An oceanographic context for the foraging ecology of eastern Pacific leatherback turtles: Consequences of ENSO

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Received 11 July 2007; received in revised form 4 February 2008; accepted 17 February 2008
Available online 29 February 2008

Abstract

We analyzed some of the primary biological and physical dynamics within the eastern Pacific leatherback turtle ( Dermochelys coriacea ) migration area in relation to ENSO and leatherback nesting ecology at Parque Nacional Marino Las Baulas (PNMB), Costa Rica. We used data from remote sensing to calculate resource availability via a net primary production (NPP) model, and to analyze the physical dynamics of the migration area via sea surface temperature fronts. Within the migration area, NPP north of 15°S was highly governed by interannual variability as indicated by the Multivariate ENSO Index while south of 15°S, production had a more seasonal signal. Nesting peaks of leatherbacks at PNMB were associated with cool, highly productive La Niña events and with large-scale equatorial phytoplankton blooms encompassing 110°W that were induced by iron enrichment following the termination of El Niño events. Resource availability in the northern migration area (eastern equatorial Pacific) appeared to determine the nesting response for the population at PNMB, Costa Rica. We suggest that ENSO significantly influences 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. Coastal foragers may be a minority in the population because of high mortality rates associated with coastal gillnet fisheries along Central and South America.

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Keywords: Coastal gillnet fisheries; Dermochelys coriacea; Eastern equatorial-southeastern Pacific; ENSO; Leatherback turtle migration; Primary production

1. Introduction

The population of leatherback turtles ( Dermochelys coriacea ) has been 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-Martínez et al., 2007). Moreover, the eastern Pacific population is the smallest in size and has the lowest reproductive output among all
populations worldwide studied to date; this is attributed to the high interannual and multidecadal climate variability in the eastern Pacific rendering resource availability highly variable (Saba et al., 2008). 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 also 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.

Leatherback turtles are among the largest reptiles in the world, yet rely on a diet consisting almost entirely of gelatinous zooplankton, which have a very low caloric value per unit volume (Doyle et al., 2007; Hsieh et al., 2001); thus subadults 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), migration to nesting beaches, and the nesting process (Hamann et al., 2002; Wallace et al., 2006). For several species of sea turtles, oceanographic conditions at their foraging areas prior to the nesting season determine their probability of nesting (Limpus and Nicholls, 2000; Broderick et al., 2001; Solow et al., 2002; Saba et al., 2007). In the eastern Pacific, the El Niño Southern Oscillation (ENSO) significantly affects the reproductive frequency of leatherbacks nesting at Parque Nacional Marino Las Baulas (PNMB), Costa Rica (Saba et al., 2007). The ENSO consists of warm and cool sea surface temperature (SST) phases in the central and eastern equatorial Pacific. Cool, highly productive La Niña events increase the nesting probability while warm, productive El Niño events decrease the probability. This relationship suggests that primary production can be used as proxy for gelatinous zooplankton abundance and distribution, or essentially, resource availability for leatherback turtles.

The equatorial Pacific is a high-nitrate low-chlorophyll region where productivity is highly limited by iron (Behrenfeld et al., 2006). Indices of ENSO are effective for predicting the number of nesting leatherbacks at PNMB; however, there were a few years during which nesting peaks occurred that were not predicted because they followed warm El Niño events (Saba et al., 2007). Recently, Ryan et al. (2006) demonstrated that very large-phytoplankton blooms (~5 × 10^5 km^2) occurred in 1998, 2003, and 2005 in the central and eastern equatorial Pacific. These unusually large-scale blooms followed El Niño events, triggered by the shoaling of the New Guinea Coastal Undercurrent (NGCUC), which resulted in a coupling of the New Guinea shelf and Equatorial Undercurrent in the western Pacific. This coupling led to enhanced iron concentrations in the euphotic zone of the central and eastern equatorial Pacific producing large-scale blooms that could not be predicted purely by SST anomalies (Ryan et al., 2006). 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).

Here we investigated some of the primary biological and physical properties of the area used during post-nesting migration by eastern Pacific leatherbacks. We identified the migration area from both published literature (Morreale et al., 1996; Eckert and Sarti 1997) and recent data (Shillinger et al., unpublished) and used the yearly response of the nesting females at PNMB as an indicator of foraging conditions (Saba et al., 2007). Resource availability in the migration area was determined by calculation of satellite derived net primary production (NPP). The physical qualities of the migration areas were characterized in terms of SST-frontal zones that could serve as physical discontinuities to aggregate gelatinous zooplankton. We provide insights to leatherback foraging ecology in the eastern Pacific with an emphasis on how this information can be applied to conservation management.

2. Data and methods

2.1. Migration area, resource availability, and nesting ecology

We identified the migration area based on satellite tagging studies that tracked post-nesting females from both PNMB (Morreale et al., 1996; Shillinger et al., unpublished) and Mexico (Eckert and Sarti, 1997). Because we were primarily interested in the migration area of post-nesting females from PNMB, we excluded the area north of 10°N where these females have yet to be commonly observed after exiting the nesting complex (Morreale et al., 1996; Shillinger et al., unpublished).
However, post-nesting females from Mexico migrate through these waters (Eckert and Sarti, 1997) and thus should be included in any future analysis that focuses exclusively on this stock within eastern Pacific population. We also excluded the single female from Mexico that traveled near 140°W (Eckert and Sarti 1997) because post-nesting females from PNMB have yet to be observed this far west. Therefore, we denoted the common migration area as being bounded by 10°N-40°S and the coastlines of Central and South America to 125°W.

To understand resource availability both spatially and temporally, we calculated NPP using satellite data. We applied the Behrenfeld–Falkowski vertically generalized production model (VGPM) (Behrenfeld and Falkowski, 1997) using the satellite software package Windows Image Manager (WIM) (Kahru, 2006) and three satellite data sets comprising 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 expanded using an edge-dilate of one pixel width to eliminate satellite data that was obtained too close to the coast, which was subject to error. We used WIM to calculate mean monthly NPP (mg C m⁻² month⁻¹) and ArcView 3.2a to calculate the size of the migration area. Along with calculating 100 monthly NPP images of the total migration area, we also divided the area into 5° × 5° squares and calculated NPP at each square to increase the resolution of the time-series. We also divided the migration area into latitudinal bands from the coastline westward at 5° latitudinal intervals to produce a zonal comparison of NPP.

We calculated composites of NPP during the 1997-1998 El Niño and during the 1998-2000 La Niña. 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°S as the center point and calculated total mean monthly NPP (Tg C year⁻¹) using each area’s size and mean monthly NPP during the two ENSO periods.

Each year, the nesting season begins in October and ends in February. We used the remigrant nesting data at Playa Grande, PNMB, from 1998-1999 to 2004-2005 from Saba et al. (2007) with the addition of the 2005-2006 nesting season. A remigrant is a turtle that was originally tagged at Playa Grande and returned to nest in a successive season. At PNMB, the number of remigrants is proportional to the number of new recruits in any given season (Santidrián-Tomillo et al., 2007); thus either measurement can be used as a season’s nesting success. 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 NPP in the migration area to discern possible foraging hot spots that influenced leatherback nesting probabilities. To discern NPP changes induced by the NGCUC shoaling, we calculated the time-series of NPP from 2.5°S to 2.5°N and 107.5°W to 112.5°W. This 5° × 5° square encompassed the area where the 1998, 2003, and 2005 NGCUC induced blooms were most pronounced, although the 1998 bloom did extend further west to the dateline (Ryan et al., 2006).

2.2. Seasonal versus interannual resource variability

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

We used the multivariate ENSO index (MEI) (Wolter and Timlin, 1998) as an indicator of ENSO strength from September 1997 to December 2005. The MEI incorporates six climatic variables in the tropical Pacific Ocean: sea-level pressure, zonal and meridional components of surface wind, SST, surface air temperature, and total cloudiness fraction of the sky. Interannual variability of NPP in each square 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 seven non-seasonal harmonic constituents of the MEI were applied in a least-squares fit to each square’s NPP time-series and r values were calculated. From the fit, two r values were calculated for each square, each of which described how much NPP
variance was explained by seasonality and the MEI separately. We then contoured the squares’ $r$ values (kriging interpolation) to visualize the temporal dynamics of NPP in the migration area.

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

2.3. SST fronts

We analyzed the distribution and frequency of SST fronts in relation to ENSO. 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). Mean SST front frequency images were produced using monthly Pathfinder 4 km AVHRR SST data (NASA, 2006). We were interested in the mean distribution and frequency of fronts during ENSO transitions. Satellite data for SST dates further back than ocean color data, thus we were able to include the 1987–1988 El Niño and 1988–1989 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.

3. Results

3.1. ENSO and primary production

Coastal areas (coastline to 80°W) were the most productive in the migration area. Net production along the coasts was reduced during the strong 1997–1998 El Niño but remained high relative to the open-ocean areas (Fig. 1A–C). The most significant NPP response to the 1997–2000 ENSO transition was north of 15°S (Fig. 1B and C). The temporal variability of NPP was dominated by the MEI ($r > 50\%$) north of the equator and west of the Gulf of Panama (Fig. 2A). High NPP 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 NPP was more seasonal towards the coast and the effect of the MEI was weak (Fig. 2A and B). The effect of the MEI on NPP weakened southward where seasonal variation dominated south of 25°S (Fig. 2A and B). The area between the Galápagos Islands and Costa Rica, where the post-nesting females migrate from PNMB (Morreale et al., 1996; Shillinger et al., unpublished), had exceptionally low seasonality (Fig. 2B). South of the equator, the MEI’s effect on coastal NPP never exceeded $r$ values greater than 50%.

The first three PCs of NPP variability in the migration area accounted for 21.6% of the total variation ($PC_1 = 10.8\%$, $PC_2 = 5.8\%$, $PC_3 = 5.0\%$) (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 eigenvectors of $PC_1$ were essentially the mirror image of the MEI, demonstrating the general trend of the MEI on NPP where warm El Niño events decreased production and cool La Niña events increased production (Fig. 3A). This relationship was strongest and most evident north of 20°S (Fig. 3D) as also demonstrated in Fig. 2A and B. The spatial mode of $PC_2$ showed the pocket NPP west of 100°W between 10°S and 20°S associated with the MEI (Fig. 3E) as also shown in Fig. 2A. There was a slight lag between the peak eigenvector variation of $PC_3$ and the MEI that followed El Niño events in 1998 and 2003; this was likely a result of the large-scale blooms that followed the 1998 and 2003 El Niño events, however, the 2005 bloom wasn’t represented in $PC_3$ (Fig. 3C). The third spatial mode also showed MEI governed PP variability in the South Pacific Subtropical Gyre (Fig. 3F).

3.2. Primary production transitions, SST fronts, and leatherback nesting response

The size of the northern migration area from 15°S to 10°N was $14.38 \times 10^6 \text{km}^2$, 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 NPP spatially, seasonal variability in the northern area was extremely low while it dominated in the south (Fig. 4A). In terms of the mean NPP generated per month by each area (Tg C month^-1) from 1997 to 2005, the north was significantly more productive (ANOVA, P < 0.0001) by 1.78 Tg C month^-1 than the south (Fig. 4B). Oceanic 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 1997-1998 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 NPP occurred August through October, which were extended during the 1998-2000 La Niña. In the south, maximum production occurred during the austral spring (October through December) of each year. The 5° latitudinal bands of NPP further demonstrated the stronger interannual variability north of 15°S and the decrease in NPP south of 15°S until an increase occurred at 35°S approaching the Southeast Pacific Subtropical Convergence (Fig. 5).

The 5° x 5° square along the equator that encompassed 110°W clearly showed the peaks in NPP 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 NPP transitions in the migration area appeared to be determined by areas north of 15°S. The largest peak in remigrants occurred in 1999-2000 and 2000-2001
Fig. 2. Seasonal versus interannual NPP at the migration area. Contoured $r$ values for each 5° × 5° square’s NPP time-series (1997–2005) derived from Fourier regression, harmonic analysis, and least-squares fit of (A) interannual variability using the MEI and (B) seasonal variability using the annual and semi-annual harmonic constituents.

(Fig. 6B) coinciding with the 1998–2000 La Niña NPP increase north of 15°S (Fig. 4B). Moreover, the nesting peaks in remigrants in 2003–2004 and 2005–2006 (Fig. 6B) were perhaps a response to the NGCUC induced large-scale blooms along the equator around 110°W (Fig. 6A). However, the small number of remigrants in 1998–1999 indicated no response to the large 1998 NGCUC induced bloom (Fig. 6A and B); nesting numbers in 1998–1999 coincided with typical ENSO indices when the 1997–1998 El Niño caused a low remigration probability in 1998–1999 (Saba et al., 2007).
Along the equator, the frequency of SST fronts was reduced during the 1987–1988 and 1997–1998 El Niño events when equatorial upwelling was reduced (Fig. 7). The frequency of fronts increased during the subsequent La Niña events in 1988–1989 and 1998–1999 when equatorial upwelling intensified. Thus, La Niña increased both NPP and the frequency of SST fronts north of 15°S.
Fig. 4. (A) Time-series of mean monthly NPP 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 1997–1998 El Niño, and the 1998–2000 La Niña. T-bars are standard deviation.
4. Discussion

4.1. ENSO and leatherback foraging areas

Leatherbacks nesting at PNMB, Costa Rica, appeared to be responding to NPP transitions in the northern part of the migration area from 15°S to 10°N. This is based on the strong relationship of their nesting response to ENSO associated NPP transitions in the northern part of the migration area. If foraging conditions south of 15°S influenced...
upwelling was intensified, and the frequency of SST fronts increased (Figs. 1C, 5, 7). 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 2003–2004 and 2005–2006 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 affected leatherbacks nesting at PNMB because no nesting response was observed in 1998 that followed the largest NGCUC induced bloom (Fig. 6A and B). The nesting probabilities in 1998 were highly influenced by the strong 1997–1998 El Niño when we observed a low number of remigrants (Fig. 6B) due to the reduction of NPP north of 15°S (Figs. 4A and B, 5). We suggest that no nesting response to the 1998 NGCUC induced bloom occurred because the overall NPP of the north was at its lowest level, whereas in 2003 and 2005 the NGCUC induced blooms occurred when NPP was closer to the mean and significantly higher than during the 1997–1998 El Niño event (Figs. 4A and 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. Finally, La Niña events not only increased NPP along the equator, but also increased the frequency of SST fronts (Fig. 7). These fronts may be important areas for leatherback foraging because they can aggregate gelatinous zooplankton (Graham et al., 2001).

4.2. Galápagos islands

At PNMB, 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 ~6 nests per season with a mean internesting interval of 9.5 days, the entire nesting season for a female lasts ~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. Based on the tracking study by Morreale et al. (1996), it takes about 40–60 days for a leatherback to reach the Galápagos Islands from PNMB, thus the majority of turtles would be arriving there 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 high during El Niño events (Fig. 1A–C). Although NPP on the west coast of the Galápagos Islands 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
Fig. 7. Small-scale SST frontal frequency during the 1987-1988 and 1997-1998 El Niño, and the 1988-1989 and 1998-1999 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 4km Pathfinder AVHRR satellite data.

upwelling where the Equatorial Undercurrent impinges the western coasts of the islands. 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 to 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). Moreover, the majority of leatherbacks recently tracked from PNMB to the Galápagos Islands migrated on the western side (Shillinger et al., unpublished).

4.3. Southeastern pacific

Among other leatherback populations in both the Atlantic and western Pacific, arrival to temperate foraging areas follows the seasonal spring bloom (Benson et al., 2007a; James et al., 2005; McMahon and Hays, 2006; Saba et al., 2008; Witt et al., 2007) when gelatinous zooplankton abundance peaks in the summer months (James and Herman, 2001; Witt et al., 2007). Production peaks in the southern part of the migration area in the austral spring (October to December), thus we would expect leatherback arrival to the southeastern Pacific in the austral summer from January to February, at least during El Niño years when production along the equator is reduced.

With the exception of the coastlines, the southeastern Pacific has very low NPP as a result of the permanent thermocline within the South Pacific Subtropical Gyre that is considerably deeper than the mixed layer (Fiedler and Talley, 2006). It is important to note that physical forcing alone is not enough to create suitable foraging; sufficient NPP is initially required to support the food web (Polovina et al., 2006). Sharp gradients in NPP along the edges of the South Pacific Subtropical Convergence and on the eastern and northern boundaries of the South Pacific Subtropical Gyre (Fig. 1A–C) 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 that lies at the boundary between low chlorophyll subtropical gyres and high chlorophyll subarctic gyres (Polovina et al., 2000, 2001, 2006). We surmise that leatherbacks migrating to the pelagic southeastern Pacific target these chlorophyll fronts that lie on the southern, eastern, and northern boundaries of the South Pacific Subtropical Gyre.

4.4. Coastal foraging and gillnet fisheries

Satellite tracking data from PNMB (Morreale et al., 1996; Shillinger et al., unpublished) and from Mexico (Eckert and Sarti, 1997) showed only a few individuals migrating to coastal areas. It is possible that more than 1.5 years of individual 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 and 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 the eastern equatorial Pacific in terms of NPP and marine fauna biomass (Pennington et al., 2006) (Fig. 1A). The Gulf of Panama was not only a highly productive coastal area; it also had a relatively high seasonal signal due to its high terrestrial run-off and wind induced mixing (Pennington et al., 2006) (Figs. 1A–C, 2B). The Costa Rica Dome is a biological 'hotspot' for many trophic levels including zooplankton, fish, and 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 and low NPP in the pelagic southeastern Pacific.

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. 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 tropical nesting areas and back was done by James et al. (2005) in the western Atlantic. They showed six adult males, seven adult females, and six 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. High levels of foraging area fidelity have also been reported for mature female loggerhead (Caretta caretta) and green (Chelonia mydas) turtles in the Mediterranean Sea (Broderick et al., 2007). This suggests that individual sea turtles typically return to the same foraging areas throughout their subadult and adult life stages.

Eckert and Sarti (1997) compiled Chilean gillnet fishery reports from Frazier and Montero (1990) and Weidner and Serrano (1997) spanning the 1980s and into the 1990s. These fisheries typically target swordfish. Eckert and Sarti (1997) 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, we conclude that coastal foragers are now a minority within the eastern Pacific leatherback population because of a high bycatch and mortality rate from past and possibly present coastal gillnet fisheries.

Leatherback bycatch and mortality have also been reported among Peruvian coastal gillnet fisheries. From 2000 to 2003, a dock-side observer program from eight Peruvian ports reported 133 incidentally caught leatherbacks of which 76% were captured in artisanal gill nets (Alfaro-Shigueto et al., 2007). Of the 133 leatherbacks caught, 55 were released alive and 78 were retained for human consumption. Moreover, 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 in both studies were juveniles and subadults [mean curved carapace length = 109.27±14 cm (de Paz et al., 2006) and 113±12 cm (Alfaro-Shigueto et al., 2007)]. This could be a function of the mesh size (up to 20 cm) or that the coast of Peru serves as an important foraging area for juveniles and subadults.
4.5. Comparison to other leatherback populations worldwide

Our analysis suggests that the eastern equatorial Pacific was the crucial zone where resource availability determined the leatherback nesting response at PNMB, Costa Rica. Whereas eastern Pacific leatherbacks relied 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 is a major migration area for western Atlantic leatherbacks (Eckert, 2006; Ferraroli et al., 2004; Hays et al., 2004; James et al., 2005) and, consequently, their reproductive output is nearly twice that of eastern Pacific leatherbacks (Saba et al., 2008). Although some western Atlantic leatherbacks may 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 among the most productive leatherback foraging area whereas the southeastern Pacific is one of the least productive (Saba et al., 2008). Similar to eastern Pacific leatherbacks, it appears that eastern Atlantic turtles from Gabon also highly rely on equatorial waters 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 areas has been a successful strategy. However, these turtles have also been observed along the eastern coast of South America (Billes et al., 2006); thus coastal foraging may be an additional strategy essential to the success of this population.

The most striking difference in the migration patterns between eastern Pacific leatherbacks and every other population worldwide is the infrequent reporting of coastal migration. Coastal waters are highly productive 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, b). These studies demonstrate the importance of coastal areas as crucial leatherback foraging areas. It is plausible that leatherback mortality among Pacific coastal fisheries off Central and South America at one time exceeded that of any other area in the world.

5. Conclusions

Our results suggest that 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. 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. Transitions in NPP along the equator extend much further west than 125°W along the equatorial cold tongue, thus the turtles could also be responding to ENSO-governed transitions in the central equatorial Pacific as well if the migration area were expanded west. However, the NGCUC induced blooms were most pronounced at 110°W suggesting that the foraging areas were most likely in the eastern equatorial Pacific. Using equatorial SST indices alone did not completely predict the number of turtles remigrating to nest at PNMB (Saba et al., 2007) because blooms induced by the NGCUC were not signaled by local climate conditions such as SST. The use of NPP 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 if mortality rates are still high. Given that this population is already subject to natural variability in their foraging areas, anthropogenic mortality needs to be eliminated. 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 Galápagos Islands are in operation during that time, appropriate action is required to avoid turtle interaction. If leatherback mortality at coastal areas is sufficiently reduced or eliminated, eventually coastal foraging may no longer be rare, reducing the entire population's sensitivity to ENSO and thus possibly enabling higher nesting rates during El Niño years.
Acknowledgments

We are very grateful to all of the people involved with the leatherback conservation project at PNMB, Costa Rica. We thank R. Piedra, E. Vélez, S. Eckert, B. Wallace, and the Ministerio de Ambiente y Energía (MINAE). M. Kahru graciously provided satellite data analysis assistance. Funding for the leatherback tagging study was provided by Earthwatch Institute and The Leatherback Trust. We thank the Tagging of Pacific Predators (TOPP) program and the TOPP sea turtle team. Leatherback tagging permits and animal care protocols were issued by MINAE, Indiana-Purdue University of Fort Wayne, Drexel University, and Stanford University.

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