

Size, growth, and reproductive output of adult female leatherback turtles *Dermochelys coriacea*

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ABSTRACT: Leatherback turtles *Dermochelys coriacea* exhibit superlative measures of size, growth, and fecundity among reptiles, yet factors affecting these variables remain poorly studied. We investigated the relationships between the leatherback's variable remigration interval and measures of growth and fecundity by analyzing 8 years of data from a population of females nesting at Parque Nacional Marino Las Baulas, Costa Rica. We hypothesized that variation in the remigration interval was due to tradeoffs with seasonal fecundity (clutch size and estimated clutch frequency) or growth rate over the interval. Nesting females grew an average of 0.2 cm yr⁻¹ (range: -1.5 to 2 cm yr⁻¹) in standard curved carapace length and 0.2 cm yr⁻¹ (range: -1.6 to 1.7 cm yr⁻¹) in curved carapace width, with smaller turtles growing significantly faster than larger ones. The small adult growth rates observed indicate that size differences within and between populations are not good indicators of age. Major differences in body size among turtles within a population appear to be set during the juvenile and subadult portions of female leatherbacks' lives. Remigration interval did not correlate with either growth or measured indices of seasonal fecundity. Because delayed remigration did not result in enhanced growth or measured indices of reproduction, variability of environmental conditions might instead determine the length of the remigration interval and thus the overall reproductive output during a female's lifetime.

KEY WORDS: Leatherback · Remigration interval · Life history traits · Fecundity · Sea turtle · Clutch size · Costa Rica

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INTRODUCTION

Leatherback turtles *Dermochelys coriacea* rank among the largest living reptiles, reaching 916 kg in mass and 257 cm in curved carapace length (Eckert & Luginbuhl 1988). Hatchlings grow to about 30 times their length at nest emergence before reaching adulthood. Growth curves fitted to skeletochronological data for leatherbacks indicate rapidly decreasing growth after leatherbacks reach reproductive maturity at about 9 yr (Zug & Parham 1996). However, aside from this growth model, little is known about the

growth rate of adult leatherbacks, although distinct variations in size exist within and among the world's nesting populations (Van Buskirk & Crowder 1994, Zug & Parham 1996). Theoretically, turtles are capable of indeterminate growth, although many turtle species do not continue to grow significantly after maturity (Carr & Goodman 1970, Avery 1994). Here, we present growth data for nesting adult females from a leatherback population that was tagged and monitored for 8 yr.

Along with growth, reproductive traits are central to understanding animal life histories. Leatherbacks lay

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the largest eggs (~80 g each), have the most massive clutches (~5 to 10 kg), and nest the greatest number of times in a given breeding season (mean of 7 clutches) of all sea turtle species (Miller 1997, Reina et al. 2002). This suite of characteristics gives leatherbacks the largest reproductive output by mass of any reptile.

Adult leatherback females typically migrate back to the same beach 2 to 7 yr after nesting to lay several clutches of eggs during a season. The causes of variation in the remigration interval of female leatherbacks are unknown, but they may involve tradeoffs between growth and current and future reproduction. Variation in remigration interval length could be a result of turtles delaying reproduction and investing more resources in growth, as this could result in increased survival or lifetime reproductive success (Congdon et al. 2001). Following this hypothesis, turtles that delay remigration and forego reproduction longer should exhibit a higher growth rate over the remigration interval.

Another hypothesis is that adult female leatherbacks delay reproduction in order to allocate energy more efficiently to fecundity in a future season (Bull & Shine 1979). Because sea turtles engage in a potentially costly breeding migration (Morreale et al. 1996, Eckert & Sarti 1997, Hughes et al. 1998), it might be advantageous for turtles to store energy resources longer, remigrate less often, and produce more eggs during the reproductive season. This hypothesis predicts that turtles with longer remigration intervals should have a greater reproductive output (clutch frequency, clutch size/mass, and egg size/mass) when they return to nest.

Alternatively, variation in the remigration interval may be a result of variation in availability of food resources, or the ability to gather enough resources and make a breeding migration (Broderick et al. 2001, Solow et al. 2002). Large-scale climatic shifts such as the El Niño Southern Oscillation (ENSO) or smaller scale variability of food resource abundance could result in variable remigration intervals.

Finally, adult size may affect both growth rate and seasonal fecundity. Hypothetically, larger turtles might be physically capable of carrying more eggs and/or storing more resources than smaller turtles. Clutch size increases with body size in various turtle species (Hirth & Ogren 1987, Hays & Speakman 1991, Congdon et al. 2001), but no such relationship existed in a previous study of Pacific leatherbacks (Reina et al. 2002).

To test these hypotheses, we examined the relationships between growth rate, seasonal fecundity (measured by both clutch frequency and clutch size), remigration interval, and size for individual female leatherbacks in the Parque Nacional Marino Las Baulas population over 8 yr. Our results on growth and

reproduction of female leatherbacks have important implications for our understanding of life history traits of this critically endangered species.

MATERIALS AND METHODS

We conducted nightly surveys of the beaches at Parque Nacional Marino Las Baulas (Las Baulas) in Guanacaste Province, Costa Rica, during the leatherback nesting season (October to February) from 1993/94 to 2001/02. Early morning patrols demonstrated that these nightly surveys encountered more than 95% of the nesting turtles (as in Steyermark et al. 1996) and leatherbacks generally nest at least 4 times per season (as found by Reina et al. 2002). Starting from 1993, we tagged all nesting turtles with 2 passive integrated transponder (PIT) tags in the muscle of the left and right shoulders, allowing accurate identification of individuals across breeding seasons. We tagged and identified turtles using hand-held PIT tag scanners (AVID Marketing) during oviposition or shortly thereafter while turtles were covering their nests. Given that we encountered all nesting leatherbacks at Las Baulas and that aerial surveys from Mexico to South America did not reveal any other major nesting beaches nearby (Spotila et al. 2000), it is likely that few turtles were nesting elsewhere between recorded nesting seasons at Las Baulas which thereby would have artificially lengthened the observed remigration interval.

We recorded successful or aborted nesting activity of each turtle after the visual observation of oviposition or the observed failure of the turtle to lay. We classified a nest as unknown if we did not observe oviposition. In these cases, we inferred oviposition if we did not identify the individual turtle in a similar nesting attempt within 6 d before or after the inferred oviposition (Reina et al. 2002). We counted eggs as they were laid and distinguished eggs from shelled albumen gobs (SAGs) by their visibly large size difference (Hirth 1980, Sotherland et al. 2003).

We measured carapace length and width while turtles were motionless, during or after laying their eggs. Standard curved carapace length (SCCL) was the distance from the center of the nuchal notch along the side of the dorsal ridge to the posterior tip of the carapace (pygal process). Curved carapace width (CCW) was the distance across the carapace from the widest point along the most lateral ridge (4th longitudinal) to the widest point on the opposite lateral ridge (Steyermark et al. 1996). We averaged multiple measurements within a season to determine a turtle's size, assuming that no detectable growth occurred during the breeding season (Broderick et al. 2003). Measurements that were ≥ 2 cm from the seasonal mean for a

given individual were considered outliers caused by observer error and were removed from analysis (fewer than 8% of measurements were removed for this reason). We determined growth by comparing an individual's mean size during a given nesting season with its mean size during its previously recorded nesting season. Only turtles with at least 2 valid measurements within both seasons were used for determining growth. We calculated growth rate by dividing the growth of a turtle by the number of years passed since it previously nested (remigration interval). Changes in body mass would likely be a better measure of growth, but the extreme size of leatherbacks makes this measurement impractical. Individual turtles that showed zero or negative growth were included in our analysis.

Estimated clutch frequency (ECF), a standard measure for sea turtles (Steyermark et al. 1996) is an estimate of the number of clutches a turtle lays during a nesting season. We used ECF instead of observed clutch frequency (OCF), because it avoids some of the underestimation associated with OCF due to variable census effort (Johnson & Ehrhart 1996, Steyermark et al. 1996). Briefly, we calculated ECF using the first and last observations of a turtle within a season and its mean internesting period to determine the number of clutches the female would have laid within that time period. In order to get the most accurate estimate of clutch frequency, we calculated ECF from only those turtles that began nesting between 15 October and 15 December (Reina et al. 2002). This allowed us to reduce the possibility that a turtle started or finished its nesting season outside of our survey period. Although not reported here, analysis of OCF in place of ECF resulted in the same conclusions. Results are presented as mean \pm 1 SE.

RESULTS

Growth rate

The sizes of turtles used in calculating growth rates ranged from 133 to 165 cm for SCCL (mean \pm SE = 147.0 cm \pm 0.48) and 93.5 to 116.8 cm (mean \pm SE = 105.1 cm \pm 0.39) for CCW (in the first year of measurement). One turtle with an obvious deformity (broken pygal process) was excluded from analyses involving size or growth. Growth rates ranged from -1.5 to 2.0 cm yr⁻¹ for SCCL and ranged from -1.6 to 1.7 cm yr⁻¹ for CCW.

Due to measurement error, it was difficult to discern growth in turtles with 2 yr remigration intervals. However, the overall data indicate that these turtles clearly do grow after maturity. Averaged across all turtles, SCCL growth rate was 0.2 ± 0.05 cm yr⁻¹ (n = 152) and

CCW growth rate was $(0.2 \pm 0.04$ cm yr⁻¹, (n = 140). These growth rates are significantly greater than zero (2-tailed Student's *t*-tests, $t_{151} = 4.577$, $p < 0.001$ and $t_{139} = 5.732$, $p < 0.001$, respectively).

Remigration interval vs. growth rate and seasonal fecundity

There was no consistent relationship between the length of the remigration interval and annual growth rate (Fig. 1). For CCW, 3 yr remigrants grew significantly faster than 2 yr remigrants (ANOVA: $F_{5, 134} = 2.980$, $p = 0.014$). However, the slow annual growth rate made it difficult to detect growth in 2 yr remigrants. Moreover, ANOVA revealed no other significant differences in growth rates between turtles grouped by remigration interval.

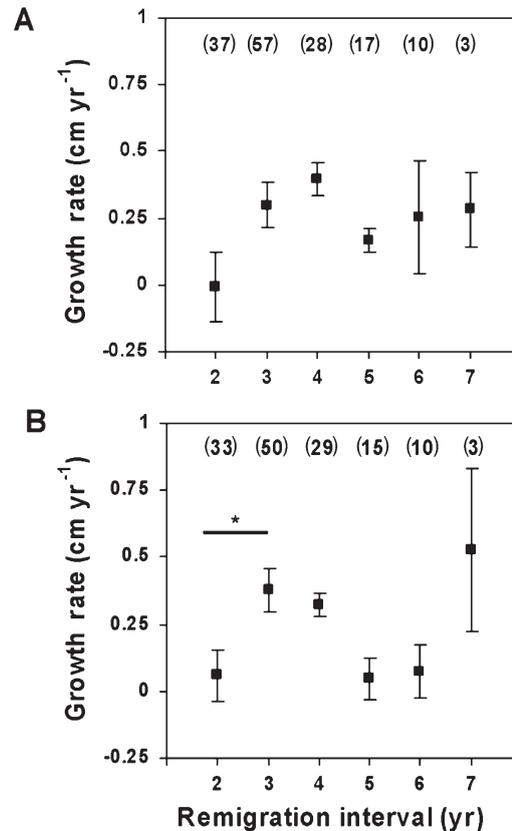


Fig. 1. *Dermochelys coriacea*. Growth rate (cm yr⁻¹) vs. remigration interval for leatherback turtles at Parque Nacional Marino Las Baulas, Costa Rica. There were no consistent relationships between growth rate of either (A) standard curved carapace length (SCCL) or (B) curved carapace width (CCW) and remigration interval for female leatherbacks nesting at Las Baulas. Values are presented as means \pm 1 SE. Sample sizes (in parentheses) for each remigration interval are shown above data. *There was a significant difference in growth rate between 2 and 3 yr remigrants only

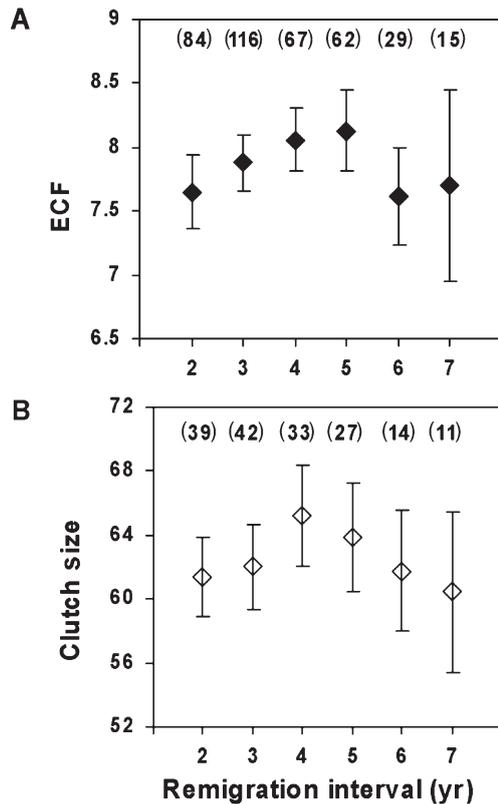


Fig. 2. *Dermochelys coriacea*. Seasonal fecundity vs. remigration interval of leatherback turtles at Parque Nacional Marino Las Baulas, Costa Rica. There were no significant relationships between either (A) estimated clutch frequency (ECF; clutches season⁻¹) or (B) clutch size (no. of eggs) and remigration interval. Values are presented as mean \pm 1 SE. Sample sizes (in parentheses) for each remigration interval are shown above data

Remigration interval had no effect on either ECF (mean \pm SE = 7.87 ± 0.1232 ; ANOVA: $F_{5,367} = 0.456$, $p = 0.809$) or mean clutch size (mean \pm SE = 62.6 ± 1.2869 ; ANOVA: $F_{5,160} = 0.288$, $p = 0.919$) (Fig. 2). Even after accounting for the effect of size (see below), remigration interval had no effect on clutch size (ANCOVA: SCCL, $F_{4,84} = 1.565$, $p = 0.191$ and CCW, $F_{4,81} = 0.842$, $p = 0.502$).

Growth rate and seasonal fecundity vs. size

Growth rate was negatively correlated with size, although size explains only a small proportion of the variation in growth rate (ANOVA: SCCL, $F_{1,150} = 10.691$, $p = 0.001$, linear regression: $r^2 = 0.067$; CCW, $F_{1,129} = 7.377$, $p = 0.008$, $r^2 = 0.054$; Fig. 3). Clutch size increased with increasing turtle length and width (ANOVA: SCCL, $F_{1,88} = 31.825$, $p < 0.001$, linear

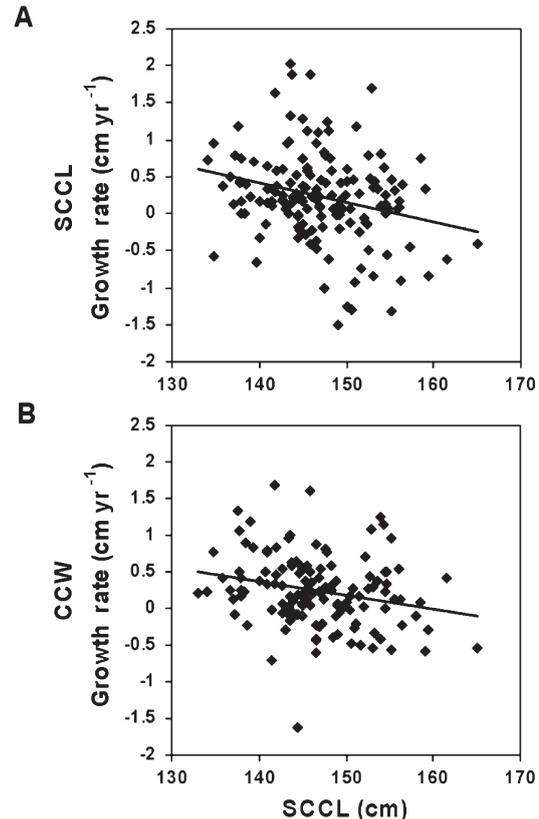


Fig. 3. *Dermochelys coriacea*. Growth rate (cm yr⁻¹) of (A) standard curved carapace length (SCCL; cm) and (B) curved carapace width (CCW; cm) vs. size (SCCL) for adult female leatherback turtles nesting at Parque Nacional Marino Las Baulas, Costa Rica. Growth rate in both SCCL ($n = 152$, growth rate = $-0.026(\text{SCCL}) + 4.1$, $p < 0.001$, $r^2 = 0.067$) and CCW ($n = 131$, growth rate = $-0.019(\text{CCW}) + 3.0$, $p = 0.008$, $r^2 = 0.054$) decreased with increasing length

regression: $r^2 = 0.266$, Fig. 4; CCW, $F_{1,85} = 15.336$, $p < 0.001$, $r^2 = 0.153$, data not shown). However, ECF did not vary with either measure of turtle size (Linear Regression, ANOVA: SCCL, $F_{1,142} = 0.108$, $p = 0.743$, $r^2 = 0.001$; CCW, $F_{1,136} = 0.686$, $p = 0.409$, $r^2 = 0.005$, Fig. 4).

DISCUSSION

Growth in adult leatherbacks

Adult female leatherbacks in the Parque Nacional Marino Las Baulas population continued to grow after reaching reproductive age, as Zug & Parham's (1996) model suggested. Furthermore, the growth rate of adults was slower for larger turtles. These results imply that reproductive female leatherbacks continue to grow slowly, but that this growth slows further over time. Most reptiles are theoretically capable of contin-

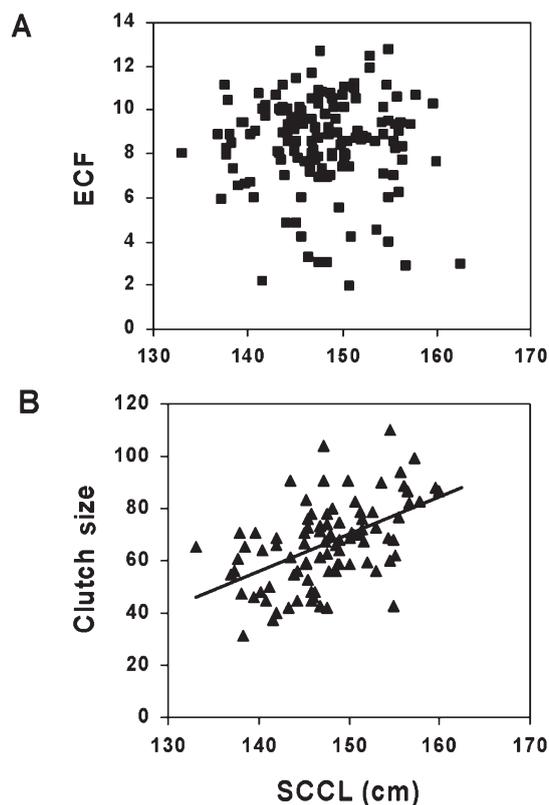


Fig. 4. *Dermochelys coriacea*. Fecundity vs. standard curved carapace length (SCCL) for adult female leatherback turtles nesting at Parque Nacional Marino Las Baulas, Costa Rica. (A) There was no significant relationship between estimated clutch frequency (ECF) and turtle length (SCCL) ($n = 144$, $p = 0.743$, $r^2 = 0.001$). (B) Clutch size increased with increasing turtle length (SCCL) ($n = 90$, clutch size = $1.43(\text{SCCL}) - 144$, $p < 0.001$, $r^2 = 0.266$)

ual growth throughout their lifetimes and many turtle species exhibit indeterminate growth (Congdon & Gibbons 1990). However, most turtle species, including green turtles, apparently do not grow indefinitely (Carr & Goodman 1970, Avery 1994, Castenet 1994). Our results indicate that growth rates of large adult leatherbacks are negligible. Similar results have been found by investigators working with other species of sea turtles (Limpus & Chaloupka 1997, Broderick et al. 2003).

Amongst individual turtles within a species, size at maturation is often variable (Carr & Goodman 1970, Frazer & Ehrhart 1985, Gibbons & Greene 1990, Congdon et al. 2001). The slow growth rate of adult female leatherbacks, compared to the range in sizes of nesting turtles in this population, implies that most variation in nesting female size is due to variation in size at maturity. Size, therefore, does not seem to be a good indicator of age. Furthermore, mean size of an entire nesting leatherback population is probably a better estimate of

mean size at onset of maturity than the mean size of just the smallest turtles in that population, as was reported for green and loggerhead turtles (Frazer & Ehrhart 1985).

Nesting leatherbacks at Las Baulas are 10 to 20 cm shorter on average than those nesting in other populations around the world (Van Buskirk & Crowder 1994, Zug & Parham 1996). Other studies of turtles have demonstrated that population differences in mean size can largely be attributed to differences in size at maturity, rather than differences in mean population age (Carr & Goodman 1970, Gibbons & Greene 1990, Tucker et al. 1999). Our results support this explanation of size differences between leatherback populations. The evolutionary and/or environmental mechanisms driving these population differences in size at maturity were beyond the scope of this study, but may include differential population density (Bjorndal et al. 2000), access to food (Gibson & Hamilton 1984), ambient temperature (Dunham & Gibbons 1990), predation (Van Buskirk & Crowder 1994), age at maturity (Gibbons & Greene 1990), environmental pollution (Albers et al. 1986), habitat productivity (Tucker et al. 1999), and length of breeding migration (Carr & Goodman 1970).

Fecundity and size

Sea turtles are expected to maximize clutch size and increase clutch size with body size due to their high energy expenditure during nesting (Hays & Speakman 1991). Large Las Baulas female leatherbacks did tend to have greater reproductive output than smaller females. These larger turtles may simply be able to carry and deposit larger clutches as a direct consequence of their size. Larger turtles might also be more efficient at accumulating fat stores. The previous finding that body size is not correlated with clutch size in the Las Baulas population (Reina et al. 2002) contradicts the current findings which are based on a subset of the data used by those authors as well as more recent data (from seasons 2000 to 2002). The cause of this contradiction is unclear; however, it is worthwhile to note the high variation in the data. We believe that high intrinsic variation in the data combined with measurement error resulted in a Type II statistical error in the Reina et al. (2002) study. The current study only used data from turtles from which multiple size measurements within a season and multiple clutch size measurements (average = 3) within a season were taken. This likely resulted in mean clutch sizes which were much less variable than those used by Reina et al. (2002), allowing the significant relationship to be detected.

Variation in remigration interval

Leatherback turtles have a variable remigration interval of 2 to 7 yr (Reina et al. 2002), and the cause of this variation is unknown. Theoretically, there may be tradeoffs among certain life history traits that explain why turtles delay remigration if they have the opportunity to reproduce more often (Bull & Shine 1979). Growth and seasonal fecundity are 2 traits subject to these tradeoffs.

Adult turtles might invest energy in growth instead of reproduction in any given year. In some species of turtles, including this leatherback population, larger turtles lay larger clutches of eggs (Frazer & Richardson 1986, Gibbons & Greene 1990, Congdon & van Loben Sels 1991, Hays & Speakman 1991, Hirth & Ogren 1991). Thus, it might be advantageous for leatherbacks to delay remigration and invest in growth in order to achieve greater lifetime fecundity by producing larger clutches in future nesting seasons (Shine 1980). Furthermore, larger size may confer greater annual survival (Congdon & Gibbons 1990, Congdon et al. 2001) and thereby increase a turtle's expected lifetime fecundity (although this may not be true for anthropogenic sources of mortality). Our data indicate that adult female leatherbacks with long remigration intervals do not generally exhibit a higher growth rate than those females with short remigration intervals. The fact that 2 yr and 3 yr remigrants differed in growth rate (for CCW) may indicate that there is a tradeoff between growth rate and remigration interval for those turtles that return most quickly to nest. However, this finding may also reflect the difficulty of detecting growth in 2 yr remigrants due to the slow rate of growth for all adult leatherbacks. The highly variable growth rates (and other variables) exhibited by leatherbacks combined with measurement error raise the possibility of Type II statistical errors. This problem could be compounded by nest beach infidelity, a situation that may be indicated by a trend in fecundity variables amongst short remigrants and not long remigrants (which may have made unrecorded interim breeding migrations to other beaches). While a possibility, it seems unlikely that the leatherbacks nested elsewhere in the eastern Pacific in interim years because the other main nesting beaches in Mexico are patrolled by biologists with PIT tag readers and only 1 Las Baulas turtle was ever found there (this turtle nested at Las Baulas the same year, L. Sarti pers. comm.). Overall, our results do not provide strong support for the hypothesis that leatherbacks delay reproduction in favor of devoting energy resources to growth.

Another benefit of delaying remigration to the nesting beach could be enhanced seasonal fecundity via energetic efficiency. Bull & Shine (1979) presented a

model of iteroparity that suggests that some animals, particularly those that engage in a breeding migration, can offset the cost of delayed reproduction with increased seasonal fecundity. Leatherbacks engage in a significant breeding migration (Morreale et al. 1996, Eckert & Sarti 1997, Hughes et al. 1998) which is probably energetically costly. Therefore, a female leatherback might delay her reproductive remigration in order to further increase her fat reserves so that the breeding migration would use a smaller proportion of her total reserves. The increased fat reserves that remain when she arrives at the beach should result in greater clutch size or frequency. Our data, however, do not support this hypothesis because leatherbacks with longer remigration intervals did not exhibit greater seasonal fecundity. It should be noted, however, that we did not examine egg size as a measure of fecundity (Hirth 1980, Van Buskirk & Crowder 1994), due to a relative paucity of data on egg size parameters. This topic merits further research.

Since delaying remigration does not appear to be advantageous to leatherbacks through either increased growth rate or greater seasonal fecundity, variable remigration intervals appear to be the consequence of other factors, such as individual differences in efficiency of energy assimilation or location of high-quality foraging grounds, with highly efficient turtles accumulating necessary energy stores faster and remigrating sooner. Such individual differences could be influenced by genetics as well as environmental effects that have been accumulated over a turtle's lifetime. Fluctuations in environmental conditions could also influence the remigration interval, with 'good' feeding years causing quicker remigrations (Hays 2000). Recent research indicates that environmental conditions, such as sea surface temperature (SST), can affect trends in nesting activity and remigration intervals for green turtles (Broderick et al. 2001, Chaloupka 2001, Solow et al. 2002). Migratory data (Morreale et al. 1996) suggest that leatherbacks nesting at Las Baulas forage in the southeast Pacific, an area subject to high spatial and temporal oceanographic variability due to ENSO. For example, shifts in skipjack tuna populations are related to the large-scale changes in SST associated with ENSO (Lehodey et al. 1998). Fluctuations in environmental conditions could potentially affect turtles population-wide, or within a subset of the nesting population, depending upon the size and transience of leatherback foraging grounds. Furthermore, remigration interval may also be affected by the length of the breeding migration, with turtles foraging more distantly from the breeding grounds requiring longer periods to acquire energy. Unfortunately, the lives of leatherbacks at sea are still poorly understood, and it is unknown whether migratory distances traveled by

individuals within a population vary significantly. Future studies should examine more closely the effects of temporally and spatially variable environmental conditions on life history traits in leatherbacks, including remigration interval, growth rate and seasonal fecundity.

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