Chelonian Conservation and Biology, 2007, 6(1): 15–27

Nesting Biology and Conservation of the Leatherback Sea Turtle (*Dermochelys coriacea*) in the State of Espírito Santo, Brazil, 1988–1989 to 2003–2004

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Abstract. – In Brazil, the only area where regular leatherback sea turtle (*Dermochelys coriacea*) nesting is known to occur is located on the northern coast of the state of Espírito Santo, around latitude 19°S. In this study, we present the field methods used by Projeto TAMAR-IBAMA (the Brazilian Sea Turtle Conservation Program) in the state of Espírito Santo and analyze data on leatherback nesting from 1988–1989 to 2003–2004. In that period, 527 nests were observed in the study area. The annual number of nests varied between 6 (in 1993–1994) and 92 (in 2002–2003). Between 1995–1996 and 2003–2004, the annual number of nests increased at about 20.4% per year on average. Among the 527 clutches observed, 358 (67.9%) were left in situ, 50 (9.5%) were relocated to another spot on the beach, 88 (16.7%) were relocated to open-air beach hatcheries, and 31 clutches (5.9%) did not have their management decision recorded. Curved carapace length of nesting females was in the range of 139–182 cm (mean = 159.8 cm). At present, there is no significant alteration of the nesting habitat in Espírito Santo, egg poaching has been reduced to very low levels, and there is no subsistence hunting for sea turtles of any species. The main challenges to leatherback conservation currently are the incidental capture in artisanal fisheries operating close to nesting beaches and in high seas fisheries operating in the South Atlantic, as well as activities related to the oil industry. An overview of Projeto TAMAR's actions addressing current sea turtle conservation issues in the State of Espírito Santo is presented.

Key Words. – Reptilia; Testudines; Dermochelyidae; *Dermochelys coriacea*; sea turtle; reproduction; nesting; conservation; community based; Brazil

The leatherback sea turtle (*Dermochelys coriacea*; in Portuguese: "tartaruga-de-couro", "tartaruga-gigante", "tartaruga-de-casco-mole", or "careba-mole") has recently been classified as critically endangered by the IUCN-World Conservation Union (Sarti Martínez 2000). Declines, sometimes catastrophic, in populations of nesting leatherbacks have been observed in several places around the world, mainly in the Pacific and Indian Oceans (Chan and Liew 1996; Sarti M. et al. 1996; Spotila et al. 1996; Spotila et al. 2000).

In the Atlantic Ocean, major leatherback nesting sites exist in French Guiana and Suriname in South America, Trinidad in the southern Caribbean, and Gabon and Congo in Africa; significant nesting also occurs in several other places in the wider Caribbean region and Africa (Fretey 1980; Fretey 2001; Girondot and Fretey 1996; Spotila et al. 1996; Eckert 2006). In Brazil, the only area where regular leatherback nesting is known to occur is located on the northern coast of the state of Espírito Santo, eastern Brazil, around latitude 19°S. Nesting occurs mainly on Comboios Beach, about 90 km north of Vitória, the state capital, but less dense nesting also occurs to the north of Comboios. Besides regular nesting in the state of Espírito Santo, occasional (very rare) leatherback nesting has been recorded in other places in Brazil (Barata and Fabiano 2002).

The Comboios region was acknowledged in the early 1950s, mainly through the work of the Brazilian naturalist Augusto Ruschi and collaborators, as an important area for conservation purposes, because of diversity of its characteristic fauna and flora, including the occurrence of sea turtle nesting there. This led to the declaration of a state biological reserve in this region in 1953 (Ruschi 1954; Ruschi 1978). Uncontrolled occupation of some of the area occurred, however, and, in 1984, only a part of the area originally protected became a federal conservation area, the Biological Reserve of Comboios (Decree no. 90222, 25 September 1984). This federal reserve includes a stretch of 15 km of Comboios Beach to the south of the mouth of the Doce River (Fig. 1). The 22 km of beach further to the south are within Indian lands, under a special legal status, with restricted access, which gives some protection to that part of the beach (Fig. 1). Although no protected areas have been declared to the north of the Doce River mouth, local, state, and federal regulations concerning the coastal zone apply to that region. Regulations for the establishment of protected areas in that region are under study by the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA, an agency of the Brazilian government), because of the presence of sea turtles there, among other reasons. There are 3 villages in or around the nesting areas; they are relatively small in

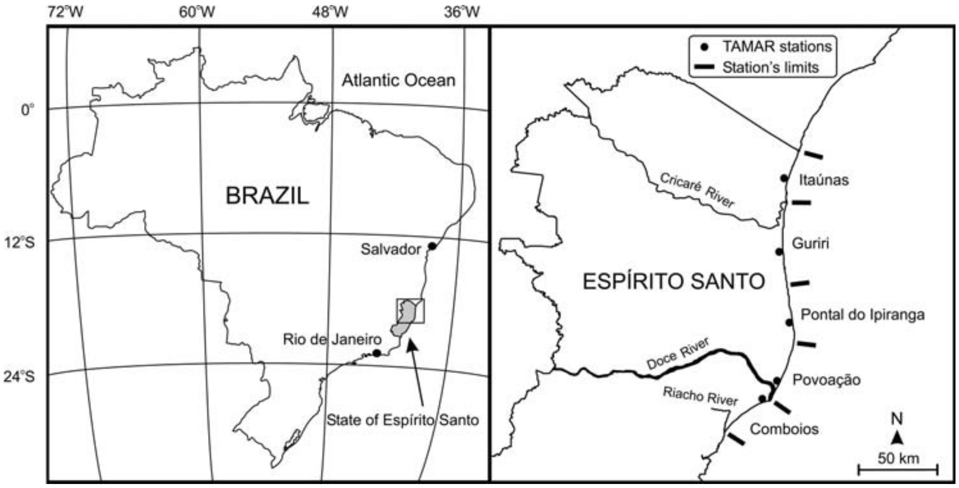

Figure 1. Maps of Brazil (left) and of the northern part of the State of Espírito Santo (right), where the limits of the 5 TAMAR stations located in that area are indicated.

size, each with about 1000 inhabitants, and with a relatively small growth rate. Tourism and, increasingly, activities related to the oil industry (both on land and at sea) present new alternatives for the economic development of the region, while posing many challenges to environmental conservation.

Projeto TAMAR-IBAMA, the Brazilian Sea Turtle Conservation Program, has been working on the northern coast of the state of Espírito Santo since 1982, initially at Comboios and later gradually extending its activities northward, up to the border with the state of Bahia. Currently, Projeto TAMAR maintains 5 field stations in that region (Fig. 1), monitoring 240 km of nesting beaches and conducting environmental conservation, and educational activities with the coastal communities (Marcovaldi and dei Marcovaldi 1999).

An early, preliminary report about leatherback conservation by Projeto TAMAR in Comboios was published by Silva and Brito (1984). Santos (1993) analyzed data for leatherback nesting on Comboios Beach between 1982 and 1993, and Morisso and Krause (2001) compared data between in situ and relocated nests in the state of Espírito Santo between 1989–1990 and 1998–1999. In the present study, we present the field methods used by Projeto TAMAR in the state of Espírito Santo and analyze the leatherback nesting data from 1988–1989 to 2003–2004: data on the spatial and temporal distributions of nests, clutch size, management practices each season, hatching success and incubation time for in situ nests, size distribution of the nesting turtles, and some remigration interval data are presented. An estimate of the number of females nesting in the state of Espírito Santo is also provided. Finally, a review of the conservation status of leatherback nesting in Brazil is presented. The analysis of hatching success and incubation period of managed nests will be the object of a future study.

METHODS

Study Area and Duration. — The study area is located on the north coast of the state of Espírito Santo, runs in a south-north direction, and has a total length of 160 km between the Barra do Riacho River (19°40′S) and the mouth of the Cricaré River (18°25′S) (Fig. 1). For management purposes, the area is divided into 4 sections, each monitored by a TAMAR station, from south to north: Comboios (CB), Povoação (PV), Pontal do Ipiranga (PG) and Guriri (GU) (Fig. 1). Most of the beaches in the study area, which is part of the Doce River coastal plains, are high-energy beaches with steep profiles and coarse sand. Beaches in the northernmost part of the area are lower-energy beaches with finer sand. Climate and vegetation in the study area were described by Baptistotte et al. (2003).

Leatherback nesting in Brazil occurs mostly around the austral summer, generally from October to February, so, each season is denoted by a 2-year code, e.g., 1994–1995. However, because nestings have been observed in all months of the year, a definite date is needed to mark the start of each season and has been arbitrarily defined as 1 July. Projeto TAMAR began its activities in Espírito Santo in 1982–1983, initially protecting nests and nesting females only on Comboios Beach. Gradually, the area under protection was expanded, and the study area has only been entirely monitored since 1988–1989. Therefore, only data from the 1988–1989 season to the 2003–2004 season will be analyzed.

Community Relations in the Study Area. — The partnership between local communities and the conservation program forms the core of TAMAR's activities in Brazil. Since the start of its work in the state of Espírito Santo, Projeto TAMAR strove for the involvement of the local communities in the conservation program, by means of environmental education and communication activities (Marcovaldi and dei Marcovaldi 1999; Marcovaldi and

Thomé 1999). Solutions to the conservation problems had to arise out of the combination of two main factors: the understanding of the local reality and the knowledge of sea turtle biology.

In the state of Espírito Santo, sea turtles were a resource for traditional people, who used to kill nesting females and/or poach the eggs (Hartt 1941; Medeiros 1983). TAMAR worked to promote alternative economic activities as a way of generating family income. Fishers who used to hunt turtles, locally called "carebeiros" ("turtlers", from "careba", which means "turtle" in the local Indian language), were hired to work for the protection of nests. This helped to integrate the local people into the conservation program by making them feel responsible for it (Almeida and Mendes 2007). TAMAR has also worked to develop other forms of alternative income sources for local inhabitants. One of the most fruitful experiences has been the production, by local people, of T-shirts and other materials with sea turtle motifs, which are sold in stores at all TAMAR stations in Brazil (Marcovaldi and Thomé 1999).

Environmental education and communication, in a broad sense, have been key points in the development of the conservation program. Local communities, as well as politicians, environmental officers, school children, university students, the scientific community, and the general public have been addressed in multiple ways through visitor centers (including small museums, display tanks with sea turtles, posters about sea turtle natural history), video films, mass media (newspapers, television, Internet, etc.), oral presentations, publications and training programs for university students, among other activities (Marcovaldi and Thomé 1999).

Field Methods. — Projeto TAMAR's field methodology was described in detail by Marcovaldi and Laurent (1996), Marcovaldi and dei Marcovaldi (1999), and Almeida and Mendes (2007). The entire study area is monitored daily at dawn by carebeiros hired by TAMAR and working under the supervision of TAMAR's technical personnel; they look for nests laid the night before, and, furthermore, their presence on the beach inhibits egg poaching. Daily patrolling of the beaches by TAMAR's technical personnel is also carried out in the early morning to mark nests found by carebeiros with wooden numbered stakes and to excavate hatched nests. Clutches threatened by tidal flooding or predation are relocated by the TAMAR technical team, although the goal is to leave every clutch in situ. Whenever necessary, the relocation of clutches to another spot on the same beach is preferred to maintain incubation conditions as close as possible to those at the original location; however, sometimes the risks of predation are deemed to be high and the clutches are then transferred to open-air hatcheries, fully exposed to sun and rain, located in beach portions similar to those used by turtles to nest and surrounded by plastic meshes to prevent animal predation. Night patrolling of the beaches occurs only infrequently.

All nests are excavated within 24 hours after the majority of hatchlings emerged. Clutch size is determined by counting egg shells and unhatched eggs, and the species is determined by examining dead hatchlings, and embryos or live hatchlings remaining in the nest; for nests without hatchlings or embryos, the species was determined by the eggs or the width of turtle tracks on the beach. Nonviable, yolkless eggs, frequently found in leatherbacks nests, are counted separately from normal (yolked) eggs.

The entire area is marked with stakes at each kilometer, and the location of each nest is recorded. The geographic location was not recorded for 17 nests at Campo Grande, a 12-km beach located around km 110. Females encountered when nesting are double tagged on the hind flippers with monel tags (Style 681, National Band and Tag Co., USA), and curved carapace length (CCL) and width are recorded with flexible plastic tapes. CCL is measured from the center of the nucal notch to the posterior tip of the carapace, alongside the central dorsal ridge. Because of the length of the beaches and restricted night patrolling, not all nesting females are intercepted on the beach.

Data Analyses. — In some analyses (temporal and spatial distributions, clutch size), all observed clutches were considered, while in other analyses (hatching success, incubation period), only in situ clutches were considered. Among in situ clutches ($n = 358$), 42 (11.7%) were excluded from the analyses because of partial or total depredation by animals, 10 clutches (2.8%) were excluded because they were harvested by humans, and 55 clutches (15.4%) were excluded because their incubation was not monitored; data for these clutches (number of eggs, number of live hatchlings, etc.) are not available. In each particular analysis, some clutches were excluded because of unrecorded values for some of the variables, so, sample sizes may vary. Clutch size and hatching success are only analyzed for the period 1994–1995 through 2003–2004, because it is unclear if yolkless eggs were recorded separately from normal (yolked) eggs for some clutches in years 1988–1989 through 1993–1994.

Yolked and yolkless eggs are treated separately in the analyses to follow. For each clutch, total clutch size is defined as yolked + yolkless eggs, and hatching success is the percentage of yolked eggs that produced live hatchlings, including live hatchlings encountered in the nest during excavation. Incubation period was calculated as the number of days between oviposition and time of emergence of the first hatchlings. To evaluate the relation between hatching success and nesting date, and between incubation time and nesting date, in each season, 1 July was set as day 1, and the days in the season were counted consecutively from that date. In the state of Espírito Santo, leatherbacks nest during the night or very early in the morning, and, in case the laying occurred in the early morning, the date of laying was recorded as the date of the night just before, e.g., 1 July was recorded as the date of

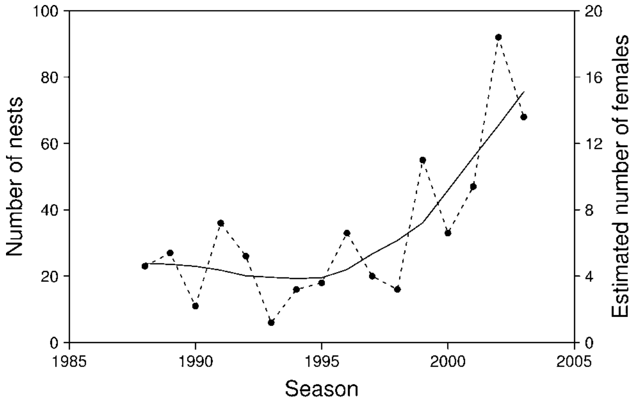

Figure 2. Number of leatherback nests (left scale) and estimated number of nesting females (right scale) per season, state of Espírito Santo, 1988–1989 through 2003–2004 ($n = 527$). The first year of each season is shown on the horizontal axis, e.g., 1995 = 1995–1996. The dots show the actual data; the solid curve, a loess regression, indicates the trend in the number of nests and estimated females.

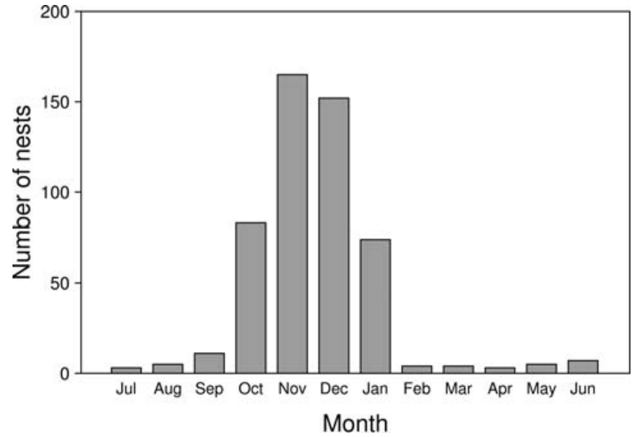

Figure 3. Distribution of nests by month, state of Espírito Santo, 1988–1989 through 2003–2004 ($n = 516$).

laying for any nesting that occurred from the night of 1 July to the early morning of 2 July.

An estimate of the number of females nesting each year was obtained by dividing the observed annual number of clutches by an estimate of the mean annual number of clutches per female (Meylan 1995). For comparison with other populations, we used a value of 5 clutches per female per year (Spotila et al. 1996). Although this figure is not universal among leatherback nesting sites (Spotila et al. 1996), it allows an order-of-magnitude estimate of the annual number of nesting females.

In the analysis of variation in clutch size, hatching success, incubation period, and carapace length among seasons, because sample sizes are small and/or data are non-normal, exact nonparametric Kruskal-Wallis tests (or Monte Carlo approximations, whenever sample sizes were relatively large) were used; in exact tests, p values are computed on the basis of permutations of the data, not through theoretical large sample approximations, so results are valid even for small sample sizes (Mehta and Patel 1998; Conover 1999). When comparing the average incubation period in Brazil with that in other countries, standard t tests were used (Zar 1996).

When analyzing variation of CCL among seasons, the first CCL measurement of a turtle in each season was included in the analysis ($n = 27$); when analyzing the complete CCL distribution (i.e., when pooling data from all seasons), only the first measurement ever of each turtle (i.e., the first measurement among all seasons) was considered ($n = 24$). CCL distribution was compared with a normal distribution through an exact nonparametric Kolmogorov-Smirnov one sample test (Mehta and Patel 1998; Conover 1999).

Nonparametric, locally weighted polynomial regressions were computed following the loess method; locally linear fitting was used throughout, and the smoothing parameter (alpha) was 0.65 in all computations. In this kind of regression, the shape of the regression curve is not established a priori, as it happens, for instance, in a standard linear regression, but is obtained from the data themselves. Points of the regression curve are computed one by one by applying weighted linear regressions to different subsets of the data whose relative sizes, with respect to the whole data set, are controlled by the smoothing parameter alpha; the greater alpha is, the larger the subset to be used in the calculation of each point and the smoother the regression curve will be; the points so calculated are then connected to produce the complete regression curve (Cleveland 1993). The loess computations assume an error structure for the data, which allows one to calculate approximate pointwise 95% confidence intervals for the regression (Cleveland et al. 1993).

Statistical analyses were carried out with the softwares R 2.4.0 (R Development Core Team 2006) and StatXact 4 (Mehta and Patel 1998). In the statistical analyses, alpha = 0.05 (probability of a type I error).

RESULTS

Number of Nests per Season. — Between 1988–1989 and 2003–2004, 527 nests were observed in the study area. The annual number of nests varied between 6 (in 1993–1994) and 92 (in 2002–2003) (Fig. 2). Nesting activity was greatest in November and December, and 91.9% of the clutches were deposited between October and January (Fig. 3). There was clearly an increasing trend since 1995–1996. An exponential function fitted to data from 1995–1996 to 2003–2004 ($R^2 = 0.675$, $n = 9$) indicated that the number of nests increased at about 20.4% per year ($p = 0.012$) in that period. Although fluctuations in the annual numbers of nests can be seen in Fig. 2, no clear pattern was evident concerning the interval between high and low nesting years in the data.

Estimated Number of Nesting Females. — By dividing the number of nests per year with a mean number of 5 nests per female per year, we obtained an estimate for the annual number of leatherback females nesting in each

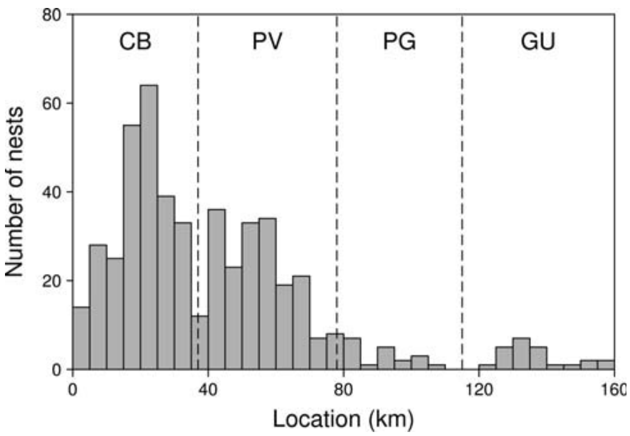

Figure 4. Geographic distribution of leatherback nests in the state of Espírito Santo, 1988–1989 through 2003–2004 ($n = 494$). Km 0 is the southernmost point of the study area. Exact location was not recorded for 17 nests laid on a 12-km stretch of beach located around km 110; these nests were not included in the figure. Dashed vertical lines indicate the boundaries of each station (see Methods for codes).

year. This number is between 1.2 and 18.4, with an increasing trend since 1995–1996, following the trend observed in the number of nests (Fig. 2).

Spatial Distribution. — Nesting was distributed unevenly in the study area (Fig. 4) and was more concentrated in the southernmost end. More than half (53.2%) of all nests were located in the first southern 37 km (under the management of the Comboios station), and 91.1% of all nests were found in the first southern 80 km of the beach (Comboios and Povoação stations).

Number of Yolked and Yolkless Eggs per Clutch. — The distribution of the number of yolked eggs per clutch was not significantly different among the seasons, between 1994–1995 and 2003–2004 (Kruskal-Wallis test, $n = 260$, $p = 0.083$). In that period, the overall average number of yolked eggs per clutch was 87.7 (range = 5–131, SD = 18.9, $n = 260$; Fig. 5a).

Leatherbacks are known to lay a substantial number of smaller, yolkless eggs, together with normal, yolked eggs. The number of yolkless eggs per clutch is generally less than that of yolked eggs, although the ratio of normal to yolkless eggs is variable (Pritchard 1971; Schulz 1975; Frazier and Salas 1984; Pritchard and Trebbau 1984). In the state of Espírito Santo, for years 1994–1995 through 2003–2004, the distribution of the number of yolkless eggs per clutch was not significantly different among the seasons (Kruskal-Wallis test, $n = 260$, $p = 0.294$). The average number of yolkless eggs between 1994–1995 and 2003–2004 was 22.1 eggs (range = 0–61, SD = 13.4, $n = 260$; Fig. 5b). The average percentage of yolkless eggs in relation to the total number of eggs (yolked + yolkless) was 19.6% (range = 0%–76.2%, SD = 11.9%, $n = 260$). Clutch parameters for leatherbacks nesting in the state of Espírito Santo and in other areas in the Atlantic are presented in Table 1.

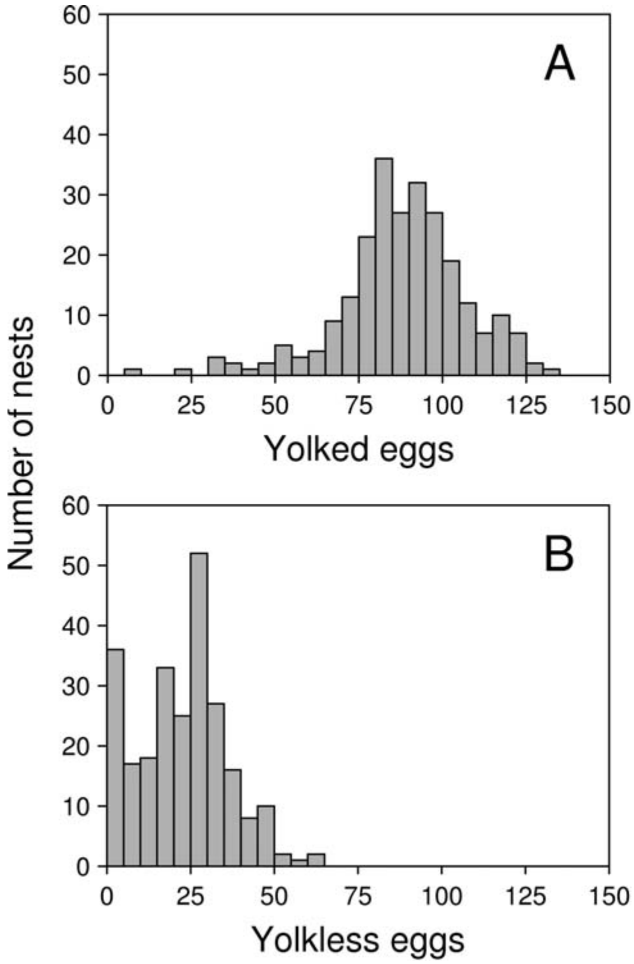

Figure 5. Distribution of the number of yolked (A) and yolkless (B) eggs per clutch for leatherbacks, state of Espírito Santo, 1994–1995 through 2003–2004 ($n = 260$).

Managements Practices. — Among 527 clutches observed between 1988–1999 and 2003–2004, 358 clutches (67.9%) were left in situ, 50 (9.5%) were relocated to another spot on the beach, 88 (16.7%) were relocated to open-air beach hatcheries, and 31 clutches (5.9%) did not have their management decision recorded. From approximately 1995 on, there was an increasing trend in the percentage of clutches left in situ and a corresponding reduction in the percentage of clutches relocated either to the beach or to an open-air hatchery (Fig. 6).

Hatching Success. — Hatching success was analyzed for in situ nests only, for seasons 1994–1995 through 2003–2004. Hatching success was significantly different among seasons (Kruskal-Wallis test, $n = 185$, $p < 0.001$; Table 2). Average hatching success ranged from 53.3% (in 1994–1995, $n = 4$) to 78.0% (in 2003–2004, $n = 30$). The overall average hatching success was 65.1% ($n = 185$, range = 0%–100%, SD = 26.9%) (Table 2).

In Fig. 7, the line representing the average hatching success is within the band defined by the approximate pointwise 95% confidence intervals, which indicates that

Table 1. Average number of yolked and yolkless eggs and total clutch size for leatherbacks in Espírito Santo (Brazil) and in other nesting populations in the Atlantic.

Area and period	Sample size (nests)	Average no. of yolked eggs	Average no. of yolkless eggs	Average total clutch size	Average no. of yolkless eggs as a percentage (%) of average total clutch size	Source
Suriname, 1967–1973	$n = 385$	84.1	24.4	108.5	22.5	Schulz 1975
St. Croix, US Virgin Islands, 1981–1995	$n = 82$–355 nests per year	79.7	36.4	116.1	31.4	Boulon et al. 1996
Playa Gandoca, Costa Rica, 1990–1997	$n = 2045$	79.3	35	114	30.7	Chacón-Chaverri 1999
Tortuguero, Costa Rica, 1990–1991 and 1995	$n = 269$	81.6	38.0	119.6	31.8	Data pooled from Leslie et al. 1996 and Campbell et al. 1996
Puerto Rico, USA, 1984–1985	$n = 212$	70.0	35.9	105.9	33.9	Hall 1990
French Guiana, circa 1980	$n = 26$	84.3	30.2	114.5	26.4	Fretey 1980
Espírito Santo, Brazil, 1994–1995 to 2003–2004	$n = 261$	87.7	22.1	109.8	20.1	This study

hatching success does not vary as the season progresses. Hatching success decreased markedly to the south, in the first 25 km of the study area (Fig. 8). However, there was a relatively small number of nests in that region.

Incubation Period. — The incubation period was analyzed for in situ nests only, for seasons 1988–1989 to 2003–04. Incubation period was significantly different among seasons (Kruskal-Wallis test, $n = 179$, $p < 0.001$; Table 2). Average incubation period ranged from 61.5 days (in 1994–1995, $n = 4$) to 78.0 days (in 1988–1989, $n = 1$). The overall average incubation period between 1988–1989 and 2003–2004 was 67.8 days ($n = 179$, range = 56–90 days, SD = 7.1 days).

The incubation period varied along the season, decreasing until the beginning of December and then remaining approximately constant (Fig. 9). In the first 100 km of beach, the average incubation period is always well within the approximate pointwise 95% confidence intervals, so the incubation period does not depend on the position of the nest along the beach (Fig. 10).

Carapace Length. — No statistically significant difference was found in CCL among seasons between 1988–1999 and 2003–2004 (Kruskal-Wallis test, $p = 0.810$, $n = 27$; n varied between 1 and 5 among seasons; there were no observations in 1988–1989, 1993–1994, 1996–1997, and 2001–2002). CCL of nesting females was in the range of 139–182 cm (mean = 159.8 cm, SD = 10.5 cm, $n = 24$, Fig. 11). The CCL distribution was not significantly different from a normal distribution (Kolmogorov-Smirnov one sample test, $p = 0.886$, $n = 24$, Fig. 11).

Turtle Tagging and Remigration Intervals. — Twenty-five females were tagged between 1988–1989 and 2003–2004, of which, 20 females were found only once on the beach in those years, and 5 females were found more than once. Among the latter, 3 were only found again in

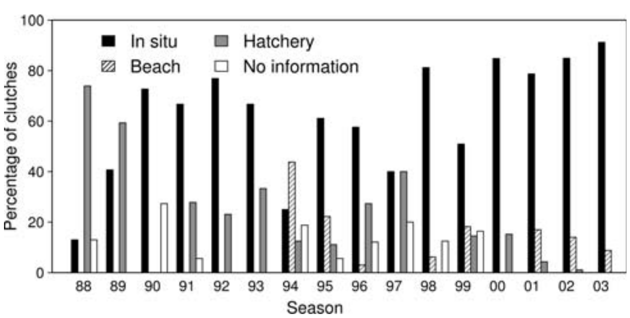

Figure 6. Percentage of leatherback clutches according to management method by season, state of Espírito Santo, 1988–1989 through 2003–2004 ($n = 527$). The first year of each season is shown on the horizontal axis, e.g., 95 = 1995–1996.

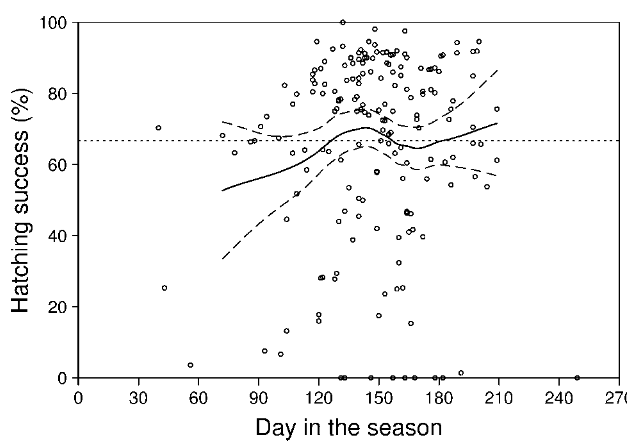

Figure 7. Hatching success by date of laying the clutch (in each season, July 1 = day 1) for in situ leatherback nests, state of Espírito Santo, 1994–1995 through 2003–2004 ($n = 179$). Center curve (solid line) is a loess regression ($n = 175$), outer curves (dashed lines) show approximate pointwise 95% confidence intervals. The 3 leftmost data points and the rightmost one were excluded from the loess computations, because there is an insufficient number of points to reliably estimate the regression curve in the extreme regions of the graph. The dotted horizontal line shows the average hatching success for data points included in the loess regression: 66.7% ($n = 175$).

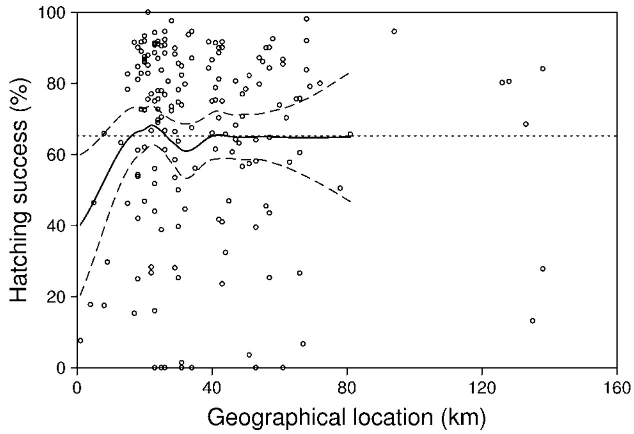

Figure 8. Hatching success by geographical location of the nest for in situ leatherback nests, state of Espírito Santo, 1994–1995 through 2003–2004 ($n = 182$). Center curve (solid line) is a loess regression ($n = 175$), outer curves (dashed lines) show approximate pointwise 95% confidence intervals. The 7 rightmost data points were excluded from the loess computations, because there is an insufficient number of points to reliably estimate the regression curve in the rightmost region of the graph. The dotted horizontal line shows the average hatching success for the data points included in the loess regression: 65.2% ($n = 175$).

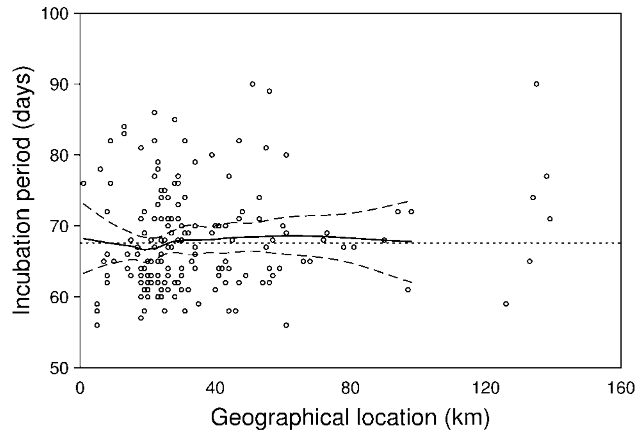

Figure 10. Incubation period by geographical location of the nest for in situ leatherback nests, state of Espírito Santo, 1988–1989 through 2003–2004 ($n = 176$). Center curve (solid line) is a loess regression ($n = 170$), outer curves (dashed lines) show approximate pointwise 95% confidence intervals. The 6 rightmost data points were excluded from the loess computations, because there is an insufficient number of points to reliably estimate the regression curve in the rightmost region of the graph. The dotted horizontal line indicates the average incubation period for data points included in the loess regression: 67.6 days ($n = 170$).

the same season as when they were first tagged. The other 2 turtles were found in different seasons: one turtle had a remigration interval of 3 years and the other turtle was seen in 3 different seasons, with remigration intervals of 2 years. No leatherbacks nesting in Espírito Santo have ever been found bearing flipper tags applied elsewhere, and no leatherbacks tagged in Espírito Santo have ever been found nesting elsewhere.

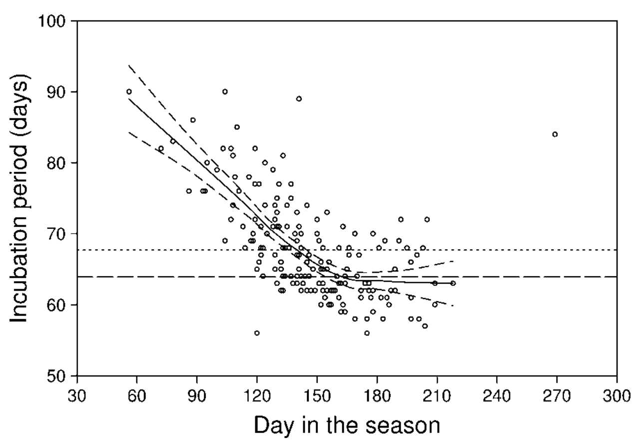

Figure 9. Incubation period by date of laying the clutch (in each season, July 1 = day 1) for in situ leatherback nests, state of Espírito Santo, 1988–1989 through 2003–2004 ($n = 179$). Center curve (solid line) is a loess regression ($n = 178$), outer curves (dashed lines) show approximate pointwise 95% confidence intervals. The rightmost data point was excluded from the loess computations, because there is an insufficient number of points to reliably estimate the regression curve in the rightmost region of the graph. The dotted horizontal line indicates the average incubation period for data points included in the loess regression: 67.7 days ($n = 178$). The dashed horizontal line indicates the estimated pivotal incubation period for leatherback turtles in Suriname: 63.9 days (Godfrey et al. 1996).

DISCUSSION

The increasing trend in the number of nests observed since 1995–1996 is noteworthy. Although, in this article, only data from 1988–1989 on are analyzed, Projeto TAMAR has been protecting sea turtle nesting on Comboios Beach (the first 37 km of the study area, the region with the highest numbers of leatherback nests) since 1982–1983. Zug and Parham (1996), by means of growth models based on skeletochronogical analysis, proposed an average age for maturity for leatherbacks of 13–14 years and a minimum of 9 years. The time interval between 1982–1983 and 1995–1996, 13 years, is compatible with the age for maturity estimates proposed by Zug and Parham (1996). The input of hatchlings provided since 1982–1983 by the conservation activities in Espírito Santo

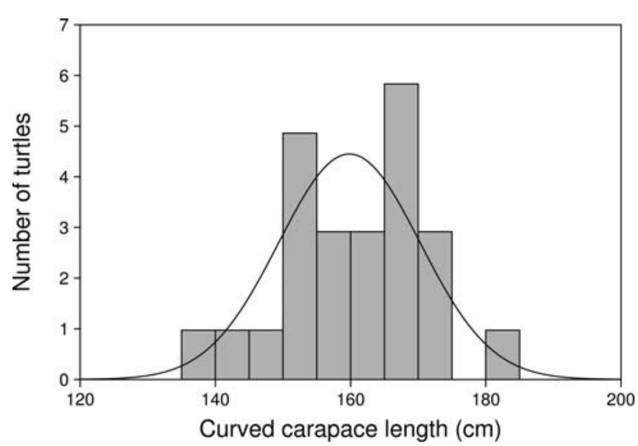

Figure 11. Curved carapace length distribution for leatherbacks, state of Espírito Santo, 1988–1999 through 2003–2004 ($n = 24$). A normal curve with the same average (= 159.8 cm) and standard deviation (= 10.5 cm) as those of the data is superimposed.

could be, at least partially, an explanation for the increase in nestings observed since 1995–1996. A marked increase in the number of leatherback nests, which has been attributed to conservation efforts leading to an increase in hatchling production (beach patrolling to avoid egg poaching and relocation of clutches laid in erosion zones or below the water mark), has also been observed at St. Croix, US Virgin Islands (Dutton et al. 2003).

A possible shift of nesting sites from other nesting areas to Brazil could be another component of an explanation for the observed increase in the number of nestings in Espírito Santo since 1995–1996. Genetic analyses through the use of mitochondrial deoxyribonucleic acid suggest that leatherbacks have a somewhat reduced sense of natal homing, when compared with other sea turtle species (Dutton et al. 1999). Tagging data gathered on relatively small-scale regions show that leatherbacks can nest on different beaches within a nesting season (Eckert et al. 1989; Boulon et al. 1996). Fretey and Lescure (1998) discussed the possibility that leatherbacks might present fidelity to a nesting region, but they could also nest in other areas, possibly quite distant, from year to year. In French Guiana, the nearest known leatherback nesting site in the western Atlantic, the main nesting season occurs between April and July, but there is a second nesting season, peaking around December, with a number of nesters much smaller than numbers in the main season (Chevalier et al. 2000). Tagging data indicate that leatherbacks nesting in the small season seem to form a population distinct from that nesting in the main season (Chevalier et al. 2000). Because the small nesting season in French Guiana occurs at about the same time as the nesting season in Brazil, Chevalier et al. (2000) raised the possibility that leatherbacks nesting in the smaller season in French Guiana are related to those nesting in Brazil. However, preliminary results of an ongoing genetic study suggest that the Brazilian population is distinct in relation to other populations in the Atlantic (P. Dutton, unpubl. data). As stated before, no leatherbacks tagged in Espírito Santo have ever been found nesting elsewhere, and no leatherbacks nesting in Espírito Santo have ever been found bearing flipper tags applied elsewhere, although, in French Guiana, passive integrated transponder tags have been used (Girondot and Fretey 1996; Chevalier et al. 2000), which cannot at the moment be detected in Brazil.

Fluctuations in the annual number of nests among seasons do not follow any clear pattern. Fluctuations in the number of nests and/or turtles, also without clear interannual patterns, have been observed in other leatherback populations (Boulon et al. 1996; Girondot and Fretey 1996; Hughes 1996; Reina et al. 2002).

The distribution of leatherback nests by month in the state of Espírito Santo is quite similar to that of loggerheads (Baptistotte et al. 2003). However, loggerheads nest in much greater numbers in the area: between 1988–1989 and 2003–2004, the number of loggerhead nests was about 24 times greater than that of leatherbacks.

Leatherbacks seem to somehow avoid the area adjacent to km 37 near the mouth of the Doce River (Fig. 1), which, through its relatively large discharge and deposition of sediments, has influence on salinity, sea currents, and beach dynamics nearby, and could, therefore, in part, explain that observation. However, loggerhead sea turtles also nest in the study area, with a geographical distribution similar to that of leatherbacks, but loggerhead nesting peaks exactly around km 37, that is, around the mouth of the Doce River (Baptistotte et al. 2003). Although leatherbacks are sometimes believed to prefer to nest on beaches with an open, deep water approach (Pritchard and Trebbau 1984; Mortimer 1995), as it happens in the southern part of the study area, in French Guiana, they nest on beaches located in river estuaries (Girondot and Fretey 1996; Fretey and Lescure 1998). Nest-site selection by leatherbacks and other sea turtle species is a poorly understood subject (Mrosovsky 1983; Mortimer 1990; Mortimer 1995). Local oceanographic features (e.g., bathymetry, ocean currents) and the distribution of villages, ports, and industrial installations along the coast could also possibly explain the observed geographical nest distribution patterns in Espírito Santo.

Although the average total clutch size for leatherbacks in Brazil is in the low end of the range of averages observed among the populations in the Atlantic, the average number of yolked eggs per clutch in Brazil seems to be higher than that of other populations, and the percentage of yolkless eggs in Brazil seems to be smaller than that in those populations (Table 1). This suggests that leatherbacks nesting in Brazil allocate a higher proportion of their egg production to viable, hatchling-producing eggs than leatherbacks nesting elsewhere in the Atlantic. However, one should bear in mind the possibility of faulty data recording with regard to yolkless eggs, as the bimodal distribution in Fig. 5b, where the first bar in the graph is due to clutches with no yolkless eggs (8.8% of the clutches, $n = 261$), seems to suggest. Furthermore, estimates of annual fecundity in Brazil are not possible, because there are no reliable data on the annual clutch frequency.

Hatching success in Espírito Santo is equal to or higher than that observed for other populations in the Atlantic. At St. Croix, US Virgin Islands, hatching success for in situ nests in 1982–1985 averaged 64.1% ($n = 178$) (Eckert and Eckert 1990), about the same as in Brazil. In Tortuguero, Costa Rica, in 1990–1991, the average in situ hatching success was 56.9% ($n = 104$) (Leslie et al. 1996), but, in Playa Gandoca and also in Costa Rica, the average in situ hatching success in 1990–1997 was 39% ($n = 418$) (Chacón-Chaverri 1999). In Suriname, the average in situ hatching success in 1970, 1971, and 1973 was 45.9% ($n = 98$) (Schulz 1975). There are differences in the methods of computing hatching success used in different places; whenever possible, comparisons between countries should allow for biases because of different methodologies. In Brazil, hatching success was computed in the same way as at St. Croix (Eckert and Eckert 1990).

Several factors could possibly be related to the lowering of hatching success in the southernmost part of the study region (Fig. 8). Sand gets coarser as one goes south. It has been observed by the TAMAR technical team that turtles sometimes have difficulty digging nests in the southernmost part of the beach, because the excavated sand often falls back into the nest hole. At Ascension Island and Aldabra Atoll, a correlation between sand coarseness (mean particle diameter and sorting coefficient) and the median number of trial nest holes dug per nesting emergence by green turtles was observed (Mortimer 1990). Sand coarseness could be related to the rate of gas exchange within the nests, hydric conditions of the sand, the possibility of sand cave-ins (collapsing of the air chamber as hatchlings emerge from the nest), and other features of the nesting environment that influence hatching success (Mortimer 1990). At Ascension Island, a negative correlation was found between sand coarseness (mean particle diameter) and green turtle hatching success in 10 biogenic beaches (Mortimer 1990). Furthermore, in the first 10 km of the study area, the width of the beach is often small, which causes the turtles to nest close to the vegetation in the highest part of the beach. Nests laid there are often subjected to invasion by plant roots, which may be an additional factor in lowering hatching success. Plant roots were implicated in the loss of a leatherback clutch in Tortuguero, Costa Rica, where nesting in the high part of the beach, among the vegetation, is not uncommon (Leslie et al. 1996).

The incubation period seems to be significantly different from that of other leatherback populations in the Atlantic. At St. Croix, US Virgin Islands, the average incubation period for in situ nests in 1982–1985 was 64.0 days ($n = 160$, SD = 3.2 days) (Eckert and Eckert 1990); this average incubation period is significantly different from that in Brazil (Welch's *t*-test, $t = 6.46$, $df = 253$, $p < 0.001$). In Suriname, the average incubation period in 1964–1971 was 64.1 days ($n = 56$, SD = 2.7 days) (Schulz 1975); this average incubation period is also significantly different from that in Brazil (*t*-test [Welch's method], $t = 5.77$, $df = 225$, $p < 0.001$).

The pivotal incubation period for leatherbacks in Espírito Santo has not been estimated. In Suriname, it has been estimated to be 63.9 days (Godfrey et al. 1996). Pivotal temperatures seem not to vary greatly among different sea turtle species and populations (estimated values are generally in the range of 29° ± 1°C; Mrosovsky 1994; Davenport 1997), and there seems to be a strong correlation between temperature and incubation period, at least for loggerhead and hawksbill turtles in Brazil (Godfrey et al. 1999). This suggests that the pivotal incubation period for leatherbacks in Suriname could be taken as an approximation to the one for the Brazilian leatherback population. Incubation periods both lower and higher than Suriname's pivotal period were found in the present study, which suggests that both male and female hatchlings are produced in Brazil, with more males being produced early in the season, when there are longer incubation periods (Fig. 9). However, this is a very tentative analysis of the incubation data with regard to the sex determination of hatchlings, and more research on this is clearly needed in Brazil.

Whatever the reasons that might explain a lower hatching success in the southern part of the study region, they seem not to have any significant influence on the incubation period, which is on average essentially constant along the first 100 km of the beach.

Leatherbacks nesting in Brazil seem to have an average CCL a little larger than those nesting in other areas in the Atlantic, but the differences are relatively small (Table 3). The measurement of leatherbacks is fraught with difficulties (Zug and Parham 1996; Bolten 1999; Godfrey 2002); slight differences in measurement methods could play a role in explaining small differences in data sets shown in Table 3. So, we believe that a detailed comparison of the measurement methods used in each nesting area should be considered, before any detailed analysis of the data presented in Table 3 could be attempted.

With regard to remigration patterns, Brazil's scant data are in accord with data obtained in other areas in the Atlantic, which indicate that the remigration interval for leatherbacks seems to be mostly from 2 to 3 years (Boulon et al. 1996; Girondot and Fretey 1996; McDonald and Dutton 1996).

Conclusions

There are oral and written accounts indicating that, in the state of Espírito Santo, sea turtles nested in large numbers in the past (Hartt 1941; Medeiros 1983), although no quantitative data are available, in particular, about leatherbacks. Although currently the contribution of Espírito Santo to leatherback demography is relatively small, protection of smaller sea turtle rookeries could be important for conservation purposes, because of the role they could play in the sex-ratio balance of larger populations (Baptistotte et al. 1999) or in maintaining genetic diversity (Dutton et al. 1999). Moreover, in a world where there are indications that the total number of leatherbacks could be declining (Spotila et al. 1996; Spotila et al. 2000), we believe that the protection of each nesting colony has an important role in the conservation of this species.

Worldwide, egg poaching, destruction or alteration of the nesting habitat, subsistence hunting, marine pollution, and the incidental capture in fisheries are some of the major threats to leatherback sea turtles (Frazier 1995; Frazier 2000; Chan and Liew 1996; Spotila et al. 1996; Suarez and Starbird 1996; Eckert and Sarti 1997; Lutcavage et al. 1997). In the state of Espírito Santo, nesting beaches have been protected since 1982. Nowa-

Table 2. Hatching success (1994–1995 to 2003–2004) and incubation period (1988–1989 to 2003–2004) for in situ leatherback clutches, Espírito Santo, Brazil. Values are mean ± standard deviation, range and sample size.

Season	Hatching success (%)	Incubation period (days) [a]
1988–1989		78.0 ± NA (78–78) (*n* = 1)
1989–1990		72.0 ± 9.7 (58–85) (*n* = 7)
1990–1991		64.0 ± NA (64–64) (*n* = 1)
1991–1992		67.3 ± 4.6 (56–76) (*n* = 20)
1992–1993		74.4 ± 7.8 (61–89) (*n* = 14)
1993–1994		77.5 ± 9.2 (71–84) (*n* = 2)
1994–1995	53.3 ± 9.1 (46.4–65.9) (*n* = 4)	61.5 ± 4.8 (57–68) (*n* = 4)
1995–1996	66.5 ± 24.1 (7.6–90.1) (*n* = 11)	67.5 ± 4.6 (61–76) (*n* = 11)
1996–1997	62.7 ± 32.7 (0–94.6) (*n* = 11)	70.0 ± 5.9 (62–79) (*n* = 9)
1997–1998	77.4 ± 32.9 (3.6–97.6) (*n* = 7)	67.0 ± 10.6 (60–90) (*n* = 7)
1998–1999	65.2 ± 24.9 (0–85.6) (*n* = 10)	71.8 ± 10.5 (58–86) (*n* = 8)
1999–2000	63.1 ± 25.1 (13.2–98.1) (*n* = 25)	68.9 ± 8.2 (58–90) (*n* = 19)
2000–2001	67.8 ± 23.5 (6.7–92.0) (*n* = 21)	64.6 ± 7.3 (56–82) (*n* = 9)
2001–2002	55.4 ± 23.3 (0–82.3) (*n* = 14)	69.2 ± 6.8 (61–82) (*n* = 9)
2002–2003	59.6 ± 29.8 (0–93.3) (*n* = 52)	63.9 ± 4.3 (58–76) (*n* = 41)
2003–2004	78.0 ± 23.8 (0–100) (*n* = 30)	67.9 ± 3.4 (63–75) (*n* = 17)
All seasons	65.1 ± 26.9 (0–100) (*n* = 185)	67.8 ± 7.1 (56–90) (*n* = 179)

[a] NA = not applicable.

days, there is no significant alteration of the nesting habitat in that area, as might be caused by the construction of buildings, roads, or ports on or near nesting beaches, and there are no significant problems caused by artificial illumination or traffic of vehicles on the beaches. Egg poaching has been reduced to very low levels, and there is no subsistence hunting for sea turtles of any species. The 5 species of sea turtles found in Brazil (leatherbacks, green turtles, hawksbills, loggerheads, and olive ridleys) are fully protected since 1986 by federal law (Marcovaldi and dei Marcovaldi 1999). The main challenges to leatherback conservation currently are the incidental capture in artisanal fisheries operating close to nesting beaches and in high-seas fisheries operating in the South Atlantic (Thomé et al. 2003), as well as activities related to the oil industry.

Around the mouth of the Doce River, gill nets pose a significant risk to leatherbacks; there are records of incidental captures in this kind of fishing gear. TAMAR is working closely with local fishermen to address this problem. A possible solution, already being investigated, is to look for places for setting gill nets where the nets could have a lower potential for impact on sea turtles, as long as no significant adverse effects on fishing are observed in the new places. Other possible solutions under study are changes in fishing methods (e.g., from nets to hooks) and fish farming. In recent years, trawl boats have increased in numbers in the northern part of the state of Espírito Santo, many of them coming from neighboring Brazilian states, but no incidental captures of leatherbacks in trawl nets have been recorded. Research on the biology of shrimp and on the fishing fleet operating in the area is greatly needed to provide a basis for fishing management and for conservation measures concerning sea turtles.

Leatherbacks are known to be incidentally captured by the longline fishery in the south Atlantic, as elsewhere in the world (Lewison et al. 2004; Domingo et al. 2006); incidental captures by Brazilian commercial longline vessels operating in the South Atlantic have been recorded (Kotas et al. 2004; Sales et al. 2004; Domingo et al. 2006;

Table 3. Curved carapace length (cm) for leatherbacks in Espírito Santo (Brazil) and in other nesting populations in the Atlantic.[a]

Area and period	Average	Range	Sample Size (turtles)	Source
St. Croix, U.S. Virgin Islands, 1982–1994	152.9 SD = 7.0	131.0–177.4	*n* = about 435	Boulon et al. 1996
Tortuguero, Costa Rica, 1990–1991	156.2 SD = 10.6	124.0–180.3	*n* = 56	Leslie et al. 1996
Tortuguero, Costa Rica, 1995	152.8 SD = 8.9	138.0–179.1	*n* = 41	Campbell et al. 1996
French Guiana, circa 1970	157.4 SD = 7.2	137.2–180.3	*n* = 192	Pritchard 1971
French Guiana, 2000–2001	156.2	137–186	*n* = 218	M. Godfrey, pers. comm. 2001
Trinidad, 1967–1969	158 SD = NA	125–185	*n* = 20	Bacon 1970
Espírito Santo, Brazil, 1988–1989 to 2003–2004	159.8 SD = 10.5	139.0–182.0	*n* = 24	This study

[a] NA = not available. Averages and SDs from Pritchard (1971) and Boulon et al. (1996) were computed from data in graphs.

Projeto TAMAR, unpubl. data). Drift nets targeting sharks are also known to incidentally capture leatherbacks off the eastern Brazilian coast (Sales et al. 2003; Projeto TAMAR, unpubl. data). TAMAR is currently assembling a database on the incidental capture of sea turtles by the Brazilian commercial high seas fisheries, with data obtained from governmental agencies, universities and NGO (nongovernmental organization) partners, to assess the levels of captures and main areas and periods of the year where they occur. Data have also been obtained through a partnership established with several major commercial Brazilian longline fishing companies operating in the southwestern Atlantic, which have allowed on-board observers on their vessels. Furthermore, experiments are underway by TAMAR to test different kinds of hooks used in longlines with regard to their potential for the incidental capture of sea turtles (Giffoni et al. 2005). TAMAR is also currently monitoring the incidental capture of sea turtles in drift nets (Sales et al. 2003) and working toward a ban on their use.

Studies are underway in the state of Espírito Santo and elsewhere in Brazil to assess the impact of seismic, drilling, and oil production activities on sea turtles. TAMAR has been working jointly with governmental environmental agencies to ensure that activities related to the oil industry that could impact sea turtles on or around nesting beaches are only licensed on the condition that measures that promote the protection of sea turtles and their habitats and guarantee the constant monitoring of possible impacts are established, to maintain the proper functioning of the ecological processes related to sea turtle reproduction.

As a strategy to ensure the conservation of the Espírito Santo nesting area in the long run, a plan for the sustainable development of the region around the Biological Reserve of Comboios has just been carried out by TAMAR in partnership with community organizations, local municipality governments, schools, universities, farmers, private corporations, and other local partners. Financial resources are being allocated to the development of alternative fishing techniques (sustainable and with less impact on sea turtles) and to properly direct the economic and social development of the area. One item of that plan is the creation of a federal protected area around the Doce River estuary, under the category "Reserve for the Sustainable Development", where natural resources would be managed by IBAMA and their use would be restricted by law to local communities.

Acknowledgments

We would like to express our special thanks to the local communities of the state of Espírito Santo for their collaboration with the conservation program and to the members of the TAMAR staff and all trainees (university students) who helped collect the data. Projeto TAMAR, a conservation program of the Brazilian Ministry of the Environment, is affiliated with IBAMA, is comanaged by Fundação Pró-TAMAR, and is officially sponsored by Petrobras. In Espírito Santo, Projeto TAMAR is supported by the municipal governments of Linhares and São Mateus.

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Received: 28 August 2004

Revised and Accepted: 4 January 2007