Bottom-up and climatic forcing on the nesting and foraging ecology of leatherback turtles (Dermochelys coriacea)

Vincent Sellitto Saba
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BOTTOM-UP AND CLIMATIC FORCING ON THE NESTING AND FORAGING ECOLOGY OF LEATHERBACK TURTLES (DERMOCHELYS CORIACEA)

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

by
Vincent Sellitto Saba
2007
This dissertation is submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

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DEDICATION

I dedicate this dissertation to my wife, Grace, for her constant support, love, and relaxing smile that kept my stress levels to a minimum over the course of my research.
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ABSTRACT

There currently exists a major dichotomy in the nesting population trends of leatherback turtles (*Dermochelys coriacea*) worldwide. Eastern Pacific populations have been declining precipitously while populations in the Atlantic and western Indian Oceans have been either stable or increasing. The populations in the western Pacific have also declined with some near extirpation. Factors attributed to the Pacific population decline are incidental fishery mortality and egg harvesting. Fishery mortality occurs throughout all basins, and with the exception of the western Pacific population, egg harvesting has not been a major factor at the major nesting complexes for almost two decades. Populations in the Atlantic and western Indian Oceans currently tolerate mortality from top-down factors, while the eastern Pacific populations continue to decline. Therefore, trophic forcing from bottom-up factors may be the major cause of this dichotomy. This study addressed the effects of bottom-up and climatic forcing on leatherback populations worldwide, with an emphasis on leatherbacks in the eastern Pacific.

Nesting leatherbacks in the eastern Pacific were highly influenced by ENSO. Cool, highly productive La Niña events caused a high nesting probability whereas warm, less productive El Niño events caused a low probability. Areas of the equatorial Pacific that produced the most accurate nesting estimates, as indicated by sea surface temperature anomalies, were located around the northeast. Foraging conditions in the eastern equatorial Pacific were a function of ENSO governed primary production transitions that determined leatherback nesting numbers in Costa Rica. It appeared that resource availability in the temperate, southeastern Pacific was not sufficient on its own to support vitellogenesis and the nesting process. While coastal foragers were common among most leatherback populations worldwide, they were rare within the eastern Pacific population, possibly from high mortality associated with coastal gillnet fisheries along Central and South America. Among populations worldwide, eastern Pacific leatherbacks had the lowest reproductive output derived from climate driven, inconsistent resource availability. This study demonstrated that the highly sensitive nature of eastern Pacific leatherbacks to anthropogenic mortality derived from interannual and multidecadal climate variation in their foraging areas, thus accounting for their decline rates despite continued beach protection.

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AUTHOR'S NOTE

The primary research chapters of this dissertation were written in the format of the respective journal under which each is either published, in review, or to be submitted. Therefore, these chapters were written in the third person to represent my co-authors. The citations for the chapters are as follows:

Chapter 2


Chapter 3


Chapter 4

BOTTOM-UP AND CLIMATIC FORCING ON THE NESTING AND FORAGING ECOLOGY OF LEATHERBACK TURTLES (DERMOCHELYS CORIACEA)
CHAPTER 1

Worldwide Status of Leatherback Turtles, Background, and Research Objective
Introduction

There currently exists a disparity in the nesting population trends of leatherback turtles (*Dermochelys coriacea*) in the Atlantic, Western Indian, and Pacific Oceans. Assessments indicate that populations of Atlantic and Western Indian leatherbacks are increasing or stable (Hughes, 1996; Girondot et al. 2002; Dutton et al., 2005; Verhage et al. 2006) while those in the Pacific continue to decline (Chan and Liew, 1996; Spotila et al., 1996; Spotila et al., 2000; Hitipeuw et al., 2007) (Fig. 1 A to F). Although the global population of leatherbacks is reported as declining (Spotila et al., 1996) and is classified as "critically endangered" by the World Conservation Union (IUCN), the decline rates observed in the Pacific are not evident in the Atlantic and Western Indian Oceans.

The nesting beaches at Parque Nacional Marino Las Baulas (PNMB), Costa Rica, of which Playa Grande is the primary nesting beach, currently supports the largest nesting population in the eastern Pacific (Reina et al., 2002). This nesting population has decreased precipitously from 1,504 individual females in 1988 to an average of 188 from 2000 to 2003 (Santidrián-Tomillo et al., 2007) (Fig. 1F). Similar nesting population trends in the Pacific Ocean have been reported at Terengganu, Malaysia (Chan and Liew, 1996) (Fig. 1D), Tierra Colorada, Mexico (Pritchard, 1982; Spotila et al., 1996), and Mexiquillo, Mexico (Márquez et al., 1981; Spotila et al., 1996) (Fig. 1E). All of the aforementioned reports concluded that nesting beach exploitation combined with incidental fishery mortality were the major factors causing dramatic decline rates.

Leatherbacks in the Atlantic and Indian Oceans have been exploited analogously to those in the Pacific, however, it has been suggested that conservation efforts at Atlantic and Western Indian nesting beaches preceded efforts in the Pacific allowing for the
observed recovery rates in the Atlantic (Boulon et al., 1996; Dutton et al., 2005; Hughes, 1996). Although beach protection at Parque Nacional Marino Las Baulas (PNMB), Costa Rica has been ongoing since 1991, Santidrián-Tomillo et al. (2007) reported observed recruitment rates from 2000 to 2003 that were half of the expected recruitment rates based on neonate production. They suggested that mortality rates in the ocean before maturation were double the levels of those of a stable population.

In the past, it was suggested that a major source of leatherback mortality at sea derived from incidental bycatch among the tuna and swordfish longline fishery. A recent paper by Lewison et al. (2004) reported significantly higher leatherback bycatch rates among pelagic longline fisheries in the Atlantic compared to those in the Pacific for the year 2000. Furthermore, the authors reported that the majority of longline fishing effort occurred in the Pacific (52%) followed by the Atlantic (37%) and Indian (11%) Oceans. These results suggest that more leatherbacks are incidentally caught in Atlantic waters with less fishing effort than in Pacific waters, yet populations in the Atlantic are still recovering while those in Pacific continue to decline.

There are a few possible explanations for this paradox. One may be that leatherback mortality rates associated with the pelagic longline fishery are being over-estimated. Leatherbacks tend to be foul hooked on longline sets because they rarely attempt to ingest the bait. The post-release survival of leatherbacks after being foul hooked in a longline set is unknown but is assumed to be low. If leatherback bycatch mortality among the longline fishery is in fact low and mortality in the ocean is still a major problem affecting Pacific leatherbacks, it is possible that other fisheries are catching and killing these turtles. Examples include coastal gill net fishing and illegal drift net fishing at
leatherback foraging areas and nesting beaches. A study near the nesting beaches at Trinidad suggested a 35% mortality risk among leatherbacks caught in the coastal gillnet fishery (Lee Lum, 2006). Based on population modeling, Kaplan (2005) suggested that coastal gillnet fisheries were the primary source of anthropogenic mortality among leatherbacks in the eastern Pacific. Procuring artisanal leatherback bycatch data worldwide is not feasible because some of these fisheries are illegal, practiced discretely, and exist in waters at or near third world countries where enforcement and conservation efforts are not functional.

Another possible explanation to this paradox that can be explored practically is that Pacific leatherbacks may be further prone to faster decline rates and/or slower recovery rates due to higher levels of environmental variability that directly affects their foraging areas. High levels of environmental variability in the Pacific Ocean can lead to fluctuations in the availability of food for certain marine animals depending on their trophic status. Analysis of leatherback stomach contents suggests that gelatinous organisms such as medusae, siphonophores, and salps are their primary food sources (Frazier et al., 1985). The gross anatomy of the leatherback digestive tract suggests a stenophagous diet of jellyfish (James and Herman, 2001). Active observations of neonates at sea also confirm a dietary preference for gelatinous prey items (Salmon et al., 2004). The high intrinsic growth rates of gelatinous organisms coupled with their extreme sensitivity to the marine environment, renders their abundance and distribution sporadic (Graham et al., 2001; Mills, 2001).

If Pacific leatherback foraging conditions are of the same variable nature as environmental conditions, growth and recruitment rates could be affected accordingly.
Seasons of poor feeding conditions could result in lower female reproductive output, therefore decreasing recruitment. These poor feeding conditions could also slow growth rates leading to delayed sexual maturity. If leatherback foraging conditions are more stable in the Atlantic and Western Indian Oceans, this may result in faster turtle growth rates, a younger age-at-maturity, higher egg production, and ultimately higher, more consistent recruitment rates.

Research demonstrating the biological consequences of environmental variability in the Pacific Ocean suggests that the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) are the primary climatic phenomena driving productivity (Behrenfeld et al., 2001; Chavez et al., 2003; Chavez et al., 1999). The major environmental phenomenon in the Atlantic Ocean is the North Atlantic Oscillation (NAO), however, the environmental consequences of NAO are not nearly as severe as those associated with ENSO (Behrenfeld et al., 2001). The highly variable nature of the Pacific Ocean could be rendering leatherback populations more vulnerable to anthropogenic disturbance.

**Background – Effects of climate variability on sea turtle nesting ecology**

Literature pertaining to the effects of environmental variability on the nesting biology of sea turtles is scarce and the majority focus on green sea turtles (*Chelonia mydas*). Limpus and Nicholls (2000) found a significant correlation between green turtle nesting numbers and ENSO at Heron Island, Australia. Additionally, Chaloupka (2001) attributed year-to-year variability of green turtle egg production in Southeast Asia to environmental factors. These studies pertained to one species of sea turtle and it has been...
suggested that trophic feeding status determines a sea turtle's sensitivity to climate variability (Broderick et al., 2001).

The remigration interval, the time in between successive nesting seasons (Limpus, 1985), is an aspect of a sea turtle's nesting behavior that can be investigated to determine the effects of the marine environment on the frequency of vitellogenesis throughout a multitude of years. Carr and Carr (1970) and Broderick et al. (2001) suggested that the ecological conditions of foraging areas modulate the length of the remigration interval. These intervals can typically range between 1 and 9 years among the seven species of sea turtle (Miller, 1997). It is during this time that mature female sea turtles migrate to foraging and breeding areas before returning to their natal beaches to nest again. Hays (2000) suggested that high levels of inter-annual variability in nesting stocks are simply a result of variable remigration intervals among the entire nesting population that are modulated by feeding conditions at sea.

Given a stock of females of the same species and colony nesting in the same year, it has been hypothesized that a synchrony in the remigration interval can occur within the nesting stock due to similar experiences to the marine environment (Solow et al., 2002). This assumes that the majority of the nesting stock has similar migration and foraging patterns between successive nesting years and that nest site fidelity remains at a high level. A direct test of this hypothesis concerning green turtles was conducted by Solow et al. (2002). Using sea surface temperature (SST) as a general indicator of oceanographic conditions or essentially, foraging conditions, they found a significant effect of SST on the remigration intervals of green turtles nesting at Tortuguero, Costa Rica. This type of approach has never been applied to leatherbacks. The foraging areas of eastern Pacific
leatherbacks nesting at Playa Grande are suggested to be along the eastern equatorial Pacific, the Chile-Peru Humboldt Current System, and the far off-shore waters of Peru and Chile. These locations are based on satellite tracking data of females leaving the nesting beaches of PNMB, Costa Rica (Morreale et al., 1996; Shillinger and Block, 2006). The productivity of these equatorial and southern latitudes in the eastern Pacific can be highly variable as determined by ENSO (Chavez et al., 1999; Behrenfeld et al., 2001; Yáñez et al., 2001; Chavez et al., 2003) and can potentially affect the nesting ecology of leatherbacks at Playa Grande.

*Background – ENSO, primary production, and leatherback prey*

The effects of ENSO on productivity in the equatorial Pacific and the west coast of the Americas have been well documented. However, satellite tracking studies showed that leatherbacks of PNMB also frequent the far off-shore waters of Peru and Chile extending to 125° W and 40° S (Shillinger and Block, 2006). The effects of ENSO on productivity in off-shore waters south of 20° S have not been investigated to the same extent as in equatorial and coastal waters. Physically, ENSO's signal weakens poleward south of 20° S where local, wind-driven forcing dominates (Strub and James, 2002; Yáñez et al., 2001). This dynamic may have implications on leatherback foraging strategies during and in between El Niño and La Niña events.

There are very few long-term time-series studies involving the abundance and distribution of gelatinous organisms, let alone research on the consequences of climatic variability on their population dynamics. A study by Raskoff (2001) found pronounced differences in the gelatinous community along the mesopelagic depths (100-1000 m) of
Monterey Bay, CA with respect to ENSO. Here, the author used 10 years of BetaCam video data to account for organism presence. The gelatinous organisms that were responding to the ENSO events were all Scyphomedusae. Furthermore, studies by Robison et al. (1998) and Silguero and Robison (2000) found that mesopelagic siphonophores in Monterey Bay had seasonal cycles that correlated with physical changes in the epipelagic waters that are subject to variability by ENSO. A 12-year study by Ozaki et al. (2004) at the Kii Channel, Japan reported that populations of hydromedusae increased in correlation with the bottom intrusion of subsurface, cold nutrient-rich water from the Pacific Ocean. The authors suggested that long-term environmental variability at the Kii Channel might be associated with ENSO, ultimately affecting the zooplankton community including Scyphomedusae.

There are, however, more numerous long-term time-series studies that have focused on the effects of climatic variability on meso- and micro-zooplankton distribution and abundance. Research in the Pacific suggests that ENSO strongly influences the biomass of meso-zooplankton communities at local ecosystems (Dessier and Donguy, 1987; Franco-Gordo et al., 2004; Mackas et al., 2004; Sheridan and Landry, 2004; Sánchez-Velasco et al., 2004). These studies showed that ENSO governed primary productivity transitions were followed by similar transitions in zooplankton abundance and distribution. Leatherback prey items, such as medusae, are primarily carnivores that feed on a wide selection of zooplankton when available (Mills, 1995). These zooplankton prey items comprise of copepods, decapods, fish larvae, fish eggs, protozoa, rotifers, and other medusae.
Background – Leatherback ecology worldwide

Research projects at both eastern Pacific and western Atlantic leatherback nesting beaches have shown extraordinary differences in the nesting ecology and size of the mature females. Atlantic and Western Indian nesting female turtles are larger (mean CCL = 154 to 162 cm) (Hughes, 1996; Girondot et al. 2002; Dutton et al., 2005; Verhage et al. 2006) and remigrate to nest more frequently (mean remigration interval = 2.2 years) (Dutton et al., 2005) compared to Pacific turtles (mean CCL = 144 to 147 cm) (Reina et al., 2002), (mean remigration interval = 3.7 years) (Santidrián-Tomillo et al., 2007). Most compelling, the remigrant return rates at St. Croix, U.S. Virgin Islands are nearly double the rates observed at PNMB, Costa Rica (St. Croix = 58.6 % return rate (McDonald and Dutton, 1996), PNMB = 29.3% return rate (Santidrián-Tomillo et al., 2007)).

There are no data demonstrating that leatherback mortality associated with fisheries is significantly higher in the Pacific Ocean. Beach protection at the major nesting beach in the eastern Pacific is also relatively equivalent. It is possible that there is higher leatherback mortality among unmonitored fisheries in the Pacific but this type of data may never surface. The dichotomies in the growth and nesting ecology of the mature females between the basins may help explain why the Atlantic and Western Indian populations do not show the decline rates observed in the Pacific Ocean. If leatherback feeding conditions in the Atlantic and Western Indian Oceans are of higher quality and temporally more consistent than in the Pacific Ocean, it is likely that the turtles in the Atlantic and Western Indian Oceans will: a) grow faster thus reaching sexual maturity at a younger age; b) remigrate to nest more frequently during the female reproductive life.
stage; and c) have a consistent and higher annual recruitment rate. All three of these statements are true according to the literature, however, a thorough review and comparison of their nesting and foraging ecology has yet to be completed.

The foraging areas and migration patterns of western Atlantic leatherbacks have been studied to a much greater extent than all other populations. Satellite tracking studies involved nesting females, mature males, and juveniles. The turtles tend to frequent the slope and shelf waters off Canada and the northeastern United States (James et al., 2005a; James et al., 2005b; James et al., 2005c), the European shelf waters (Witt et al. 2007), ocean frontal zones in the central north Atlantic, and the coastal waters of northwest Africa (Ferraroli et al., 2004; Hays et al., 2004).

**Research objective**

Here I investigate the effects of bottom-up and climatic forcing on leatherback populations worldwide with an emphasis on the eastern Pacific population nesting at PNMB, Costa Rica. I hypothesize the following: 1) mature female foraging areas in the eastern Pacific are highly inconsistent resulting in variable nesting remigration probabilities; thus variable annual egg production; 2) the nesting probabilities of females in the eastern Pacific are foremost a function of ENSO governed primary production transitions in the equatorial and southeastern Pacific Ocean; 3) mature female foraging areas in the Atlantic and Western Indian Oceans are more productive and more stable thus resulting in consistently higher annual egg production; 4) The higher female reproductive output, and ensuing higher recruitment rates of Atlantic and Western Indian
leatherbacks enabled population recovery and stability in the face of continued anthropogenic mortality from fisheries.

To test these hypotheses, I first modeled the effects of ENSO on the nesting remigration intervals of eastern Pacific leatherbacks at Playa Grande, Costa Rica (Chapter 2) (Saba et al., 2007). I then elucidated the relationship of ENSO to productivity transitions at female leatherback foraging areas in the eastern equatorial and southeastern Pacific (Chapter 3). Finally, I reviewed all of the published nesting data from the major beaches of the leatherbacks worldwide to a) summarize the differences in nesting ecology; b) compare the stability and production of mature female foraging areas in all basins; and c) elucidate the role of inter-annual climate variability in the population biology of eastern Pacific leatherbacks (Chapter 4) (Saba et al., In Review).
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Figure 1. Nesting population trends of leatherback turtles in the Atlantic Ocean: (A) French Guiana and Suriname (Chevalier and Girondot, 1998; Fretey and Girondot, 1989), (B) St. Croix (Alexander et al., 2004; Boulon et al., 1996); the Western Indian Ocean: (C) South Africa (Hughes, 1996; Hughes, pers. comm.); the Pacific Ocean: (D) Malaysia (Chan and Liew, 1996), (E) Mexico (Pritchard, 1982; Sarti et al., 1999), and (F) Costa Rica (Reina et al., 2002; Santidrián-Tomillo et al., 2007; Spotila et al., 2000).
Number of nesting females

(A)

(B)

Year

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(E)  
Number of nesting females

(F)  
Year

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CHAPTER 2

The Effect of the El Niño Southern Oscillation on the Reproductive Frequency of Eastern Pacific Leatherback Turtles
Abstract

1. Pacific leatherback turtle populations *Dermochelys coriacea* have been declining precipitously. It has been suggested that fishery associated mortality is the leading factor causing the decline; however, the sensitivity of leatherbacks to climate variability relative to their population ecology is unknown.

2. We investigated the effects of interannual climate variability, as governed by the El Niño Southern Oscillation (ENSO), on leatherback nesting ecology. We used equatorial Pacific sea surface temperature (SST) anomaly data over various time-scales derived from both moored buoys and remote satellites as signals of ENSO. We then incorporated these data into a remigration probability model for the largest nesting population of eastern Pacific leatherbacks at Parque Nacional Marino Las Baulas (PNMB), Costa Rica.

3. Our results showed that nesting females of PNMB exhibited a strong sensitivity to ENSO as reflected in their nesting remigration probabilities. Cool La Niña events corresponded to a higher remigration probability and warm El Niño events corresponded to a lower remigration probability.

4. We suggest that productivity transitions at leatherback foraging areas in the eastern equatorial and southeastern Pacific in response to El Niño/La Niña events resulted in variable remigration intervals thus variable annual egg production. This phenomenon may render the eastern Pacific leatherback population more vulnerable to anthropogenic mortality than other populations.

5. *Synthesis and applications.* Physical indices of environmental variation can be used to estimate the probability of leatherbacks remigrating to nest at PNMB, Costa Rica. This type of modelling approach can be extremely useful to understand the effects of climatic variations on leatherback populations.
variation on the population dynamics of sea turtles. Our remigration probability model can be applied to any monitored sea turtle nesting population where nesting site-fidelity and beach monitoring coverage remains high. This modelling approach can help nesting beach monitoring programmes forecast remigrant numbers based on prior climate data and can further quantify anthropogenic mortality by validating survival estimates.
Introduction

Understanding the effects of large-scale climate variation on marine life is essential in order to single out anthropogenic influences. The highly stochastic nature of the Pacific Ocean, as governed by atmospheric and oceanic forcing, renders the productivity of its ecosystems variable (Chavez et al. 2003). Pacific leatherback turtle *Dermochelys coriacea* Vandelli 1761 populations have been declining precipitously over the past 15 years (Spotila et al., 2000), thus it is important to understand their sensitivity to climate variability relative to their population ecology. Incidental mortality among coastal gillnet fisheries is thought to be the major anthropogenic influence on leatherback survival in the eastern Pacific (Kaplan 2005), however, the effect of environmental stochasticity on this population has yet to be described.

Assessments of sea turtle populations are based primarily on the census of nesting females at specific beaches. Mature female leatherbacks migrate to nesting beaches where they lay several clutches of eggs within a nesting season. The remigration interval is the time between successive nesting seasons for a particular female and is heavily influenced by the ecological conditions in the turtle’s foraging areas (Broderick, Godley & Hays 2001; Carr & Carr 1970; Chaloupka 2001; Limpus & Nicholls 2000; Solow, Bjorndal & Bolten 2002). Mature female sea turtles require a specific level of energy reserves to migrate to nesting beaches, undergo vitellogenesis (egg formation), and successfully nest. If these energy requirements are not met, nesting will be delayed until feeding conditions improve (Solow, Bjorndal & Bolten 2002). Egg fertilization by mature male leatherbacks usually occurs near nesting beaches (Reina et al. 2005)
suggesting that females have already met their vitellogenesis energy requirements upon arrival.

The El Niño Southern Oscillation (ENSO) is the major climatic phenomenon that governs the overall interannual productivity of the equatorial Pacific (Chavez et al. 1999; Turk et al. 2001). The consequences of ENSO on the marine environment have also been demonstrated in the temperate latitudes of the North Pacific (Franco-Gordo et al. 2004; Marinovic et al. 2002; Raskoff 2001; Ruhl & Smith 2004) and South Pacific (Blanco et al. 2002; Carr et al. 2002; Escribano et al. 2004; Yáñez et al. 2001). Green turtles Chelonia mydas Linnaeus 1758 in the western Pacific have been shown to exhibit a sensitivity to ENSO that is reflected in their egg production and nesting numbers (Chaloupka 2001; Limpus & Nicholls 2000).

In the north tropical Atlantic, sea surface temperature (SST) anomalies are related to both ENSO and the North Atlantic Oscillation (Czaja, Van Der Vaart & Marshall 2002). Fluctuations in western Atlantic green turtle annual nesting numbers at Tortuguero, Costa Rica, were attributed to a high sensitivity of their modelled remigration intervals to SST anomalies in southwestern Puerto Rico (Solow, Bjorndal & Bolten 2002). This implies that populations of Atlantic sea turtles can also be influenced by interannual climate variation derived from the tropical Pacific.

Among the leatherback nesting sites in the eastern Pacific, the beach complex at Parque Nacional Marino Las Baulas (PNMB), Costa Rica, hosts the largest population of mature females (Reina et al. 2002). Satellite tracking studies of post-nesting females at PNMB suggest that the turtles follow a southwestern migration corridor along the Cocos Ridge towards the Galapagos Islands (Morreale et al. 1996; Shillinger & Block 2006)
followed by an open migration through the eastern equatorial Pacific, the Chile-Peru Humboldt Current System, and the far off-shore waters of Peru and Chile (Shillinger & Block 2006), all of which are subject to environmental variation via ENSO (Chavez et al. 1999; Escribano et al. 2004; Turk et al. 2001; Yáñez et al. 2001).

Leatherbacks are foraging specialists relying on gelatinous zooplankton such as medusae, siphonophores, and salps (Frazier, Meneghel & Achaval 1985). The high intrinsic growth rates of gelatinous organisms coupled with their extreme sensitivity to the marine environment, renders their abundance and distribution sporadic (Graham, Pagès & Hamner 2001; Mills 2001). Given the low caloric content of gelatinous organisms (Hsieh, Leong & Rudloe 2001; Lutcavage & Lutz 1986), mature female leatherbacks require large aggregations of prey or areas that favour large prey items to build their energy reserves required for nesting. If the marine environment of the equatorial and southeastern Pacific is highly governed by ENSO, favourable leatherback foraging areas are most likely stochastic both spatially and temporally.

Here we introduce the first empirical analysis investigating the effects of interannual climate variability on leatherback ecology. We used equatorial Pacific SST anomaly data as signals of ENSO and incorporated these data into a leatherback remigration probability model for the nesting female population at PNMB. Information-theory principles (Burnham & Anderson 2002) were applied to identify areas of the equatorial Pacific that produced the best signal strength of ENSO for leatherback remigration probabilities. The spatial and temporal dynamics of SST anomalies at these areas were examined through an empirical orthogonal function analysis and we elucidated their relationship to potential eastern Pacific leatherback foraging areas and ENSO strength.
Methods

TAGGING DATA

Leatherbacks on the Pacific coast of Costa Rica maintain a high site-fidelity to their nesting beach (Santidrián-Tomillo et al. 2007). The nesting season at PNMB begins in late September and ends in early March. Nesting females were tagged with passive integrated transponder tags from 1993 to 2004. The majority of the females were tagged in both flippers in case of single tag failure.

The nesting complex at PNMB consists of two main beaches: Playa Langosta and Playa Grande. Because 90% of the females nest at Playa Grande in a given year (Santidrián-Tomillo et al. 2007), we based our remigrant analysis only on turtles that were originally tagged at Playa Grande. There is a small amount of beach exchange at PNMB (Santidrián-Tomillo et al. 2007); if a turtle originally tagged at Playa Grande nested exclusively at Playa Langosta in a later year, we still counted the event as a remigration. We did not include turtles that were originally tagged at Playa Langosta and nested at Playa Grande either within a year or thereafter. We then calculated remigration intervals for 10 nesting seasons from 1995 to 2004.

At PNMB, the mean observed internesting period, which is the time between ovipositions by an individual female, is 9.5 (± 0.04) days and does not significantly vary from year to year (Reina et al. 2002). The number of nests laid by an individual female in a particular nesting season can be measured by calculating the Estimated Clutch Frequency (ECF) and/or the Observed Clutch Frequency (OCF). The ECF is the preferred method because, unlike the OCF, it will not underestimate clutch frequency if nesting events are missed in between a turtle's first and last nesting. The study by Reina
*et al.* (2002) analyzed ECF at PNMB from 1993 to 1999, therefore, we calculated ECF from 2000 to 2004 by using the first and last appearance dates for an individual female and the mean observed internesting period, as in the previous study. This included females that were observed nesting only once, resulting in an ECF of 1. Because ECF at PNMB is positively correlated with beach coverage (Reina *et al.* 2002), we only incorporated prior ECF data into our analysis from 1997 to 1999 where beach coverage was relatively high.

**INDICES OF CLIMATE VARIATION**

The predominating physical indices of ENSO are anomalies of SST in the equatorial Pacific (Burgers, Jin & Oldenborgh 2005; Chavez *et al.* 1999; McPhaden & Yu 1999; Zelle *et al.* 2004). We used mean monthly SST anomaly data from 59 individual moored buoys that are part of the Tropical Atmosphere and Ocean / Triangle Trans-Ocean Buoy Network (TAO/TRITON) array (McPhaden *et al.* 2001) stretching across the equatorial Pacific from 95° W to 156° E and 8° S to 8° N. We incorporated the effect of SST on a turtle's remigration probability by using a linear logistic model (Solow, Bjorndal & Bolten 2002):

\[
P_y = \frac{\exp[\beta_0 + \beta_1(SST_y)]}{1 + \exp[\beta_0 + \beta_1(SST_y)]}
\]

where \(\beta_0\) and \(\beta_1\) are estimated parameters and \(SST_y\) is a predictor variable representing the mean monthly SST anomaly (°C) from a particular TAO buoy averaged from September of each year \(y\) to September of \(y-13, y-25,\) and \(y-37\) months. This allowed us to analyze

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the effects of mean environmental conditions on female remigration approximately 1 year, 2 years, and 3 years prior to each nesting season.

**REMIGRATION PROBABILITY MODEL**

We developed remigration models that determined the probability of a turtle remigrating to Playa Grande in year \( y \) after \( i \) years using the following variables: annual survival \( s' \), the effect of environmental conditions on the probability of remigrating \( p_y \), the effect of environmental conditions on the probability of not remigrating in previous years \( \prod_{j=1}^{i-2} (1-p_{y-j}) \), and a time at sea influence \( t \). We constructed two models of remigration:

For \( i = 2 \) yrs

\[
R_y = s'p_y
\]

Model A

For \( i \geq 3 \) yrs

\[
R_y = s'p_y \prod_{j=1}^{i-2} (1-p_{y-j})
\]

and

For \( i = 2 \) yrs

\[
R_y = s'p_y
\]

Model B

For \( i \geq 3 \) yrs

\[
R_y = s'p_y \prod_{j=1}^{i-2} (1-p_{y-j})
\]

where model B differs only by adding the \((1/i)t\) term indicating that turtles who did not remigrate after 2 years may have still benefited from previous years' foraging. Two year remigrant probabilities are missing the term \( \prod_{j=1}^{i-2} (1-p_{y-j}) \) from both models because they do not account for 1 year remigrants.

To estimate the random variable \( R_y \) for 2 to 7 year remigrants using the empirical tagging data from Playa Grande, we derived the binomial likelihood probability function

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where \( r_y \) is the number of remigrants nesting in year \( y \) that have not been observed nesting since year \( y-i \), and \( N_{y-i} \) is the number of tagged turtles (both new and remigrant) from year \( y-i \). The term \( R_y \) is the probability of turtles surviving to year \( y \) and remigrating in year \( y \) after 2 to 7 years while \( 1 - R_y \) is the probability of turtles surviving 2 to 7 years but not remigrating to nest. The summarized log likelihood function of eqn 1 is

\[
L_y (r_y, N_{y-i}, R_y) = \left( \frac{N_{y-i}}{R_y} \right) \prod_{i=2}^{7} (R_y)^{r_y} (1 - R_y)^{N_{y-i} - r_y}
\]

Eqn 1

\[
\ln L = \sum_{i=2, y=1993}^{7, 2004} \left[ r_y \ln(R_y) + (N_{y-i} - r_y) \ln(1 - R_y) \right]
\]

Eqn 2

accounting for 12 years of tagging data from 1993 to 2004. Equation 2 is maximized by adjusting the parameters \( \beta_0, \beta_1, \sigma, \) and \( t \) (model B only). Models A_0 and B_0 represent A and B under the condition that \( \beta_1 = 0 \) eliminating the effect of \( SST_y \) (Solow, Bjorndal & Bolten 2002). Each model's remigrant estimate was ranked using the corrected Akaike Information Criterion (AICc) among 59 TAO buoys over three time scales and without the inclusion of \( SST_y \).

MODEL DETAILS

The binomial random variable \( r_y \) can result in two possible outcomes (remigrating or not remigrating) from a trial size of \( N_{y-i} \) turtles. The outcome of remigrating has a probability \( R_y \) and an outcome of not remigrating with probability \( 1 - R_y \) for each turtle where \( R_y \) is
a function of the estimated parameters $\beta_0$, $\beta_1$, $s$, $t$ (model B only), and the empirical predictor variable $SST_y$. The likelihood function (eqn 2) was maximized for each TAO buoy's $SST_y$ using the empirical data set from Playa Grande comprising of $N_{y,i}$ and $r_y$ for $y = 1993$ to 2004 and $i = 2$ to 7 years. For each buoy's set of $SST_y$, we calculated remigrant estimates $E$ for each year $y$ given its respective $R_y$ ($i = 2$ to 7 years) that is based on the estimated parameters $\beta_0$, $\beta_1$, $s$, and $t$ from the maximum likelihood of $L$ (eqn 2). The estimated number of remigrants for each year $y$ is given by

$$E_y = \sum_{i=2}^{7} R_i N_{y,i}$$

where $N_{y,i}$ is the sum of new recruits (from the tagging data) and estimated remigrants $E_{y,i}$ from previous years.

**MODEL APPLICATION**

The linear logistic equation $p_y$ is the probability of remigration based purely on $SST_y$ whereas $R_y$ is the total probability of remigration based on $p_y$, $s$, and $t$ (model B). We used the empirical remigrant data from Playa Grande to calculate the likelihood function (eqn 2) and then maximized it by adjusting the parameters $\beta_0$, $\beta_1$, $s$, and $t$ (model B only). This gives a significant advantage over the model by Solow, Bjorndal & Bolten (2002) because they did not maximize their likelihood function using empirical remigrant data, they only used annual nesting numbers whereas we used both annual nesting numbers $N_{y,i}$ and the annual remigrant numbers $r_y$ for 2 to 7 year remigrants. We also used the number of turtles that did not remigrate ($N_{y,i} - r_y$) from the empirical data set so that our
model did not assume that a female must remigrate in 2 to 7 years if she survives. By setting $\beta_1 = 0$ in $p_y$ (model $A_0$ and $B_0$), we eliminated the $SST_y$ effect on remigration leaving a constant probability for $p_y$ such that $R_y$ is purely a function of time since annual survival is also constant. The remigration probability $R_y$ can be applied to any remigration interval but it should be based on the typical remigration interval range of the nesting population in question.

MODEL SELECTION

We applied information-theory principles to evaluate each TAO buoy’s model performance (Burnham & Anderson 2002). Conventional hypothesis testing (use of $P$ values) should never accompany information-theory (Burnham & Anderson 2002) hence the absence of ‘significance’ terms when we discussed each model’s strength. Our approach estimated the Kullback-Leibler (K-L) (Kullback & Leibler 1951) distance between reality (observed number of remigrants) and each TAO buoy’s remigrant number estimate, and between the remigrant number estimate without the inclusion of $SST_y$ (model $A_0$ and $B_0$).

The AIC method (Akaike 1973) ranks each model by approximating the K-L distance between the model’s estimated number of remigrants and the observed where the smallest AIC value corresponds to the most parsimonious model. The $AIC_c$ (Hurvich & Tsai 1989) was used as opposed to AIC where

$$AIC_c = -2\log(L) + 2V + \frac{2V(V + 1)}{(n - V - 1)}$$
because it corrects for small sample sizes \((n/V < 40)\) where \(V\) is the number of estimated parameters and \(n\) is the empirical data set sample size.

We calculated \(\Delta AIC_{c}\) values (\(AIC_{c} - AIC_{m}\)) and Akaike weights for each TAO buoy using the three \(SST_{y}\) time periods and for models \(A_{0}\) and \(B_{0}\) (total of 356 models) to determine which buoy's \(SST_{y}\) produced the best remigrant estimate (Table 1 and 2). The \(\Delta AIC_{c}\) values could have also been applied by subtracting each TAO buoy's \(AIC_{c}\) (model A and B) from the \(AIC_{c}\) of model \(A_{0}\) and \(B_{0}\) respectively. These \(\Delta AIC_{c}\) values demonstrate the power of each buoy's \(SST_{y}\) in fitting the number of remigrants as opposed to the fit without \(SST_{y}\). The resulting \(\Delta AIC_{c}\) values followed the exact same contours described in Figure 3 a-c.

Normalized Akaike weights \(w_{m}(AIC_{c})\) (Burnham & Anderson 2002) were used to interpret the probability of model \(m\) minimizing the K-L distance where

\[
 w_{m}(AIC_{c}) = \frac{\exp(-0.5 \Delta_{m}AIC_{c})}{\sum_{k=1}^{K} \exp(-0.5 \Delta_{k}AIC_{c})}
\]

and \(K\) is the number of candidate models. The evidence ratios (Burnham & Anderson 2002) were obtained by dividing the candidate model's Akaike weights resulting in strength of evidence in favor of one model over another. These ratio values indicated the probability of selection \((pos)\) that one model is more likely to be the best K-L model over another.
REMOTE SATELLITE DATA AND EMPIRICAL ORTHOGONAL FUNCTION ANALYSIS

We used Pathfinder 4 km Advanced Very High Resolution Radiometer (AVHRR) satellite data (NASA 1985) to increase the resolution of SST in the equatorial Pacific. Anomalies of SST were calculated at 5° x 5° grids encompassing the same area as the 59 TAO buoys and each grid was analyzed under the remigration probability model over the three SST time periods. Pathfinder AVHRR 4 km SST data comprised of version 5.0 mean monthly daytime ascending pass files from January 1985 to September 2004 (NASA 1985). The data set was used from its beginning in 1985 to produce the best SST anomaly calculations. We used satellite imaging software (Kahru 2005) to calculate mean SST anomalies for 5° x 5° grids covering the same area as the 59 TAO buoys resulting with 88 individual grids. The mean SST anomaly for each grid was used as an SST predictor value in model B to produce the ΔAICc contours (kriging interpolation).

We computed the first two principal components (PCI and PC2) of AVHRR SST anomaly data via an empirical orthogonal function analysis that extended from 20° N to 40° S. This enabled us to distinguish patterns of SST variation in the equatorial and southern Pacific that exhibited the greatest levels of SST variation. We then applied a harmonic analysis via a least-squares method to compare the eigenvectors of the TAO array area (95° W to 156° E and 8° S to 8° N) to the Multivariate ENSO Index (MEI) (Wolter & Timlin 1998). This enabled us to elucidate the relationship of SST variation in the equatorial Pacific to ENSO strength variation. We chose the MEI as an indicator of ENSO strength because it incorporates six climatic variables in the tropical Pacific comprised of sea-level pressure, zonal and meridional components of surface wind, SST,
surface air temperature, and total cloudiness fraction of the sky (Wolter & Timlin 1998). We determined the harmonic constituents of the MEI using a Fourier analysis (Emery & Thomson 1998) and then applied them to a regression of the eigenvectors of PC1 and PC2 to determine their variance explained by the MEI.

Results

The remigration intervals of leatherbacks tagged at Playa Grande typically ranged from 2 to 7 years (Fig. 1a). In some seasons, we observed 1 year, 8 year, and 9 year remigrants but they accounted for a very small percentage of the total remigrant data set (1 year = 0.52 %, 8 year = 0.69 %, 9 year = 0.52 %). The number of remigrants from 1995 to 1997 was a function of the number of turtles tagged since 1993 but did not explain the oscillations from 1998 to 2004 (Fig. 1b). Furthermore, when sufficient time passed to allow the observance of 7 year remigrants, the remigrant composition was not consistent from 2000 to 2004 ($P < 0.05$) (Fig. 1a).

From 1997 to 2004, the mean beach coverage was 87.25 % and the mean ECF was 6.50 ($\pm 0.37$) clutches per season. The ECF did not significantly vary from 1997 to 2004 ($P = 0.16, n = 1,183$) and was not correlated to beach coverage (Pearson's $r = 0.36$). Furthermore, the ECF did not vary significantly between years that followed El Niño (1997, 1998, and 2001 to 2004) and the years that followed La Niña (1999, 2000) ($P = 0.16, n = 1,183$).

Both models A and B, under all three $SST_y$ time periods, outperformed $A_0$ and $B_0$ respectively [probability of selection (pos) of A over $A_0 = 1.00$, and of B over $B_0 = 1.00$] suggesting that the predictor variable $SST_y$ strongly influenced the probability of
leatherbacks remigrating to Playa Grande (Table 1). Model B outperformed model A for all time periods of SST$_y$ ($\text{pos} = 1.00$). This extremely large weight of evidence suggested that the parameter $t$ was an important component affecting remigration, meaning that turtles remigrating after more than two years still benefited from prior years' foraging.

All of the 59 TAO buoys signalled ENSO, but we singled out individual buoys for each of the three SST$_y$ time periods that produced the best remigrant estimates under model B (Table 2). Our estimate of remigrants without SST$_y$ ($B_0$) (Fig. 2a) fitted the observed data relatively well from 1995 to 1997 but did not account for the oscillations thereafter. The top-ranked models for each of the three time periods of SST$_y$ accounted for the remigrant oscillations after 1997 to various degrees (Fig. 2 b-e). The TAO buoys located at 5° N 125° W and 8° N 110° W using SST$_{yn}$ produced the best estimates (Table 2, Fig. 2 b,c). Their respective annual survival estimates (Fig. 2 b,c) were similar to those reported for Playa Grande leatherbacks based on tag return rates of 1993-98 cohorts (Santidrián-Tomillo et al., 2007). The best fits under model B for SST$_{y,25}$ and SST$_{y,37}$ analyses were ranked within the top 10 (Table 2) (Fig. 2 d,e). Values of $t$ for the top-ranked models indicated that as the remigration interval $i$ increased from 3 to 7 years, the value of prior years' foraging decreased (Fig. 2 b-e).

Certain areas of the equatorial Pacific served as better signals than others over specific time periods of SST$_y$ (Fig. 3 a-c). The spatial structure of the $\Delta$AIC$_c$ values from the satellite analysis followed the same general pattern as the TAO buoy analysis with similar areas of the equatorial Pacific producing better remigrant estimates than others. For SST$_{y,13}$, the area between 0° N to 10° N and 110° W to 125° W produced excellent signal strength of ENSO for leatherback remigration probabilities (Fig. 3a, blue areas) as
did the TAO buoys in the same area (Fig. 2 b,c) (Table 2). Cool SST anomalies corresponded to high remigration probabilities whereas warm SST anomalies corresponded to low probabilities (Fig. 3 d-f). The sensitivity of the 2 to 7 year remigration probability to equatorial Pacific SST variation was not subtle given that a -2°C anomaly change increased the probability over 500% (Fig. 3d). The first and second principal components of SST variation in the TAO array area accounted for 52.9% of the total variation within that area (PCI = 34.8%, PC2 = 18.1%) (Fig. 4 a,b). The variance explained by the MEI for PCI was 74.43% (Fig. 4c) and 66.22% for PC2 (Fig. 4d). The regression was based on 8 harmonic constituents of the MEI.

Discussion

LEATHERBACK REMIGRATION AT PNMB

Females nesting at PNMB tended to remigrate within 2 to 7 years, however, on rare occasion, we did observe 1, 8, and 9 year remigrants. These 1 year remigrants (a total of 3 females) may have migrated to highly productive foraging areas close to the nesting beach and were able to nest in successive seasons. The 8 and 9 year remigrants (total of 7 females) were either at sea for those time periods without nesting or they may have nested elsewhere. Reports of females tagged at PNMB nesting exclusively outside of the park in later nesting seasons are scarce (Santidrián-Tomillo et al. 2007), therefore we did not include a nesting site-fidelity parameter in our model; doing so would not have affected our remigrant estimates.

Our values of ECF from 1997 to 2004 did not vary and were not correlated to beach coverage like those calculated by Reina et al. (2002) from 1993 to 1999. We suggest
that the high beach coverage from 1997 to 2004 (mean = 87.25 %) resulted in a stable
ECF for each year. For this reason, we did not include the ECF values from 1993 to 1996
in our analysis because they were calculated based on relatively low beach coverage
(mean = 66.00 %). A full representation of the 2 to 7 year remigrants was not possible
until 2000. The 2 to 7 year remigration intervals and ECF were not correlated suggesting
that a leatherback’s time at sea between nesting years does not affect its clutch frequency
upon re-nesting.

ENSO'S EFFECT ON LEATHERBACK REMIGRATION

Our results suggest that interannual climate variability, as governed by ENSO, highly
influenced the probability of leatherbacks remigrating to nest at Playa Grande, Costa
Rica. Cool periods of SST that corresponded to high remigration probabilities were
indicative of highly productive La Niña events when the thermocline of the central and
eastern Pacific was elevated resulting in an increased upwelling magnitude of cold,
nutrient rich water. Warmer episodes were less productive El Niño events when the
thermocline was depressed. Leatherback remigration probabilities exhibited a strong
reaction to the 1997-98 El Niño\1998-99 La Niña transition that was evident in all three
SST, time periods (Fig. 3 d-f). The peak in the number of remigrants (Fig. 2 b-e) in 2000
was a result of the strong 1998-99 La Niña event. Biological production rates in the
equatorial Pacific were substantially affected during the transition (30% decrease during
El Niño, 40% increase during La Niña) (Turk et al. 2001). The effect of the 1998-99 La
Niña on productivity south of 15° S was also evident (Escribano et al. 2004; Yáñez et al.
2001) but not of the same magnitude observed near the equator (Chavez et al. 1999; Turk
et al. 2001). Without tracking data from the late 1990s, we cannot confirm where the turtles were feeding during the productivity transitions, we can only assume they followed similar migration corridors suggested by the studies in the mid 1990s (Morreale et al. 1996) and more recently (Shillinger & Block 2006). Moreover, the tracking study by Shillinger & Block (2006) took place during warm El Niño events and their tracks may describe a migration that is specific to El Niño periods. The turtles may spend more time at or near the equator during La Niña events but further satellite tracking during these episodes will be required to confirm this.

The time at sea influence \( t \) was an important component affecting remigration. Individuals that benefitted the most from this factor were the 3-year remigrants and this benefit decreased with increasing remigration interval. This means that if a turtle does not remigrate after 2 years due to insufficient energy reserves, it can still use those initially acquired energy reserves plus what it gains from an additional year of foraging for a 3 year remigration; however, the more time the turtle spends at sea, the more energy it invests in foraging.

The best remigrant estimates failed to fit the peak observed in 2003 (Fig. 2 b-e) because of a low remigration probability for that season due to the 2002-03 El Niño. It is possible that some females at PNMB migrate to foraging areas that are still highly productive during El Niño events (V. Saba unpublished data). These areas are located along the west coast of South America where productivity is dominated by coastal upwelling. Interestingly, only one of the post-nesting females from PNMB had a migration pattern close to the coast (Shillinger & Block 2006). This suggests that a small portion of the females at PNMB migrate to the coastal areas, which may explain why a
peak in migration occurred in 2003 that our model did not estimate. Moreover, the lack of coastal foragers from PNMB may be a result of high mortality rates from coastal gillnet fisheries, rendering these foragers a minority within the population.

DYNAMICS OF ENSO SIGNAL STRENGTH FOR LEATHERBACK REMIGRATION

The wide area of signal strength for both $SST_{y-13}$ and $SST_{y-25}$ (Fig. 3 a,b) and their similar $\Delta AIC_c$ values (Table 1) suggested that environmental conditions approximately one to two years prior to each nesting season determined whether or not leatherbacks remigrated to Playa Grande. Furthermore, the area of signal strength moved east as the $SST_y$ time period decreased (Fig. 3 a-c). The eastward progression existed because equatorial thermocline depth anomalies during the 1997-98 El Niño, and possibly others, originated in the west and propagated east (McPhaden & Yu 1999). Additionally, there was a longitude-dependent time lag of up to 1 year between thermocline depth variations in the west and SST anomalies in the east, consistent with large scale ocean dynamics that control the ENSO cycle (Meinen & McPhaden 2000; Zelle et al. 2004).

The signal strength contour pattern shows that certain areas of the equatorial Pacific signalled the effect of ENSO on leatherback remigration better than others (Fig. 3 a,b). Similarities between Figure 3 a,b and Figure 4 a,b can be observed. Dominated by equatorial and coastal upwelling, the equatorial cold ‘tongue’ structure (Jin 1996) that extends to 165° E in Figure 4a is evident in Figure 3a. The pocket of SST variation (blue-purple) in the east was similar in structure to the pocket of moderate ENSO signal strength (dark green) in Figure 3a, both of which extended to about 100° W. The TAO

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buoys that produced excellent ENSO signal strength for leatherback remigration (Fig. 3a, blue areas) were on the contour interval of SST variation in the northeastern equatorial Pacific (Fig. 4b). These isotherms extended south to the off-shore areas of Peru and Chile, which the turtles have also been shown to frequent (Shillinger & Block 2006). Furthermore, ENSO governed interannual SST variability in the northeastern equatorial Pacific was in synchrony with SST variability in the southeastern areas near Peru and Chile extending from 10° N to 20° S and the coast to 140° W (Montecinos, Purca & Pizarro 2003). The empirical orthogonal function analysis confirmed that the similarity between the ENSO signal strength patterns (Fig. 3 a,b) and the first two principal components of SST variation in the TAO area (Fig. 4 a,b) was a result of the physical dynamics of ENSO in the equatorial Pacific. This is because the majority of the variance in the eigenvectors of PC1 and PC2 derived from the MEI (Fig. 4 c,d).

APPLICATIONS TO MANAGEMENT

Our model is not limited to any one population or one species of sea turtle. In this context, it is important that turtle nesting site-fidelity and monitoring coverage remains high at the nesting beach in question to avoid over-estimates of remigration intervals. The clutch frequencies of the females also need to be taken into consideration when investigating reproductive frequency. Furthermore, the general location of the foraging areas of the post-nesting females should be known in order to focus any environmental variation analysis.

The $SST_y$ predictor variable in the equation for $p_y$ can be replaced with any environmental parameter. Moreover, additional environmental parameters can be
incorporated into the remigration model through multiple $p_i$ linear logistic equations. It is important, however, to minimize the number of parameters in the model to conserve parsimony.

The results will give nesting beach managers insight as to which environmental variables are influencing turtle remigration and allow them to predict the coming season's number of remigrants using the appropriately lagged environmental data. Forecasting remigrant numbers prior to a nesting season may help managers quantify their necessary beach patrolling and hatchery effort. Most importantly, mature female survival estimates can be made by exposing the nesting population's sensitivity to environmental variation. This can help to quantify the influence of anthropogenic mortality and validate conservation strategies focused on reducing it.

CONCLUSIONS

We stress that SST anomalies in the equatorial Pacific served as 'surrogate' indicators of leatherback foraging conditions. The foraging areas of mature females probably have a widespread distribution throughout the eastern equatorial and southeastern Pacific; therefore it is difficult to single out specific areas to use as direct signals. It has been shown that ENSO can affect the distribution and abundance of gelatinous organisms (Ozaki et al. 2004; Raskoff 2001; Silguero & Robison 2000), and the structure of the deep-sea megafaunal community (Ruhl & Smith 2004) in the north Pacific. It is likely that ENSO has similar effects in the equatorial and southeastern Pacific where leatherbacks are migrating and potentially foraging on gelatinous prey at various depths.
extending to the mesopelagic zone. The high sensitivity of the food-resource dependent remigration probability strengthens the validity of this notion.

The exact relationship between increased primary productivity from La Niña and leatherback prey availability in the equatorial and southeastern Pacific is unknown; however, our results suggest that the increased rates of primary production and subsequent increase of secondary production leads to an increase in the abundance, distribution, and size of the gelatinous zooplankton that the turtles feed on throughout the water column. There are, however, other factors in addition to food availability that can regulate the size and density of gelatinous zooplankton populations, particularly for medusae (Graham, Pagès & Hamner 2001; Lucas 2001).

Our low estimates of annual survival suggests that anthropogenic mortality needs to be reduced. If coastal gillnet fisheries are in fact the primary anthropogenic source of mortality (Kaplan 2005), conservation policy effort should be targeted at these fisheries. Eastern Pacific leatherbacks are highly susceptible to any form of anthropogenic mortality due to the stochastic nature of mature female foraging areas rendering annual egg production variable. The ability for a population to recover depends on sufficient recruitment rates. Because ENSO affects productivity and ultimately leatherback egg production in the eastern Pacific, any negative anthropogenic influence on leatherback mortality needs to be minimized or eliminated in order to maintain the highest egg production rates possible and allow for population recovery in the face of reduced reproduction related to El Niño events.
Literature Cited


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Table 1. AICc analysis results from both models A and B using model averaging. For each of the three SSTy time periods, each model’s mean ΔAICc and mean annual survival estimate $\hat{s}$ are listed. Models $A_0$ and $B_0$ represent A and B without the inclusion of SSTy, respectively. The number of parameters estimated is represented by $V$.

<table>
<thead>
<tr>
<th>Model</th>
<th>$V$</th>
<th>SSTy Time Period (months)</th>
<th>Mean ΔAICc</th>
<th>Mean $\hat{s}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>4</td>
<td>13</td>
<td>82.33</td>
<td>0.85</td>
</tr>
<tr>
<td>B</td>
<td>4</td>
<td>25</td>
<td>93.66</td>
<td>0.85</td>
</tr>
<tr>
<td>B</td>
<td>4</td>
<td>37</td>
<td>123.68</td>
<td>0.86</td>
</tr>
<tr>
<td>B_0</td>
<td>3</td>
<td>-</td>
<td>160.13</td>
<td>0.89</td>
</tr>
<tr>
<td>A</td>
<td>3</td>
<td>13</td>
<td>162.96</td>
<td>0.90</td>
</tr>
<tr>
<td>A</td>
<td>3</td>
<td>25</td>
<td>169.08</td>
<td>0.89</td>
</tr>
<tr>
<td>A</td>
<td>3</td>
<td>37</td>
<td>189.95</td>
<td>0.89</td>
</tr>
<tr>
<td>A_0</td>
<td>2</td>
<td>-</td>
<td>224.89</td>
<td>0.90</td>
</tr>
</tbody>
</table>
Table 2. AICc analysis results from model B. Ranks are based on normalized Akaike weights ($w_m(AIC_c)$) that are a function of each model's $\Delta AIC_c$ where values of $w_m(AIC_c)$ < $1 \times 10^{-5}$ are virtually 0.00 when compared to the top-ranked model. Akaike weights are normalized using models A, B, A0, and B0, for all three time periods of SST$_y$ from 59 TAO buoys (Ranks range from 1 to 356).

<table>
<thead>
<tr>
<th>Model</th>
<th>V</th>
<th>SST$_y$ Time Period (months)</th>
<th>$\Delta AIC_c$</th>
<th>TAO Buoy SST$_y$</th>
<th>Rank</th>
<th>$w_m(AIC_c)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>B 4</td>
<td>13</td>
<td>0.00</td>
<td>5°N 125°W</td>
<td>1</td>
<td>0.68</td>
<td></td>
</tr>
<tr>
<td>B 4</td>
<td>13</td>
<td>1.55</td>
<td>8°N 110°W</td>
<td>2</td>
<td>0.32</td>
<td></td>
</tr>
<tr>
<td>B 4</td>
<td>25</td>
<td>13.49</td>
<td>0°N 140°W</td>
<td>3</td>
<td>8.06 x 10$^{-4}$</td>
<td></td>
</tr>
<tr>
<td>B 4</td>
<td>13</td>
<td>16.96</td>
<td>8°N 95°W</td>
<td>4</td>
<td>1.42 x 10$^{-4}$</td>
<td></td>
</tr>
<tr>
<td>B 4</td>
<td>13</td>
<td>22.02</td>
<td>8°N 125°W</td>
<td>5</td>
<td>1.13 x 10$^{-5}$</td>
<td></td>
</tr>
<tr>
<td>B 4</td>
<td>37</td>
<td>31.61</td>
<td>8°N 180°W</td>
<td>9</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>B$_0$</td>
<td>3</td>
<td>-</td>
<td>160.13</td>
<td>236</td>
<td>0.00</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 1. Leatherback remigrant dynamics at Playa Grande. (a) The percentage of 2 to 7 year remigrants and (b) the total number of individual 2 to 7 year remigrants observed nesting at Playa Grande during each nesting season from 1995 to 2004.
Fig. 2. Comparison of observed with model B’s estimated number of remigrants at Playa Grande. The estimated number of 2 to 7 year remigrants (a) without the inclusion of $SST_y$ (model $B_0$), with the inclusion of $SST_y$ from TAO buoy’s (b) $5^\circ N 125^\circ W$ ($SST_{y,13}$), (c) $8^\circ N 110^\circ W$ ($SST_{y,13}$), (d) $0^\circ N 140^\circ W$ ($SST_{y,25}$), and (e) $8^\circ N 180^\circ W$ ($SST_{y,37}$). The estimated number of remigrants for each year $y$ were calculated using each model’s $R_0$ ($i = 2$ to 7 years) and $N_{p,k}$. Values for parameters $\beta_0$, $\beta_1$, $t$, and $s$ were based on each model’s maximized $L$. 

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Number of remigrants

\[
\begin{align*}
(a) \quad &\hat{\beta}_0 = -2.56 \\
&\beta_1 = 0.00 \\
&t = 6.93 \\
&\hat{s} = 0.88 \\
&\text{Observed} \\
&\text{Estimated}
\end{align*}
\]

\[
(b) \quad &\hat{\beta}_0 = -2.48 \\
&\beta_1 = -0.94 \\
&t = 8.69 \\
&\hat{s} = 0.80 \\
&\text{Observed} \\
&\text{Estimated}
\]

\[
(c) \quad &\hat{\beta}_0 = -2.61 \\
&\beta_1 = -1.86 \\
&t = 8.15 \\
&\hat{s} = 0.83 \\
&\text{Observed} \\
&\text{Estimated}
\]

\[
(d) \quad &\hat{\beta}_0 = -2.46 \\
&\beta_1 = -0.78 \\
&t = 8.19 \\
&\hat{s} = 0.80 \\
&\text{Observed} \\
&\text{Estimated}
\]

\[
(e) \quad &\hat{\beta}_0 = -1.98 \\
&\beta_1 = -2.59 \\
&t = 7.74 \\
&\hat{s} = 0.80 \\
&\text{Observed} \\
&\text{Estimated}
\]

\[
\text{Nesting season}
\]

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Fig. 3. ENSO signal strength for leatherback remigration probabilities $R_p$ and the relationship of $SST_y$ to $R_p$. (a) Model B's contoured $\Delta$AICc values from 88 $5^\circ$ x $5^\circ$ grids using $SST_y$ values from satellite AVHRR 4 km SST data 13 months, (b) 25 months, and (c) 37 months prior to each nesting season. Locations of the 59 TAO buoys are overlaid the contours with small black circles. Lower $\Delta$AICc values correspond to higher ranked grids whose $SST_y$ values produced better remigrant estimates. The relationship between $SST_y$ and $R_p$ for the top-ranked TAO buoys (d) $5^\circ$ N 125$^\circ$ W ($SST_{y,13}$), (e) 0$^\circ$ N 140$^\circ$ W ($SST_{y,25}$), and (f) 8$^\circ$ N 180$^\circ$ W ($SST_{y,37}$) under model B. The remigration probability is the mean $R_p$ for 2 to 7 year remigrants each year. Anomalies of SST are not in real-time. They are in the form of $SST_y$ thus they are lag corrected.
Fig. 4. Principal components of AVHRR 4 km SST variation in the Pacific Ocean comprised of the TAO array area and potential leatherback foraging areas in the southeastern Pacific from 1985 to 2004. (a) The first principal component (PC1) and (b) second principal component (PC2) of SST variation from 20° N to 40° S and the west coast of the Americas to 140° E. The colour bar is unitless and represents the strength of eigenvector variability. The locations of the 59 TAO buoys are overlaid the PCs with small black circles. The red star indicates the location of Playa Grande, Costa Rica and the white enclosure is the potential migration area of the nesting females (Morreale et al. 1996; Shillinger & Block 2006). The relationship of (c) PCI's and (d) PC2's eigenvector of SST variation in the TAO array area to the standard departure of the MEI.
CHAPTER 3

Abstract

The eastern Pacific leatherback turtle (*Dermochelys coriacea*) population has been continually declining over the past two decades. This population is extremely sensitive to anthropogenic mortality because of inconsistent food resource availability due to the El Niño Southern Oscillation (ENSO). The effects of ENSO are reflected in the nesting ecology of leatherbacks at the major nesting complex in the eastern Pacific at Parque Nacional Marino Las Baulas (PNMB), Costa Rica. However, an oceanographic analysis of their migration area in relation to their nesting response has yet to take place. We analyzed the biological and physical dynamics of the leatherback migration area in relation to ENSO and leatherback nesting ecology at PNMB, Costa Rica. We used remote satellite data to calculate resource availability via a primary production model, and to analyze the physical dynamics of the migration area via sea surface temperature (SST) fronts and sea surface height anomalies. The migration area ranged from 10° N to 40° S and from the coastlines of Central and South America to 125° W. Primary production north of 15° S was highly governed by interannual variability as indicated by the Multivariate ENSO Index (MEI) while south of 15° S, production had a more seasonal signal. Nesting leatherbacks at PNMB positively responded to cool, highly productive La Niña events throughout the eastern equatorial Pacific. The turtles also responded to large-scale equatorial phytoplankton blooms encompassing 110° W that were induced by iron enrichment following the termination of El Niño events. Although resources were seasonally consistent in the southern migration area and there was a relatively higher frequency of physical discontinuities such as SST fronts and eddies, alone it did not appear to provide nesting females adequate energy requirements for
nesting. Thus primary production in the northern, equatorial migration area determined the nesting response at PNMB, Costa Rica. Coastal foragers appeared to be a minority within the population due to high mortality rates associated with coastal gillnet fisheries along South America and possibly Central America. We suggest that ENSO significantly influenced the nesting ecology of leatherbacks at PNMB because the majority of the population consists of pelagic foragers that strictly rely on the eastern equatorial Pacific for prey consumption prior to the nesting season. Compared to every other leatherback nesting population worldwide, the eastern Pacific population was the only one that lacked coastal migration. Leatherback mortality from coastal gillnet fisheries needs to be eliminated so that coastal foraging may occur and reduce the population's sensitivity to ENSO by enabling higher nesting rates during El Niño years.
1. Introduction

The population of leatherback turtles (*Dermochelys coriacea*) has been precipitously declining in the eastern Pacific Ocean (Spotila et al., 2000). Nesting population trends at the major beaches in Costa Rica and Mexico have both shown similar declining trends over the past 15 years (Santidrián-Tomillo et al., 2007; Sarti et al., 1999). Moreover, the eastern Pacific population is the smallest in size and has the lowest reproductive output among all other populations worldwide; this is attributed to the high rate of interannual and multidecadal climate variability in the eastern Pacific rendering resource availability highly variable (Saba et al., 2007; Saba et al., In Review). It has been suggested that the major anthropogenic source of leatherback mortality derives from coastal gillnet fisheries along Central and South America (Eckert and Sarti, 1997; Kaplan, 2005). However, it is important to understand the relationship of climate variability, resource availability, and the migration and foraging ecology of leatherbacks to provide a foundation for conservation management in the eastern Pacific Ocean.

Satellite tracking of post-nesting females from Parque Nacional Marino Las Baulas (PNMB), Costa Rica and Mexiquillo, Mexico showed leatherbacks migrating through the equatorial and southeastern Pacific Ocean (Eckert and Sarti, 1997; Morreale et al., 1996; Shillinger and Block, 2006). Round-trip migration from the nesting beach to foraging areas and back has yet to be described; this would be a difficult task given that the mean remigration interval (time between successive nesting seasons) in the eastern Pacific is 3.7 years (Saba et al., In Review; Santidrián-Tomillo et al., 2007). Satellite tracking of post-nesting females at PNMB in the mid-1990's and more recently suggests that the majority migrate southwest from the nesting complex following the Cocos Ridge until
they reach the vicinity of the Galápagos Islands where they then diverge to the equatorial and southeastern Pacific. Post-nesting females from Mexico do not appear to follow the Cocos Ridge although they do exit the nesting complex southwest and then diverge to similar areas as those from Costa Rica once they reach the equator (Eckert and Sarti, 1997).

Leatherback turtles are among the largest reptiles in the world, yet rely on a diet comprised almost entirely of gelatinous zooplankton which have a very low caloric content (Hsieh et al., 2001), thus sub-adults and adults require large patches of prey to fulfill their energy demand (Lutcavage and Lutz, 1986; Wallace et al., 2006). Mature female sea turtles have an even higher energy demand prior to reproduction to fulfill resource allocation requirements for vitellogenesis (egg formation) (Hamann et al., 2002; Wallace et al., 2006). For multiple species of sea turtles, oceanographic conditions at their foraging areas prior to the nesting season determine their probability of nesting (Limpus and Nicholls, 2000; Saba et al., 2007; Solow et al., 2002). In the eastern Pacific, the El Niño Southern Oscillation (ENSO) significantly affects the reproductive frequency of leatherbacks nesting at PNMB, Costa Rica (Saba et al., 2007). Cool, highly productive La Niña events increase their nesting remigration probability while warm, less productive El Niño events decrease the probability. This relationship strongly suggests that primary production can be used as proxy for gelatinous zooplankton abundance and distribution, or essentially, resource availability for leatherback turtles.

Using only ENSO indices in a model to predict the number of nesting leatherbacks at PNMB is very effective, however, there were a few nesting seasons during which small nesting peaks occurred that were not predicted due to warm El Niño events (Saba et al.,
2007). Recently, Ryan et al. (2006) demonstrated that very large phytoplankton blooms ($\sim 5 \times 10^5 \text{ km}^2$) occurred in 1998, 2003, and 2005 in the central and eastern equatorial Pacific that were not in sync with the typical ENSO signal. These unusually large-scale blooms followed El Niño events, triggered by the shoaling of the New Guinea Coastal Undercurrent (NGCUC) that resulted in a coupling of the New Guinea shelf and Equatorial Undercurrent. This coupling led to enhanced iron concentrations in the euphotic zone of the central and eastern equatorial Pacific producing these large-scale blooms that could not be predicted purely by ENSO indices (Ryan et al., 2006).

Furthermore these equatorial blooms were most pronounced at 110° W (Ryan et al., 2006), well within the migration area of eastern Pacific leatherbacks. It is possible that leatherbacks nesting at PNMB responded to Western Pacific modulated blooms along the equator that were not accounted for in the remigration probability model (Saba et al., 2007).

The effect of ENSO on eastern Pacific leatherbacks is reflected in their nesting ecology, however, an extensive analysis exposing the relationship of the dynamics of their foraging areas to their nesting ecology has yet to take place. Here we investigated the biological and physical properties of the migration area used by post-nesting eastern Pacific leatherbacks. We used the yearly response of the nesting females at PNMB as an indicator of foraging conditions (Saba et al., 2007) and focused our oceanographic analysis on the migration areas described for post-nesting females (Morreale et al., 1996; Shillinger and Block, 2006). The effect of ENSO on the biological production of the migration area was determined by calculation of satellite derived primary production (PP). We explored the physical qualities of the migration areas through sea surface
temperature (SST)- and sea surface height (SSH)- frontal zones that could serve as physical discontinuities to aggregate gelatinous zooplankton. We then provided insights to leatherback foraging ecology in the eastern Pacific with an emphasis on conservation management of this declining population.

2. Data and methods

2.1 Migration area, primary production, and nesting ecology

We determined the migration area of eastern Pacific leatherbacks from PNMB through a review of satellite tracking studies by Morreale et al. (1996) and Shillinger and Block (2006). We did not analyze individual tracks separately because we were interested in how the entire population could have utilized the migration area. To understand resource availability both spatially and temporally, we calculated PP using remote satellite data. We applied the Behrenfeld-Falkowski vertically generalized production (VGP) model (Behrenfeld and Falkowski, 1997) using the satellite software package Windows Image Manager (WIM) (Kahru, 2006) and three satellite data sets comprised of sea surface chlorophyll, SST, and photosynthetically active radiation (PAR). We used monthly SeaWiFS level three (9 km) sea surface chlorophyll-a and PAR data (Feldman and McClain, 2006) and monthly Pathfinder 4 km Advanced Very High Resolution Radiometer (AVHRR) SST data (NASA, 2006) from September 1997 to December 2005 resulting in 100 monthly images. The coastlines were slightly expanded to avoid satellite data that was obtained too close to the coast, which was subject to error. We used WIM to calculate mean monthly PP (mg C m$^{-2}$ month$^{-1}$) and ArcView 3.2a to calculate the size of the migration area. Along with calculating 100 monthly PP images.
of the total migration area, we also divided the area into $5^\circ \times 5^\circ$ grids and calculated PP at each grid to increase the resolution of the time-series. We also divided the migration area into latitudinal bands from the coastline westward at $5^\circ$ latitudinal intervals to produce a zonal comparison of PP.

Leatherbacks nesting at PNMB exhibited a strong response to the 1997-98 El Niño and 1998-2000 La Niña (Saba et al., 2007), therefore we were interested in how their migration area changed relative to these events. We calculated composites of PP during the 1997-98 El Niño and during the 1998-2000 La Niña based on indices of the MEI. The El Niño composite ranged from September 1997 to June 1998 while the La Niña composite ranged from October 1998 to October 2000. We also divided the migration area in half using $15^\circ$ S as the center point and calculated total mean monthly PP (Tg C year$^{-1}$) using each area's size and mean monthly PP during the two ENSO periods.

We used the remigrant nesting data at Playa Grande, PNMB from 1998-99 to 2004-05 from Saba et al. (2007) with the addition of the 2005-06 nesting season. Each year, the nesting season begins in October and ends in February. A remigrant is a turtle that was originally tagged at Playa Grande that returned to nest in a successive season. Given that the number of remigrants at PNMB can be closely predicted using ENSO indices prior to each nesting season, we compared peaks in remigrants to peaks in PP in the migration area to discern possible foraging hot spots that influenced leatherback nesting probabilities.
2.2 Seasonal versus interannual resource variability

To understand the temporal dynamics of PP at the migration area, we applied a harmonic analysis and Fourier regression (Emery and Thomson, 1998) to each 5° x 5° grid. Seasonality was determined by using the annual and semi-annual harmonic constituents of the PP time-series from each grid. A least-squares method was used to fit the estimated PP time-series to the observed and produce $r$ values to determine the variance explained by the harmonic constituents.

Because ENSO influences the reproductive frequency of leatherbacks at PNMB, we used the multivariate ENSO index (MEI) (Wolter and Timlin, 1998) as indicator of ENSO strength from September 1997 to December 2005. The MEI incorporates six climatic variables in the tropical Pacific Ocean comprised of sea-level pressure, zonal and meridional components of surface wind, SST, surface air temperature, and total cloudiness fraction of the sky. Interannual variability of PP in each grid was determined by using the primary non-seasonal harmonic constituents of the MEI at 14, 17, 20, 25, 33, 50, and 100 month amplitudes that, by themselves, explained 96% of the variance of the MEI. The 7 non-seasonal harmonic constituents of the MEI were applied in a Fourier regression to each grid's PP time-series and $r$ values were calculated. From the harmonic analysis, two $r$ values were calculated for each grid, each of which described how much PP variance was explained by seasonality and the MEI separately. We then contoured the grids' $r$ values (kriging interpolation) to visualize the temporal dynamics of PP in the migration area.

We applied an empirical orthogonal function analysis to the 100 monthly PP images of the migration area using WIM (Kahru, 2006) to expose the primary sources of
variability. The harmonic analysis and Fourier regression of the MEI was applied to the eigenvectors of the first three principal components (PCs) of PP variability; this demonstrated the amount of PP variability in the foraging area influenced by the MEI. Along with the first three principal components, their corresponding spatial modes were calculated using WIM (Kahru, 2006). The spatial modes demonstrated the strength and location of PP eigenvector variability in the migration area.

2.3 Sea surface temperature and sea surface height

Physical discontinuities such as SST frontal zones and meso-scale eddies are important features that are known to physically aggregate gelatinous zooplankton (Graham et al., 2001). We analyzed the distribution and frequency of SST fronts and SSH anomalies in the migration area. For SST fronts, we used WIM's SST edge detection method (Kahru, 2006) that incorporates a modified version of the single-image edge detection (Cayula and Cornillon, 1992) by using a variogram analysis to detect small-scale fronts (Diehl et al., 2002). We calculated mean SST front frequency images for the 12 months using 252 monthly Pathfinder 4 km AVHRR SST data from 1985 to 2005 (NASA, 2006). We were also interested in the mean distribution and frequency of fronts during the ENSO events analyzed in the PP analysis. Satellite data for SST dates further back than ocean color data, thus we were able to include the 1987-88 El Niño and 1988-89 La Niña for further comparison. The frequency and distribution of SST fronts is a function of the number of monthly images used in the analysis, therefore, we designated equal time periods for each ENSO event based on the MEI. We used monthly SST from April to the following March of each ENSO event; this not only kept the time period...
consistent, but also analyzed the fronts over a similar seasonal range so that local climate variability remained consistent. Images of SST edge frequency were created for the four ENSO events. Finally, we calculated a composite of SST in the migration area using 252 monthly Pathfinder SST images from January 1985 to December 2005.

To analyze large-scale eddy dynamics in the migration area, we used weekly remote satellite altimetry data comprised of SSH anomaly (± cm) images that were merged from TOPEX/Poseidon, Jason, and ERS-1/2 created by Ssalto/Duacs and distributed by Archiving Validation and Interpretation of Satellite Data in Oceanography (AVISO) (ftp://ftp.cls.fr/pub/oceano/AVISO/SSH/duacs/global/dt/ref/msla/merged/h/). The images used ranged from December 2003 to December 2005. Our goal was to understand the typical distribution of eddies throughout a typical year, not during the strong ENSO transition when SSH changes along the equator were exceptionally strong and large-scale eddies were not evident. We used WIM to calculate monthly averages from each month's weekly image set and then calculated 3-month averages for each austral season.

3. Results

3.1 ENSO and primary production

The migration area of eastern Pacific leatherbacks from PNMB, Costa Rica ranged from 10° N to 40° S extending from the coast to 125° W, based on the general movement patterns described by Morreale et al. (1996) and Shillinger and Block (2006). The movements of post-nesting females from Mexico extended further north, however the western longitudinal range was similar with the exception of one individual that moved past 140° W (Eckert and Sarti, 1997). With the exception of leatherbacks tracked near
the Galápagos Islands, migration directly along coastal areas was not a typical pattern observed by these studies thus the majority of the turtles remained far off-shore.

Coastal areas were the most productive in the migration area. Production along the coasts was reduced during the strong 1997-98 El Niño but remained high relative to the open-ocean areas (Fig. 1A-C). The most significant PP response to the 1997-2000 ENSO transition was north of 15° S (Fig. 1B,C). The temporal variability of PP was dominated by the MEI \((r > 50\%)\) north of the equator and west of the Gulf of Panama (Fig. 2A).

High PP variability governed by the MEI was also evident west of 100° W between 10° S and 20° S (Fig. 2A). In the Gulf of Panama, the cycle of PP was more seasonal towards the coast and the effect of the MEI was weak (Fig. 2A,B). The effect of the MEI on PP weakened southward where seasonal variation dominated south of 25° S (Fig. 2A,B).

The area between the Galápagos Islands and Costa Rica, which includes the Cocos Ridge where the post-nesting females migrate from PNMB, had exceptionally low seasonality (Fig. 2B). South of the equator, the MEI's effect on coastal PP never exceeded \(r\) values greater than 50%.

The first three PCs of PP variability in the migration area accounted for 21.6% of the total variation (PC1 = 10.8%, PC2 = 5.8%, PC3 = 5.0%) (Fig. 3A-F). The amount of variability explained by the MEI for the first three PCs was 90.53%, 86.87%, and 84.82% respectively (Fig. 3A-C). The spatial mode of PC1 demonstrated the general trend of the MEI on PP where warm El Niño events decreased production and cool La Niña events increased production (Fig. 3D). The eigenvectors of PC1 were essentially the mirror image of the MEI (Fig. 3A). This relationship was strongest and most evident north of 20° S (Fig. 3D) as also demonstrated in the harmonic analysis (Fig. 2A,B). The spatial
mode of PC2 showed the pocket of MEI governed PP west of 100° W between 10° S and 20° S (Fig. 3E) as also shown in Fig. 2B. For PC3, the spatial mode (Fig. 3F) demonstrated PP variability along the equator that, as indicated by the eigenvectors, was not as in sync with the MEI (Fig. 3C). There was a slight lag between the peak eigenvector variation of PC3 and the MEI that followed El Niño events; this was likely a result of the large-scale blooms that followed the 1998, 2003, and 2005 El Niño events (Fig. 3C). The third spatial mode also showed MEI governed PP variability in the South Pacific Subtropical Gyre (SPSG) (Fig. 3F).

3.2 Primary production transitions and leatherback nesting response

The size of the northern migration area from 15° S to 10° N was 14.38 x 10^6 km^2, slightly smaller than the southern area from 15° S to 40° S which was 16.48 x 10^6 km^2. In terms of mean production throughout the area, seasonal variability of PP in the northern area was extremely low while seasonality dominated in the south (Fig. 4A). In terms of the mean PP generated per month by each area (Tg C month^-1) from 1997 to 2005, the north was significantly more productive (P < 0.0001) by 1.78 Tg C month^-1 than the south (Fig. 4B). Production in the south was not significantly affected during the 1997-2000 ENSO transition (P = 0.75) while there was a significant increase in the north between the 1997-98 El Niño and the 1998-2000 La Niña (+ 2.6 Tg C month^-1) (P < 0.0001) (Fig. 4B). Mean production in the north was also significantly higher during the 1998-2000 La Niña relative to the entire time-series from 1997 to 2005 (+ 0.55 Tg C month^-1) (P < 0.005) (Fig. 4B). Even though there was a weak seasonal signal in the north, periods of maximum PP occurred August through October, which were extended

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during the 1998-2000 La Niña (Fig. 4A). In the south, maximum production occurred during the austral spring (October through December) of each year (Fig. 4A).

The 5° latitudinal bands of PP further demonstrated the stronger interannual variability north of 15° S and the decrease in PP south of 15° S until an increase occurred at 35° S approaching the South Pacific Subtropical Convergence (SPSC) (Fig. 5). The 5° x 5° grid along the equator that encompassed 110° W clearly showed the peaks in PP just after El Niño events that were influenced by the shoaling of the NGCUC (Fig. 6A).

The response of the nesting numbers at PNMB to PP transitions in the migration area appeared to be primarily a function of areas north of 15° S. The largest peak in remigrants occurred in 1999-2000 and 2000-01 (Fig. 6B) that were a response to the 1998-2000 La Niña PP increase north of 15° S (Fig. 4B). Moreover, the smaller peaks in remigrants in 2003-04 and 2005-06 (Fig. 6B) appeared to be a response to the NGCUC induced large-scale blooms along the equator around 110° W (Fig. 6A). However, the small number of remigrants in 1998-99 indicated no response to large 1998 NGCUC induced bloom (Fig. 6A,B); nesting numbers in 1998-99 were in sync with typical ENSO indices when the 1997-98 El Niño caused a low remigration probability in 1998-99 (Saba et al. 2007).

3.3 Oceanic fronts

The composite of monthly SST from 1985 to 2005 demonstrated the general, large-scale horizontal temperature gradients in the migration area (Fig. 7). The typical SST range of the migration area was from 30° C north of the equator to about 12° C at 40° S (Fig. 7). The highest mean monthly frequencies of small-scale SST fronts were typically

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concentrated around the SPSC, the coast of South America, and along the equator (Fig. 8A). The highest concentration of SST fronts occurred between May and July of each year (Fig. 8A). Along the equator, the frequency of SST fronts was reduced during the 1987-88 and 1997-98 El Niño events when equatorial upwelling was reduced (Fig. 8B). From the composite of PP from 1997 to 2005, fronts of PP (i.e. chlorophyll fronts, nutraclines) concentrated around equatorial and coastal upwelling zones, the Costa Rica Dome, the Gulf of Panama, and the SPSC (Fig. 9).

The majority of large-scale eddy abundance occurred south of 20° S (Fig. 10). Positive anomalies of SSH were warm core, anticyclonic eddies and negative anomalies were cold core, cyclonic eddies (Fig. 10). Along the equator, positive SSH anomalies moved east from 2004 to 2005 because of the 2004-05 El Niño. Towards the end of 2005 in the austral spring, SSH anomalies in the eastern equatorial Pacific started to decrease from the ensuing 2006 weak La Niña (Fig. 10). Eddies were not as frequent in the north where SSH dynamics were dominated by interannual ENSO events.

4. Discussion

4.1 ENSO and eastern Pacific leatherback foraging areas

Leatherbacks nesting at PNMB, Costa Rica were responding to PP transitions in the northern part of the foraging area from 15° S to 10° N. This is based on the strong relationship of their nesting response to highly ENSO governed PP transitions in the northern part of the migration area. If foraging conditions south of 15° S influenced the nesting probability for leatherbacks at PNMB, we would not expect to observe such a large influence of ENSO on their remigration given its weakened signal in the south. The
small peaks in remigrant numbers in 2003 and 2005 can be attributed to ENSO, although in a different context than the peaks observed in 1999-00 and 2000-01 (Fig. 6B). The peaks in 1999-00 and 2000-01 were a response to the cool, La Niña conditions in the equatorial Pacific when the thermocline was shallow and the magnitude of upwelling was intensified (Figs. 1C, 5). The effect of this event on leatherbacks nesting at PNMB was captured in the remigration probability because the model used SST in the equatorial Pacific as an indicator of ENSO (Saba et al., 2007). The remigrant peaks in 2003-04 and 2005-06 were not captured by the model because the NGCUC induced blooms in the eastern equatorial Pacific were not detectable through SST. During these blooms, the thermocline depth was not anomalously shallow as it was during La Niña; they followed the termination of El Niño events and were caused by iron enrichment to the Equatorial Undercurrent from the El Niño induced shoaling of the NGCUC in the western equatorial Pacific (Ryan et al., 2006). We cannot, however, suggest that these NGCUC induced blooms consistently affect leatherbacks nesting at PNMB because no nesting response was observed in 1998 that followed the largest NGCUC induced bloom (Fig. 6A,B). The nesting probabilities in 1998 were highly influenced by the strong 1997-98 El Niño when we observed a low number of remigrants (Fig. 6B) (Saba et al., 2007) due to the reduction of PP north of 15°S (Fig. 4A,B). We suggest that no nesting response to the 1998 NGCUC induced bloom occurred because the over-all PP of the north was at its lowest level, whereas in 2003 and 2005 the NGCUC induced blooms occurred when PP was closer to the mean and significantly higher than during the 1997-98 El Niño event (Figs. 4A,B, 5). This suggests that foraging conditions throughout the entire northern
part of the migration area need to be at a minimum threshold to cause any nesting response from an NGCUC induced bloom.

4.2 Coastal foraging and gillnet fisheries

The satellite tracking data from both Mexico and Costa Rica showed only a few individuals migrating to coastal areas (Eckert and Sarti, 1997; Shillinger and Block, 2006). It is possible that more than 1 year of tracking is required to observe a higher frequency of coastal migration. Coastal upwelling is affected by ENSO, however, these areas still remain much more productive than equatorial areas during El Niño (Fig. 1B,C). Moreover, the coastal areas are typically more productive than equatorial areas regardless of ENSO (Fig. 1A). The Peruvian Coastal Upwelling region, extending 1000 km from the coast, is the richest area in eastern equatorial Pacific in terms of PP and biomass (Pennington et al., 2006) (Fig. 1). The Gulf of Panama was not only a highly productive coastal area, it also had a relatively high seasonal signal due its high terrestrial run-off and wind induced mixing (Pennington et al., 2006) (Figs. 1, 2). The Costa Rica Dome is a biological 'hotspot' for many trophic levels from zooplankton to fish to marine mammals (Fiedler, 2002) and lies in very close proximity to PNMB (Fig. 1A). In this context, coastal areas should be a common migration destination for eastern Pacific leatherbacks where they can take advantage of the high production opposed to the vastly reduced production along the equator during El Niño.

We surmise that high rates of leatherback mortality among gillnet fisheries along the Central and South American coasts drastically reduced the number of coastal foragers, thus rendering the pelagic foragers a population relic. This theory assumes that
leatherbacks maintain a high site fidelity to their foraging areas year after year. Presently, the only leatherback study that reported round-trip migration from foraging areas to nesting beaches and back was done by James et al. (2005) in the western Atlantic. The authors showed 6 adult males, 7 adult females, and 6 juveniles migrating from the coastal waters of Nova Scotia, Canada to southern tropical waters and then back north to within several hundred kilometers of where they occurred the previous year.

Eckert and Sarti (1997) compiled Chilean gillnet fishery reports from Frazier and Montero (1990) and Weidner and Serrano (1997) spanning the 1980's and into the 1990's. These fisheries typically target swordfish. They suggested that over 800 leatherbacks were caught in 1990 and that number doubled in 1997 with increasing fishing effort. The leatherback mortality rate associated with their incidental capture among these fisheries was 80% (Frazier and Montero, 1990). Given these high mortality rates from Chile alone, and taking into account the effects of gillnet fisheries from the entire coastline of South and Central America spanning to Costa Rica, we conclude that coastal foragers are now a minority within the eastern Pacific leatherback population due to a high bycatch and mortality rate from coastal gillnet fisheries.

There is less documentation of leatherback bycatch along Peru although Eckert and Sarti (1997) suggested a substantial amount of leatherback mortality from the Peruvian fisheries. A study at San Andrés, Peru among a gillnet fishery for small sharks and rays suggested a historical mortality of 200 leatherbacks per year at this location alone (de Paz et al., 2006). Interestingly, the majority of leatherbacks caught were large juveniles (mean curved carapace length = 109.27 ±14.4 cm) (de Paz et al., 2006). This could be a
function of the mesh size (up to 20 cm) or suggest that the coast of Peru serves as major foraging area for juveniles and sub-adults.

4.3 Conceptual leatherback foraging strategy in the eastern Pacific

At PNMB, Costa Rica, the nesting season spans from October to February with the peak nesting period from November to January (Reina et al., 2002). Given that leatherbacks at PNMB lay an average of about 6 nests per season with a mean internesting interval of 9.5 days, the entire nesting process for a female lasts approximately 2 months (Reina et al., 2002). Therefore, the majority of females would be leaving the nesting beach area between January and March and swimming towards the Galápagos Islands along the Cocos Ridge. Based on the study by Morreale et al. (1996), it takes about 40 days for a leatherback to reach the Galápagos Islands from PNMB, thus the majority of turtles would be arriving at or near the archipelago between February and April. Peak production along the equator was typically between August and October, however, production along the west coast of the Galápagos Islands is twice that of the equatorial upwelling areas year-round (Pennington et al., 2006) and remains productive during El Niño events (Fig. 1). Although PP on the west coast of the archipelago was highly governed by the MEI, the area was more productive than the surrounding equatorial upwelling areas because macronutrients are supplied via equatorial upwelling and island upwelling where the Equatorial Undercurrent impinges the western coasts of the archipelago. Furthermore, the islands provide iron to their surrounding surface waters releasing primary producers from micronutrient limitation (Pennington et al., 2006). We suggest that the western coasts of the Galápagos Islands provide post-nesting females...
from PNMB with a highly dependable foraging area, especially after the completion of a nesting season when their energy reserves are highly depleted. One of four leatherbacks tracked past the Galápagos Islands remained along the western coasts of the islands for nearly two weeks before continuing south while almost all the others remained on the western side of islands when passing through (Morreale et al., 1996). More recent studies indicate that all post-nesting females tracked to the Galápagos Islands from PNMB migrated along the west side of the archipelago (Shillinger and Block, 2006). Although leatherbacks leaving the nesting beaches of Mexico did not traverse along the Cocos Ridge, many did make their way towards the western side of the Galápagos Islands (Eckert and Sarti, 1997). Females that did not migrate to the Galápagos Islands after the nesting season must have strictly relied on equatorial upwelling unless they were one of the minority of coastal foragers. For leatherbacks at PNMB, highly productive coastal areas in close proximity to the nesting complex are the Costa Rica Dome and Gulf of Panama (Fig. 1). Only one turtle from PNMB migrated directly to the Gulf of Panama after the nesting season and remained there for over a year (Shillinger and Block, 2006).

Among other leatherback populations in both the Atlantic and western Pacific, arrival to temperate foraging areas follows the seasonal spring blooms and arrival time is in the summer months (Benson et al., 2007a; James et al., 2005; McMahon and Hays, 2006; Saba et al., In Review; Witt et al., 2007) when gelatinous zooplankton abundance peaks (James and Herman, 2001; Witt et al., 2007). Production peaks in the southern part of the migration area in the austral spring (September to November) (Fig. 4A), thus we would expect leatherback arrival in austral summer from December to February. Consequently,
Shillinger and Block (2006) reported leatherbacks south of 30° S during the austral summer.

4.4 Southeast Pacific and physical forcing

Our results suggest that resource availability in the southern part of the migration area was not sufficient on its own to support the energy requirements for leatherback nesting. With the exception of the coastlines, the southeastern Pacific has very low PP as a result of the permanent thermocline within the SPSG that is considerably deeper than the mixed layer (Fiedler and Talley, 2006). However, the southeastern Pacific contains many physical frontal features that can aggregate gelatinous zooplankton (Figs. 7-10). Our analysis clearly demonstrated both the large-scale (Fig. 7) and small-scale (Fig. 8) SST frontal features, fronts associated with eddies (Fig. 10), and the frontal zones associated with PP (Fig. 9). It is important to note that physical forcing alone is not enough to create suitable foraging; sufficient PP is initially required to support the food web (Polovina et al., 2006). Sharp gradients in PP along the edges of the SPSG (Fig. 9) could aggregate gelatinous prey along the zone of convergence (Polovina et al., 2001). Pacific loggerhead turtles (Caretta caretta) migrate along chlorophyll frontal zones, most importantly the Transitional Zone Chlorophyll Front (TZCF) that lies at the boundary between low chlorophyll subtropical gyres and high chlorophyll subarctic gyres (Polovina et al., 2006; Polovina et al., 2001; Polovina et al., 2000). In the southeastern Pacific, the TZCF lies between 35° S and 45° S depending on the season. We suggest that leatherbacks utilize the TZCF during the austral summer along with the many other physical frontal zones in the south.
The SST frontal zones in the south were not affected by ENSO as they were in the north. Moreover, a substantial number of eddies occurred in the south that could also serve as prey hotspots (Polovina et al., 2006) (Fig. 10). In this region, eddies derive from the Chile-Peru Current near the coastline of South America where warm, anticyclonic eddies propagate northwestward and cool, cyclonic eddies propagate westward (Chaigneau and Pizarro, 2005). Post-nesting leatherbacks from South Africa utilize both cyclonic and anticyclonic eddies suggesting that both eddy types can aggregate prey (Luschi et al., 2003). Eddies were observed in the SPSG during the austral summer (Fig. 10) and may serve as the only features within the gyre where leatherbacks can find prey aggregations; we suggest that the northern, eastern, and southern edges of the SPSG serve as the main targets for leatherback foraging due the strong frontal systems (Figs. 8,9).

4.5 Eastern equatorial Pacific and leatherback nesting response

Although the southern area of the migration area serves as a seasonally productive foraging area that contains many physical features for aggregating prey, mature female leatherbacks still rely on equatorial areas to support the nesting process. As with western Atlantic leatherbacks (James et al., 2005), eastern Pacific leatherbacks likely leave the temperate area in the austral fall and return to the tropics. Peak production in the north was typically between August and November, thus the turtles would be arriving at an advantageous time (Fig. 4A). Furthermore, the NGCUC induced blooms along the equator at 110° W typically begin May through August after El Niño (Ryan et al., 2006). The lag between increased PP and gelatinous zooplankton growth is shorter in tropical
regions (Purcell, 2005) thus leatherbacks could arrive closer to PP maximums and still take advantage of gelatinous zooplankton aggregations. This has been demonstrated with leatherback arrival at the Mauritania upwelling system in the tropical eastern Atlantic (Eckert, 2006). Therefore, the timing of PP transitions in the northern foraging area may be the primary reason that the peak nesting at PNMB occurs from November to January. This suggests that leatherbacks could build their energy reserves for nesting about 5 to 7 months prior to the nesting season. Leatherback energy budget calculations suggest that females in the eastern Pacific would need approximately 151 days to build energy reserves for nesting (Wallace et al., 2006), and our oceanographic analysis confirms these findings.

4.6 Comparison to other leatherback populations worldwide

Our results suggest that the northern migration area of eastern Pacific leatherbacks was the crucial zone where resource availability determines the nesting response at PNMB, Costa Rica. Whereas eastern Pacific leatherbacks rely on a tropical area for resources required for nesting, it appears other populations rely on temperate areas. In the Atlantic Ocean, the highly productive North Atlantic serves as a major migration area for western Atlantic leatherbacks (Eckert, 2006; Ferraroli et al., 2004; Hays et al., 2004; James et al., 2005) that have a reproductive output nearly twice that of eastern Pacific leatherbacks (Saba et al., In Review). Although some western Atlantic leatherbacks migrate only to tropical areas (Ferraroli et al., 2004; Hays et al., 2004), the majority migrate to the North Atlantic. In terms of the spatial availability of resources, the North Atlantic is the most productive leatherback foraging area whereas the southeastern
Pacific is one of the least productive (Saba et al., In Review). Similar to eastern Pacific leatherbacks, it appears that eastern Atlantic turtles from Gabon also highly rely on equatorial upwelling with no observation of these turtles in the temperate North Atlantic (Witt et al., unpublished). The robust size and stable trend of the eastern Atlantic population suggests that foraging at equatorial upwelling areas has been a successful strategy. However, these turtles have also been observed along the eastern coast of South America (Billes et al., 2006) suggesting that coastal foraging may be an additional strategy essential to the success of this population.

The most striking difference in the foraging ecology between eastern Pacific leatherbacks and every other population worldwide is their lack of coastal migration. Coastal areas are highly productive, especially for gelatinous zooplankton where leatherback occurrence is highly correlated to jellyfish presence in the eastern North Atlantic (Houghton et al., 2006; Witt et al., 2007), the western North Atlantic (James and Herman, 2001), and the northeastern Pacific (Benson et al., 2007a). Western Pacific leatherbacks nesting in Papua migrate across the entire Pacific Ocean to the coastlines of northwest North America where the turtles are commonly observed foraging on scyphomedusae (Benson et al., 2007a; Benson et al., 2007b). These studies demonstrate the importance of coastal areas as crucial leatherback foraging areas. It is highly likely that leatherback mortality among coastal fisheries off Central and South America exceeds that of any other area in the world. Furthermore, the relatively low and variable nature of resources at eastern Pacific leatherback foraging areas exacerbates their negative response to anthropogenic mortality (Saba et al., In Review).
5. Conclusions

Our results suggest that the oceanographic conditions in the eastern equatorial Pacific determined whether or not females successfully nest at PNMB, Costa Rica. These results likely apply to the nesting population in Mexico given their similar foraging areas and nesting season duration. The lack of coastal migration combined with the strong ENSO signal in the nesting ecology of leatherbacks at PNMB suggests that the nesting population consists primarily of pelagic foragers that rely on the equatorial Pacific for resources needed for vitellogenesis and the nesting process. The turtles' migration area probably expands further west than 125° W as our area was based on just over a 1-year duration of tracking. Transitions in PP along the equator extend much further west than 125° W along the equatorial cold tongue, thus the turtles could also be responding the ENSO governed transitions in the central equatorial Pacific as well. However, the NGCUC induced blooms were most pronounced at 110° W suggesting that the foraging areas were typically in the eastern equatorial Pacific. Using equatorial SST indices alone did not completely predict the number of turtles remigrating to nest at PNMB because blooms induced by the NGCUC are not signaled by local climate conditions. The use of PP transitions at 110° W at the termination of El Niño events should increase the nesting prediction accuracy.

Conservation measures aimed at reducing leatherback bycatch among coastal fisheries need to increase substantially. Given that this population is already subject to natural variability in their foraging areas as governed by ENSO, anthropogenic mortality needs to be eliminated, especially in coastal areas, to allow for a thriving foraging
population. Our analysis suggests that the majority of females nesting at PNMB are typically pelagic foragers. The western side of the Galápagos Islands may serve as a potential hotspot for leatherbacks between February and April of each year. If coastal fisheries at the archipelago are in operation during that time, they need to take appropriate action to avoid turtle interaction. We also suggest that any leatherbacks migrating to the coast of Chile would likely arrive during the austral summer as the others do far-off shore, thus the Chilean coastal swordfish fishery could reduce their leatherback take by either changing or closing fisheries during specific times. Coastal gillnet fisheries along Peru also incidentally kill leatherbacks and that is another fishery within which leatherback mortality needs to be minimized. If leatherback mortality among coastal gillnet fisheries is sufficiently reduced or eliminated, eventually coastal foraging may no longer be rare, reducing the entire population's sensitivity to ENSO and thus enabling higher nesting rates during El Niño years.
Literature Cited


Figure 1. Mean monthly primary production at the migration area (A) from September 1997 to December 2005; (B) during the 1997-98 El Niño from September 1997 to June 1998; (C) during the 1998-2000 La Niña from October 1998 to October 2000. Values in red can be greater than 1400 mg C m\(^{-2}\) month\(^{-1}\) because we scaled down the range to show PP outside of the highly productive coastal areas. The location of PNMB is indicated by the white star.
Figure 1 A to C.

(A) Costa Rica Dome

(B) Gulf of Panama

(C) Galápagos Islands

Equatorial Upwelling

Coastal Upwelling

South Pacific Subtropical Gyre

South Pacific Subtropical Convergence
Figure 2. Seasonal versus interannual primary production at the migration area.

Contoured $r$ values for each $5^\circ \times 5^\circ$ grid's PP time-series (1997 to 2005) derived from a harmonic analysis of (A) interannual variability using the MEI and (B) seasonal variability using the annual and semi-annual harmonic constituents.
Figure 2 A to B.
Figure 3. First three principal components and corresponding spatial modes of primary production variability from 1997 to 2005. Relationship of the standard departure of the MEI to the eigenvectors of (A) PC1, (B) PC2, and (C) PC3. Periods of the MEI shown in red are warm El Niño events while those in blue are cool La Niña events. Corresponding spatial modes of PP variability from (D) PC1, (E) PC2, and (F) PC3. The red-blue color bar represents eigenvector variability strength (unitless) and does not correspond to cool and warm temperatures.
Figure 3 A to F.

(A) MEI and PC 1

(B) MEI and PC 2

(C) MEI and PC 3

Year

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Figure 4. (A) Time-series of mean monthly primary production from 1997 to 2005 in the north and south of the migration area and the seasonal harmonic fit. (B) Comparison of total monthly production in the north and south during the entire time-series, the 1997-98 El Niño, and the 1998-2000 La Niña. T-bars are standard deviation.
Figure 4 A to B.

(A) 10 N to 15 S

Observed
Seasonal fit

Seasonal variance = 16.73%

PNMB nesting complex

10 N to 15 S

Year


1000
500
0
-500
-1000

Mean PP (mg C m⁻² month⁻¹)

(B) 15 S to 40 S

Observed
Seasonal fit

Seasonal variance = 66.31%

15 S to 40 S

Year


1000
500
0
-500
-1000

Mean PP (mg C m⁻² month⁻¹)
Figure 5. Time-series of mean monthly primary production from 1997 to 2005 at each 5° latitudinal band that stretches from the west coastline of Central and South America to 125° W. The dotted line represents each band's mean primary production.
Figure 6. (A) Mean monthly primary production at the most pronounced area of the NGCUC induced bloom along the equator encompassing 110° W. (B) Number of remigrant turtles at Playa Grande, PNMB from 1998-99 to 2005-06 (October to February) and their response to ENSO and NGCUC induced primary production transitions in the eastern equatorial Pacific.
Figure 6 A to B.

(A) Mean PP (mg C m⁻² month⁻¹) for NGCUC induced equatorial bloom.

- 2.5 S to 2.5 N
- 107.5 W to 112.5 W

(B) Number of remigrants over nesting seasons.

- 1998-2000 La Niña response
- 2003 NGCUC equatorial bloom response
- 2005 NGCUC equatorial bloom response
Figure 7. Mean sea surface temperature in the migration area from January 1985 to December 2005 using monthly 4 km Pathfinder AVHRR satellite data.
Figure 8. Smal-scale sea surface temperature frontal frequency (A) by month from 1985 to 2005 and (B) during the 1987-88 and 1997-98 El Niño, and the 1988-89 and 1998-99 La Niña (April to the following March of each ENSO event). Frequency of SST fronts are the number of fronts detected per the number of valid SST values for each pixel using monthly 4 km Pathfinder AVHRR satellite data.
Figure 8A-B.
(B)

87-88 El Niño
88-89 La Niña
97-98 El Niño
98-99 La Niña
Figure 9. Mean distribution of fronts associated with primary production in the migration area from 1997 to 2005. Each contour line represents a PP gradient of 50 mg C m$^2$ month$^{-1}$ calculated from a range of 0 to 1000 mg C m$^2$ month$^{-1}$. 

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**Figure 10.** Seasonal sea surface height anomalies in the migration area from 2004 to 2005. Red areas represent positive anomalies associated with warm core eddies while blue area represent negative anomalies associated with cold core eddies. Each seasonal image was composited using weekly AVISO merged satellite altimetry data.
Figure 10.
CHAPTER 4

Bottom-up and Climatic Forcing on the Worldwide Population of Leatherback Turtles


Abstract

Nesting populations of leatherback turtles (*Dermochelys coriacea*) in the Atlantic and western Indian Oceans are increasing or stable while those in the Pacific are declining. It has been suggested that leatherbacks in the eastern Pacific may be resource limited due to environmental variability derived from the El Niño Southern Oscillation (ENSO), but this has yet to be tested. Here we explored bottom-up forcing and the responding reproductive output of nesting leatherbacks worldwide. We achieved this through an extensive review of leatherback nesting and migration data; and by analyzing the spatial, temporal, and quantitative nature of resources as indicated by primary production at post-nesting female migration areas. Leatherbacks in the eastern Pacific were the smallest in body size and had the lowest reproductive output due to foraging areas that were less productive and temporally more variable. This derived from natural interannual and multidecadal climate variability together with an influence of anthropogenic climate warming that is possibly affecting these natural cycles. The reproductive output of leatherbacks in the Atlantic and western Indian Oceans was nearly twice that of turtles in the eastern Pacific. The inconsistent nature of the Pacific Ocean may also render western Pacific leatherbacks susceptible to a lower and more variable reproductive output, however, it appears that egg harvesting on nesting beaches is their major threat. We suggest that the eastern Pacific leatherback population is more sensitive to anthropogenic mortality due to recruitment rates that are lower and more variable, thus accounting for much of the population differences compared to Atlantic and western Indian turtles.
INTRODUCTION

There is a clear dichotomy in the nesting population sizes and trends of Atlantic, Indian, and Pacific leatherback turtles (*Dermochelys coriacea*). Populations of nesting females in the eastern Atlantic Ocean (EA), western Atlantic Ocean (WA), and western Indian Ocean (WI) are increasing or stable (Hughes 1996, Girondot et al. 2002, Dutton et al. 2005, Verhage et al. 2006) while those in the eastern Pacific Ocean (EP) have been declining precipitously (Sarti et al. 1999, Spotila et al. 2000). In the western Pacific Ocean (WP), some populations have also declined (Hitipeuw et al. 2007) while others have been extirpated (Chan and Liew 1996). Furthermore, the population in the Atlantic is much larger than in the Pacific (Spotila et al. 2000, Girondot et al. 2002, Verhage et al. 2006).

Major anthropogenic threats to leatherback populations include egg poaching, incidental fishery mortality, loss of nesting beaches, and in some areas, nesting female harvesting. Increasing population trends in the Atlantic and WI have been attributed to nesting beach protection (Hughes 1996, Dutton et al. 2005). Although this has been in place at the major nesting complex in the EP over a time period that should allow for adult recruitment, population recovery has not occurred there (Santidrián-Tomillo et al. 2007). Incidental mortality from coastal fisheries, particularly gillnets, appear to be the major anthropogenic influence on adult survival (Kaplan 2005). Whereas these fisheries exist in all basins, they have not precluded population recovery in the Atlantic and WI. This is most evident among pelagic longline fisheries where leatherback bycatch rates are significantly higher in the Atlantic with less fishing effort when compared to the Pacific (Lewison et al. 2004). One theory to explain this paradox suggests that leatherbacks in
the EP may be resource limited due to climatic variability derived from the El Niño Southern Oscillation (ENSO) (Wallace et al. 2006), but this has yet to be tested. Moreover, we have shown that ENSO highly influences the reproductive frequency of the major EP population nesting in Costa Rica (Saba et al. 2007).

Leatherbacks are foraging specialists relying on large patches of gelatinous zooplankton (Lutcavage and Lutz 1986) that typically occur at areas of high primary production (PP) (Ménard et al. 1994, Lucas et al. 1997, Vinogradov and Shushkina 2002, Lynam et al. 2004). Migration to nesting beaches and vitellogenesis among female sea turtles is dependent upon their level of energy reserve, which is a function of foraging area condition prior to the nesting season (Solow et al. 2002, Broderick et al. 2003, Saba et al. 2007). Given the low caloric content of gelatinous zooplankton (Lutcavage and Lutz 1986), leatherbacks likely rely on areas that have high concentrations of prey. While these areas need to retain specific physical features that support gelatinous zooplankton growth and aggregation (Graham et al. 2001, Lucas 2001), they must foremost be high in PP to support a high biomass (Ménard et al. 1994, Lucas et al. 1997, Vinogradov and Shushkina 2002, Lynam et al. 2004). Recently, we have shown that nesting leatherbacks in the EP respond to ENSO governed PP transitions (Saba et al. 2007). In this context, PP can be used as a proxy for gelatinous zooplankton abundance.

Here we explore the foraging and nesting ecology of leatherback populations worldwide to determine differences in resource quantity and consistency, and reproductive output that may be influencing the population dichotomy. We calculate PP over the entire extent of leatherback migration areas based on a review of post-nesting female satellite tracking studies in the Atlantic, Pacific, and Indian Oceans. The
reproductive outputs of populations worldwide are calculated from an extensive review of leatherback nesting ecology at the major nesting beaches and we present an explanation for the population dichotomy that derives from both bottom-up and climatic factors.

METHODS

Migration review

We reviewed all available literature on the post-nesting migration of leatherbacks worldwide. The majority of our migration review comprised of long-term (~1 year) satellite tracking studies except for a few cases where we used recent tracking data (Witt et al. unpublished) and nesting female tag return data (Billes et al. 2006) from western Africa in Gabon and observational data in the Mediterranean (MED) (Casale et al. 2003). The latitudinal and longitudinal ranges of the foraging areas were based on the furthest extent in the tracking studies except where we used observational data in the MED and Western South Atlantic (WSA). We did not conduct a fine-scale migration analysis because we were interested in how the entire population utilized the respective ocean basin. Therefore, we did not impose fine-scale limits on where leatherbacks could and could not migrate, we rather designated large areas shown to be used by post-nesting females from each population. This was essential to generate large foraging areas for each population, especially given the wide-ranging nature of leatherback migration.
Remote satellite data analysis

To calculate PP, we applied the Behrenfeld-Falkowski vertically generalized production (VGP) model (Behrenfeld and Falkowski 1997) using the satellite software package Windows Image Manager (WIM) (Kahru 2006). The model requires three satellite data sets comprised of sea surface chlorophyll, sea surface temperature (SST), and photosynthetically active radiation. We used monthly SeaWiFS level three (9 km) sea surface chlorophyll-a and photosynthetically active radiation data (Feldman and McClain 2006) and monthly Pathfinder 4 km Advanced Very High Resolution Radiometer (AVHRR) SST data (NASA 2006) from September 1997 to December 2005 resulting in 100 monthly images. We used WIM to calculate mean monthly PP (mg C m$^{-2}$ month$^{-1}$), and ArcView 3.2a to calculate the size of each migration area. Total mean yearly PP was calculated using each migration area's size and mean monthly value. To understand the seasonality of each PP time-series, we applied a least-squares regression to each data set using semi-annual and annual harmonic constituents (Emery and Thomson 1998). From this, we denoted $r$ values greater than 50 % as seasonal variation and $r$ less than 50 % as interannual.

We assumed turtles foraged on the way to and from areas of high PP (Hays et al. 2006); therefore, we calculated values over the entire migration area and denoted it as a foraging area. Calculating PP over the entire migration area was necessary to understand the spatial availability of resources. The energetic cost of round-trip migration to and from nesting beaches dominates the energy budget of nesting females (Wallace et al. 2006); therefore, it is crucial to understand the spatial distributions of PP throughout the total migration area.
We applied an empirical orthogonal function analysis to 252 mean monthly Pathfinder SST images from January 1985 to December 2005 (NASA 2006) using WIM (Kahru 2006) producing the first spatial mode of SST variation across three ocean basins. This allowed us to demonstrate environmental variability, as indicated by SST, of the Atlantic, Indian, and Pacific Oceans. To illustrate the strength of ENSO events in the EP over the past 50 years as influenced by both natural and anthropogenic factors, we used the multivariate ENSO index (MEI) (Wolter and Timlin 1998) as an indicator of multidecadal regime shifts (Chavez et al. 2003) that can affect EP leatherbacks. The MEI incorporates six climatic variables in the tropical Pacific comprised of sea-level pressure, zonal and meridional components of surface wind, SST, surface air temperature, and total cloudiness fraction of the sky.

**Nesting ecology review**

Our nesting review was based on the most recent literature pertaining to available time-series of the nesting ecology of leatherbacks. We included almost all major nesting complexes in the review with the exception of Florida for the WA population and Sri Lanka for the Indian Ocean population due to data limitations. The majority of data were long-term except for Gabon, Papua, and Papua New Guinea. Egg clutch frequencies were based on mean estimated clutch frequencies (ECFs) when possible. The ECF is a more accurate assessment of clutch frequencies because it accounts for missing nesting events due to a lack of beach coverage (Reina et al. 2002), and is based on a female's first and last appearance dates and the mean inter-nesting interval of leatherbacks (typically 9 to 10 days).
Given that foraging area condition highly affects the remigration intervals of sea
turtles (Solow et al. 2002, Saba et al. 2007), we assumed mean remigration intervals for
Trinidad and Mexico based on tracking data similarities to their population cohorts in the
WA and Costa Rica, respectively.

RESULTS

Our review and PP analysis showed that post-nesting females among all populations
migrated to systems of high PP (Table 1; Fig. 1a and b) driven by coastal upwelling
et al. 2007a, b), equatorial upwelling (Morreale et al. 1996, Eckert and Sarti 1997,
Ferraroli et al. 2004, Shillinger and Block 2006, Witt et al. unpublished), and strong
wind-driven vertical mixing along coastal shelves and temperate pelagic zones (Ferraroli
et al. 2007b, c). Among all of the foraging areas worldwide, the north Atlantic (NA) had
the highest mean and maximum PP (Table 1; Fig. 1a, 2 a-d) and is where the majority of
the WA females tended to migrate. Among the least productive foraging areas were the
western tropical Pacific (WTP), southeastern Pacific (SEP), and eastern sub-tropical
Pacific (ESTP) (Table 1; Fig. 1b, 2 a-d). All of the foraging areas had seasonal PP except
the eastern tropical Pacific (ETP) and ESTP (Fig. 2 a-d).

The most extensive data regarding both nesting and migration comprised were for
WA and EP populations. Seasonality accounted for the majority of PP variation among
all of the foraging areas of WA females (Fig. 2a) while, with the exception of the SEP,
interannual variation dominated in the EP (Fig. 2b). Mean PP among all foraging areas of WA females was significantly higher than those of the EP ($P \ll 0.0001$, $n = 100$ months) (Fig. 3a). The difference between WA and EP foraging area quality and consistency was reflected in the nesting female reproductive output where the egg production of WA females was twice that of EP females (Table 2; Fig. 3a). Given almost equal size in total foraging area of WA and EP females, the total yearly PP of the WA foraging area was almost 150% greater than that of the EP (Fig. 3b).

Migration patterns of WA females were more variable, with some individuals relying on coastal shelf and temperate pelagic areas and others relying on equatorial and coastal upwelling zones (Ferraroli et al. 2004, Hays et al. 2004, Eckert 2006). In the EP, female leatherbacks relied on equatorial upwelling in the tropics and wind-driven mixing at the sub-tropical convergence (Morreale et al. 1996, Eckert and Sarti 1997, Shillinger and Block 2006). Although only a few individuals utilized coastal upwelling areas (Eckert and Sarti 1997, Shillinger and Block 2006), we still included them in the PP analysis (Fig. 1b). The lack of coastal foragers in the EP may be a result of high mortality rates among coastal gillnet fisheries along Peru and Chile (Eckert and Sarti 1997, Kaplan 2005), essentially reducing the number of these foraging cohorts.

Females in the WI were the largest in body size and produced the highest reproductive output (1518.4 eggs/female/5 years) (Table 2). On average, EA females tended to be slightly smaller than WA females and produced smaller egg clutches (Table 2). Nesting remigration intervals of EA females have yet to be described, hence we could not calculate reproductive output over multiple years. Nesting females in the EP were the smallest in body size and had the lowest reproductive output among all populations.
(Table 2). Nesting data in the WP were too limited for an accurate assessment of nesting ecology.

From 1985 to 2004, the first principal component (spatial mode) of SST variability among all three basins accounted for 13.6% of the total variation (Fig. 4a). Within the first principal component, the majority of SST variability occurred in the Pacific Ocean while the Atlantic and Indian Oceans remained relatively stable (Fig. 4a). The area of intense variability occurred in the equatorial Pacific where EP leatherbacks forage; however, high variability occurred throughout the entire basin relative to the Atlantic and Indian Oceans. In the EP, reproductive output and PP were calculated towards the end of an El Viejo regime and possibly during a regime shift when El Niño events were more frequent (Fig. 4b).

DISCUSSION

**Western Atlantic and eastern Pacific populations**

Our analysis revolved around WA and EP leatherbacks because of their extensive nesting and migration data and we were able to statistically compare PP at their total foraging area because the sizes were nearly equal (Fig. 3b). The higher reproductive output of WA females derived from shorter remigration intervals (time between successive nesting seasons) and larger egg clutch sizes than those of the EP (Table 2). We suggest that females in the WA can afford to expend more energy on reproduction and migration due to their consistent, high quality foraging areas. Our results confirm the leatherback energy budget calculations by Wallace et al. (2006) where they showed WA leatherbacks nesting at St. Croix, despite having higher energy costs and higher feeding
rates from larger body size, still had remigration intervals half as long as EP leatherbacks nesting in Costa Rica. The lack of seasonality from ENSO events in the ETP and ESTP renders resource availability inconsistent and less reliable, likely leading to a higher rate of gelatinous zooplankton patchiness, thus forcing EP females to expend more energy on finding food and less on reproduction. This has been demonstrated among EP females nesting in Costa Rica where ENSO events strongly influence their nesting remigration probabilities (Saba et al. 2007).

Larger female leatherbacks typically lay larger egg clutches than smaller individuals (Price et al. 2004) and this relationship has been demonstrated with other sea turtles (Broderick et al. 2003). Reptiles undergo indeterminate growth, and their growth rates are highly correlated with food quantity and distribution (Avery 1994); therefore, we suggest that the difference in turtle body size between the WA and EP is a function of resource availability. Moreover, WA females may reach sexual maturity at an earlier age from faster growth rates, further enhancing population growth rate.

**Eastern Atlantic population**

Possibly the largest population in the Atlantic, EA leatherbacks nesting in Gabon appear stable (Table 2) although a longer time-series of tagging data is required to confirm this. Both tag returns (Billes et al. 2006) and satellite tracking (Witt et al. unpublished) indicate that post-nesting females migrate in both the eastern south Atlantic (ESA) and WSA along the coast of South America (Table 1; Fig. 1a). However, the sample size of post-nesting female tracks and tag returns was low and may only represent a portion of their migration patterns. The smaller body size and smaller egg clutch size
of EA leatherbacks relative to those in WA (Table 2) was also likely due to resource availability. Presently, no tracks or tag-returns show EA leatherbacks occurring in the highly productive NA (Table 1) and their remigration intervals have yet to be described. However, given their seasonally productive foraging areas in the ESA and WSA (Fig. 2c), extremely high population size, larger egg clutch, and larger body size relative to the EP (Table 1 and 2), it is likely their reproductive output is near those reported for WA and WI females.

**Western Indian population**

The small, stable WI nesting population on the east coast of South Africa (Table 2) has been shown to migrate along the Agulhas Current System (ACS) and into the ESA (Luschi et al. 2006) (Table 1; Fig. 1a). Females migrate along the ACS to various seasonally high PP zones driven by coastal upwelling in the Benguela Current, and wind-driven mixing off the eastern coast of South Africa and the sub-tropical convergence (Luschi et al. 2006) (Table 1; Fig. 1a, 2c). The total foraging area size of the post-nesting females was the smallest among all other nesting populations ($2.58 \times 10^7$ km$^2$) (Table 1). Given that migration dominates the energy budget of nesting females (Wallace et al. 2006), we suggest that WI leatherbacks achieve the largest body size and the highest reproductive output because they expend less energy on migration by foraging in seasonally productive areas in close proximity to the nesting beaches. Although this population is currently stable (Hughes pers. comm.), it has substantially recovered over the past 40 years (258% population size increase) because egg exploitation is no longer a threat (Hughes 1996).
Western Pacific population

The WP population of leatherbacks is among the least studied, but research has been increasing in Papua and Papua New Guinea. Short-term nesting data suggest a possible decline in Papua (Hitipeuw et al. 2007) and Papua New Guinea (Benson pers. comm.), however, further monitoring is needed for accurate assessment. Satellite tracking suggests that WP females (Benson et al. 2007b, c) have more variability in their migration patterns than EP females (Morreale et al. 1996, Eckert and Sarti 1997, Shillinger and Block 2006). Post-nesting females from Papua New Guinea migrate to the southwestern Pacific (SWP) targeting the sub-tropical convergence zone near New Zealand whereas Papua females frequent the central and western north Pacific (CWP), northeastern Pacific (NEP), and the WTP (Benson et al. 2007a, b, c). These turtles may also frequent the ESTP and ETP but not to the same extent as EP turtles. Although nesting data are limited, recent results suggest that WP females are larger than EP females (Hitipeuw et al. 2007) and possibly lay larger egg clutches. It is likely that Papua females migrating across the Pacific to the NEP have longer remigration intervals than those migrating closer to nesting beaches rendering their reproductive output lower than others within the nesting population. In general, however, WP females appear to have a higher reproductive output than EP females due to their multiple foraging areas with seasonal PP (Table 1, Fig. 2d) and larger body size, however, their population is declining and they are far less abundant than turtles in the Atlantic. High egg harvesting rates occur in both Papua and PNG (Kinan pers. comm.) and were a major factor in the dramatic decline of the Malaysian population (Chan and Liew 1996).
The effects of climate variability on WP leatherbacks have not been studied. The North Pacific appears to be a major migration area for these turtles and regime shifts triggered by climate change have been extensively documented in this ecosystem (Chavez et al. 2003). The high variability of the Pacific Ocean relative to the Atlantic and Indian Oceans (Fig. 4a) may be a major factor for the population size difference between Atlantic and Pacific turtles. This suggests that the WP population may also be affected by resource variability, although presently, it appears egg harvesting is their primary threat.

**Climate variability and eastern Pacific leatherbacks**

Our results suggest that the EP leatherback population is less tolerant of anthropogenic mortality due to its reduced recruitment rates from both low reproductive output and possibly slower growth rates. The interannual nature of resource availability in the ESTP and ETP combined with the low productivity of the SEP are likely the major factors rendering EP leatherback reproductive output lower and more variable. Interannual climate variability in the eastern equatorial Pacific is primarily ENSO driven. There is, however, multidecadal climate variability where ocean temperatures fluctuate between warmer (El Viejo) and cooler (La Vieja) regimes (Chavez et al. 2003). Biological consequences of these regime shifts are foremost evident in the high fishery yields of anchovies during La Vieja and sardines during El Viejo (Chavez et al. 2003). Cooler, more productive La Niña events have been shown to enhance the reproductive frequency of EP females (Saba et al. 2007) thus La Vieja regimes should favor a higher reproductive output (Fig. 4b). The last peak La Vieja occurred in the early 1960's and
likely caused a more productive EP. Large-scale productivity data during a La Vieja regime are not available, however, a 40-year time series from Peruvian coastal waters showed a precipitous decline in zooplankton volume from 1964 to 2001 (Ayon et al. 2004), likely a result of decreasing PP. Our PP calculations were based on data recorded during the end of an El Viejo and during a possible regime shift (Chavez et al. 2003) when less productive El Niño events dominated, suggesting we may have observed the lower threshold of reproductive output and nesting numbers in the EP. Therefore, this population may experience major fluctuations in its size over long time periods purely through trophic forcing as influenced by climate. In the Pacific, climate induced population fluctuations over long periods have been documented for fish, birds, and mammals (Chavez et al. 2003, Trites et al. 2007). In the North Pacific, major population abundance shifts of Steller sea lions (*Eumetopias jubatus* Steller 1741) over the past 4000 years were attributed to bottom-up forcing through changes in ocean climate (Trites et al. 2007). In the SEP, the population fluctuations of seabirds were attributed to changes in the abundance of anchovy (Chavez et al. 2003).

Over the past century, anthropogenic forcing through greenhouse gas input has resulted in a weakening of tropical Pacific circulation (Vecchi et al. 2006). The equatorial Pacific zonal wind stress weakening has led to a reduction in the intensity of equatorial upwelling, likely reducing PP (Vecchi et al. 2006). This suggests that anthropogenic climate change may be disrupting the natural regime shifts in the eastern equatorial Pacific leading to more frequent, less productive El Niño events (Timmermann et al. 1999). These studies were based on climate models that can be subject to errors, therefore it is still unclear how greenhouse gas induced climate warming will affect
ENSO variability (McPhaden et al. 2006). If, however, El Niño events do become more frequent, the reproductive output of EP leatherbacks will remain at its lower threshold, further delaying population recovery.

**Primary production, physical forcing and leatherback prey**

Gelatinous zooplankton such as *Cnidaria* (siphonophores and medusae) and *Ctenophora* (comb jellies) that feed on secondary producers (e.g. copepods) are typically at their highest biomass a few months after phytoplankton blooms (Sullivan et al. 2001, Lynam et al. 2004, Decker et al. 2007). Gelatinous organisms that can feed directly on phytoplankton, such as pelagic tunicates (salps, larvaceans, and pyrosomes), respond even sooner (Ménard et al. 1994). The lag is derived from the time required for bottom-up trophic forcing to cascade, which is a function of both biological and physical factors (Purcell et al. 1999, Graham et al. 2001).

The most common observation of leatherback predation on gelatinous zooplankton in both Atlantic and Pacific basins involves scyphomedusae, particularly of the genera *Aurelia, Chrysaora*, and *Cyanea* (James and Herman 2001, Benson et al. 2007a). Leatherbacks from the WP have been observed feeding on scyphomedusae in Monterey Bay (Benson et al. 2007a) and are likely doing the same at coastal areas further north along the northwest coast of North America (NMFS 1998). Similar foraging has also been observed in eastern Canada where WA leatherbacks are found close to the coast of Nova Scotia (James and Herman 2001). With the exception of EP females, both satellite tracking (Ferraroli et al. 2004, Hays et al. 2004, James et al. 2005a, Eckert 2006, Luschi
and tag returns (Billes et al. 2006) confirm that a portion of post-nesting females migrate to coastal areas.

The majority of scyphomedusae have a benthic polyp stage, thus a hard bottom substrate is required for polyp attachment thus are restricted to coastlines. There are, however, scyphomedusae such as those from the genera *Pelagia* that are holoplanktonic and do not have a benthic polyp stage, thus can be found in the open ocean. In temperate coastal zones, the small scyphomedusae (ephyrae) release from the benthic polyps in the spring when temperatures warm and resources becomes more abundant (Purcell 2005). Ephyrae production is positively correlated to resource availability (Purcell et al. 1999) and may be determined by the size and timing of the spring bloom (Lynam et al. 2004). The population densities of large scyphomedusae in northern coastal zones are typically highest in July and August (Purcell et al. 2000, Purcell 2005, Purcell and Decker 2005). Peaks in the biomass of salps in the Slope Water off the northeastern United States also take place in the summer months (Madin et al. 2006). In this context, leatherbacks would need to time their arrival to temperate waters after peak periods of PP (spring blooms) to take advantage of the large patches of adult scyphomedusae. Consequently, peak leatherback abundance occurs at Monterey Bay in August (Starbird et al. 1993, Benson et al. 2007a) and from June to August off of eastern Canada (James and Herman 2001, James et al. 2005b). Studies along the European continental shelf also showed leatherback peak occurrence during the summer months (McMahon and Hays 2006, Witt et al. 2007).

The physical characteristics of the water in the summer months also favor aggregations of prey. Temperature and salinity are significant factors controlling
distributions of scyphomedusae both intrinsically (growth rate, ephyrae release) and extrinsically (zooplankton prey abundance and distribution) (Purcell 2005, Decker et al. 2007). Moreover, discontinuities such as shelf breaks, upwelling and downwelling fronts, thermal gradients, haloclines, and meso-scale eddies are typically associated with large aggregations (Graham et al. 2001). However, without adequate resources ultimately derived from PP, a large gelatinous zooplankton biomass is not possible (Lucas et al. 1997, Madin et al. 2006).

Among coastal areas in the tropics, Eckert (2006) reported WA leatherback arrival at the West African Mauritania upwelling system in February. The peak period of PP in the eastern tropical Atlantic (ETA) occurred between February and March of each year (Fig. 2a) when wind-driven coastal upwelling peaks. Eckert (2006) suggested that the initiation of upwelling concentrated gelatinous zooplankton through enhanced physical discontinuities. This theory, however, is not consistent for leatherbacks foraging in other coastal upwelling areas. In Monterey Bay, coastal upwelling typically peaks in June (Croll et al. 2005) yet leatherback peak abundance occurs in August (Starbird et al. 1993, Benson et al. 2007a). We suggest that the difference in leatherback arrival time at Mauritania and Monterey Bay is a function of the temperature-mediated lag between enhanced PP and medusae abundance and/or the turtles are foraging on herbivorous macro-zooplankton (salps and pyrosomes) that respond quickly to phytoplankton blooms. In tropical waters, gelatinous zooplankton growth rates are enhanced due to a faster metabolism from warmer temperatures (Purcell 2005). Therefore, the response time of gelatinous zooplankton (both carnivorous and herbivorous) to increased PP would be
faster in the Mauritania upwelling system and may explain why leatherbacks arrive closer to PP maximums then they do in Monterey Bay.

Migration to coastal areas represents just a portion of leatherback behavior. Among equatorial upwelling systems, both WA (Ferraroli et al. 2004) and EA (Witt et al. unpublished) leatherbacks migrate through the equatorial Atlantic (Table 1; Fig. 1a), and EP leatherbacks through the equatorial Pacific (Morreale et al. 1996, Eckert and Sarti 1997, Shillinger and Block 2006) (Table 1; Fig. 1b). There are very few studies that have characterized the gelatinous zooplankton at equatorial upwelling systems. In the pelagic equatorial Atlantic, one study showed that siphonophores, tunicates, and crustaceans contributed up to 65% of the macrozooplankton species diversity (Piontkovski et al. 2003). This study, however, used an 80 cm net diameter that was likely too small to catch larger macrozooplankton such as medusae.

**Geographic range and temperature**

Our migration data review showed that the typical latitudinal range of Atlantic and WI females exceeded that of Pacific turtles by approximately 5° north and south (Fig. 1a and b, 5a and b). The reason for the smaller latitudinal range of Pacific turtles is likely the result of fewer sampling numbers in the tracking studies, or the result of a few individuals traveling outside the typical range in the Atlantic and Indian Oceans. Pacific leatherbacks, likely of the WP population, have been sighted or incidentally captured near Alaska as far north as 60° N but these are rare occasions (NMFS 1998). We didn't include these northern areas in our PP analysis because the tracking studies do not show
the turtles anywhere near this latitude. Our analysis primarily focused on WA and EP females, thus expanding the northern range of WP females would not affect our results.

There have been recent studies regarding the minimum temperature threshold of adult leatherbacks, primarily focused on WA turtles foraging in the eastern and western NA. Two different studies in the NA suggested that adult leatherbacks may be thermally constrained by SST of 15°C (McMahon and Hays 2006) or 10 to 12°C (Witt et al. 2007) and that global warming could expand their range (McMahon and Hays 2006). It is important to note, as these studies do, that the temperature constraints represent surface water temperatures and do not include the cooler temperatures encountered during dives. A study off northeastern Canada in the Gulf of St. Lawrence showed a leatherback diving continuously for many weeks in near-freezing water down to 0.4°C while SST averaged 17.5°C and water depth averaged 50 to 100 m (thermocline depth averaged 15 to 30 m) (James et al. 2006). Leatherbacks can tolerate these low temperatures because of their thermal inertia via large body size and counter-current circulatory system (gigantothermy) (Paladino et al. 1990). The turtle diving in near-freezing water was actually smaller than average for Atlantic leatherbacks (CCL = 148 cm) suggesting that this tolerance may apply to the smaller EP population. Leatherbacks foraging in the Gulf of St. Lawrence have been well documented and it is evident that these turtles frequent cooler waters (James and Herman 2001, James et al. 2005a, b, c, James et al. 2006) than those foraging off of western Europe in the eastern NA (McMahon and Hays 2006, Witt et al. 2007), primarily because warming from the Gulf Stream occurs further east of coastal Canada following the NA gyre (Fig. 5a). Further research is required to
understand the thermal constraints of leatherbacks and if there are in fact differences among populations.

Conclusions

Ecosystem regime shifts are not limited to the Pacific Ocean. There is growing evidence showing that the northwest Atlantic Ocean experienced a regime shift in the early 1990s driven by bottom-up and climatic factors and led to an overall increase in PP via enhanced stratification from higher rates of freshwater influx (Greene and Pershing 2007). Off northwest Africa, the intensity of coastal upwelling has increased through the 20th century (McGregor et al. 2007), likely increasing biological production. Studies have shown that the North Atlantic Oscillation (NAO) can affect the abundance and distribution of both ctenophores and cnidarians in the Atlantic Ocean (Sullivan et al. 2001, Lynam et al. 2004, Purcell 2005). It is possible that the foraging areas of WA leatherbacks are currently in a favorable climate regime, which may partially explain the population increase at some nesting beaches.

Our analysis focused on bottom-up forcing via resource availability, but there is clearly pressure emanating from top-down factors such as egg poaching in the WP and incidental fishery mortality throughout all basins. Further reduction of anthropogenic mortality in the Pacific should take priority if any population recovery is to occur, especially in the EP. At the major nesting complex for EP leatherbacks located in Costa Rica, egg harvesting is no longer a factor and even though beach protection has continued there for almost 15 years, no recovery has been observed (Santidrián-Tomillo et al. 2007). It is possible that more time is required to observe any recovery in the EP due to the inconsistent nature of resources.
We conclude that the highly variable nature of the EP exacerbates the sensitivity of its leatherback population to fishery mortality despite continued beach protection. Moreover, we may have observed the lower threshold of nesting numbers and reproductive output in the EP due to an unfavorable climate regime, suggesting that this population may naturally experience major shifts in abundance over time.


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Table 1. Migration of leatherback turtles and primary production. We calculated total PP using migration/foraging area size and mean monthly PP, thus is an annual mean (1 Tg = 10^{12} \text{ g}). The cycle of PP was based on the harmonic analysis results such that variance explained by seasonality > 50% is considered seasonal and << 50% is interannual.

<table>
<thead>
<tr>
<th>Population</th>
<th>Migration/Foraging areas</th>
<th>Nutrient forcing</th>
<th>Mean primary production (mg C/m²/month)</th>
<th>Maximum primary production (mg C/m²/month)</th>
<th>Migration/Foraging area size (km² x 10²)</th>
<th>Total primary production (Tg C/year)</th>
<th>Primary production cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western Atlantic</td>
<td></td>
<td>Wind-driven mixing &amp; eutrophic shelf</td>
<td>680.7 (± 282.7)</td>
<td>1209.7</td>
<td>15.6</td>
<td>127.2 (± 52.8)</td>
<td>Seasonal</td>
</tr>
<tr>
<td></td>
<td>North Atlantic (NA)</td>
<td>Eutrophic shelf</td>
<td>360.9 (± 50.2)</td>
<td>440.1</td>
<td>20.6</td>
<td>89.1 (± 12.4)</td>
<td>Seasonal</td>
</tr>
<tr>
<td></td>
<td>Western Tropical Atlantic (WTA)</td>
<td>Coastal/Equatorial upwelling</td>
<td>554.3 (± 83.8)</td>
<td>786.1</td>
<td>8.7</td>
<td>55.6 (± 8.7)</td>
<td>Seasonal</td>
</tr>
<tr>
<td>Eastern Atlantic</td>
<td>Mediterranean (MED)*</td>
<td>Coastal upwelling</td>
<td>463.8 (± 87.4)</td>
<td>695.3</td>
<td>3.2</td>
<td>17.8 (± 3.4)</td>
<td>Seasonal</td>
</tr>
<tr>
<td></td>
<td>Eastern Atlantic</td>
<td>Eutrophic shelf</td>
<td>360.9 (± 50.2)</td>
<td>440.1</td>
<td>20.6</td>
<td>89.1 (± 12.4)</td>
<td>Seasonal</td>
</tr>
<tr>
<td></td>
<td>Eastern South Atlantic (ESA)</td>
<td>Wind-driven mixing &amp; eutrophic shelf</td>
<td>525.9 (± 76.5)</td>
<td>656.3</td>
<td>19.7</td>
<td>124.0 (± 18.0)</td>
<td>Seasonal</td>
</tr>
<tr>
<td>Western Indian</td>
<td>Western South Atlantic (WSA)</td>
<td>Wind-driven mixing &amp; eutrophic shelf</td>
<td>474.4 (± 93.9)</td>
<td>676.7</td>
<td>14.6</td>
<td>83.0 (± 16.4)</td>
<td>Seasonal</td>
</tr>
<tr>
<td></td>
<td>Agulhas Current System (ACS)</td>
<td>Coastal/Equatorial upwelling</td>
<td>561.8 (± 113.8)</td>
<td>772.9</td>
<td>6.1</td>
<td>41.3 (± 8.4)</td>
<td>Seasonal</td>
</tr>
<tr>
<td></td>
<td>ESA (See above)</td>
<td>Wind-driven mixing &amp; eutrophic shelf</td>
<td>360.9 (± 50.4)</td>
<td>492.7</td>
<td>5.9</td>
<td>25.4 (± 4.3)</td>
<td>Interannual</td>
</tr>
<tr>
<td>Eastern Atlantic</td>
<td>Eastern Sub-Tropical Pacific (ESTP)</td>
<td>Coastal upwelling</td>
<td>455.7 (± 85.1)</td>
<td>601.9</td>
<td>15.0</td>
<td>83.8 (± 11.7)</td>
<td>Interannual</td>
</tr>
<tr>
<td></td>
<td>Eastern Tropical Pacific (ETP)</td>
<td>Coastal/Equatorial upwelling</td>
<td>316.4 (± 33.8)</td>
<td>386.7</td>
<td>25.4</td>
<td>96.4 (± 10.3)</td>
<td>Seasonal</td>
</tr>
<tr>
<td>Western Pacific</td>
<td>Southeastern Pacific (SEP)</td>
<td>Coastal upwelling &amp; wind-driven mixing</td>
<td>402.5 (± 74.6)</td>
<td>562.9</td>
<td>47.1</td>
<td>227.4 (± 42.1)</td>
<td>Seasonal</td>
</tr>
<tr>
<td>Papua</td>
<td>Central &amp; Western North Pacific (CWNP)</td>
<td>Wind-driven mixing &amp; eutrophic shelf</td>
<td>438.5 (± 83.5)</td>
<td>601.9</td>
<td>8.1</td>
<td>42.8 (± 8.2)</td>
<td>Seasonal</td>
</tr>
<tr>
<td></td>
<td>Northeastern Pacific (NEP)</td>
<td>Coastal upwelling &amp; wind-driven mixing</td>
<td>292.9 (± 25.0)</td>
<td>334.3</td>
<td>24.2</td>
<td>82.2 (± 7.3)</td>
<td>Seasonal</td>
</tr>
<tr>
<td></td>
<td>Western Tropical Pacific (WTP)</td>
<td>Coastal/Equatorial upwelling</td>
<td>415.4 (± 53.5)</td>
<td>524.9</td>
<td>30.7</td>
<td>152.9 (± 19.7)</td>
<td>Seasonal</td>
</tr>
</tbody>
</table>

* Assumed leatherbacks observed in the MED were part of the WA given their migration patterns near the Strait of Gibraltar.
Table 2. Nesting ecology of leatherback turtles. All values reported are means.

Population trends were based on nesting numbers over the past 5 to 10 years depending on the data set length. Because turtles nesting in Trinidad share the same migration areas as the rest of the WA population, we assumed their mean remigration interval was also similar. This also applied to leatherbacks nesting in Mexico and Costa Rica. Clutch frequencies reported are ECFs except in St. Croix and Gabon where they are based on observed clutch frequencies (OCFs) and are likely under-estimates. The clutch frequencies in Trinidad and Caribbean Costa Rica/Panama were based on the mean clutch frequency from the WA.

<table>
<thead>
<tr>
<th>Population (complex)</th>
<th>Population size (females/year)</th>
<th>Population trend</th>
<th>Remigration interval (years)</th>
<th>CCL (cm)</th>
<th>Reproductive output (eggs/clutch)</th>
<th>Clutch frequency (clutches/season)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western Atlantic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>St. Croix</td>
<td>150</td>
<td>Increasing</td>
<td>2.5</td>
<td>152</td>
<td>80</td>
<td>5.3</td>
<td>Dutton et al. 2005; Alexander et al. 2004; Boulon et al. 1996</td>
</tr>
<tr>
<td>Trinidad</td>
<td>4,300</td>
<td>Increasing</td>
<td>2.5*</td>
<td>156</td>
<td>84</td>
<td>6.4f</td>
<td>Livingstone and Downie 2006; Maharaj 2004</td>
</tr>
<tr>
<td>French Guiana &amp; Suriname</td>
<td>5,000</td>
<td>Stable</td>
<td>2.5</td>
<td>155</td>
<td>85</td>
<td>7.5</td>
<td>Rivlin et al. 2005; Hillemann and Goverse 2004; Girondot et al. 2002</td>
</tr>
<tr>
<td>Caribbean Costa Rica and Panama</td>
<td>1,300</td>
<td>Stable</td>
<td>2.5</td>
<td>154</td>
<td>82</td>
<td>6.4f</td>
<td>de Haro and Troeng 2006; Troeng and Chaloupka 2006; Troeng et al. 2004; Chacon et al. 1998</td>
</tr>
<tr>
<td>Eastern Atlantic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gabon</td>
<td>6,000</td>
<td>Stable</td>
<td>-</td>
<td>151</td>
<td>73</td>
<td>5.0</td>
<td>Verhage et al. 2006</td>
</tr>
<tr>
<td>Western Indian</td>
<td>South Africa</td>
<td>125</td>
<td>Stable</td>
<td>2.5</td>
<td>160</td>
<td>104</td>
<td>Hughes pers. comm.; Hughes 1973, 1974, 1996</td>
</tr>
<tr>
<td>Eastern Pacific</td>
<td>Mexico</td>
<td>200</td>
<td>Decreasing</td>
<td>3.7</td>
<td>145</td>
<td>64</td>
<td>Sarl et al. 1999; NMFS 1998</td>
</tr>
<tr>
<td>Costa Rica</td>
<td>200</td>
<td>Decreasing</td>
<td>3.7f</td>
<td>145</td>
<td>64</td>
<td>6.1</td>
<td>Santidrián-Tomillo et al. 2007; Reina et al. 2002</td>
</tr>
<tr>
<td>Western Pacific</td>
<td>Papua</td>
<td>1,250</td>
<td>Decreasing</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Hilpouët et al. 2007</td>
</tr>
<tr>
<td>Papua New Guinea</td>
<td>250</td>
<td>Decreasing</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Benson pers. comm.</td>
</tr>
</tbody>
</table>

*Used mean RI from WA.
†Used mean clutch frequency from WA.
‡Used mean RI from Costa Rica.
§Nesting complex has not been extensively studied.
Figure 1. Mean monthly PP at Atlantic, Pacific, and Western Indian foraging areas.

Nesting complexes in (a) the Atlantic and Western Indian are numbered for the WA population: (1) French Guiana and Suriname, (2) Trinidad, (3) Caribbean Costa Rica and Panama, (4) St. Croix; the EA population: (5) Gabon; and the WI population: (6) South Africa; (b) the Pacific nesting complexes are numbered for the EP population: (7) Pacific Costa Rica, (8) Pacific Mexico; and the WP population: (9) Papua New Guinea, and (10) Papua. Mean monthly PP values are scaled down such that red areas can range from 1400 to 4000 mg C m$^{-2}$ month$^{-1}$ and are typically coastal areas. Coastal edges were slightly expanded to avoid satellite errors associated with remote sensing close to the coast. Foraging areas comprise of the North Atlantic (NA), Eastern Tropical Atlantic (ETA), Western Tropical Atlantic (WTA), Mediterranean (MED), Western South Atlantic (WSA), Eastern South Atlantic (ESA), Agulhas Current System (ACS), Northeastern Pacific (NEP), Eastern Sub-Tropical Pacific (ESTP), Eastern Tropical Pacific (ETP), Southeastern Pacific (SEP), Southwestern Pacific (SWP), Western Tropical Pacific (WTP), and the Central and Western North Pacific (CVPN).
Figure 2. Primary production from 1997 to 2005 at the foraging areas of (a) WA, (b) EP, (c) EA and WI, and (d) WP leatherback populations. Seasonal harmonic fits were obtained from a Fourier regression using semi-annual and annual harmonic constituents of the mean monthly PP time-series from each foraging area. Solid lines are the observed PP and dashed lines are the seasonal harmonic fit.
Figure 2a to d.

(a) NAtlantica (Seasonal variance = 65.81%) - Observed
Harmonic fit

(b) ESTP (Seasonal variance = 32.18%) - Observed
Harmonic fit

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Figure 3. (a) Reproductive output of WA and EP females and mean monthly PP at their respective total foraging area. Total foraging area is a summation of all foraging areas for the respective population from Table 1. Error bars represent standard deviation. (b) Size and PP of the total foraging area of WA and EP females.
Figure 3a to b.

(a) Reproductive output (eggs female$^{-1}$ 5 years$^{-1}$) and primary production (mg C m$^{-2}$ month$^{-1}$) for Western Atlantic and Eastern Pacific regions.

(b) Foraging area size (km$^{2} 	imes 10^{6}$) and total primary production (Tg C year$^{-1}$) for Western Atlantic and Eastern Pacific regions.
Figure 4. Variability of SST in the Pacific, Atlantic, and Indian Oceans and
multidecadal regime shifts in the EP. (a) First principal component (spatial mode) of
SST variation derived from an empirical orthogonal function analysis using 21 years of
Pathfinder AVHRR satellite data. Eigenvector variability is represented in the color scale
bar and is unitless. (b) Time-series of the Multivariate ENSO Index (MEI) with regimes
shifts in the EP (Chavez et al. 2003) and their likely influence on leatherback
reproductive output. The influence is based on the results from (Saba et al. 2007) that
showed cooler, more productive La Niña events increased the reproductive frequency of
EP leatherbacks.
Figure 4a to b.

(a) £

(b) £

El Viejo warm phase: reduced reproductive output for EP leatherbacks

La Vieja cool phase: enhanced reproductive output for EP leatherbacks

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Figure 5. Mean SST from January 1985 to December 2005 in the (a) Atlantic Ocean and (b) Pacific Ocean. The composite is based on 252 monthly Pathfinder AVHRR satellite images.
Figure 5a to b.

(a)
**Summary**

Eastern Pacific leatherbacks have continued to decline despite the elimination of egg harvesting over 15 years ago. If the mean age of maturity of leatherbacks ranges from 9 to 13 years (Zug and Parham, 1996), signs of population recovery should have been evident by now. This study demonstrated that natural interannual and multidecadal climate variability, combined with a possible influence of global warming on these natural cycles, causes variable recruitment rates within the eastern Pacific population.

Resource availability in the eastern equatorial Pacific was highly variable as governed by ENSO. In the pelagic southeastern Pacific, although the cycle of resources was seasonal, production was much lower compared to the temperate areas where other leatherback populations forage. Moreover, if global warming is in fact causing more frequent El Niño events (Timmermann et al., 1999; Vecchi et al., 2006), leatherback recruitment rates may continue to be at the lowest threshold.

The number of post-nesting females tracked in the eastern Pacific exceeds that of most other populations (Benson et al., 2007a; Benson et al., 2007b; Eckert and Sarti, 1997; Ferraroli et al., 2004; Hays et al., 2004; Luschi et al., 2006; Morreale et al., 1996; Shillinger and Block, 2006) yet a lack of coastal foragers was observed among these turtles. If leatherback mortality among coastal gillnet fisheries is a major factor causing the decline, conservation effort associated with these fisheries needs to increase. This may be a difficult task given that some of these fisheries are artisanal, unmonitored, and unregulated.

The analysis of this study revolved around nesting females and did not include neonates, juveniles, sub-adults, or male leatherbacks although the results likely apply to
these cohorts as well. It has been shown that male leatherbacks in the western Atlantic have similar migration patterns to mature females (James et al., 2005), thus were exposed to similar foraging conditions. Among neonates and juveniles, their migration and ecology is unknown worldwide, however, given their smaller size and lack of thermal inertia they are restricted to warmer temperatures in tropical waters (> 26° C) (Eckert, 2002). Therefore, neonates and juveniles of the eastern Pacific leatherback population would likely be restricted to the eastern tropical Pacific where climatic variability is highest. Thus, these life history stages would also be affected by variable resource availability, further reducing population growth rate.

The reproductive output of eastern Pacific turtles was calculated during an El Viejo regime when El Niño events were more frequent. If the climate and ecosystem of the eastern Pacific shifts to a cooler La Vieja regime in the near future, leatherbacks nesting at Costa Rica and Mexico should experience larger pulses in recruitment from increased resource availability, thus population recovery may then become evident.

Primary production calculations in this study were calculated using the most widely accepted and applied model (Behrenfeld and Falkowski, 1997). Recently, Behrenfeld et al. (2006) showed that satellite derived primary production estimates in the eastern tropical Pacific Ocean may be over-estimated because this area is extremely iron limited. Therefore, resource availability for eastern Pacific leatherbacks is likely lower than calculated in this study, ultimately strengthening the argument that these turtles are highly resource limited (Saba et al., In Review; Wallace et al., 2006).

There have been recent, unpublished laboratory studies using long-term captive turtles that suggest the main factor limiting leatherback growth rate is strictly resource
availability (T. Jones pers. comm.). In this context, if a female neonate eastern Pacific leatherback was left to forage in the western Atlantic, it is likely the turtle would grow to a comparable size and have a reproductive output of a western Atlantic turtle. Thus, the smaller size and lower reproductive output of eastern Pacific turtles would not be due to genotype, but rather a phenotype response to low resource availability.

**Future direction**

The majority of tracking studies from Costa Rica took place during El Niño events. It would be interesting to observe migration during not only La Niña, but also during a transition. Moreover, as leatherbacks are continually monitored in Costa Rica, the longer-term trends will begin to surface and their relationship to large-scale, multidecadal climate change will become more evident as will any response to global warming.

Most importantly, leatherback research along the Peruvian and Chilean coastlines should be intensified. These areas are highly unstudied regarding leatherbacks; the northern areas in Peru are quite possibly foraging hotspots for juveniles and sub-adults. Finally, more information is required on the global impacts of coastal gillnet fisheries on leatherback populations and if there are in fact differences in mortality between ocean basins.
Literature Cited


