5-2008

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Recommended Citation

Saba, VS; Spotilia, JR; Chavez, FP; and Musick, JA, "Bottom-up and climatic forcing on the worldwide population of leatherback turtles" (2008). *VIMS Articles*. 1728.
https://scholarworks.wm.edu/vimsarticles/1728

Ecology, 89(5), 2008, pp. 1414–1427

BOTTOM-UP AND CLIMATIC FORCING ON THE WORLDWIDE POPULATION OF LEATHERBACK TURTLES

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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 net primary production at post-nesting female migration and foraging areas. Leatherbacks in the eastern Pacific were the smallest in body size and had the lowest reproductive output due to less productive and inconsistent resources within their migration and foraging areas. 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 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.

Key words: climate variability; Dermochelys coriacea; *ENSO; gelatinous zooplankton; global warming; jellyfish; leatherback sea turtles; multidecadal regimes; primary production; reproductive output; resource availability; trophic forcing.*

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, Livingstone and Downie 2006, Verhage et al. 2006), while those in the eastern Pacific Ocean (EP) have been declining precipitously (Spotila et al. 2000, Sarti-Martinez et al. 2007). 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, Livingstone and Downie 2006, Verhage et al. 2006, Hitipeuw et al. 2007).

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 Oceans 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 (Parque Nacional Marino Las Baulas, Costa Rica) over a time period that should allow for adult recruitment (~16 years), population recovery has not occurred there (Santidrián-Tomillo et al. 2007). In the EP, incidental mortality from coastal fisheries, particularly gillnets, appear to be the major anthropogenic influence on adult survival (Eckert and Sarti 1997, Kaplan 2005, Alfaro-Shigueto et al. 2007). Whereas these fisheries exist in all basins, they have not precluded population recovery in the Atlantic and WI Oceans. Among pelagic longline fisheries, leatherback bycatch rates are significantly higher in the Atlantic with less fishing effort when compared to the Pacific (Lewison et al. 2004), likely a result of a higher probability of bycatch due to more leatherbacks present. Among Atlantic coastal gillnet fisheries in Trinidad, Lee Lum

Manuscript received 5 March 2007; revised 17 August 2007; accepted 13 September 2007. Corresponding Editor: M. Wikelski.

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(2006) reported ~3000 adult leatherbacks caught as bycatch in a single year with a 30% mortality rate. Although this mortality rate is likely not sustainable for a long period of time, the Trinidad population currently appears to be robust and not declining (Livingstone and Downie 2006). 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, ENSO highly influences the reproductive frequency of the major EP population nesting in Costa Rica, a consequence that may exacerbate their sensitivity to anthropogenic mortality (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 net primary production (NPP; 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, Doyle et al. 2007*b*), 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, Doyle et al. 2007*a*), they must foremost be high in NPP to support a high biomass (Ménard et al. 1994, Lucas et al. 1997, Vinogradov and Shushkina 2002, Lynam et al. 2004). Nesting leatherbacks in the EP respond to ENSO-governed NPP transitions in the equatorial Pacific (Saba et al. 2007); in this context, NPP 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 NPP 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 (*Dermochelys coriacea*) worldwide. The majority of our migration review was comprised of long-term (~1 year) satellite tracking studies, except for a few cases where we used recent tracking data (M. Witt and B. Godley, *unpublished data*) and nesting female tag return data (Billes et al. 2006) from Gabon and observational data in the Mediterranean (MED; Casale et al. 2003). The latitudinal and longitudinal ranges of the migration 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 migration areas for each population, especially given the wide-ranging nature of leatherbacks.

Remote satellite data analysis

To calculate net primary production (NPP), we applied the Behrenfeld-Falkowski vertically generalized production model (VGPM; Behrenfeld and Falkowski 1997) using the satellite software package Windows Image Manager (WIM, Microsoft, Redmond, Washington, USA; 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 and photosynthetically active radiation data (*available online*)[5] and monthly Pathfinder 4-km Advanced Very High Resolution Radiometer (AVHRR) SST data (*available online*)[6] from September 1997 to December 2005 resulting in 100 monthly images. We used WIM to calculate mean monthly NPP (mg $\mathrm{C \cdot m^{-2} \cdot month^{-1}}$) and ArcView 3.2a (ESRI, Redlands, California, USA) to calculate the size of each migration area. Total mean yearly NPP was calculated using each migration area's size and mean monthly value. To understand the seasonality of each NPP time series, we applied a least-squares regression to each data set using semiannual and annual harmonic constituents (Emery and Thomson 1998). From this, we denoted r values greater than 0.5 as seasonal variation and r much less than 0.5 as interannual.

We assumed turtles foraged in transit to and from areas of high NPP (Hays et al. 2006); therefore, we calculated NPP both at the entire migration area and at individual foraging areas. Calculating NPP 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 NPP throughout the total migration area. To discern foraging areas within the

[5] ⟨http://oceancolor.gsfc.nasa.gov⟩

[6] ⟨podaac.jpl.nasa.gov/sst⟩

TABLE 1. Net primary production, nutrient forcing, and seasonality within the migration areas of post-nesting female leatherback populations worldwide

Population and migration area	Nutrient forcing	Mean NPP (mg C·m^{-2}·month^{-1})	Maximum NPP (mg C·m^{-2}·month^{-1})
Western Atlantic			
North Atlantic (NA)	wind-driven mixing and eutrophic shelf	680.7 ± 282.7	1209.7
Western Tropical Atlantic (WTA)	eutrophic shelf	360.9 ± 50.2	440.1
Eastern Tropical Atlantic (ETA)	coastal/equatorial upwelling	534.3 ± 83.8	786.1
Mediterranean (MED)†	coastal upwelling	463.8 ± 87.4	685.3
Eastern Atlantic			
Eastern South Atlantic (ESA)	coastal/equatorial upwelling and wind-driven mixing	525.9 ± 76.5	656.3
Western South Atlantic (WSA)	wind-driven mixing and eutrophic shelf	474.4 ± 93.9	676.7
Western Indian			
Agulhas current system (ACS)	wind-driven mixing and eutrophic shelf	561.6 ± 113.8	772.9
Eastern South Atlantic (ESA)	coastal/equatorial upwelling and wind-driven mixing	525.9 ± 76.5	656.3
Eastern Pacific			
Eastern subtropical Pacific (ESTP)	coastal upwelling	360.5 ± 60.4	492.7
Eastern tropical Pacific (ETP)	coastal/equatorial upwelling	465.7 ± 65.1	601.9
Southeastern Pacific (SEP)	coastal upwelling and wind-driven mixing	316.4 ± 33.8	386.7
Western Pacific, Papua			
Central and western North Pacific (CWNP)	wind-driven mixing and eutrophic shelf	402.5 ± 74.6	562.9
Northeastern Pacific (NEP)	coastal upwelling and wind-driven mixing	438.5 ± 83.5	601.9
Western Tropical Pacific (WTP)	island/equatorial upwelling	282.9 ± 25.0	334.3
Western Pacific, Papua New Guinea			
Southwestern Pacific (SWP)	wind-driven mixing and eutrophic shelf	415.4 ± 53.5	524.9

Notes: Each population's migration area was based on the review of satellite telemetry studies of post-nesting females from their respective nesting beaches. Total NPP was calculated using migration area size and mean monthly NPP and thus is an annual mean (1 Tg = 10^{12} g). Data shown are ±SD. The cycle of NPP was based on the least-squares regression such that variance explained by seasonality >50% is considered seasonal and ≪50% is interannual.

† We assumed that leatherbacks observed in the MED were part of the WA population, given their migration patterns near the Strait of Gibraltar.

migration areas, we reviewed studies that incorporated high-use horizontal habitat utilization analysis from leatherback satellite telemetry. This enabled us to compare NPP among entire migration areas and among smaller foraging areas.

We applied an empirical orthogonal function analysis to 252 mean monthly Pathfinder SST images from January 1985 to December 2005 using WIM (Kahru 2006) producing the first spatial mode of SST variation across three ocean basins (data *available online*).[6] 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 55 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), which 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 the nesting ecology of leatherbacks over a time series. 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 because of 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). It is based on a female's first and last appearance dates and the mean inter-nesting interval of leatherbacks (typically 9–10 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.

Table 1. Extended.

Migration area size (10^6 km^2)	Total NPP (Tg C/yr)	NPP cycle
15.6	127.2 ± 52.8	seasonal
20.6	89.1 ± 12.4	seasonal
8.7	55.6 ± 8.7	seasonal
3.2	17.8 ± 3.4	seasonal
19.7	124.0 ± 18.0	seasonal
14.6	83.0 ± 16.4	seasonal
6.1	41.3 ± 8.4	seasonal
19.7	124.0 ± 18.0	seasonal
5.9	25.4 ± 4.3	interannual
15.0	83.8 ± 11.7	interannual
25.4	96.4 ± 0.3	seasonal
47.1	227.4 ± 42.1	seasonal
8.1	42.8 ± 8.2	seasonal
24.2	82.2 ± 7.3	seasonal
30.7	152.9 ±19.7	seasonal

Results

Our review and NPP analysis showed that post-nesting females among all populations migrated to systems of high NPP (Table 1; Fig. 1a, b) driven by coastal upwelling (Ferraroli et al. 2004, Hays et al. 2004, Eckert 2006, Luschi et al. 2006, Benson et al. 2007*a*, *b*), equatorial upwelling (Morreale et al. 1996, Eckert and Sarti 1997, Ferraroli et al. 2004; G. Shillinger, D. Palacios, H. Bailey, S. Bograd, A. Swithenbank, J. Spotila, B. Wallace, F. Paladino, S. Eckert, R. Piedra, and B. Block, *unpublished data*; M. Witt and B. Godley, *unpublished data*), and strong wind-driven vertical mixing along eutrophic coastal shelves and temperate pelagic zones (Ferraroli et al. 2004, Hays et al. 2004, James et al. 2005*a*, Billes et al. 2006, Eckert 2006, Luschi et al. 2006, Benson et al. 2007*b*, *c*, Evans et al. 2007). Among all of the migration areas worldwide, the North Atlantic (NA) had the highest mean and maximum NPP (Table 1; Fig. 1a) and is where the majority of the WA females tended to migrate. Among the least productive migration areas were the western tropical Pacific (WTP), southeastern Pacific (SEP), and eastern subtropical Pacific (ESTP) (Table 1; Fig. 1b). All of the migration areas had seasonal NPP except the eastern tropical Pacific (ETP) and ESTP (Table 1; Fig. 2a, b).

The most extensive data regarding both nesting, migration, and foraging was comprised of the WA and EP populations. Seasonality accounted for the majority

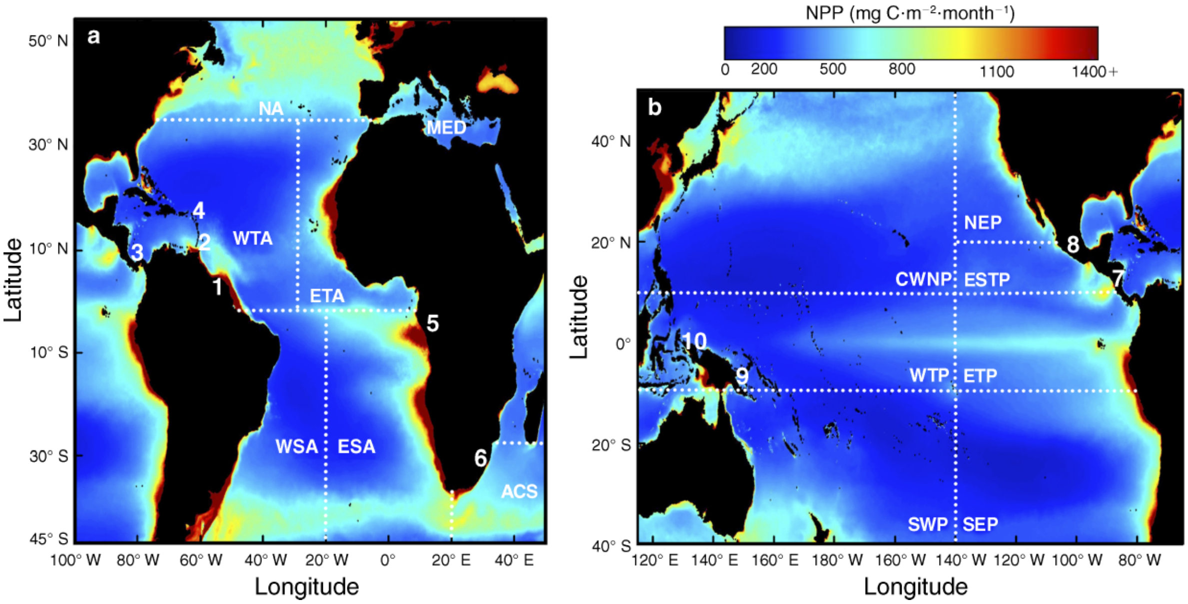

Fig. 1. Mean monthly net primary production (NPP) at Atlantic, Pacific, and western Indian migration areas. (a) Nesting complexes in the Atlantic and western Indian are numbered as follows: for the western Atlantic Ocean (WA) population, (1) French Guiana and Suriname, (2) Trinidad, (3) Caribbean Costa Rica and Panama, (4) St. Croix; for the Atlantic Ocean (EA) population, (5) Gabon; and for the western Indian (WI) population, (6) South Africa. (b) Nesting complexes in the Pacific are numbered as follows: for the eastern Pacific (EP) population, (7) Pacific Costa Rica, (8) Pacific Mexico; for the western Pacific (WP) population, (9) Papua New Guinea and (10) Papua. Mean monthly NPP 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.

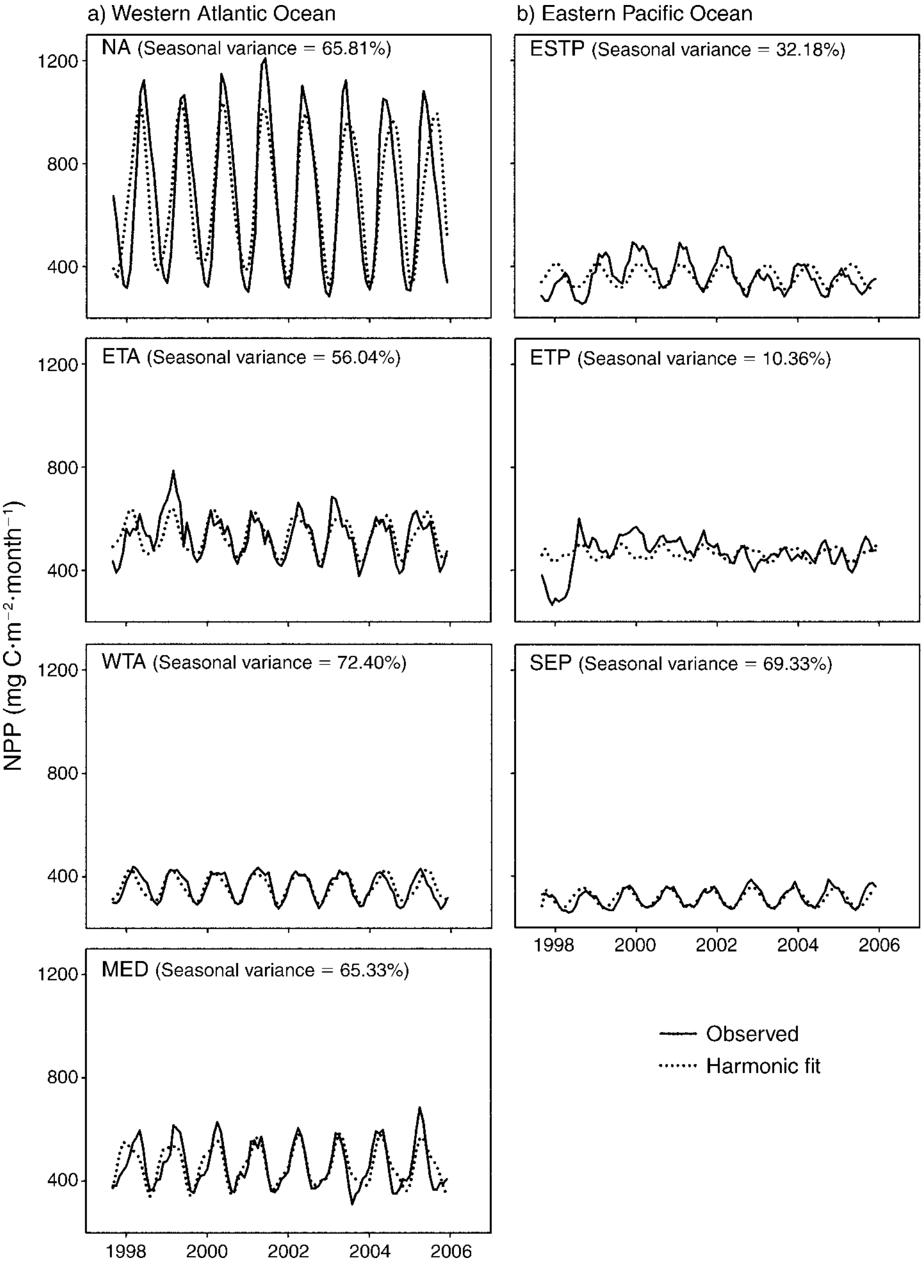

FIG. 2. Time series of net primary production from 1997 to 2005 at (a) western Atlantic Ocean (WA) and (b) eastern Pacific (EP) migration areas. Seasonal harmonic fits were obtained from a least-squares regression using semi-annual and annual harmonic constituents of the mean monthly NPP time-series from each migration area. Solid lines are the observed NPP, and dotted lines are the seasonal harmonic fit.

of NPP variation among all of the migration areas of WA females (Fig. 2a) while, with the exception of the SEP, interannual variation dominated in the EP (Fig. 2b). Mean NPP among all migration 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 migration area NPP quantity 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 migration area of WA and EP females, the total yearly NPP of the WA migration 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

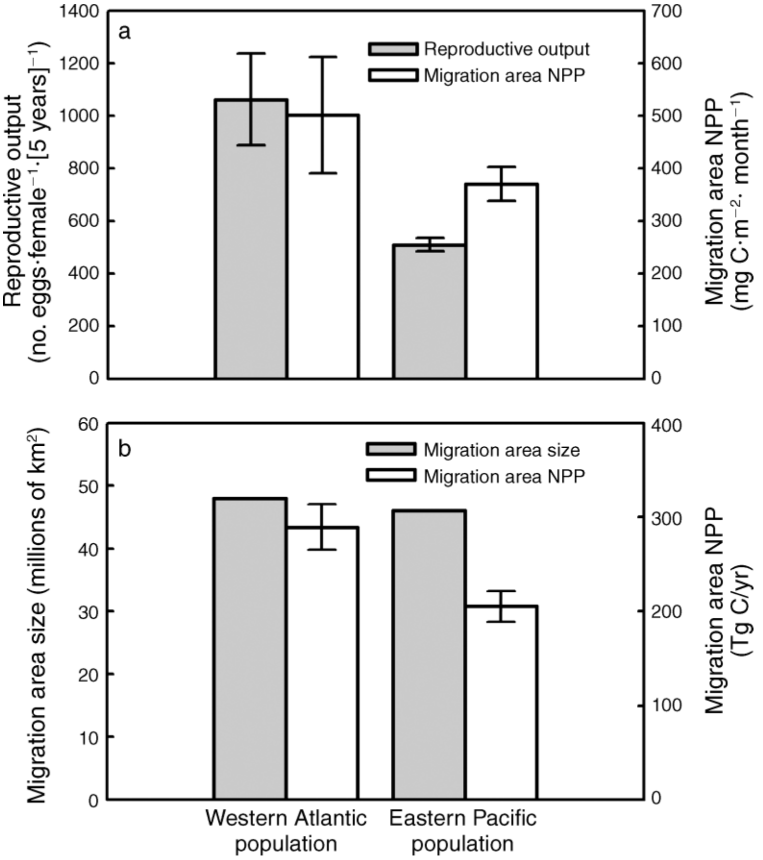

FIG. 3. (a) Reproductive output of western Atlantic (WA) and eastern Pacific (EP) females and mean monthly NPP at their respective total migration area. Total migration area is a summation of all migration areas for the respective population from Table 1. (b) Size and NPP of the total migration area of WA and EP females. There are no error bars for migration area size because it is constant. In both panels, data are shown as mean ± SD.

equatorial and coastal upwelling zones (Ferraroli et al. 2004, Hays et al. 2004, James et al. 2005*a*, Eckert 2006, Evans et al. 2007). In the EP, female leatherbacks relied on equatorial upwelling in the tropics and wind-driven mixing at the subtropical convergence (Morreale et al. 1996, Eckert and Sarti 1997; Shillinger et al., *unpublished data*). Although only a few individuals utilized coastal upwelling areas (Eckert and Sarti 1997; Shillinger et al., *unpublished data*), we still included them in the NPP analysis of the migration area (Fig. 1b).

Evident foraging areas within the migration area of WA turtles consisted of the pelagic and coastal NA (Ferraroli et al. 2004, Hays et al. 2004, James et al. 2005*a*, *b*, Eckert 2006), the Mauritania coastal upwelling system (Eckert 2006) within the ETA, and the northern Gulf of Mexico (Evans et al. 2007) within the WTA. High-use areas within the MED have not been described for leatherbacks thus we did not include foraging areas within this migration area. Among the EP population, foraging areas consisted of the pelagic eastern equatorial Pacific (Morreale et al. 1996; Shillinger et al., *unpublished data*) within the ETP, and the pelagic southeastern Pacific (Shillinger et al., *unpublished data*) within the SEP. The least productive foraging area among WA leatherbacks was the northern Gulf of Mexico, however, this area had significantly higher mean NPP than both the northern and southern pelagic southeastern Pacific ($P < 0.0001$; Fig. 4a). Total NPP among all foraging areas of WA leatherbacks was nearly 370% greater than those of the EP (Fig. 4b). Although the total foraging area size of WA leatherbacks was larger than that of the EP, the ratio of total NPP to foraging area size among WA leatherbacks was twice the EP ratio (Fig. 4b).

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. Moreover, high-use areas for EA, WI, and WP leatherbacks have not been

TABLE 2. Nesting ecology of leatherback turtles worldwide.

Population and nesting complex	Population size (females/yr)	Population trend	Remigration interval (yr)	CCL (cm)	Reproductive output (eggs/clutch)
Western Atlantic					
St. Croix	150	increasing	2.5	152	80
Trinidad	4300	increasing	2.5†	156	84
French Guiana and Suriname	5000	stable	2.5	155	85
Caribbean Costa Rica and Panama	1900	stable	2.5	154	82
Eastern Atlantic					
Gabon	6000	stable		151	73
Western Indian					
South Africa	125	stable	2.5	160	104
Eastern Pacific					
Mexico	200	decreasing	3.7§	144	62
Costa Rica	200	decreasing	3.7	145	64
Western Pacific					
Papua‖	1250	decreasing			78
Papua New Guinea‖	250	decreasing			

Notes: All values reported are means. Population trends were based on nesting numbers over the past 5–10 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 estimated clutch frequencies (ECFs) except in St. Croix and Gabon, where they are based on observed clutch frequencies (OCFs) and are likely underestimates. The clutch frequencies in Trinidad and Caribbean Costa Rica/Panama were based on the mean clutch frequency from the western Atlantic (WA).

† Used mean RI (remigration interval) from WA (western Atlantic).

‡ Used mean clutch frequency from WA.

§ Used mean RI from Costa Rica.

‖ Nesting complex has not been extensively studied.

reported, thus we could not discern foraging areas within their respective migration areas.

From 1985 to 2005, the first principal component (spatial mode) of SST variability among all three basins accounted for 13.6% of the total variation (Fig. 5a). 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. 5a). 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 NPP were calculated toward the end of an El Viejo regime and possibly during a regime shift when El Niño events were more frequent (Fig. 5b).

DISCUSSION

Western Atlantic and eastern Pacific populations

Our analysis revolved around WA and EP leatherbacks because of their extensive nesting and migration data. 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 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

TABLE 2. Extended.

Clutch frequency (clutches/season)	References
5.3	Dutton et al. (2005), Alexander et al. (2004), Boulon et al. (1996)
6.4‡	Livingstone and Downie (2006), Maharaj (2004)
7.5	Rivalan et al. (2005), Hilterman and Goverse (2004), Girondot et al. (2002)
6.4‡	de Haro and Troëng (2006), Troëng and Chaloupka (2006), Troëng et al. (2004), Chacón et al. (1996)
5.0	Verhage et al. (2006)
7.3	Hughes (1973, 1974, 1996); G. R. Hughes, *personal communication*
5.5	Sarti-Martinez et al. (2007)
6.1	Santidrián-Tomillo et al. (2007), Reina et al. 2002
	Hitipeuw et al. (2007), Tapilatu and Tiwari (2007)
	S. R. Benson, *personal communication*

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.

Given the nearly equal size of the total migration area between WA and EP leatherbacks (Fig. 3b), we surmise that a WA female can potentially travel the same distance as an EP female over a similar time period yet encounter a larger quantity of resources, especially those foraging in the coastal and pelagic NA and the Mauritania upwelling system (Fig. 4a). This explains the higher reproduction energy allocation of WA females. The foraging areas of EP females were pelagic and did not include coastal upwelling zones along Central and South America. Long-term satellite tracking of EP females ($n = 46$) has recently demonstrated that coastal migration appears to be a very rare occurrence (Shillinger et al., *unpublished data*). Shorter-term studies also demonstrate a lack of coastal migration among EP post-nesting females (Morreale et al. 1996, Eckert and Sarti 1997). This is likely due to high mortality rates among coastal gillnet fisheries along Peru (Alfaro-Shigueto et al. 2007) and Chile (Eckert and Sarti 1997) rendering pelagic foragers the majority within the EP mature female population. It is clear that coastal foraging is a common strategy among every other leatherback population worldwide (James et al. 2005*b*, Billes et al. 2006, Eckert 2006, Houghton et al. 2006, Luschi et al. 2006, Benson et al. 2007*a*, *b*, Evans et al. 2007, Witt et al. 2007) thus the EP population may be lacking an essential foraging community.

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 (M. Witt and B. Godley, *unpublished data*) 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 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

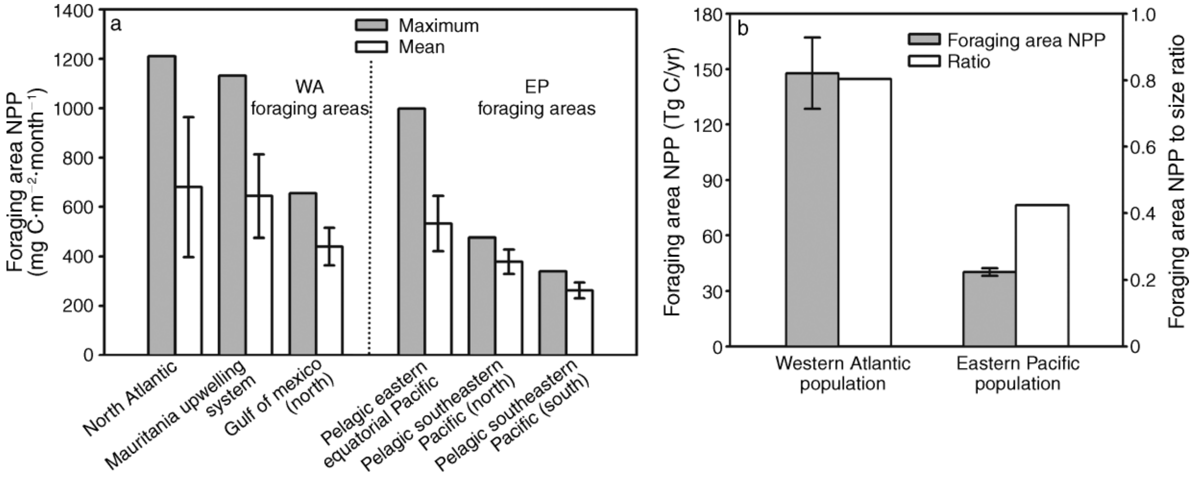

FIG. 4. (a) Mean and maximum NPP at individual foraging areas of western Atlantic (WA) and eastern Pacific (EP) leatherbacks. (b) Total NPP among all foraging areas for WA and EP populations and the ratio of total NPP to the foraging area size. Each ratio was multiplied by 10^5 to increase the scale.

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, robust population size, stable trend, larger egg clutch, and larger body size relative to the EP population (Tables 1 and 2), it is likely their reproductive output is closer to 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 seasonal high-NPP zones driven by coastal upwelling in the Benguela Current and wind-driven mixing off the eastern coast of South Africa and the subtropical convergence (Luschi et al. 2006; Table 1, Fig. 1a). The total foraging area size of the post-nesting females was the smallest among all other nesting populations (2.58×10^7 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 (G. R. Hughes, *personal communication*), 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 decline in Papua (Hitipeuw et al. 2007) and Papua New Guinea (S. R. Benson, *personal communication*); however, further monitoring is needed for accurate assessment. Satellite tracking suggests that WP females (Benson et al. 2007*b*, *c*) have more variability in their migration patterns than EP females (Morreale et al. 1996, Eckert and Sarti 1997; Shillinger et al., *unpublished data*; Table 1, Fig. 1b). Post-nesting females from Papua New Guinea migrate to the southwestern Pacific (SWP), targeting the subtropical convergence zone near New Zealand; whereas, Papua females frequent the central and western North Pacific (CWNP), northeastern Pacific (NEP), and the WTP (Benson et al. 2007*a*, *b*, *c*). Some females from Papua also frequent the coastal waters of the Philippines and Malaysia (Benson et al. 2007*b*) and may also frequent some parts of 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 (Benson et al. 2007*b*, *c*) and possibly lay larger egg clutches (Tapilatu and Tiwari 2007). 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 NPP (Table 1) and larger body size, although the population trend and size of the WP is much different than in the Atlantic. High egg harvesting rates occur in both Papua and Papua New Guinea (I. Kinan, *personal communication*) 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. 5a) 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 a low reproductive output and possibly a slower growth rate. 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. 5b). The last peak La Vieja occurred in the early 1960s 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 since 1965 (Ayón et al. 2004), likely a result of decreasing NPP. Our NPP 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

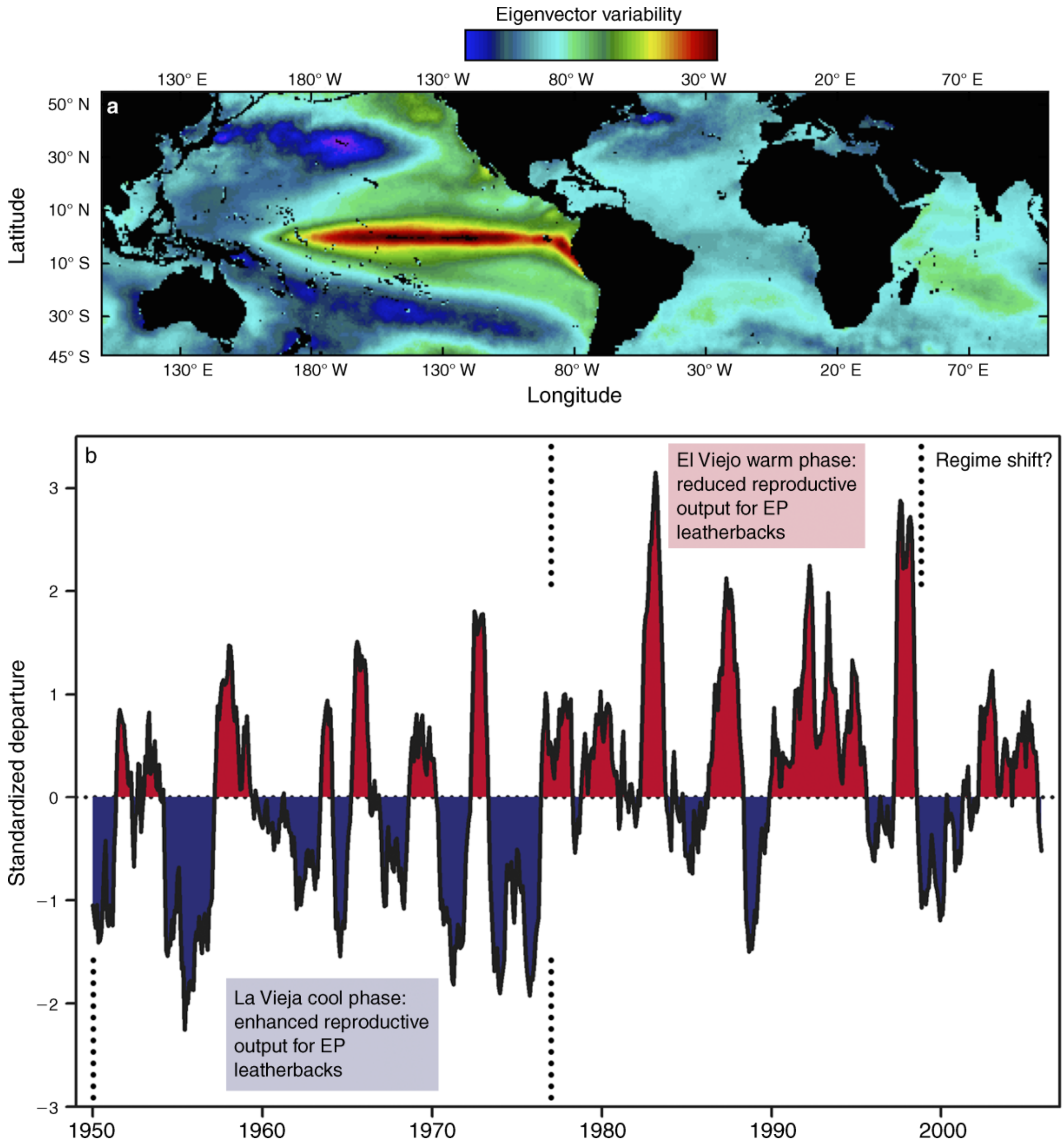

FIG. 5. Variability of SST (sea surface temperature) in the Pacific, Atlantic, and Indian oceans and multidecadal regime shifts in the eastern Pacific (EP). Dark red and dark blue represent highest variability while aqua blue to light green represents little to no variability. (a) First principal component (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) from 1950 to 2005 with regimes shifts in the EP (Chavez et al. 2003) and their likely influence on EP leatherback reproductive output. The influence is based on results from Saba et al. (2007) showing that cooler, more productive La Niña events increased the reproductive frequency of EP leatherbacks.

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*) 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 NPP (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. 2007*a*). Leatherbacks from the WP have been observed feeding on scyphomedusae in Monterey Bay (Benson et al. 2007*a*) and are likely doing the same at coastal areas further north along the northwest coast of North America (Benson et al. 2007*b*). 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).

The majority of scyphomedusae have a benthic polyp stage, and a hard bottom substrate is required for polyp attachment, and 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 zones are typically highest in July and August (Purcell et al. 2000, Purcell 2005, Purcell and Decker 2005). In this context, leatherbacks would need to time their arrival to temperate waters after peak periods of NPP (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. 2007*a*) and from June to August off of eastern Canada (James and Herman 2001, James et al. 2005*b*). Studies along the European continental shelf also showed leatherback peak occurrence during the summer months (Houghton et al. 2006, 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 mesoscale eddies are typically associated with large aggregations (Graham et al. 2001). However, without adequate resources derived from NPP, a large biomass is not possible (Lucas et al. 1997).

Migration to coastal areas represents a portion of leatherback behavior. Among equatorial upwelling systems, both WA (Ferraroli et al. 2004) and EA (M. Witt and B. Godley, *unpublished data*) 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 et al., *unpublished data*; 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.

Primary production estimates

It is important to note that there is a degree of uncertainty when estimating NPP using satellite data and respective algorithms. The equatorial Pacific is a high-nitrate, low-chlorophyll region where algorithms, including the VGPM, can underestimate NPP (Campbell et al. 2002). In the context of our results, if NPP were underestimated in the equatorial Pacific, it is unlikely that the difference would be substantial enough between the foraging areas of WA and EP leatherbacks, especially given that highly productive coastal areas were not part of EP foraging areas (Fig. 4a, b). Moreover, phytoplankton growth in the equatorial Pacific is highly regulated by iron, which can affect the accuracy of satellite chlorophyll fields; thus productivity in the equatorial Pacific may be 1.2–2.5 Pg C/yr lower than previous estimates (Behrenfeld et al. 2006*a*). Finally, it is clear that the level of interannual variability in the ETP exceeded that of the foraging areas of WA leatherbacks. Therefore, even if maximum resource availability were equal between WA and EP foraging areas, the temporal consistency of resources would still be greater for WA leatherbacks rendering their foraging areas more reliable.

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 NPP 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. 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). Although the relationship between the MEI and NPP is substantial in the equatorial Pacific, global ocean NPP is also correlated to the MEI (Behrenfeld et al. 2006*b*); thus leatherback populations in the Atlantic and Indian Oceans may be responsive to climate indices from the tropical Pacific Ocean. It is possible that the foraging areas of WA leatherbacks are currently in a favorable regime, which may partially explain the population increase at some nesting beaches. Research investigating the relationship between detailed leatherback nesting ecology (i.e., remigration interval variability), migration ecology (i.e. high use areas, dive behavior), and climate-governed variability at foraging areas in the Atlantic, Indian, and western Pacific Oceans is currently lacking yet is necessary to fully understand the level to which each population responds to climate-driven foraging quality shifts.

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 16 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 foraging 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.

Acknowledgments

We thank the Pacific–Atlantic Sea Turtle Assessment (PASTA) working group led by Selina Heppell and Molly Lutcavage for their effort that led to a collaboration on this paper. Special thanks to Deborah Steinberg for helpful manuscript comments and Mati Kahru for satellite analysis assistance. We also thank Graeme Hays and two anonymous reviewers for their comments which improved the quality of this paper.

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