al. (2011) used an inverse weighting of track length to account for tag loss. To account for fewer track positions in the South Pacific, where leatherbacks are estimated to be foraging on gelatinous zooplankton along fronts (Saba et al. 2008a), we included a distance from release site parameter. Distance from release site and locations only below the equator were included as parameters in separate models to attempt to overcome this bias, but they did not perform better based on AIC values.

The satellite telemetry data covered a long time period, resulting in the need to use separate environmental products for SST. Further, the availability of remote sensing products, such as the time period covered, the frequency of coverage, and access to the data, is a limitation to model building and predictions. Sea surface height altimetry and derived products, such as frontal probability index, may assist in predicting prey distribution and, therefore, leatherback movement. However, some of these products have a lag until they are available, making it more challenging to use in near real-time tools. Further, we had to scale the environmental covariates in order to be able to obtain model convergence. Issues can arise if this step is not completed properly, with bias introduced and seasonal variability removed. Finding the

appropriate scaling method proved difficult and still remains a challenge.

Leatherbacks undergo seasonal movements, but predicting all the drivers of these movements is challenging (Schick et al. 2013). SST is a proxy and will likely not sufficiently capture leatherback movement alone because of other processes involved (Schick et al. 2013). We did not incorporate chlorophyll-*a* measurements because it can be a poor indicator with an inverse relationship to Eastern Pacific leatherback distribution (Shillinger et al. 2008, 2011), issues with missing values due to cloud cover, and lack of information relating net primary production to gelatinous zooplankton abundance (Lilley et al. 2011). Other environmental variables, such as upwelling indices, effects of the El Niño Southern Oscillation, as well as frontal systems and convergence zones where gelatinous zooplankton may aggregate may help to improve the explanatory power and predictive capability of the model (Polovina et al. 2000, Lambardi et al. 2008).

Fisheries sightings and data from the inter-nesting period were not incorporated in the model. The irregular sampling of fisheries sightings means that these data would need to be run as a spatial point process model that may potentially be overlain on the CTMC model due to the differences in data types (Hooten et al. 2016). This may require complex pattern analysis if a grid overlay with spatial point process is completed for the fisheries sightings because a point process model would output sightings per unit area, while the CTMC model outputs transition per unit time. Different types of inference on the distribution of the leatherback population result from fisheries sightings and telemetry data, and incorporation of both data types is complex.

The amount of telemetry data becoming available is ever-expanding, as are the complex models relating animal behaviour to environmental cues, but the computational power required of these models may be high. Therefore, it is essential to use a predictive model capable of incorporating robust model estimates of movement over large tracking datasets and vast amounts of environmental information. We used a novel technique to address the needs for more advanced observation techniques without super-computing computational requirements. Previous studies have conveyed the complex relationship between satellite-derived environmental variables and leatherback distribution (e.g. Shillinger et al. 2008, 2011, Bailey et al. 2012a), particularly resulting from the lack of understanding of prey distribution (Schick et al. 2013, Wallace et al. 2015). The inability to measure and predict gelatinous zooplankton abundance via extracted environmental characteristics increases the difficulty of predicting leatherback turtle distribution. Leatherbacks move from convergence zones to frontal zones with aggregations of gelatinous zooplankton in the South Pacific (Saba et al. 2008a), but predicting movement and distribution within and between these areas is challenging. The resulting prediction map from our model can eventually be used to help understand Eastern Pacific leatherback movements and provides a tool that can be used internationally with managers and local groups on efforts such as mandatory or voluntary fishing restrictions and awareness of the critically endangered status of leatherbacks to prevent extirpation of this Eastern Pacific population. Dynamic management of highly migratory marine species relies on understanding their movement and distribution under shifting oceanic conditions and resource demands.

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Tables

Table 4.1. Eastern Pacific leatherback positional information modified from Bailey et al. (2012a). All tracks were included in initial analyses (see Appendix), which included Argos satellite tag data from starting locations in Costa Rica, Mexico, Peru, as well as fisheries sightings from the IAATC. Post-nesting tracks represent Argos satellite tag data included in the movement model for motility estimate predictions. Obs stands for observations and Min for minimum.

| Location | Data Type | Years | Total Point Obs | No. Tags | Track Duration (Days) | | |
|---|---|-------------------------|--------------------|-------------|--------------------------|-----|-----|
| | | | | | Mean | Min | Max |
| Playa Grande, Costa Rica | Argos Satellite Tag | 1992-1995; 2004-2008 | 11600 | 54 | 215 | 4 | 568 |
| Mexiquillo, Cauhitan, and Agua Blanco Mexico | Argos Satellite Tag | 1993-1994; 1997-2003 | 3710 | 25 | 148 | 10 | 481 |
| Peruvian Driftnet Fisheries | Argos Satellite Tag | 2014-2015 | 251 | 4 | 63 | 6 | 112 |
| Fisheries Sightings | GPS coordinates | 1990-2012 | 209 | NA | NA | NA | NA |
| Post-nesting Tracks | Argos Satellite Tag; Geolocation Tag | 1992-1995 | 12338 | 74 | | | |

Table 4.2. Environmental products used throughout the modelling efforts. Netcdf files were downloaded at a monthly temporal resolution. All data were downloaded from coastwatch.pfeg.noaa.gov/erddap/.

| Variable | ERDDAP Name | Resolution | Years Extracted | Satellite |
|---|----------------------------|-------------------|----------------------------|--|
| Sea Surface Temperature | erdPHsstamday_ LonPM180 | 0.042 | 1990-2002 | Global High Resolution AVHRR Pathfinder V5.1 |
| | erdMH1sstmdmday | 0.042 | 2003-2015 | MODIS/Aqua |
| Bathymetry | usgsCeSrtm30v1 | 0.0083 | NA | ASTER/Terra |
| Ekman Upwelling | erdQAstressmday | 0.125 | Aug 1998- 2009 | SeaWinds/ QuikSCAT |
| | erdQAstressmday* | 0.25 | Oct 2009- 2015 | ASCAT |
| Sea Surface Height Anomaly | erdTAsshmday* | 0.25 | 1993-Jan 2010 | Merged (TOPEX/ Poseidon, ERS-1/- 2, Geosat FO, Envisat, Jason-1) |
| Frontal Probability Index | erdGAtfntmday | 0.05 | 2001-2015 | Imager/GOES |

*Notes: Ekman upwelling has not been downloaded beyond 2009. Sea surface height anomaly is available from AVISO on a daily time-step for all dates.

Table 4.3. Estimates of predicted individual-level beta coefficients for June and December 2016. Mean, median, standard deviation, and upper and lower quantiles for each beta regression coefficient used in motility predictions are presented. Data are log transformed as a result of the log-link Poisson GLM.

| Parameter | Mean | Standard Deviation | 2.5th Quantile | Median | 97.5th Quantile |
|---|-------------|-------------------------------|--------------------------------------|---------------|---------------------------------------|
| SST June 2016 | -0.0000078 | 0.0057 | -0.011 | -0.000016 | 0.011 |
| Bathymetry June 2016 | -0.000016 | 0.0056 | -0.011 | 0.0000092 | 0.011 |
| SST December 2016 | -0.000034 | 0.0056 | -0.011 | 0.0000010 | 0.011 |
| Bathymetry December 2016 | 0.00015 | 0.0057 | -0.019 | 0.000063 | 0.012 |

Figures

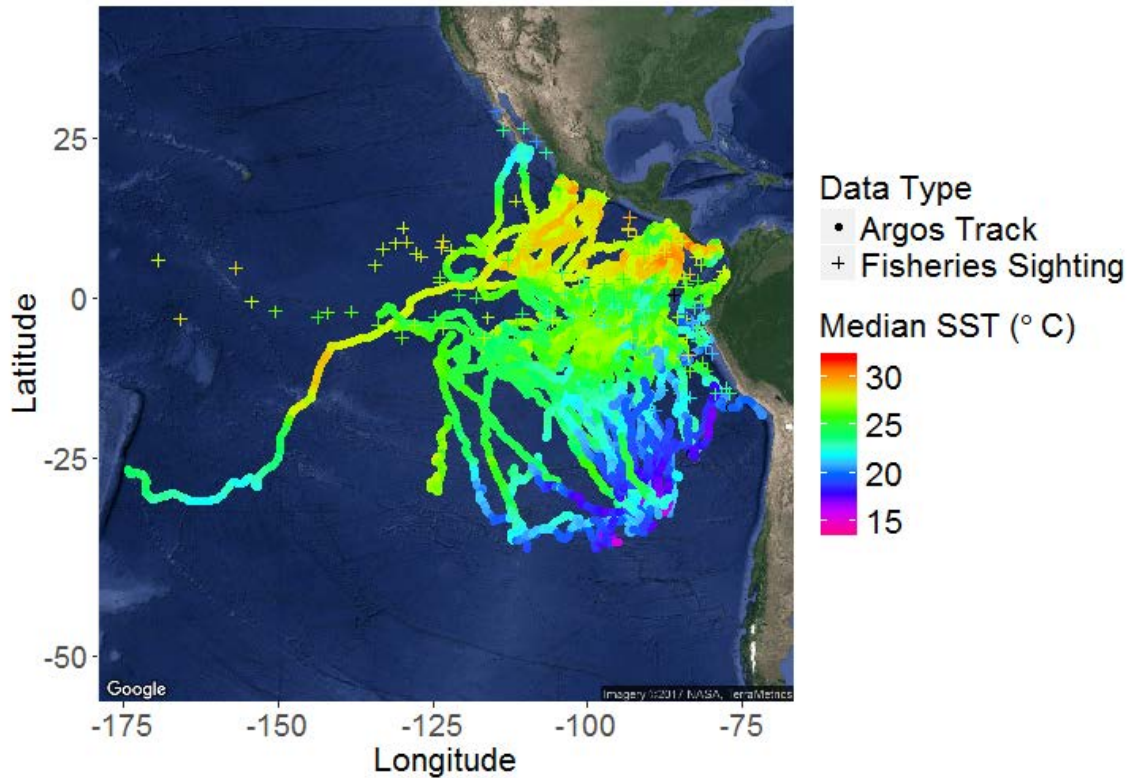


Figure 4.1. Median monthly sea surface temperature (°C) for each leatherback observation from Advanced Very High Resolution Radiometer (AVHRR) Pathfinder Version 5.0 and Moderate Resolution Imaging Spectroradiometer (MODIS) based on the estimated mean daily positions from the switching state-space model. Fisheries sightings are represented by a plus symbol, and tracks from Argos tags are represented by circles. Maps were generated using ‘ggmap’ in R (Kahle & Wickham 2013).

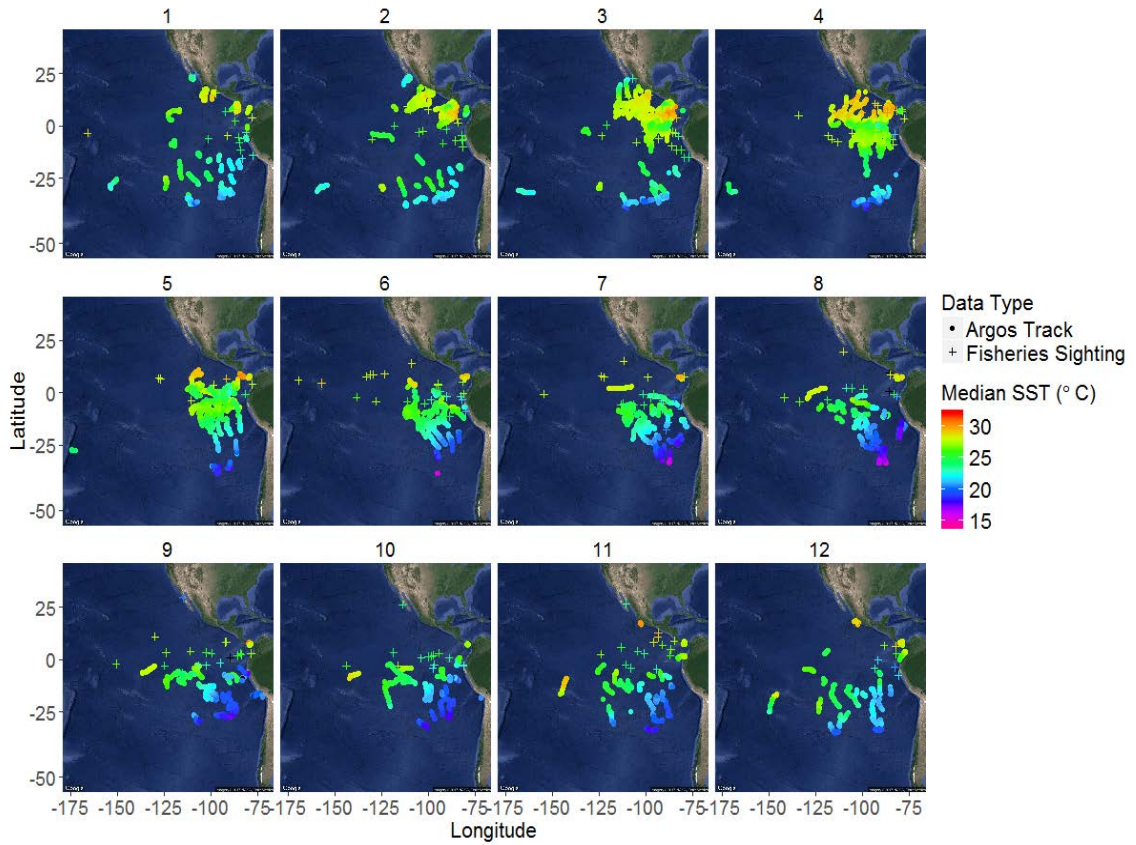


Figure 4.2. Median monthly sea surface temperature (°C) for each leatherback observation by each month. Observations span 1990 through 2015. Fisheries sightings are represented by a plus symbol, and tracks from Argos tags are represented by circles. Maps were generated using ‘ggmap’ in R (Kahle & Wickham 2013).

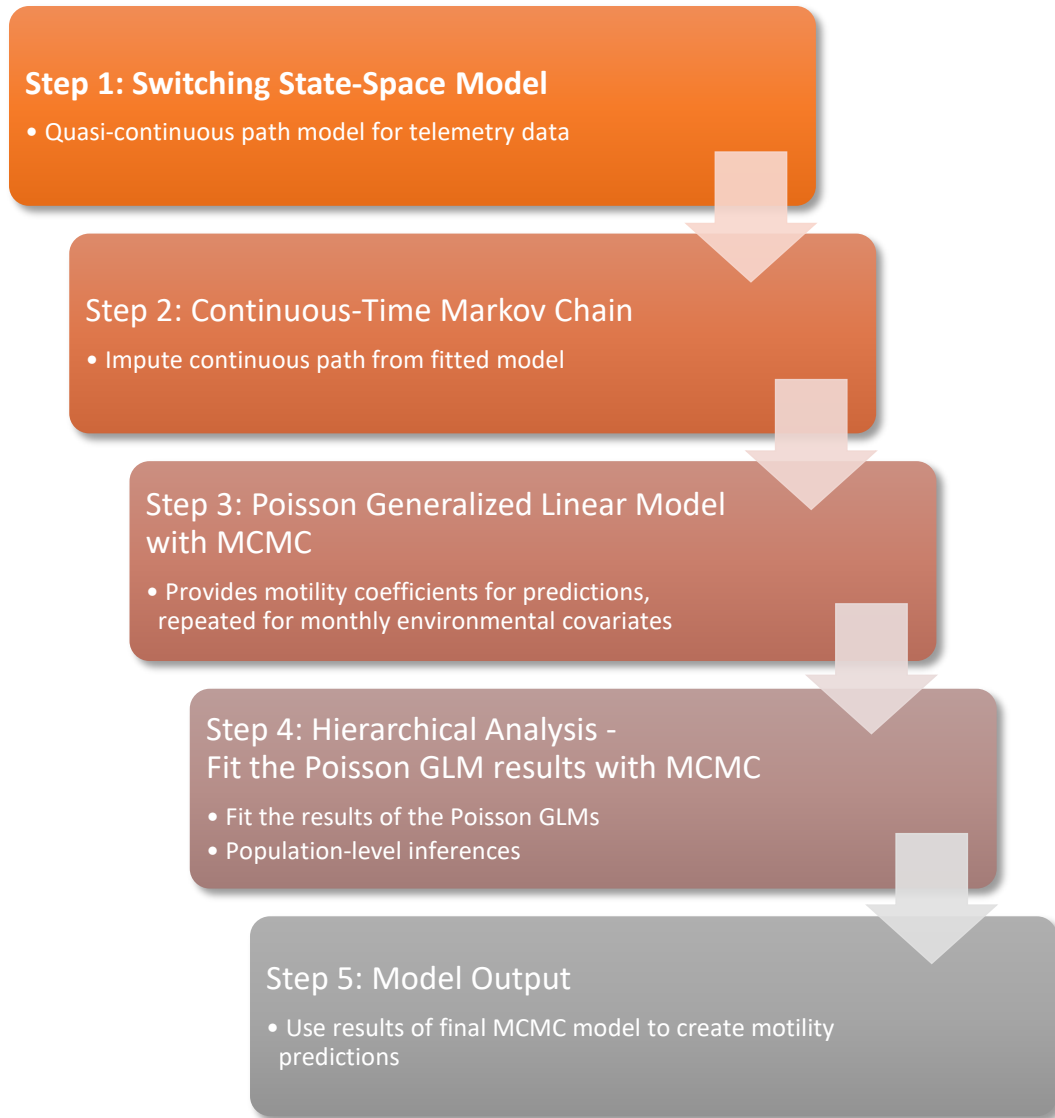


Figure 4.3. Model workflow for obtaining monthly predicted motility estimates of Eastern Pacific leatherbacks. This relatively new approach is based off methods used in Hooten et al. (2010, 2016) and Hanks et al. (2015) and expanded upon to provide population-level estimates of leatherback motility.

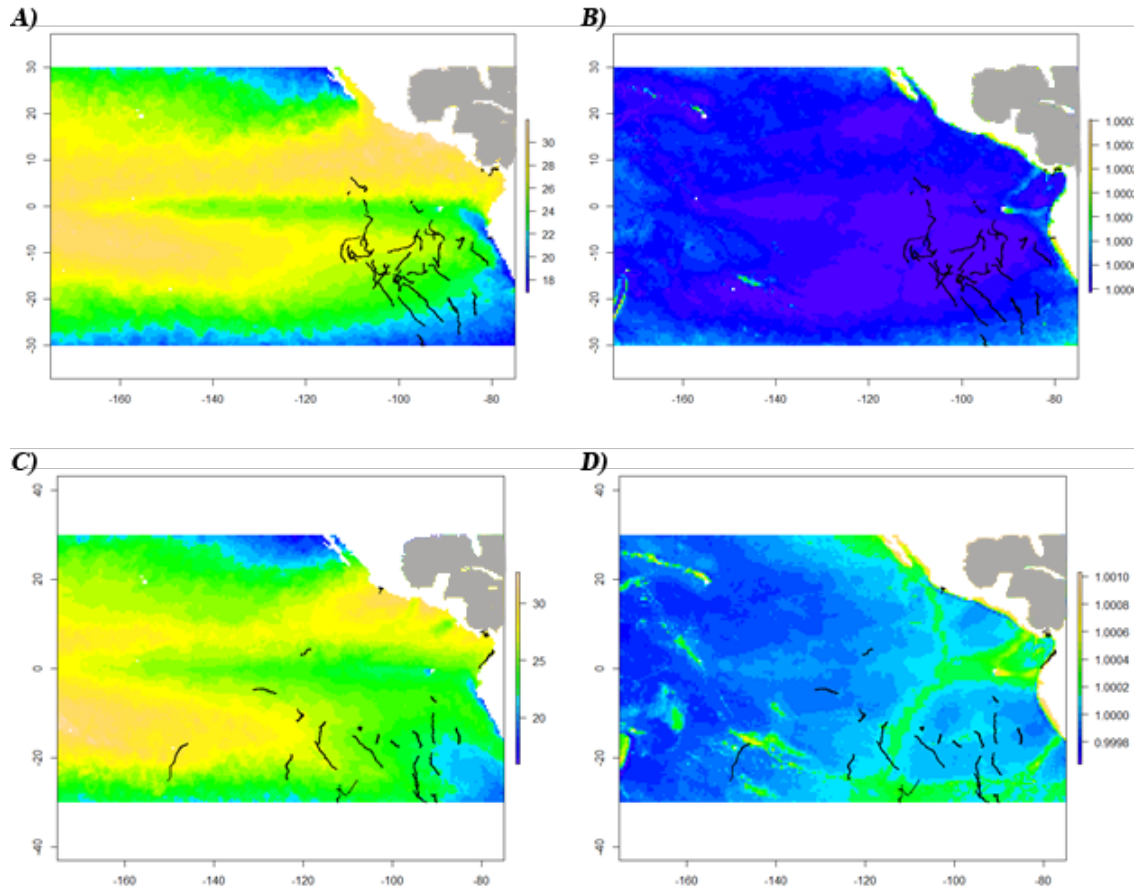


Figure 4.4. Sea surface temperature ($^{\circ}\text{C}$) for A) June and C) December 2016. Leatherback predicted posterior motility estimates for B) June and D) December are based on sea surface temperature and bathymetry. The lower the predicted values, the more likely leatherbacks will stay in the area. Black dots represent each month's leatherback location outputs from the switching state-space model that were input as location estimates.

Appendix

Modeling the movement of Eastern Pacific leatherbacks

Methods

Kernel densities

Monthly kernel densities of SST were estimated and used to determine relative use, in an approach similar to that by Howell et al. (2008, 2015). The SST data were integrated with the leatherback turtle location data, and each temperature degree (in °C) was assigned a scaled density value obtained from the ‘density’ function (R Core Team 2016). In the example month chosen, the nearest January 2016 SST was matched with the SST from January tracking data, and the scaled density estimate for this month was extracted. This estimate was used as a prediction of leatherback relative use in development of a thermal habitat model.

Regression models and generalized additive mixed models

Models of increasing complexity were explored to determine the approach most effective at accounting for the complexities of the dataset and most effectively predicting leatherback turtle distribution. Data, which included all leatherback locations, were separated into training and testing (20% of data) sets to predict the latitude of leatherback turtles based on SST values within a regression tree framework. This is useful to break data into small regions to fit models. Trees had a response variable of latitude and combinations of predictor variables that included SST, longitude, group (i.e. Mexico, fisheries sightings, Peru, CR), and season (R package 'rpart'; Therneau et al. 2015). Season was defined as quarterly intervals

throughout the year, with January through March as the first of the four seasons.

Regression trees are a common approach to create predictions when there are multiple influential variables, but the initial trials were unable to capture the variability in leatherback latitudinal movement. The Random Forest algorithm was also applied in an attempt to improve the regression tree results because this technique considers many scenarios and averages a ‘forest’ of trees to create the best predictive model. The Random Forest model combines regression tree models that may not predict well individually and combines them to create a better overall model. Two thousand trees were run for each model. Errors were calculated via jackknife estimation. The same response and predictor variables were attempted as in the regression tree models (R package “randomForest”; Liaw & Wiener 2002). Thirdly, a comparable generalized additive mixed model (GAMM) was used as in previous telemetry studies predicting distributions (e.g. Willis-Norton et al. 2015, Hazen et al. 2016). GAMMs are used to aid in explaining complex datasets. Some benefits of GAMMs include flexibility to allow fits with relaxed assumptions on the relationship between the response and predictor, the potential for better fits to data than purely parametric models, and a quick means of analysis and prediction. The response variable in each GAMM was again latitude, with predictor variables different combinations of SST, longitude, month, group, and season. A random intercept of leatherback identity was included in all model runs. The best GAMM was chosen through Akaike Information Criterion (AIC). However, all of the model types seemed to have flaws given they had poor predictive power. GAMMs, although commonly used, are a general means of analysis and can encounter interpretability issues. GAMMs also have limitations of

computationally intensive false-absence estimations required for telemetry data (e.g. Willis-Norton et al. 2015, Hazen et al. 2016).

Results

Kernel densities

Kernel density plots of SST were created for each month from the corresponding temperature for each leatherback location (Fig. A.1). There was a unimodal SST distribution only in June - August as tagged leatherbacks were outside warmer nesting areas in waters of a similar temperature range. Bimodal SST distributions during other months resulted from the leatherbacks being present both at nesting beaches (warmer temperatures) and throughout the foraging ground in the South Pacific Ocean (cooler temperatures) for those not remigrating to breed. Kernel density estimates were extracted and incorporated with January 2016 SST to create a leatherback relative use thermal habitat model (Fig. A.2).

Regression models

The regression trees described the influence of SST on latitude with 61% of the leatherback locations in waters greater than 25°C, and 22% were less than 23°C. Therefore, 17% of leatherback latitudinal positions were between 23°C and 25°C (Fig. A.3). This included inter-nesting tracks, as well as fisheries sighting positions. Nearly one-third of the tracks in waters warmer than 25°C occurred in January through mid-April, likely inter-nesting leatherbacks in tropical waters. Predictions were estimated from the 20% testing set, and some of the leaves on the tree suggested 30 degree latitude variability in the confidence intervals across the regression tree

components. The median predicted latitude was lower than the median latitude from the training data, and the confidence intervals for the prediction set were much greater than those of the training set. Overall, the regression tree models could not adequately predict the seasonal movements of leatherbacks.

The Random Forest analysis provided the amount of influence of each variable on the latitude leatherbacks, but the models were unable to capture known seasonal north-south movements. The error within Random Forest models increased as the number of trees increased, and large confidence values were obtained, limiting model performance (Fig. A.4). For example, coverage of the 95% confidence interval was only 23.9% for a Random Forest model of latitude as a function of SST, group, and month, whereas a model meeting all assumptions would be near 95% (Dodge & Marriott 2003). The predicted best fit and the associated standard error did not result in a linear relationship with the observed latitudinal positions (Fig. A.4).

Generalized additive mixed models

To determine the relationship between the latitudinal movement of the turtles and SST using a GAMM, a Gaussian distribution with identity link was run given residual and Q-Q plots. The best GAMM was chosen using AIC, which predicted latitude as the response as a function of SST, longitude, month, and group with a random effect for each individual leatherback. The adjusted r-squared value for this model was 0.723. However, the model did not meet the goal of a robust population-level prediction, nor did the seasonal prediction of leatherback movement match the distribution of the tracking data.

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Figures

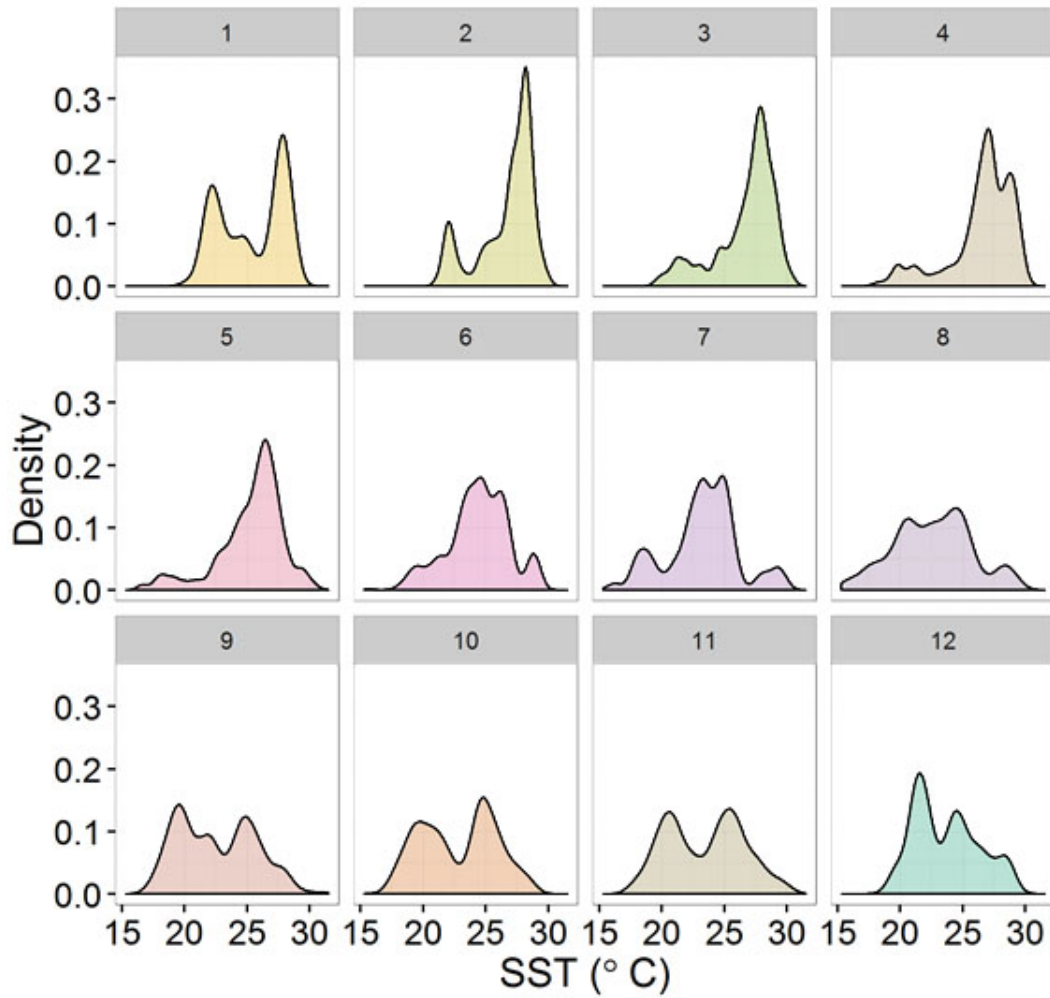


Figure A.1. Median monthly sea surface temperature ($^{\circ}\text{C}$) density by month based on observed leatherback positions between 1990 and 2015.

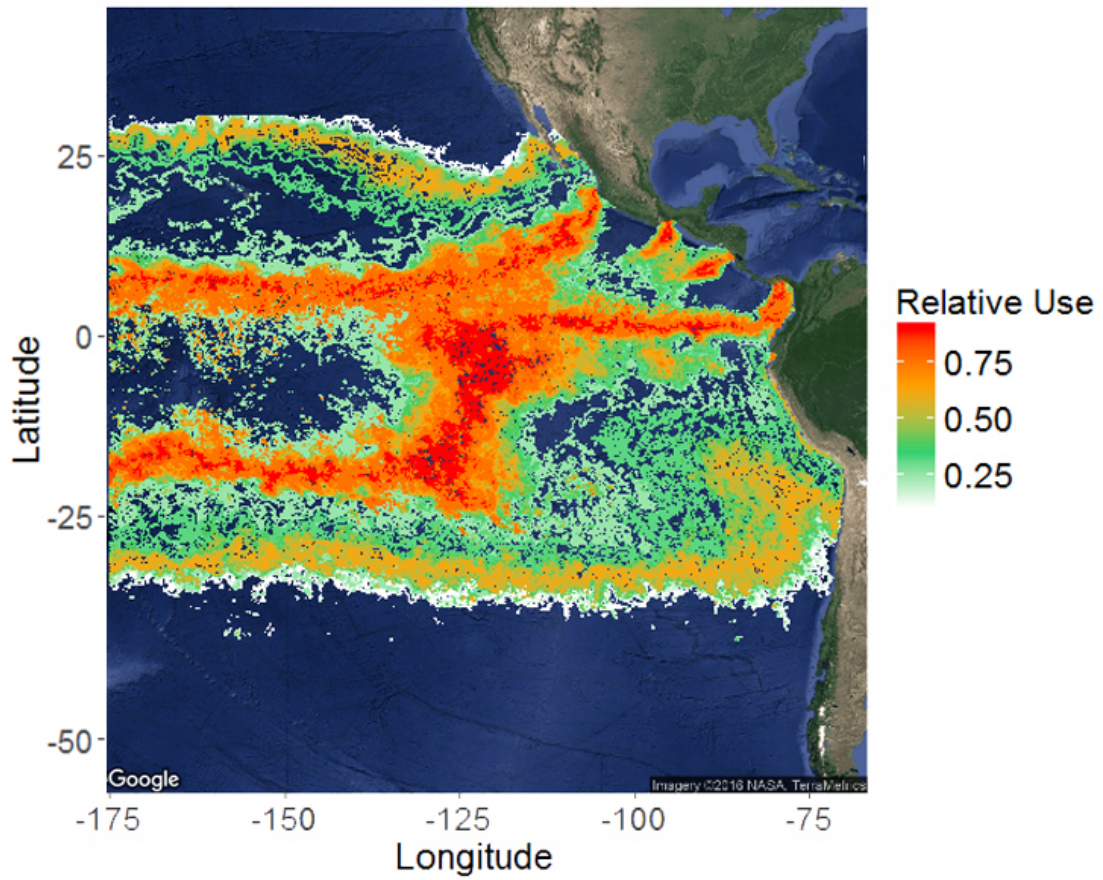


Figure A.2. Relative use map by Eastern Pacific leatherback turtles based on January 2016 SST and kernel density estimates of SST. Maps were generated using ‘ggmap’ in R (Kahle & Wickham 2013).

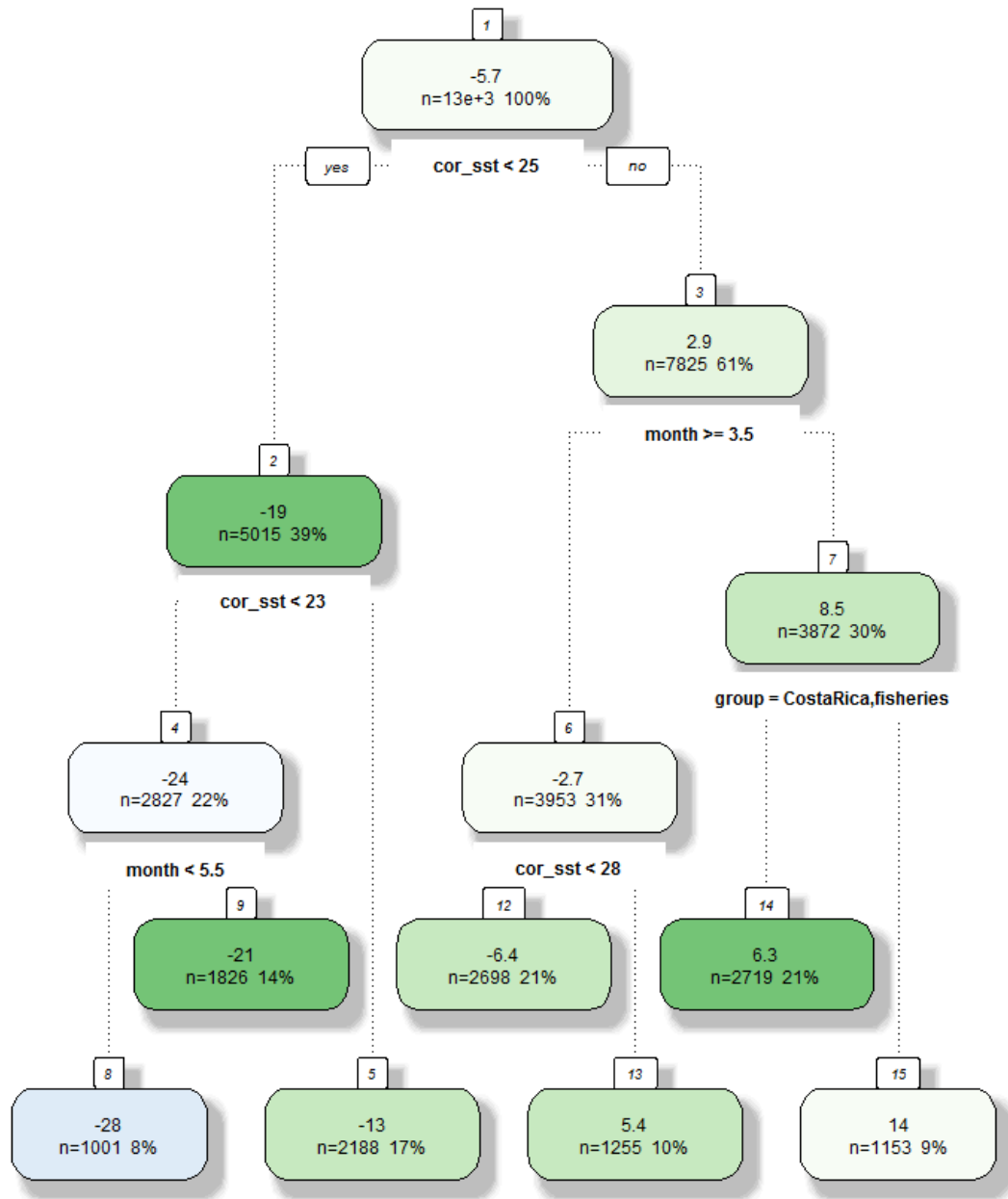


Figure A.3. Regression tree output for leatherbacks for latitude based on SST, month, and group (release site) of each leatherback.

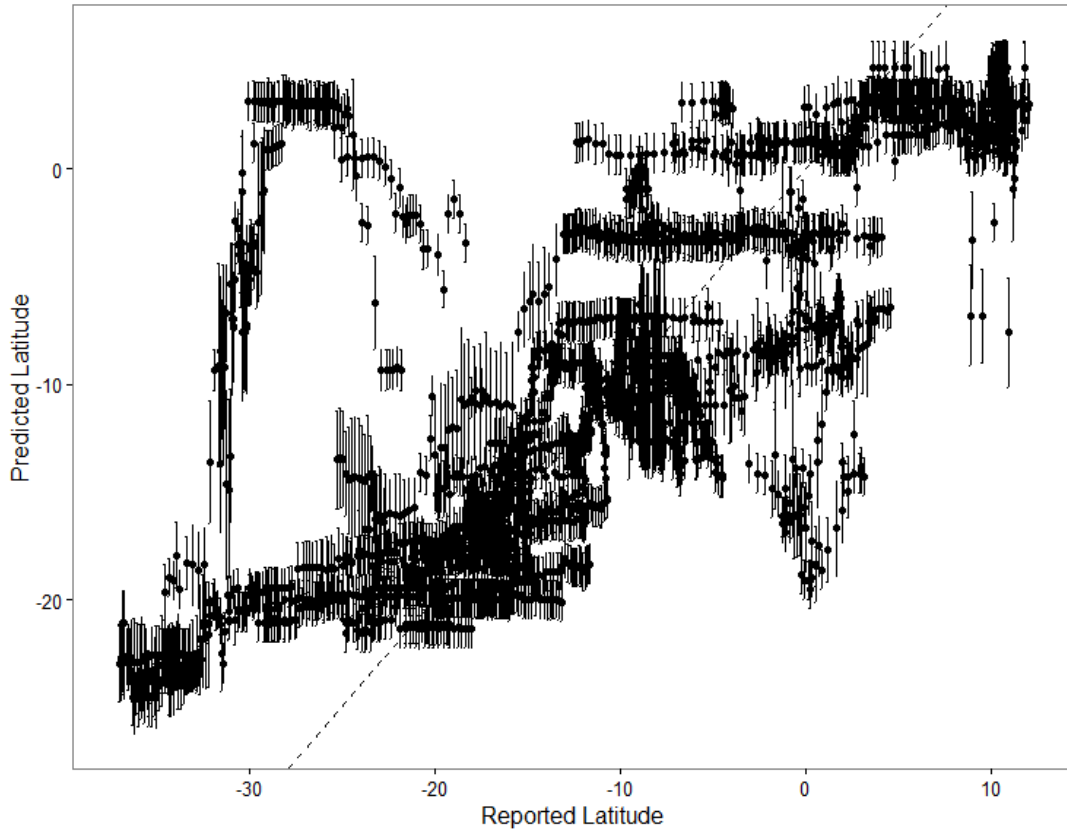


Figure A.4. Leatherback predicted latitudinal positions versus known leatherback latitudes. Error bars surrounding the estimate indicate the standard error. A linear relationship would suggest a good model fit. Wide errors bars are present at many predicted latitudes.

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