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The Influence of Beach Sand Characteristics on the Nesting Behavior and Clutch Survival of Green Turtles (*Chelonia mydas*)

JEANNE A. MORTIMER

I examined the influence of chemical and physical characteristics of beach sands on nesting behavior and clutch survival of green turtles (*Chelonia mydas*) at covehead beaches differing in substrate composition on Ascension Id. and Aldabra Atoll. In coarse, dry sand, females have difficulty digging egg chambers, and typically make multiple trial nest holes and re-emerge on successive nights before depositing eggs. At Ascension, clutch mortality is highest at beaches with low substrate water potentials. Calculated substrate water potentials range from -2--320 kPa, and high mortality in the drier conditions suggests that green turtle eggs may be particularly sensitive to desiccation. At the biogenic beaches, mortality is positively correlated with mean particle diameter of the sand, suggesting physiological stress (perhaps desiccation) in coarser sands; sand cave-ins also may cause mortality. Gas diffusion apparently does not limit hatching success at Ascension Id. Clutch survival is positively correlated with nest depth, and negatively correlated with electrical conductivity and volume of air-filled pore space in the substrate. Structure and composition of sand from 34 green turtle nesting beaches from around the world (Atlantic, Indian and Pacific oceans) were analyzed and, together with the Ascension Id. and Aldabra data, indicate that green turtles nest in sands that vary greatly. Factors other than the physiognomy of sand on nesting beaches may be as important, or more important, in nest site selection.

ALTHOUGH the substrates of sea turtle nesting beaches vary considerably (Hendrickson and Balasingam, 1966; Stancyk and Ross, 1978; Mortimer, 1982), few studies examine how substrate characteristics influence the biology of nesting females and incubating eggs. Laboratory experiments show that the physical conditions to which reptilian eggs are

exposed—particularly temperature, moisture, and gas concentrations—have a profound effect on growth and sexual differentiation (Packard and Packard, 1988). Apart from temperature (Packard and Packard, 1988), the environment inside natural nests is not well known, hence the ecological relevance of much of the laboratory work has yet to be demon-

strated. Although water potentials have been measured inside natural nests of *Chelydra* and *Conolophus* (G. Packard et al., 1985; Snell and Tracy, 1985) most studies examine the hydric environment under field conditions by determining water content of soil samples taken from the nest walls (Bustard and Greenham, 1968; McGehee, 1979; Lutz and Dunbar-Cooper, 1984). Unfortunately, water mass alone is not a good measure of the availability of water for uptake by eggs because substrate water potential differs according to physical and (or) chemical properties of the substrate (Narayana and Shah, 1966).

I examined the effects of various physical and chemical properties of the nesting substrate—in particular, sand texture (particle size distribution and particle shape), water content, and water potential on nesting behavior and clutch survival of green turtles. I also surveyed and compared the physical and chemical characteristics of sand from a variety of important green turtle beaches around the world to determine patterns which might help explain peculiarities of sea turtle nesting.

THE STUDY SITES

Most of the work was done at Ascension Id., an isolated volcanic peak on the mid-Atlantic ridge in the South Atlantic Ocean (7°57'S, 14°22'W). Diversity among the 32 covehead beaches of Ascension Id. provides an ideal natural laboratory in which to study the effects of various environmental parameters on hatching success and adult nesting behavior. Data on the influence of different sands on adult nesting behavior also were gathered at Aldabra Atoll in the Indian Ocean (9°24'S, 46°20'W) where green turtles nest on 46 covehead beaches (Mortimer, 1988). Other locations from which beach sands were sampled include some of the most important green turtle rookeries in the world. They are: Tortuguero, Costa Rica (Carr et al., 1978); Surinam (Schulz, 1975); Hawkesbay-Sandspit, Pakistan (Salm, 1976); Terengganu, Malaysia (Hendrickson and Balasingam, 1966); Heron Id., Australia (Limpus, 1980); Hawaii (Balazs, 1982, 1985); and American Samoa (Balazs, 1982).

METHODS

Nesting behavior at Ascension Id. and Aldabra Atoll.—During early morning track counts made as part of a study to estimate nesting density at

Ascension Id. (Mortimer and Carr, 1987) and at Aldabra Atoll (Mortimer, 1988) I recorded the numbers of body pits associated with individual turtle tracks. The data were collected at Ascension Id. during the 1977–78 nesting season, and at Aldabra Atoll during July 1981, June–July 1982, April 1983, and March–April 1987. At both sites, I correlated the median numbers of body pits per nesting emergence per beach with the mean particle diameter of the beach sand (see below), and at Aldabra Atoll, with levels of precipitation. Precipitation at Aldabra Atoll was measured with a rain gauge mounted behind Anse Mais, and by the Meteorological Station at Ile Picard.

Clutch viability at Ascension Id.—Although an effort had been made to mark egg clutches at the time they were deposited, and then to excavate them at the end of their incubation period, the combined high nesting density and tendency of the Ascension Id. turtles to dig multiple nest pits made finding the marked nests nearly impossible. Instead, I determined the relative rates of hatching and emergence success of egg clutches deposited on 13 of the Ascension Id. beaches by examining the contents of nests from which young had emerged during April–July 1977 and Feb.–June 1978. Nests were located by back-tracking the seaward paths of hatchlings or by digging into the saucer shaped depressions in the sand indicative of hatchling activity below the surface. I sampled every third nest thus encountered during random transects across the beach. At Spire and Pebbly West beaches, the rate of hatchling emergence was so low that I located nests by digging trenches.

For each of the 87 nests excavated, the following data were recorded: the numbers of empty egg shells, unhatched eggs, embryos that died in the process of hatching, and dead and living hatchlings remaining in the egg chamber and in the sand column above the nest. Unhatched eggs were opened and examined visually for signs of development, and the lengths of any embryos were measured. At the time of excavation, the depth to the bottom of each nest and its distance from the high spring tide line were recorded and later correlated with the observed rates of hatching success. I collected sand (~500 g) from the wall of the egg chamber of 56 of the 87 egg clutches for analyses of water content, electrical conductivity, pH, and particle size distribution.

Characterization of sands.—Sand from all 32 beaches at Ascension Id. (see map in Mortimer and Carr, 1987), from the 23 most important nesting beaches at Aldabra Atoll (Mortimer, 1988), and from green turtle beaches at 12 other localities (Tables 2–3) were collected for analysis. At both Ascension Id. and Aldabra Atoll, from each beach less than 150 m long, at least three sand samples were collected, at nest depth, at regular intervals along a transect parallel to the shoreline in the zone of greatest density of body pits. Longer beaches were sampled at 50 m intervals. At each sample station, 500 g of sand were taken. Samples from the same beach were mixed and a subsample selected. At the other localities, from one to five grab samples were collected, usually at clutch depth.

To describe the texture of each sample I used mean particle diameter and sorting coefficient (a measure of the uniformity or sorting of the particles). I determined particle-size distribution by fractionating the sand with sieves with mesh sizes 20.00, 12.70, 7.93, 4.00, 2.00, 1.00, 0.50, 0.25, 0.105, and 0.045 mm. I measured the clay fraction of the Ascension Id. samples by the hydrometer method and that of the other samples by the pipette method (Day, 1965). A cumulative frequency was plotted showing the percent of sediment (from coarsest to finest) on the ordinate and the sieve size in phi units on the abscissa—where ϕ (phi) = $-\log_2(\text{mm})$. The intercepts of the 5, 16, 50, 84, and 95 percentiles with the cumulative curve were used to calculate the mean particle diameter and sorting coefficient according to the following formulas (Folk, 1966). Mean diameters were transformed to mm units for presentation.

Mean diameter ($M_n\phi$)

$$= \frac{(\phi_{16} + \phi_{50} + \phi_{84})}{3} \quad (1)$$

Sorting Coefficient ($S\phi$)

$$= \frac{(\phi_{95} + \phi_{05})}{6.6} + \frac{(\phi_{84} + \phi_{16})}{4} \quad (2)$$

I categorized the shape of sand particles from each of 26 beaches from nesting sites around the world in terms of sphericity and roundness. Sphericity was determined using the chart and methodology of Rittenhouse (1943), in which particle classification ranges from 0.44 (elongated particles with a length to width ratio of approx. 5:1) to 0.98 (spherical particles).

Roundness, a measure of the curvature of the corners and edges (i.e., the smoothness) of the particles, was determined using the classification of Krumbein (1941) which includes nine categories ranging from 0.1 (the least smooth) to 0.9 (the most smooth).

I measured the electrical conductivity (in mmhos/cm) of a saturated extract of each sand sample, with a YSI Model 32 conductance meter. I determined the percent organic carbon by the Walkley-Black method (Allison, 1965), the percent calcium carbonate by the titrimetric method using HCl and NaOH (Soil Survey Staff, 1984), and pH with an Orian Research Model 601/Digital Ionalyzer using the water dilution method. The mineral composition of those samples containing less than 75% calcium carbonate was determined by x-ray diffraction (Whittig, 1965). The amount of inorganically bound iron present in the Tortuguero sample was measured by dithionate-citrate extraction (Soil Survey Staff, 1984). The total phosphorus of the French Frigate Shoals East Id. sample was determined by the alkaline oxidation method (Dick and Tabatabai, 1977). I evaluated sand color with a GSA Rock-Color Chart (Rock-Color Chart Committee, 1975).

The hydraulic properties of selected Ascension Id. beach sands were examined for water content, total water potential, and porosity. Total water potential is defined as the sum of matric potential and osmotic potential—a function of salinity (Bresler et al., 1982). At each beach, I took measurements of electrical conductivity and of water content, expressed as a percentage of the dry weight of the substrate, from the following two types of sand samples: those collected for characterization of the Ascension Id. sands (between 24 June–18 Aug. 1977), and those taken from the walls of individual egg chambers (over a 9 mo period spanning both nesting seasons). The mean and range of these measurements at each beach were used to calculate the substrate matric and osmotic potentials, and also the air-filled pore space.

In the laboratory, I used the pressure plate method (Klute, 1965) to derive curves describing substrate matric potential as a function of substrate water content, for pressures between 0.34 and 1471 kPa. I fit equations to these data and then used them to solve for substrate matric potentials that would correspond to substrate water contents measured in the field. I used the following formula to estimate osmotic potentials (kPa) of the soil solutions in the field:

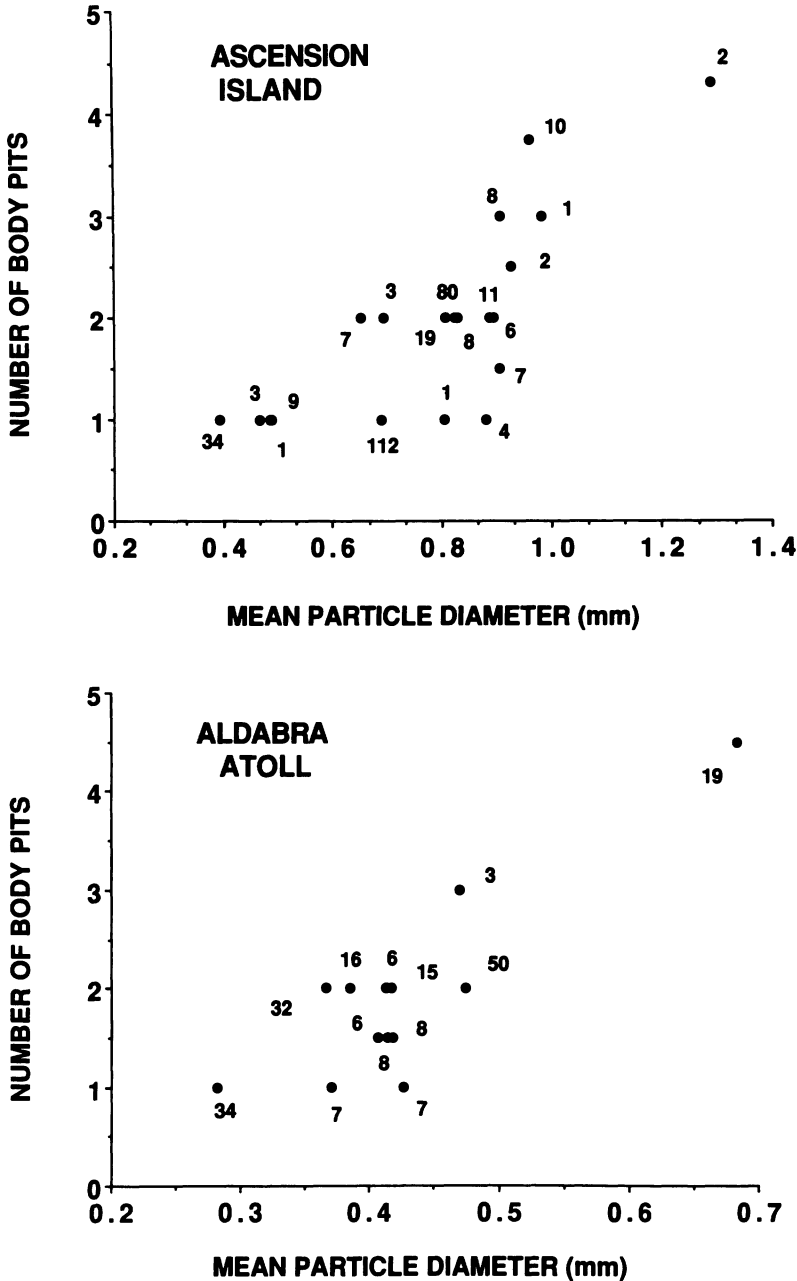


Fig. 1. Relationship between median number of body pits per nesting emergence and the mean particle diameter (mm) of sand on beaches at Ascension Id. (A) and Aldabra Atoll (B). Numbers indicate sample sizes.

$$\psi_o = -0.36 EC (\theta_s/\theta) \quad (3)$$

where EC is electrical conductivity in mmhos/cm, and θ and θ_s are the water content (g H₂O/g dry sand) in the field and the water content of the saturation extract (Bresler et al., 1982).

I determined total porosity (St) (% cm³) and total air filled pore space under field conditions (S) (% cm³) as follows:

$$St = 100 [1 - (Db/\rho p)] \quad (4)$$

$$S = St - Pv \quad (5)$$

TABLE 1. MEAN NUMBERS OF BODY PITS PER NESTING EMERGENCE RECORDED AT BEACHES OF ALDABRA ATOLL DURING PERIODS OF RELATIVELY HIGH AND LOW RAINFALL.

| Beach | Low rainfall ^a | | | High rainfall ^b | | |
|------------------|---------------------------|------|----|----------------------------|------|----|
| | \bar{x} | SD | n | \bar{x} | SD | n |
| Anse Mais | 2.85 | 1.83 | 13 | 1.76 | 1.04 | 23 |
| Anse Des Coco | 3.50 | 1.15 | 4 | 2.00 | 1.44 | 9 |
| Anse Badamier IV | 4.00 | 2.12 | 8 | 2.38 | 1.26 | 12 |

^a During 7–30 July 1981, an average of 0.8 mm of rain fell daily.

^b During 7 June–7 July 1982, an average of 3.0 mm of rain fell daily.

where Db (bulk density) is the mass of the oven dry soil in bulk volume (g/cm^3), ρ_p (particle density) is the density of the solid particles collectively (g/cm^3), and Pv is the substrate water content on a volume basis ($\text{g H}_2\text{O}/\text{cm}^3$) (Vomocil, 1965). I used the handbook density values of $2.711 \text{ g}/\text{cm}^3$ for calcite and $2.65 \text{ g}/\text{cm}^3$ for feldspars (Berry and Mason, 1959).

RESULTS

Characteristics of sand and nesting behavior.—The median number of trial nest holes dug per nesting emergence and the mean particle diameter of the beach sands at Ascension Id. were positively correlated (Spearman rank test; $r_s = 0.815$; $P = 0.0001$; $n = 20$) (Fig. 1A). Although Aldabran turtles tended to dig more trial nest holes in the coarser grained beach sands (Fig. 1B), this relationship was not statistically significant (Spearman rank; $r_s = 0.505$; $P = 0.078$; $n = 13$).

At Aldabra Atoll during the low rainfall period of 7–30 July 1981, the numbers of body pits recorded per nesting emergence were significantly higher than during 7 June–7 July 1982, when precipitation was greater (Table 1) (Mann-Whitney U-test; $z = 3.314$; $P = 0.0009$; $n = 69$). More turtles also re-emerged on two or more consecutive nights during the 1981 dry period than in 1982 (Mortimer, 1988).

Characteristics of the beach sand and clutch viability at Ascension Id.—The relative mortality and stages at which death was recorded in 87 egg clutches distributed among 15 beaches at Ascension Id. show that sand texture and mineral composition were the properties most obviously correlated with clutch survival. The relationship between the average total survival (i.e., percentage of a clutch yielding viable hatchlings) and the sorting coefficients and mean particle

diameters (Fig. 2) shows lowest survivorship at three volcanic beaches composed of the most poorly sorted sand—Pebbley East, Pebbley West, and Spire beaches. These sands contained large amounts of very coarse and very fine particles (Table 2). Among the other 12 beaches, all composed of sands with mean sorting coefficients lower than 1.10, a Spearman rank test showed no statistical correlation between any of the parameters of clutch survivorship and sorting coefficient ($P > 0.05$).

Because the variance of the mean particle diameters of the poorly sorted sand is greater than that of the better sorted ones (Fig. 3), only the 12 beaches having average sorting coefficients less than 1.10 were examined to determine the relationship between mean particle diameter and clutch survival. When all 12 beaches were considered, a Spearman rank test demonstrated no significant correlation between mean particle diameter and survivorship ($P > 0.05$). But, when only the 10 biogenic beaches were considered, highly significant correlations were observed between mean particle diameter and median percentages of the following: emergence success ($r_s = -0.8424$; $P = 0.0011$), hatching success ($r_s = -0.7939$; $P = 0.0042$), mortality during pipping ($r_s = 0.7454$; $P = 0.0109$), mortality just prior to pipping ($r_s = 0.6727$; $P = 0.0309$), and mortality at earlier embryonic stages ($r_s = 0.7091$; $P = 0.0192$). Neither the percentages of unhatched eggs nor the percentages of hatchlings that died in the sand column were significantly correlated with the mean particle diameters ($P > 0.05$), although the greatest percentages of hatchlings died in the sand of those beaches with mean particle diameters greater than 0.75 mm. For the 10 biogenic beaches, regressions showed a positive correlation between mean particle diameter and rates of mortality incurred before pipping, and during and after pipping (Fig. 4).

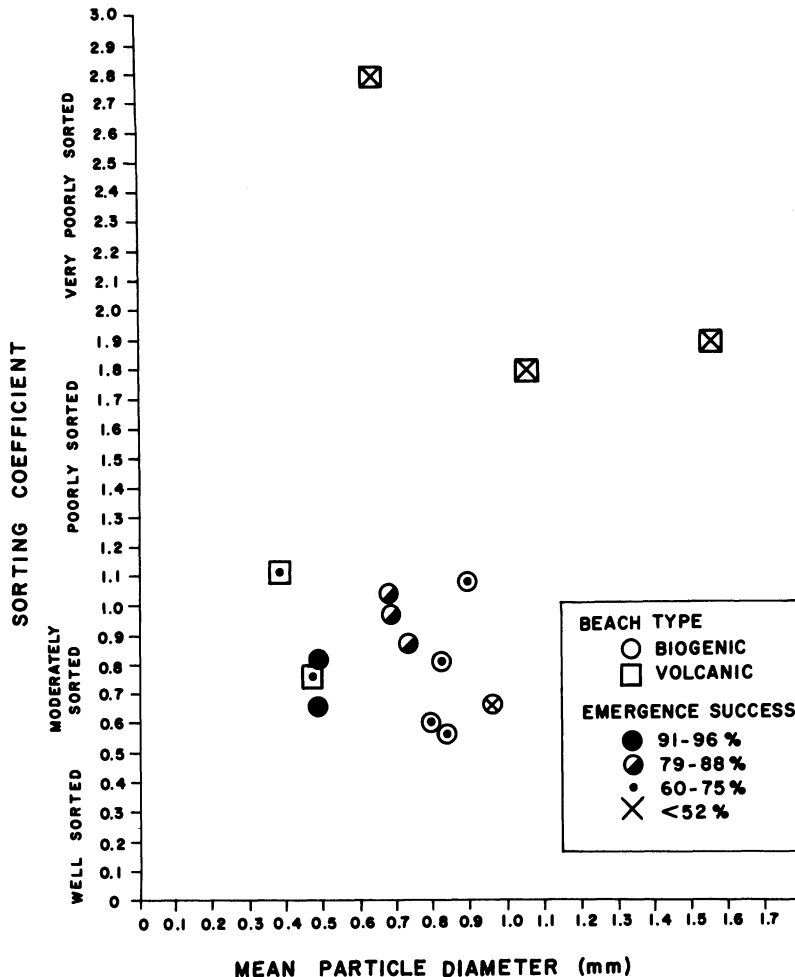


Fig. 2. Relationship between the mean emergence success of clutches at 15 Ascension beaches, and the sorting coefficients and mean particle diameters (mm) of the sands at those beaches.

The slopes of the two lines were not significantly different at the 95% confidence interval (Fig. 4).

Egg clutches suffered higher mortality when incubated in volcanic sands than they did in sands which have similar particle size distribution but are composed of biogenic parent material (Fig. 2). Volcanic and biogenic sands at Ascension Id. differ from each other in color, mineral composition and sand particle shape (Tables 2-3). Both types of Ascension Id. sands show similar values for sphericity, but the biogenic sand particles are generally rounder (i.e., smoother) than are those of volcanic sand (Table 2).

None of the parameters of clutch survival was significantly correlated with pH, with levels of organic carbon in the sand, or with clutch size (Spearman rank test; $P > 0.05$). For electrical conductivity, a Spearman rank test showed weak negative correlation with both the median percentages of emergence success ($r_s = -0.5071$; $P = 0.0529$; $n = 15$) and hatching success ($r_s = -0.5500$; $P = 0.0322$; $n = 15$), and a positive correlation with the median percentages of mortality that occurred during pipping ($r_s = 0.7890$; $P = 0.0004$; $n = 14$).

Nest depth at the time of excavation was positively but weakly correlated with percent hatching success (Spearman rank; $r_s = 0.2485$;

TABLE 2. PHYSICAL CHARACTERISTICS OF GREEN TURTLE NESTING BEACHES IN THREE OCEANS.

| Beaches | % particles >2 mm | % silt/clay | Particle shape | |
|--------------------------------------|---------------------------|---------------------------|------------------------|------------------------|
| | | | Sphericity | Roundness |
| Atlantic Ocean | | | | |
| Ascension Id. | | | | |
| Biogenic beaches | 0.9–12.6 ^a | 0.9–3.4 ^a | 0.76–0.80 ^a | 0.42–0.65 ^a |
| Volcanic beaches | 3.1–35.4 ^b | 1.0–9.0 ^b | 0.75–0.78 ^b | 0.11–0.36 ^b |
| Tortuguero, Costa Rica | 0 | 1.0 | 0.77 | 0.26 |
| Surinam | 6.7 | 1.5 | 0.74 | 0.36 |
| Pacific Ocean | | | | |
| Penarik, Terengganu, Malaysia | 1.0 | 1.1 | 0.80 | 0.39 |
| Heron Id., Australia | 0.9 | 3.2 | 0.78 | 0.35 |
| Sand Id., Rose Atoll, American Samoa | 74.4 | 1.7 | 0.72 | 0.36 |
| Hawaii | | | | |
| Trig Id., French Frigate Shoals | 30.2 | 4.5 | 0.75 | 0.29 |
| East Id., French Frigate Shoals | 36.2 | 15.5 | 0.79 | 0.32 |
| Tern Id., French Frigate Shoals | 13.0 | 2.8 | 0.80 | 0.38 |
| S.E. Id., Pearl & Hermes Reef | 76.8 | 1.1 | 0.69 | 0.39 |
| Polihua Bch., Lanai Id. | 2.0 | 1.4 | — | — |
| Indian Ocean | | | | |
| Aldabra Atoll | 1.1 ^c (1.0) | 2.1 ^c (0.5) | 0.77–0.80 ^d | 0.36–0.50 ^d |
| Hawkesbay-Sandspit Bch., Pakistan | 0.5 | 1.4 | 0.75 | 0.22 |

^a Range measured among 10 beaches.

^b Range measured among five beaches.

^c Mean and SD measured among 23 beaches.

^d Range measured among five beaches.

$P = 0.0278$; $n = 78$). Only at Long Beach, which has the widest beach platform on the island (150 m) and which was especially prone to inundation by storm swells or "rollers" (Mortimer and Carr, 1987; Mortimer, 1981), was there a significant (positive) correlation between distance from the nest to the high tide line and percent hatching success (Spearman rank; $r_s = 0.4773$; $P = 0.0519$; $n = 17$).

Curves and equations describing the substrate water potentials of those eight Ascension Id. beaches at which the most complete survivorship data were gathered range from what is typical of very coarse sand to that of sand loam (Narayana and Shah, 1966). Electrical conductivity ranged from 0.12–12.80 mmhos/cm, and water content ranged from 2.57–12.87 g H₂O/g dry sand. The range of values calculated for matric potential (–188.4––1.45 kPa) were similar to those calculated for osmotic potential (–130.9––0.80 kPa) (Table 4). There was a positive relationship between total water potential of the substrate and clutch survival (Fig. 5). At the same eight Ascension Id. beaches (excluding Spire beach where the high sorting coef-

ficient precluded a reliable determination of porosity), there was a significant positive correlation between the median percent prepping mortality and the mean total air-filled pore space of the substrate (Spearman rank; $r_s = -0.8571$; $P = 0.0103$; $n = 7$) (Fig. 6).

Characteristics of sand from other nesting beaches around the world.—Descriptions of the texture, chemical composition, and color of the sand of 50 green turtle nesting beaches from around the world show that turtles nest in a wide range of conditions (Tables 2–3). The global range of particle size distributions in nesting substrates is greater than that found at Ascension Id. (Fig. 7).

DISCUSSION

Characteristics of sand and nesting behavior.—Turtles have apparent difficulty constructing suitable nests in beaches composed of coarse, dry sand. At Ascension Id. where the mean annual precipitation is only 194 mm (SD = 130) (Mortimer and Carr, 1987) and at Aldabra Atoll,

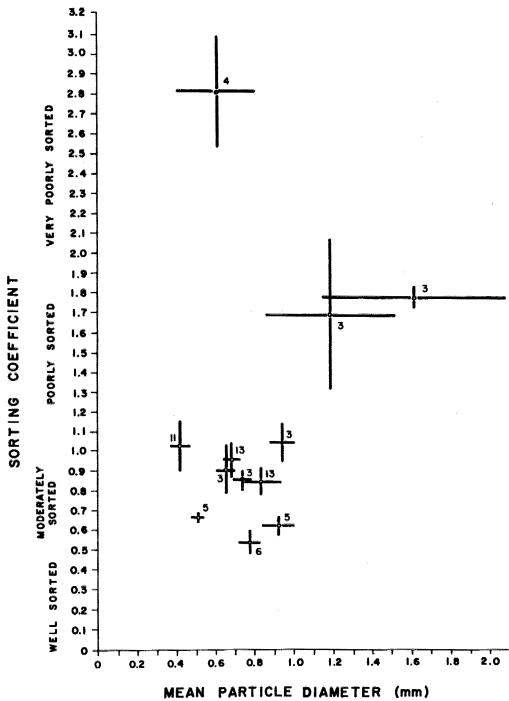


Fig. 3. Means and SD of the mean particle diameters (mm) and the sorting coefficients measured at 15 Ascension Id. beaches.

where it averages 1065 mm (SD = 286) (Stoddart, 1983; Seychelles Meteorological Station, pers. comm.) turtles construct multiple trial nest holes and re-emerge on as many as six successive nights ($\bar{x} = 1.4-3.2$) before finally laying eggs (Mortimer and Carr, 1987; Mortimer, 1988). The tendency to dig multiple nest holes and to re-emerge on successive nights also has been reported at the coarse-grained beaches of French Frigate Shoals (George Balazs, pers. comm.), on the Great Barrier Reef of Australia (Bustard and Tognetti, 1969; Bustard and Greenham, 1968) (Fig. 7), and in Sarawak, Malaysia (Hendrickson, 1958). In contrast, on the fine-grained nesting beach at Tortuguero, Costa Rica (Fig. 7) where an average of 5000–6000 mm of rain falls annually (Carr, 1979), turtles rarely emerge on more than one night, or construct more than one egg chamber before laying eggs (pers. observ.; Hirth and Samson, 1987).

Bustard and Tognetti (1969) showed that destruction of egg clutches increases with the density of turtles nesting on a beach. Green turtles which are iteroparous within a season, and tend

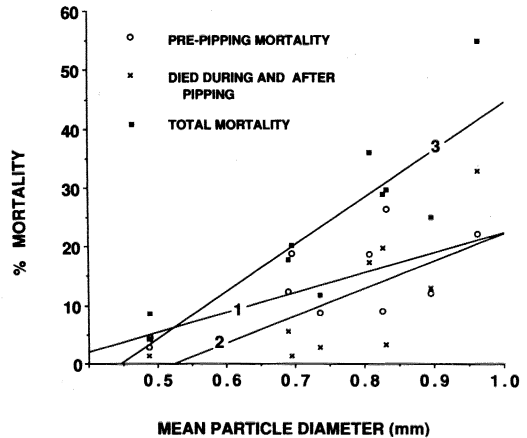


Fig. 4. Regressions of the relationship between mean particle diameter (mm) and the mean rates of mortality incurred before pipping (1) and during and after pipping (2) at 10 biogenic Ascension beaches. Total mortality (3) at each beach is also indicated. 1: $Y = -11.43 + 33.7X$, $r^2 = 0.48$, $P = 0.026$; 2: $Y = -24.32 + 46.54X$, $r^2 = 0.50$, $P = 0.022$; 3: $Y = -35.71 + 80.12X$, $r^2 = 0.74$, $P = 0.002$.

to make repeated emergences onto the same nesting beach (Mortimer, 1981) risk digging up their own egg clutches, especially when they dig multiple trial nest holes. Perhaps by nesting during the months of heaviest rainfall (Mortimer and Carr, 1987), Ascension turtles minimize such mortality.

Characteristics of sand and clutch viability at Ascension Id.—Temperature, water, and respiratory gases are considered the most important physical variables affecting the survival of reptilian embryos (Packard and Packard, 1988). Temperature was not measured during the present study, but it probably did not adversely affect survivorship. At the time of excavation, average depth to the bottom of the nest was 85 cm (SD = 18.8; range = 21–155; $n = 78$); the diameter of an egg clutch is about 24 cm (Ackerman, 1977). Carr and Hirth (1962) determined that below a depth of 30 cm, sand temperatures at South West Bay beach stayed between 27–29.5 C over a 61 d period during the nesting season. Thus, the eggs would not be exposed to temperatures likely to induce mortality—i.e., above 33 C or below 25 C (Miller, 1982). An exception might be Spire, a dark volcanic beach, at which the average nest depth was only 48 cm. The

TABLE 3. CHEMICAL CHARACTERISTICS OF GREEN TURTLE NESTING BEACHES IN THREE OCEANS.

| Beaches | Electrical conductivity (mmhos/cm) | % organic carbon | % calcium carbonate | Mineral composition | Color |
|--------------------------------------|------------------------------------|------------------------|------------------------|---|---|
| Atlantic Ocean | | | | | |
| Ascension Id. | | | | | |
| Biogenic beaches | 0.12–2.39 ^a | 0.11–0.22 ^a | 73.7–97.4 ^a | Calcite; quartz; volcanic fragments | 10YR 6/5; 10YR 7/2; 10YR 7/4; 10YR 7/5 |
| Volcanic beaches | 0.18–12.8 ^b | 0.07–0.14 ^b | 0.9–61.4 ^b | Quartz; volcanic fragments; assorted oxides; plagioclase; calcite | 5Y 4/2; 10YR 4/2; 10YR 5/4 |
| Tortuguero, Costa Rica | 0.14 | 0.05 | 2.5 | Quartz; volcanic glass; volcanic fragments; opaline; silica; plagioclase & assorted oxides; rare rhodochrosite; 4% iron | 5Y 3/2 |
| Surinam | — | 0.06 | 13.6 | Quartz; calcite | 5Y 6/4 |
| Pacific Ocean | | | | | |
| Penarik, Terengganu, Malaysia | 0.40 | 0.03 | 0.8 | Quartz | 10YR 7/5 |
| Heron Id., Australia | 0.16 | 0.40 | 95.2 | Calcite | 5GY 7/1 |
| Sand Id., Rose Atoll, American Samoa | — | 0.28 | 97.7 | Calcite | 5Y 9/1 |
| Hawaii | | | | | |
| Trig Id., French Frigate Shoals | 0.96 | 0.73 | 94.8 | Calcite | 10YR 6/3 |
| East Id., French Frigate Shoals | 5.89 | 2.40 | 79.6 | Calcite; seabird guano ^c | 10YR 6/3 |
| Tern Id., French Frigate Shoals | 0.25 | 0.27 | 97.3 | Calcite | 5Y 8/1 |
| S.E. Id., Pearl & Hermes Reef | — | 0.28 | 97.5 | Calcite | 5Y 9/1 |
| Polihoa Bch., Lanai Id. | 1.96 | 0.09 | 95.8 | Calcite | 10YR 5/5 |
| Indian Ocean | | | | | |
| Aldabra Atoll | 0.11–0.62 ^a | 0.08–0.16 ^a | 96.6–97.4 ^a | Calcite | 5Y 8/1; 5Y 7/1 |
| Hawkesbay-Sandspit Bch., Pakistan | 0.72 | 0.03 | 52.8 | Calcite; quartz | 10YR 6/4 |

^a Range measured among 10 beaches.^b Range measured among five beaches.^c Phosphate levels of 37,203 ppm recorded.^d Range measured among nine beaches.

TABLE 4. ESTIMATES OF MEANS AND RANGES (IN PARENTHESES) OF MATRIC POTENTIALS AND OSMOTIC POTENTIALS OF BEACH SUBSTRATES AT NEST LEVELS. Figures were calculated using field measurements of water content and electric conductivity, and water potential curves derived in the laboratory by the pressure plate method.

| Beach | ψ_m matric potential (-kPa) | ψ_o osmotic potential (-kPa) |
|----------------|--|---|
| Porpoise Pt. 1 | 4.06 (3.20-6.14) | 2.69 (1.00-6.74) |
| Long Beach | 2.88 (1.97-4.12) | 3.89 (1.10-17.65) |
| South West Bay | 5.61 (7.67-2.54) | 3.74 (0.84-14.16) |
| English Bay | 3.17 (1.45-5.31) | 2.35 (0.80-5.52) |
| Hannay | 6.27 (4.17-10.81) | 4.73 (2.01-10.71) |
| North East Bay | 13.12 (10.89-17.20) | 4.39 (1.58-17.83) |
| Pebble West | 20.73 | 17.68 (14.12-21.24) |
| Spire | 24.35 (4.42-188.38) | 42.41 (11.07-130.93) |

relationship between total air filled pore space and hatching success among the Ascension Id. beaches (Fig. 6), where the highest success rates were found in sands having the lowest air-filled pore space, suggests that neither would the diffusion rate of respiratory gases through the substrate be likely to impede hatching success.

Hydric conditions, however, might explain the relative rates of clutch mortality observed on Ascension Id. beaches where the highest mortality occurred on those beaches with the lowest substrate water potentials (Fig. 5). The fact that egg clutch survival at Ascension Id. was negatively correlated with measurements of electrical conductivity in the substrate, and positively correlated with nest depth at excavation also implies that water availability limits hatching and emergence success. If so, the lower limit of tolerance for green turtle embryos may be higher than that so far reported for other species of reptiles. Tolerance limits have been examined for relatively few species, however, and among them there is great variability. Eggs of the iguana *Conolophus* survive exposure to substrates at -7500 kPa ($T_a = 30$ C) (Tracy and Snell, 1985), whereas the flexible shelled eggs of some of the small lizards are more sensitive to desiccation; those of *Callisaurus draconoides*, for example, require substrates above -240 kPa (at $T_a = 35$ C) (M. Packard et al., 1980). Among turtles, the flexible shelled eggs of both *Chelydra serpentina* and *Chrysemys picta* experience increased mortality at water potentials below -500 kPa, while the embryos of turtles with rigid eggs will survive a wider range of hydric conditions (G. Packard et al., 1981).

Marine turtles produce larger egg clutches and deposit them deeper in the substrate than

any other turtles. Gas conductance of sea turtle egg shells is high as a compensation for conditions of hypoxia and hypercapnia within the egg chamber (Seymour and Ackerman, 1980). Eggs adapted to such conditions might be particularly sensitive to desiccation. Greater loss of water vapor might be expected from eggs buried in sands characterized by larger volumes of air-filled pore space, and in fact, there was a positive relationship between total air-filled pore space and clutch mortality at Ascension (Fig. 6). Ackerman (1977) predicted that coarse grained beach sand would be more conductive to gas. So, the negative correlation between mean particle diameter and clutch survival among the biogenic beaches at Ascension Id. might be related to the physiological stress of desiccation.

A possible second cause of mortality in the coarser grained biogenic sands would be sand cave-ins. Normally sea turtle hatchlings emerge from the nest as a group within an air chamber that they maintain as they move vertically from the nest to the surface of the sand (Carr and Hirth, 1961). Such chambers constructed in coarse sand may be structurally unsound and liable to collapse onto the hatchlings, making escape from the nest difficult (Mann, 1977). Mortality induced by cave-ins would impact the pipping and post-pipping stages. If, on the other hand, physiological stress from desiccation (or some other factor) is an important cause of death, mortality could occur at any stage (Miller et al., 1987). In the biogenic beaches of Ascension Id., the fact that the mortality rate prior to pipping and that which occurred during and after pipping were both positively correlated with the mean particle diameter of the sand (Fig. 4) implicates physiological stress as a mor-

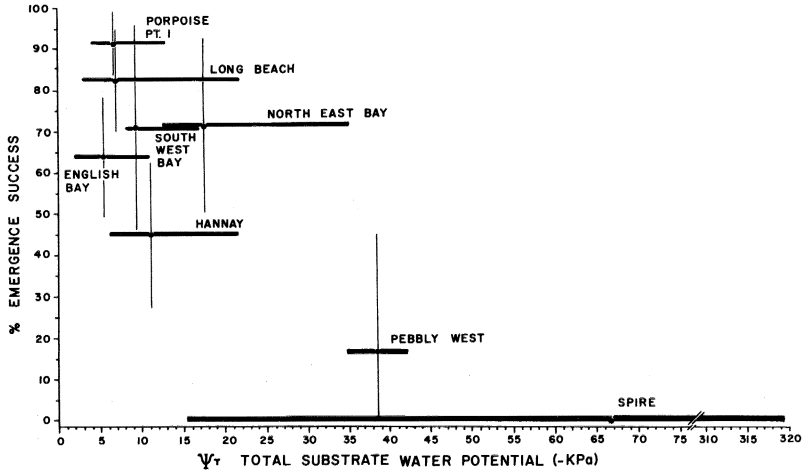


Fig. 5. Relationship between total substrate water potential and the mean percent emergence success of clutches at eight Ascension Id. beaches. Horizontal bars indicate the range of values for total water potential. Vertical bars indicate SD for survivorship. Mean values are indicated by a closed circle (●). The numbers of egg clutches sampled at each beach are the following: Porpoise Pt. 1, 4; Long Beach, 17; North East Bay, 13; South West Bay, 14; English Bay, 6; Hannay, 9; Pebbly West, 6; and Spire 7.

tality factor, but does not rule out sand cave-in as an additional cause of death.

Nest site selection.—Considering that the quality of beach sand can so strongly influence reproductive success, one would expect turtles to use sand texture as a criteria in nesting site selection. Data gathered at Ascension Id., however, suggest otherwise (Mortimer, 1982). There is no correlation between the average percent hatchling emergence at the Ascension Id. beaches and nesting density at those beaches—evidence that grain size is not of over-riding importance to a turtle in her choice of nesting beach. Turtles even nest in substrate that produces zero hatching success (Mortimer, 1982). When digging in coarse sand, turtles frequently abandon the construction of an egg chamber. According to Bustard and Greenham (1968), this is in response to either the collapse of an egg chamber or an obstruction to the digging action. Digging usually recommences after the turtle moves a few meters away. At both Ascension Id. and Aldabra Atoll, individuals may spend the entire night on one beach digging as many as 12 trial nest holes (Mortimer, 1981; Mortimer and Carr, 1987). Even after failing to nest, turtles commonly re-emerge onto the same section of beach on the following night. In fact, at Ascension Id., turtles usually show greater site fidelity after an aborted nesting at-

tempt than they do when re-emerging seven or more days later to lay a new clutch of eggs (Mortimer, 1981; Mortimer and Portier, 1989). Although such behavior may appear maladaptive, excessive density dependent mortality to egg clutches would surely occur if all the turtles searched for and laid their eggs at the few beaches most conducive to successful nesting.

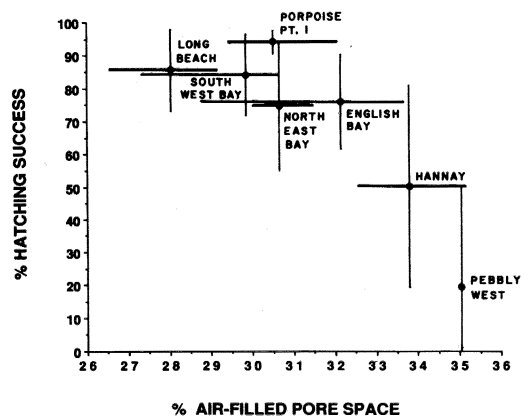


Fig. 6. Relationship between percent air-filled pore space in the substrate and percent hatching success. Horizontal bars indicate ranges for percent air-filled pore space. Vertical bars indicate SD for percent hatching success. Mean values are indicated by closed circles (●). The numbers of egg clutches sampled at each beach are indicated in Figure 5.

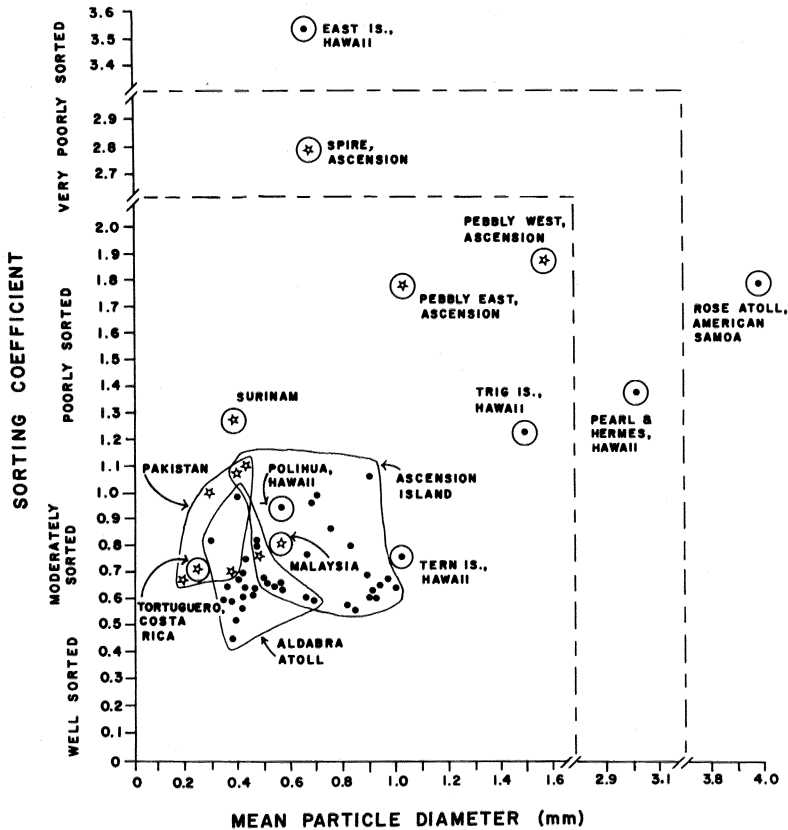


Fig. 7. Relationship between sorting coefficients and mean particle diameters (mm) at each of the 65 beaches examined. Biogenic beaches are indicated by closed circles (●) and volcanic or pyrogenic beaches by open stars.

Moreover, strong site fidelity probably ensures that the turtles do not stray from their tiny, isolated, mid-oceanic breeding grounds.

Green turtle beaches vary remarkably in terms of color, mineral composition and texture, ranging from the fine-grained, moderately well sorted, black volcanic sand at Tortuguero, to the coarse-grained, very poorly sorted, white, calcium carbonate sands found in the South Pacific (Fig. 7; Tables 2–3). Mainland beaches tend to be composed of volcanic or pyrogenic parent materials, while those on tropical islands are more often composed of calcium carbonate derived from crushed shells, corals and calcareous algae. Some sands within these groups possess unusual properties that may or may not be of biological significance to the turtles. Tortuguero sand has a high iron content, for example; whereas that of East Id., French Frigate Shoals is composed of approx. 20% sea-bird

guano (Balazs, 1980) (Table 3). The beaches do share some similarities, however. Most of the major nesting beaches, with the exception of some in Hawaii and Rose Atoll, are composed of moderately sorted sand with mean particle diameters ranging from 0.2–1.0 mm. In all cases, the percent organic carbon is low, as is the salt content at nest level (based on the values for electrical conductivity). In terms of particle shape, the sphericity values are high, ranging from 0.75–0.80, except at Rose Atoll and Pearl and Hermes Reef where the substrate is composed of elongated particles of coral. The calcium carbonate beaches of Ascension Id. and Aldabra Atoll comprise the roundest (i.e., smoothest) particles. Those of the pyrogenic substrates tend to be more angular.

The range of sand textures utilized worldwide (Fig. 7) is greater than one might expect, considering that a limited range of textures at

Ascension Id. produced the best hatching success; but, moisture availability and conductivity to respiratory gases are not simply functions of sorting coefficient and mean particle diameter. In fact, complex interactions between most of the sand features examined in the present study determine the water potential and diffusion capacity of a substrate. Both these properties are strongly influenced by pore size and shape, which in turn, are determined by particle size and shape. (In general, well sorted, coarse grained substrates composed of spherical particles are the most porous.) The effect of pore size and shape, however, can be moderated by other factors. Saline substrates and those composed of hydrophilic minerals, for example, can retain water in the pores, thereby inhibiting gas diffusion and even diminishing water availability. Excessive air-filled pore space, on the other hand, can also lead to desiccation. Precipitation and characteristics of the water table play an important role. Annual precipitation at Ascension Id., for example, is so sparse ($\bar{x} < 194$ mm) (Mortimer and Carr, 1987), mean relative humidity at sea level so low (64.8%) (Duffey, 1964), and the nest depth so great ($\bar{x} = 85$ cm), that rainfall probably seldom percolates to nest level in the manner described by G. Packard et al. (1985) for snapping turtles (*Chelydra serpentina*). At Ascension Id., substrate moisture at nest depth more likely originates as water vapor moving upwards from the water table by the process of "internal dew formation" (De Jong, 1979; Johannes and Rimmer, 1984). Hence, the positive correlation between nest depth and clutch survival. In Georgia (Ragotzkie, 1959; Kraemer and Bell, 1980) and at Tortuguero, Costa Rica (K. Horikoshi, pers. comm.), on the other hand, heavy precipitation commonly raises the water table and saturates the sand to such an extent that large scale suffocation of eggs occurs.

The reproductive strategy of the Ascension Id. population seems to have evolved in response to a complex interplay between edaphic conditions on the nesting beach and biotic factors. At Ascension Id., beach erosion and inundation by rollers cause high mortality, but hatchlings and eggs also enjoy extremely low levels of natural terrestrial and offshore predation (Mortimer, 1981). Because the Ascension Id. sand is coarse and dry, the eggs are subjected to desiccation, cave-ins and a high risk of being exhumed by females digging multiple

nest holes. On the other hand, coarse-grained sand may have a greater diffusion capacity and thus be able to support larger clutch biomass (Ackerman, 1975). At Ascension, both the average clutch size ($\bar{x} = 120.9$) (Mortimer and Carr, 1987) and the average hatchling weight ($\bar{x} = 30$ g) (Ackerman, 1975) are greater than at the fine-grained Tortuguero nesting beach ($\bar{x} = 112.2$ eggs; $\bar{x} = 22$ g) (Bjorndal, 1980; Ackerman, 1975).

The highest nesting density at Ascension Id. occurs on beaches with open offshore approaches and foreshores relatively free of rock clutter that are not illuminated by artificial light (Mortimer, 1982). Turtles may also prefer beaches with high sand platforms (Kraemer and Bell, 1980; Johannes and Rimmer, 1984). To this extent, they may actively "choose" a nesting beach. But overall, the distribution of turtle nesting worldwide is probably not determined simply by the physiognomy of the nesting beach, but rather by a suite of selective pressures to which the turtles respond. These may include temperature, moisture availability and gas conductivity in the beach substrate, erosion or inundation by fresh or salt water, and terrestrial and offshore predation. Access to offshore currents of the proper temperature that would carry hatchlings to appropriate foraging habitat may be just as important. Adult sea turtles are generally believed to return to their natal beach to breed. The occasional breakdown in site-fidelity would permit colonization of new nesting grounds (Carr and Carr, 1972), but new rookeries could only be established when conditions allow sufficient numbers of both sexes to survive to adulthood and return to breed in subsequent seasons.

Laboratory work is clearly needed to define the hydric requirements of marine turtle eggs and to determine how different substrates affect moisture availability and exchange of respiratory gases. From a practical standpoint, we could then better identify which are the most important nesting beaches to save from coastal development, and we could conduct beach renourishment at turtle rookeries in a manner compatible with the biological needs of the animals. Too often such projects, which are undertaken to replace sand lost to erosion, are carried out with little regard for, or knowledge of, what impact the new, and often completely foreign, substrates will have on turtle reproduction (Raymond, 1984). Optimal particle size

distribution probably varies from one locality to another depending on patterns of precipitation, and on mineral composition and shape of the particles composing the substrate. Nevertheless, my study shows that most of the world's major green turtle nesting beaches are characterized by moderately sorted sand with mean particle diameters ranging from 0.2–1.0 mm, by particles having high sphericity values, and by low levels of organic carbon. My findings also suggest that neither poorly sorted substrates containing a large silt/clay component, nor those that are highly saline are likely to accommodate successful incubation. Unfortunately, the fill used for many beach renourishment projects comprises poorly sorted, fine grained sediment dredged from the nearshore sea bed. In general, a better understanding of the requirements of turtle embryos will enable us to determine what types of environmental disturbance to avoid in order to protect features critical to the reproductive success of nesting turtles.

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