

Sedimentary characteristics and their effects on hatching success and incubation duration of *Caretta caretta* (Testudines: Cheloniidae) in Espírito Santo, Brazil

Lauana Schneider Fadini¹; Ary Gomes Silva¹ & Paulo Dias Ferreira-Júnior^{1,2}

¹ Centro Universitário Vila Velha, Rua Comissário José Dantas de Melo, 21, Boa Vista, 29102-770, Vila Velha, ES, Brazil.

² Corresponding author. E-mail: pdfj@hotmail.com

ABSTRACT. The beaches of Espírito Santo encompass the most important nesting sites of the loggerhead sea turtle, *Caretta caretta* (Linnaeus, 1758), in the South Atlantic Ocean. Previous research has shown that, unlike other nesting sites in Brazil, Espírito Santo harbors a large percentage of male individuals, which play an important role in maintaining the equilibrium of *C. caretta* populations in the South Atlantic. During the 2006/2007 reproductive season, four beaches presenting considerable geologic differences were monitored. The sedimentary features of the nesting sites (mineral composition, albedo, and grain size), nesting dates, and clutch sizes were correlated with hatching success and incubation duration. Results show that hatching success is mostly affected by clutch size – and to a lesser extent, by grain size and albedo. Incubation duration is more sensitive to the characteristics of the nesting site, being affected by nesting date, clutch size, mineral composition, and grain size. However, results from one nesting site cannot be generalized or extended to other sites, because sediment properties are functions of the geological framework of the area and the interaction among environmental variables is far too complex. Our results reveal the importance of protecting areas with large geologic diversity, since sedimentary characteristics may affect incubation duration and embryo survival. Our findings are important in the scope of management activities, as nest transfer may alter nest microenvironment, impacting incubation duration and hatching success.

KEY WORDS. Loggerhead sea turtle; ecology; nest; sediment; hatchling.

The loggerhead sea turtle, *Caretta caretta* (Linnaeus, 1758), is the main species nesting on the beaches of Espírito Santo, southeastern Brazil, clustering its nests at the mouth of the Doce River (BAPTISTOTTE *et al.* 1999, 2003, ALMEIDA & MENDES 2007). Five stations of Projeto TAMAR/ICMBio, the Brazilian Sea Turtle Conservation Program, operate in the area, protecting and monitoring 240 km of nesting beaches (MARCOVALDI & MARCOVALDI 1999, BAPTISTOTTE *et al.* 2003). The conservation efforts started in the past decades have reduced predation against nests and females. In recent years, these efforts have also increased the number of hatchlings of *C. caretta* (see MARCOVALDI & CHALOUPKA 2007) and of *Dermochelys coriacea* (Vandelli, 1761). This is the only area where regular leatherback sea turtle nesting is known to occur in Brazil (THOMÉ *et al.* 2007, SANTOS & FERREIRA JÚNIOR 2009). The transfer of nests under erosion and predation risks to adjacent areas or rookeries with sedimentary characteristics similar to the original nest site is one of the management strategies adopted by Projeto TAMAR/ICMBio (MARCOVALDI & LAURENT 1996, MARCOVALDI & MARCOVALDI 1999). The location where to transfer the nests is important because effects of incubation on sex ratio and hatching success have to be minimized (NARO-MACIEL *et al.* 1999, HAWKES *et al.* 2007, SERAFINI *et al.* 2008).

The sex in *C. caretta* is determined by the incubation temperature. The species' pivotal temperature in Brazil has been established as 29.2°C (MARCOVALDI *et al.* 1997). There is a direct relationship between incubation temperature and embryonic development rate (GEORGES *et al.* 1994, 2004), and an inverse correlation between incubation temperature and incubation duration (MROSOVSKY *et al.* 1984). The pivotal temperature and pivotal incubation duration have been defined similarly – the temperature and the duration of incubation that yields 50% of hatchlings from each sex, respectively (MARCOVALDI *et al.* 1997, MROSOVSKY *et al.* 1999). Because sea turtles hatchlings and juveniles are not sexually dimorphic (WYNEKEN *et al.* 2007), the pivotal incubation duration constitutes a significant parameter used to estimate sex ratio (GODFREY *et al.* 1999, GODLEY *et al.* 2001a, MROSOVSKY *et al.* 2002). The duration of pivotal incubation for *C. caretta* in Brazil is 59.3 days under fixed conditions in the lab as described by MARCOVALDI *et al.* (1997). In field conditions, the duration of pivotal incubation is 59.9 days (MROSOVSKY *et al.* 1999). In the latter studies, hatchlings from the beaches of Espírito Santo state were used.

When choosing the beach for nesting, a sea turtle has to consider several factors that can affect the hatching success and

sex ratio of its offspring. The factors that lead to the nesting site choice and the consequences that the characteristics of the site have on reproductive success are not fully understood, and there is no single feature that can be generalized to all nesting sites (MILLER *et al.* 2003). However, the following factors are known to be relevant: grain size (MORTIMER 1990, FERREIRA JÚNIOR *et al.* 2008); beach vegetation cover (SPOTILA *et al.* 1987, SERAFINI *et al.* 2008); albedo (HAYS *et al.* 2001); mineral composition of the sand (MILTON *et al.* 1997, NARO-MACIEL *et al.* 1999); nest inundation (FOLEY *et al.* 2006); height above sea level, and distance from the sea (HORROCKS & SCOTT 1991, LOPEZ-CASTRO *et al.* 2004). Sites with coarse sand have higher temperatures, shortening incubation duration; by contrast, the lower temperatures characteristic of fine sands increase incubation duration (FERREIRA JÚNIOR & CASTRO 2003). Another factor affecting nest temperature is the sand's mineral composition—nests on quartz-rich sediments have temperatures up to 3.4°C higher than those located on biogenic sands (MILTON *et al.* 1997). According to HAYS *et al.* (2001), sand albedo, which is the capacity of the sand to reflect the solar radiation it receives, also affects nest temperature. Nests in darker sands absorb more solar radiation and therefore have increased temperatures when compared with nests that lie in lighter sand, which reflects more of the incoming radiation. Shadowing may also affect sand temperature and cause differences in sex ratio within the same nesting site (MORREALE *et al.* 1982, SPOTILA *et al.* 1987). The present study evaluates the physical factors affecting the nest environment of *C. caretta* across different beaches on the coast of Espírito Santo, Brazil, by associating the sediment properties of the nesting sites with hatching success and incubation duration.

MATERIAL AND METHODS

The present study was carried out in four nesting sites of *C. caretta*, on the shores of Espírito Santo, southeastern Brazil, during the 2006/2007 reproductive season (Fig. 1). The nesting sites examined were at the Jacaraípe (20°08'S, 40°11'W) and Mole (20°15'S, 40°13'W) beaches in the town of Serra, and two areas to the north, the Pontal do Ipiranga (19°12'S, 39°42'W) and Povoação (19°34'S, 39°46'W) beaches, in the municipality of Linhares. In geologic and geomorphologic terms, the beaches monitored in this study can be grouped into two distinct regions: the northern area, which is under the influence of the mouth of the Doce River, and the southern area, with abounding contribution of biogenic sediments (MUEHE 2006, ALBINO & SUGUIO 2010). Biogenic sediments are in part formed by mineral grains and organism parts, like organic skeletons of mollusk shell, echinoderms and fragments of corals and coralline algae. Biogenic sediments present lower thermal conductivity and nests located in these sediments are colder than nest in quartz-rich sediments (MILTON *et al.* 1997).

The northern side of the mouth of the Doce River, where the Povoação and Pontal do Ipiranga beaches are located, receives a significant load of siliciclastic sediments, especially

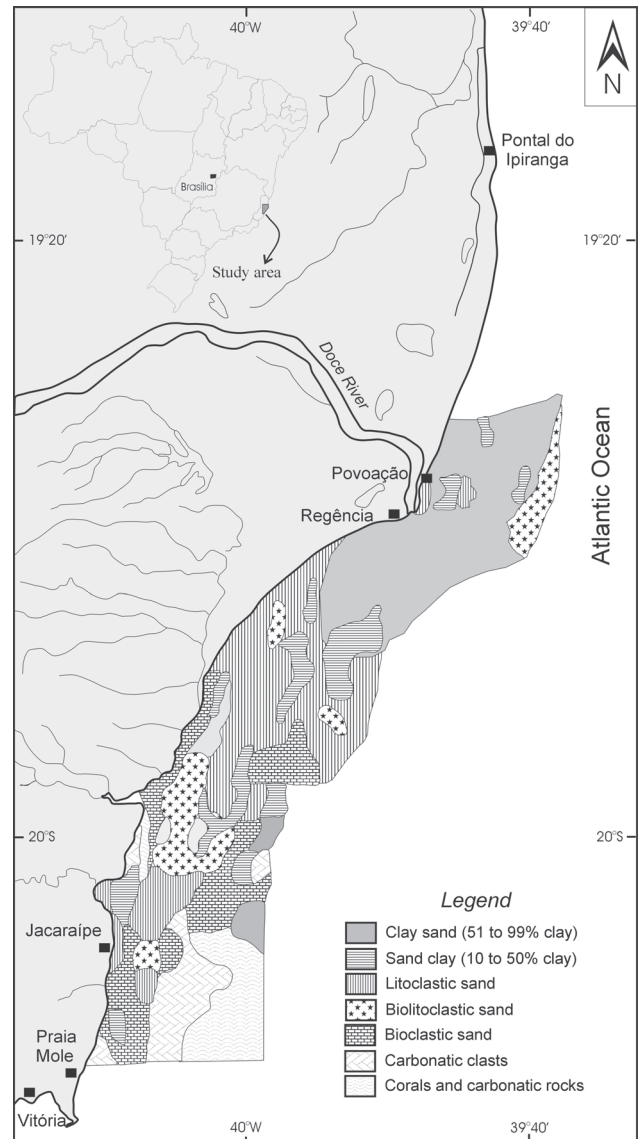


Figure 1. The map of facies of the sediments from the continental shelf between Vitória and Povoação, near the Doce river mouth (after ALBINO & SUGUIO 2010). It show that bioclasts sediments predominate in the southern region while sandy-muddy sediments are the majority at the northern region.

quartz, from the river and from the reworking of the of pleistocenic sand-beach ridges. The beaches are long and straight, often ending in steep borders, shaped by the erosion of the sand ridges. The grain size of sediments provides hints about wave speed in the environment, as judged from the composition of medium to coarse sand grains. Beaches are extensive in length, reaching tens of kilometers, and have no rocky outcrops on the shoreline; they are quite well-preserved, with

a zone of scarce wild bushes called 'Restinga' (sandbank), composed of *Ipomea pes-caprae* Linnaeus and *Blutaparon portulacoides* St. Hill. The word 'Restinga' was originally used in reference to a geological formation of leached sandy soils poor in nutrients (SUGUIO 1999). It has also been used in reference to a group of ecosystems ranging from flooded herbaceous land, hallophyllous-psamophyllous costal shores, open and close shrublands, and forests. The Restingas are under constant focus of conservationists, because they are believed to be extremely fragile environments that are very susceptible to disturbances (LACERDA *et al.* 1984, PEREIRA 2003).

The southern shore that comprises the Mole and Jacaraípe beaches is composed of biogenic sediments, which characterizes the mineralogy of the area. Marine bioclasts in Espírito Santo are mainly formed by coralline algae fragments. The Jacaraípe and Mole beaches receive siliclastic sediments (mainly quartz) from small rivers, but the contribution of the latter is fairly small when compared to the influence of the Doce River on the northern beaches. In geomorphologic terms, the southern beaches are shorter and limited by rocky outcrops and sandstone cliffs. Rocky outcrops extend into the sea and, along with reef formations, restraining female turtles from accessing parts of the beach. The "Restinga" vegetation zone has dense vegetation that shade part of the beaches and the berm.

Variations in sea hydrodynamics and in wave energy lead to changes in nest sites and in the sedimentary profile of beaches presenting fine and coarse sand layers. The sediments of the beach zone above high tide level are continually reworked by winds, which remove the finer fractions of sand, blowing these to the berm. When digging and closing their nests, turtles homogenize sediments that will cover the eggs by blending different sandy layers. In order to assess the influence of sediment size on the duration of incubation and on the hatching success of *C. caretta*, approximately 200 g samples were collected from all nests monitored. Sediments were collected at a depth of 10 cm in nests, in order to obtain a homogenous sample free of eolic influence. Data on the number of hatchlings (alive and dead), and unhatched eggs were obtained from the Projeto TAMAR/ICMBio. We used this data to calculate hatching success (the quotient of the number of live hatchlings to the total number of eggs in each nest), and incubation duration (the period that extends from nesting to the first emergence of hatchlings).

Albedo is the percentage of the incident solar radiation reflected by a surface. Darker sands tend to absorb more radiation, reaching higher temperatures when compared to light-colored sands (HAYS *et al.* 2001). Albedo readings were obtained on clear, cloudless days, under similar luminosity conditions. A photographic lightmeter (Luxímetro ITLD-260) was placed 25 cm above the ground to measure the reflected solar radiation at visible wavelengths. The standard used was the 18% grey card, and the protocol was that proposed by HAYS *et al.* (2001). Albedo was then calculated as the mean of five con-

secutive readings of sand reflection, and compared with the 18% standard grey card. Since albedo of the grey card is known, it is possible to conduct comparisons with the albedo from the sand. This affords standardized measurements at the different beaches, at different moments. Albedo was examined for all monitored nests.

Calculation of the volumetric content of bioclasts was accomplished through the dissolution of calcium carbonate in hydrochloric acid. Samples were homogenized and 5 g from each nest was selected. They were weighed both before and after dissolution, and the amount of bioclast was calculated by the difference between the initial and final weights of the sample. The grain-size analysis was carried out by sieving and the subsequent application of FOLK'S (1974) scale. Because the quantity of clay was fairly small, usually less than 1% of the sample volume, the contents of silt and clay were not considered individually.

When data showed a normal distribution, differences among the beaches, including the biological (nesting date, number of alive and dead hatchlings, and clutch size) and physical (bioclast volume, albedo, and grain size) features were further investigated using the One-way ANOVA, followed by the Bonferroni *post hoc* test. For datasets that significantly strayed from the mean, differences were examined by the Kruskal-Wallis nonparametric ANOVA *on Ranks*, followed by the Dunn *post hoc* test. Variables expressed as percentages (biogenic volume, albedo, grain size, hatching success), were transformed by the arcsine of its square root, in order to achieve data normalization (ZAR 2008). When necessary, data normality was tested by K^2 and data homoscedasticity was tested by Bartlett χ^2 (ZAR 2008). The predicting contribution of sedimentological factors and biological factors (nesting date and clutch size) in incubation duration and hatching success was estimated among all beaches and in each beach individually by stepwise backwards multiple regression, independently taking the number of days of incubation duration and the proportion of success in hatching, as dependent variables. The goodness of fit of regression residuals to the normal distribution was tested by K^2 . Normality tests were run on a programmed electronic sheet and all other statistical analysis were run in Systat, version 9.0.

RESULTS

Analyses of the properties of sediments from the nesting sites were carried out on 116 samples collected from October 2006 to March 2007, from nests in Mole ($n = 24$), Jacaraípe ($n = 16$), Povoação ($n = 43$), and Pontal do Ipiranga ($n = 34$) beaches. The nesting period (Kruskal-Wallis test $H = 6.243$, $p = 0.101$) and the hatching period ($R = 4.82$, $p = 0.187$) did not show significant differences among the four beaches, indicating that incubation took place around the same time throughout the shores being monitored. On the northern coast, the Povoação and Pontal do Ipiranga beaches, associated with the mouth of Doce River, presented a larger number of nesting

sites of *C. caretta* when compared with the southern Jacaraípe and Mole beaches.

Grain size differed among beaches (Tab. I). The Mole beach showed the coarsest sediments, with the coarse-sand fraction comprising, on average, over 80% of sediment. The finest sediments were from the Jacaraípe and Pontal do Ipiranga beaches, which were also the most similar in size. The amount of biogenic sediments varied among beaches, which we grouped in two pairs: 1) Mole and Jacaraípe beaches, with high contents of bioclast, constituting more than 35% of sediment volume and reaching as far up as 65% in Jacaraípe alone; and 2) the Pontal do Ipiranga and Povoação beaches, showing a bioclastic sediment volume proportion below 3%, constituted mainly by siliciclastic minerals (mostly quartz) and heavy minerals (especially iron oxyhydroxides). Jacaraípe presented the highest reflection rate of solar radiation.

Clutch size and hatching success were the same throughout the beaches (Tab. I). Incubation duration differed considerably among the beaches and was longer in the southern beaches, Mole and Jacaraípe ($n = 32$, $\chi^2 = 62.8 \pm 4.29$ days), than in the Povoação and Pontal do Ipiranga beaches ($n = 74$, $\chi^2 = 58.1 \pm 5.06$ days), located at the mouth of the Doce river.

When each beach was analyzed individually, the influence of environmental factors on hatching success varied across the areas, which makes it impossible to draw a common pattern across the nesting sites (Tab. II). Clutch size exerted a positive effect on hatching success in all beaches, except for Jacaraípe beach. Sediment grain size did not affect hatching success only at Pontal do Ipiranga. Albedo correlated positively with hatching success at the Jacaraípe and Pontal do Ipiranga beaches. When the four beaches were analyzed collectively, as if they represented a single nesting site, hatching success correlated to clutch size and grain size.

Table II. Stepwise backwards multiple linear regression for hatchings success of *C. caretta* in all beaches and in each individually.

Variable	Coefficient	Standard coefficient	P
All beaches ($r^2 = 0.9498$)			
Clutch size	0.0072	0.7328	<0.0001
Granule	0.6335	0.1820	<0.0001
Fine sand	1.4672	0.1274	<0.0001
Mole beach ($r^2 = 0.9367$)			
Clutch size	0.0091	1.0500	<0.0010
Fine sand	6.3100	0.2851	0.0114
Very fine sand	-27.6543	-0.3601	0.0071
Jacaraípe beach ($r^2 = 0.9304$)			
Albedo	16.2312	0.5649	0.0118
Fine sand	1.1265	0.4237	0.0451
Povoação beach ($r^2 = 0.9666$)			
Clutch size	0.0031	0.3046	0.0385
Coarse sand	0.6684	0.4282	0.0001
Medium sand	0.5741	0.2733	0.0045
Pontal do Ipiranga beach ($r^2 = 0.9818$)			
Clutch size	0.0037	0.3792	0.0004
Albedo	16.9770	0.6192	<0.0001

The influence exerted on incubation duration by grain fractions varied across the beaches sampled. At Povoação beach, the nests located in coarse sand took less time to hatch. At Jacaraípe beach, incubation duration correlated positively with

Table I. Variation of biological and environmental factors across the nesting sites of *C. caretta* during the 2006/2007 reproductive season. Mean \pm standard deviation (sample size) * and means, followed by distinct letters at the same position, denote significance at the 0.05 level.

Variables	Mole (24)	Jacaraípe (16)	Povoação (43)	Pontal do Ipiranga (33)	Parameter	p
Incubation duration (days)	62.26 \pm 4.60 ^a	63.69 \pm 3.79 ^{a,c}	58.52 \pm 3.63 ^{b,d}	57.88 \pm 6.84 ^{b,d}	F = 7.81	< 0.010*
Hatching success (%)	66.41 \pm 30.19	79.11 \pm 27.04	82.5 \pm 18.91	80.53 \pm 14.56	H = 7.43	0.059
Clutch size	113.79 \pm 31.28	115.36 \pm 19.75	115.05 \pm 22.76	111.44 \pm 27.39	F = 0.085	0.932
Albedo (%)	18.5 \pm 0.95 ^a	16.3 \pm 2.24 ^{b,c}	18.1 \pm 0.75 ^{a,e}	17.8 \pm 1.31 ^{a,e}	H = 9.85	< 0.006*
Biogenic sediment (%)	37.3 \pm 8.22 ^a	56.7 \pm 7.55 ^{b,c}	0.77 \pm 0.57 ^{b,d}	1.15 \pm 0.89 ^{b,d}	H = 9.43	< 0.010*
Grain size						
Gravel	0.71 \pm 1.09 ^a	0.14 \pm 0.22 ^{b,c}	2.19 \pm 2.21 ^{a,d,e}	0.12 \pm 0.20 ^{b,c,f}	H = 54.41	< 0.010*
Very coarse sand	10.44 \pm 8.45 ^a	3.58 \pm 5.51 ^{b,c}	12.58 \pm 8.11 ^{a,d,e}	2.21 \pm 2.47 ^{b,c,f}	H = 47.86	< 0.010*
Coarse sand	83.93 \pm 8.32 ^a	21.40 \pm 21.32 ^{b,c}	47.03 \pm 14.93 ^{b,d,e}	27.77 \pm 14.84 ^{b,c,f}	H = 117.20	< 0.010*
Medium sand	4.72 \pm 3.55 ^a	58.66 \pm 21.70 ^{b,c}	28.96 \pm 13.61 ^{b,d,e}	51.39 \pm 9.44 ^{b,c,f}	H = 75.12	< 0.010*
Fine sand	0.18 \pm 0.50 ^a	15.12 \pm 12.12 ^{b,c}	8.05 \pm 9.51 ^{b,c}	15.73 \pm 9.50 ^b	H = 58.46	< 0.010*
Very fine sand	0.02 \pm 0.02 ^a	1.09 \pm 1.43 ^{b,c}	1.18 \pm 2.32 ^{b,c,e}	2.77 \pm 1.88 ^{b,c,f}	H = 57.87	< 0.010*

the grain fractions very coarse sand and medium sand, which suggests that the nests made in coarser sands take longer to hatch (Tab. III). In Mole and Povoação beaches clutch size presented a negative correlation with incubation duration, and nests with more eggs had shorter incubation duration.

When the beaches were examined collectively, incubation duration was affected by the nesting date, albedo, mineral composition and grain size (Tab. III). Clutches laid in the beginning of the reproductive season (October and November) had a longer incubation duration ($n = 45$, $\chi^2 = 62.1 \pm 4.86$ days) than clutches laid toward the end of it (December and January; $n = 61$, $\chi^2 = 57.6 \pm 4.78$ days). The amount of biogenic sediments also showed a positive correlation with incubation duration at the Mole beach, and a negative correlation at the Jacaraípe beach (with high volumes of bioclast).

DISCUSSION

Our results on the influence of most sediment characteristics and nesting date on incubation duration and hatching success differed depending on whether beaches were analyzed individually or collectively. Clutch size and grain size, however, were found to be affected by sediment characteristics in both types of analyses. Nests containing greater number of eggs presented higher hatching success, which may reflect the differences in gas volume among eggs, and gas exchange between the egg chamber and the surrounding medium (ACKERMAN 1980, ACKERMAN *et al.* 1985). Considering sediment size, although some correlations between grain fractions and the hatching success were highly significant, the volumetric contribution of these fractions to sediment size is very small, which makes it difficult to predict how they could lead to changes in nest environment and affect embryo survival. It was only at Povoação beach that the grain fractions coarse sand (47%) and medium sand (28%) are volumetrically representative and nests located in coarser sediments presented a higher hatching success. Sediment size plays a direct role on hydraulic conductivity, total porosity, air-filled pore space, salinity (FOLEY *et al.* 2006) and heat transfer (SOUZA & VOGT 1994) with consequences to embryo survival. Apart from this, coarser sediments tend to be drier (MORTIMER 1990) and to present higher temperatures, which may reach lethal levels, reducing hatchling survival (GODLEY *et al.* 2001b, HAWKES *et al.* 2007). The coarser sediment in the surroundings of the mouth of the Doce River indicates a more dynamic environment. In this environment, tidal variation may affect the microenvironment of the nests, leading to nest flooding, which negatively impacts hatching success (ÖZ *et al.* 2004, MARGARITOU 2005, FOLEY *et al.* 2006).

The influence of the nesting site on hatching success greatly varies among the various species of sea turtle and the sites themselves (MILLER *et al.* 2003). For instance, no differences are found in the hatching success of *Eretmochelys imbricata* (Linnaeus, 1766), a species that lays eggs in open beaches as

Table III. Stepwise backwards multiple linear regression for incubation duration of *C. caretta* in all beaches and in each beach individually.

Variable	Coefficient	Standard Coefficient	p
All beaches ($r^2 = 0.9933$)			
Nesting date	-0.0741	-0.1947	0.0005
Albedo	1355.2900	0.9568	< 0.0001
Biogenic sediments	-8.4933	-0.1885	< 0.0001
Very coarse sand	10.1355	0.0488	0.0500
Coarse sand	14.0154	0.1816	0.0277
Medium sand	12.6632	0.1413	0.0068
Fine sand	16.6645	0.0923	0.0191
Mole beach ($r^2 = 0.9988$)			
Nesting date	-0.2051	-0.5103	< 0.0001
Clutch size	-0.1319	-0.2490	0.0001
Albedo	3329.6600	2.2944	< 0.0001
Biogenic sediments	-54.3680	-0.8007	0.0012
Very coarse sand	51.6410	0.2664	0.0014
Fine sand	-96.8030	-0.0718	0.0015
Very fine sand	23.2090	0.0496	0.0100
Jacaraípe beach ($r^2 = 0.9988$)			
Albedo	-1160.5000	-0.7338	0.0040
Biogenic sediments	74.8447	0.8457	< 0.0001
Granule	-120.9120	-0.0632	< 0.0001
Very coarse sand	78.9139	0.2347	< 0.0001
Medium sand	53.0503	0.7758	0.0001
Povoação beach ($r^2 = 0.9978$)			
Nesting date	-0.0906	-0.2539	0.0009
Clutch size	-0.0740	-0.1467	0.0008
Albedo	938.0900	0.6790	0.0005
Biogenic sediments	36.2720	0.9276	< 0.0001
Coarse sand	-16.4720	-0.2168	< 0.0001
Pontal do Ipiranga beach ($r^2 = 0.9963$)			
Nesting date	-0.2530	0.6629	< 0.0001
Biogenic sediments	64.8720	1.6508	< 0.0001

well as in the vegetation fringe. This constancy is attributed to the greater stability and homogeneity of the sediments in the Guadeloupe beaches, French West Indies (KAMEL & MROSOVSKY 2005). In Barbados, by contrast, *E. imbricata* shows a preference for beach zones, wherein hatching success is the highest in nests closest to mean elevation in the berm (HORROCKS & SCOTT 1991).

In Bahia, Brazil, beach vegetation cover negatively influences the hatching success of *E. imbricata* (SERAFINI *et al.* 2008). The hatching success of *Lepidochelys olivacea* (Eschscholtz, 1829) in Baja California is affected by both distance from the sea and humidity in the nest (LOPEZ-CASTRO *et al.* 2004). For *C. caretta* in Patara beach, Turkey, hatching success is lower in the open beach than inland, with erosion and nest flooding being the main factors responsible for this difference (ÖZ *et al.* 2004). In Laganas Bay, Greece, hatching success varies among six beaches that are close to one another and all within 5.5 km of the coast. This variation has been attributed to differences in the physiographic features of the sites such as grain size, plant cover, and the presence of rocky outcrops between beaches (MARGARITOU LIS 2005). The beaches of Espírito Santo monitored in this study are more than 125 km apart and show remarkable geologic differences, and the discrepancies in sediment properties among the beaches of Espírito Santo affect the survival of embryos. In the present study, nests that could be eroded or flooded by the tide and that have been transferred as part of the methodology developed by Projeto TAMAR/ICMBio (MARCOVALDI & MARCOVALDI 1999) were excluded. When comparing these results with those from other studies, it should be noted that only nests that had completed incubation and remained *in situ* have been used in the analyses, and the important role of the variation with relation to the dynamism of the beach (especially, the capacity of tides to flood or erode nests) has not been evaluated.

Incubation duration varied widely among the beaches and was greatly influenced by the properties of the sediments. However, it is not possible to draw a pattern that can be generalized. For instance, at Mole beach, the nesting date, clutch size, albedo, mineralogical composition and grain size affected incubation duration, whereas at Pontal do Ipiranga beach, only nesting date and mineralogical composition affected it. This fact shows the importance of extensively protecting nesting sites or even those areas that, in spite of being geographically small or close by, present great geologic diversity to the point of affecting the thermal environment of nests, with drastic consequences for both incubation duration (MARGARITOU LIS 2005), sex ratio (HORROCKS & SCOTT 1991) and hatching success (FOLEY *et al.* 2006).

When the beaches were analyzed collectively, nesting date, albedo, grain size and mineral composition (volume of biogenic sediments) were observed to have influence on incubation duration. Nesting date has been selected as one of the main factors influencing nest temperature and embryonic development rate, having a direct effect on incubation duration (PIKE *et al.* 2006, HAWKES *et al.* 2007). Thus, incubation duration is longer in the beginning of the reproductive season of sea turtles, because the mean daily temperature is lower. In the course of the subsequent months, days become longer and warmer, and the nest temperatures tend to increase, shortening the incubation duration (HEWAVISENTHI & PARMENTER 2002, BAPTISTOTTE *et al.* 2003). This correlation is common across the

areas of reproduction of *C. caretta* (MROSOVSKY & PROVANCHA 1989, NARO-MACIEL *et al.* 1999, ÖZ *et al.* 2004). The negative correlation between clutch size and incubation duration at Mole and Povoação beaches is attributed to metabolic heat: larger clutches lead to higher temperatures and shortened incubation duration (MAXWELL *et al.* 1988, KASKA *et al.* 1998, GODLEY *et al.* 2001b, ÖZ *et al.* 2004).

Albedo was the sedimentary variable that had the greatest influence on incubation, when beaches were analyzed together and individually. Of the four beaches analyzed, only Pontal do Ipiranga was not influenced by albedo. In general, in the nests situated in sediments with lower albedo (Povoação and Mole beaches), incubation duration was shorter, as indicated by other studies (NARO-MACIEL *et al.* 1999, HAYS *et al.* 2001). At Jacaraípe beach this trend was reversed, and the nests located in sediments with lower albedo presented longer incubation duration. This inversion is explained by the mineral composition of the sediments, which presented the highest levels of biogenic sediments at Jacaraípe beach. Fragments of coralline algae, abundant in this beach, are lighter in color than quartz minerals, which increase albedo. Nevertheless, biogenic sediments presented lower conductivity, leading to a lower incubation temperature (MILTON *et al.* 1997) and increased incubation duration. More specifically, mineral composition was more important and surpassed the influence of albedo on incubation duration at Jacaraípe beach. At Mole beach, which presented intermediate levels of bioclasts, the increase in biogenic sediment levels increased incubation duration.

The influence of grain size on incubation duration varied across beaches. At Povoação beach the increase in coarse sand fraction ($x = 47 \pm 14.9\%$ of the total volume) lead to a decrease in incubation duration, indicating that nests located in these sediments, predominantly quartz sediments, hatch sooner than nests located in fine sandy sediments (SOUZA & VOGT 1994, NARO-MACIEL *et al.* 1999). At Mole and Jacaraípe beaches, the very coarse sand fraction ($x = 10.4 \pm 8.45\%$ and $x = 3.5 \pm 5.51\%$ of total volume, respectively) correlated positively with incubation duration. In these beaches, the levels of biogenic sediments are high and the variation in grain size is not homogeneous across the different mineral components. The quartz grains are smaller and better selected than fragments of mollusk shell, corals and coralline algae. Therefore, the increase in grain size leads to a shift in mineral composition, favoring biogenic sediments that tend to decrease incubation duration due to the differences in heat absorption and transmission at depths (MILTON *et al.* 1997).

The results of this research show the importance of protecting areas with great geologic diversity, wherein the features of the environment can affect the microenvironment of nests, with consequences on incubation duration and hatching success. The manner in which sediment properties vary depends largely on the geologic setting of the region and can hardly be generalized (FOLEY *et al.* 2006). MARGARITOU LIS (2005) points to

significant differences in the incubation duration in small beaches located near each other, attributing the differences to the quality of the sediment. The areas considered in this study, the Povoação and Pontal do Ipiranga beaches associated with the mouth of Doce River are very long, and their geologic features affect the hatching success and incubation duration. The southern beaches, which are associated with the biogenic sediments, are shorter, and show greater sediment variation due to the estuaries, cliffs, or old sand ridges that provide quartz sediments and alter the mineral composition of the beaches, with great consequences that affect incubation duration and hatching success.

The sex ratio of *C. caretta* is generally female-biased (MROSOVSKY & PROVANCHA 1992, HANSON *et al.* 1998, GODLEY *et al.* 2001b). At the Beaches of Bahia, Brazil the sex ratio is strongly biased towards females -, but at the beaches of Espírito Santo associated with the mouth of Doce River, the sex ratio is not similarly biased (MARCOVALDI *et al.* 1997, MROSOVSKY *et al.* 1999, NARO-MACIEL *et al.* 1999, BAPTISTOTTE *et al.* 1999). Beside Heron Island, Australia (LIMPUS *et al.* 1983) and Bald Head Island, NC, USA (HAWKES *et al.* 2007) the Espírito Santo coastline is one of the few sites in the world where sex ratios are not highly female biased (BAPTISTOTTE *et al.* 1999). Incubation duration is longer at the Mole and Jacaraípe beaches than at the beaches associated with the mouth of the Doce River. Considering the pivotal incubation duration of 59.9 days (MROSOVSKY *et al.* 1999) and that the data were collected in one same reproductive season and under similar climatic conditions, the difference in incubation duration suggests a higher proportion of male hatchlings being born in the south beaches, when compared to the beaches to the north of the Doce River. Although constituting a smaller nesting total, hatchlings from the southern Espírito Santo beaches may be important to maintain the populations of *C. caretta*, evidencing the need to protect these nesting sites. Therefore, protection should not be restricted to the major nesting sites, but should also encompass the beaches with sparse distribution of nests, which present peculiar features that may affect the sex ratio and hatching success. The physiographic differences in nesting areas may add to hatchling variability and phenotypical characteristics like size and growth rates at juvenile stages may be useful considering hatchling and adult survival (MCGEHEE 1990, FOLEY *et al.* 2006). In a scenario where most rookeries of *C. caretta* produce a female-biased sex ratio, it is important to protect the areas where a higher male production is observed (HAWKES *et al.* 2007). These areas may play an important role in the viability of *C. caretta* populations in the southern Atlantic Ocean.

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