

# The Effect of Beach Nourishment with Aragonite Versus Silicate Sand on Beach Temperature and Loggerhead Sea Turtle Nesting Success

Sarah L. Milton,<sup>†</sup> Alexis A. Schulman<sup>‡</sup> and Peter L. Lutz<sup>†</sup>

<sup>†</sup>Department of Biological Sciences  
Florida Atlantic University  
Boca Raton, FL 33431, U.S.A.

<sup>‡</sup>Marine Biology and Fisheries  
Rosenstiel School of Marine and Atmospheric Science  
University of Miami  
4600 Rickenbacker Causeway  
Miami, FL 33149, U.S.A.

## ABSTRACT



MILTON, S.L.; SCHULMAN, A.A., and LUTZ, P.L., 1997. The Effect of Beach Nourishment with Aragonite Versus Silicate Sand on Beach Temperature and Loggerhead Sea Turtle Nesting Success. *Journal of Coastal Research*, 13(3), 904-915. Fort Lauderdale (Florida), ISSN 0749-0208.

Heavy erosion and dwindling offshore sand sources have resulted in increased pressure to find alternate sand sources for Florida beach renourishment. One potential economically viable source is oolitic aragonite commercially mined in the Bahamas, however the environmental impacts of aragonite sand on Florida beaches has not been determined. This study was undertaken to examine the effects of oolitic aragonite on one organism, the threatened loggerhead sea turtle (*Caretta caretta*), which nests in great numbers on beaches of the southeastern United States. Temperature, grain size distribution, and hydric potential were measured, and the effects of these physical factors on loggerhead nest hatching and emergence success were compared for nests buried in aragonite versus native Florida silicate sand. There were no significant differences in grain size distribution or water potential between nests in each sand type; however temperature regimes in the two sands differed significantly. While both sand types had similarly high hatching and emergence success rates of 86% to 97%, the study raises important questions concerning the possible effects of observed nest temperature differences on hatchling sex ratios.

**ADDITIONAL INDEX WORDS:** Beach renourishment, loggerhead sea turtle, hatchling sex ratio, incubation period, aragonite.

## INTRODUCTION

For many coastal states, beach preservation in the face of severe erosion has a high commercial value in order to protect coastal residences and generate tourist dollars. Florida, for example, attracts about 40 million tourists per year, adding in 1992 alone 26.9 billion dollars to the state's gross regional product (STRONGE, 1994). Beach renourishment on Miami Beach alone helped increase beach attendance from 8 million people in 1978 to 21 million in 1983 (WIEGEL, 1992). Due to extensive erosion, however, up to one-third of Florida beaches are in critical condition (OLSEN and BODGE, 1991). In order to combat this erosion, extensive beach renourishment projects have been undertaken in coastal Florida communities in which sand is "borrowed" from offshore sites and placed on the eroded beach. But suitable offshore sources are becoming scarce and pressure is building to find suitable alternative solutions. One of the most attractive sources from an economic point of view is to utilize the vast aragonite sand sources of the Bahamas Banks (OLSEN and BODGE, 1991; SEALEY, 1994). The aragonite deposit around Ocean Cay, Bahamas (just south of the Bimini Islands), is estimated to contain 1

billion tonnes alone, and is located only 50-60 miles from Miami, Florida, making it an attractive source of fill material. Bahamian aragonite sand is composed of calcium carbonate (97.0%, (SEALEY, 1994)) crystallized through natural physicochemical processes into smooth ellipsoidal or spherical shapes (oolites). Most beaches in southeastern Florida, however, are composed of quartz sand and carbonate shell, or the calcitic carbonate sand present around Biscayne Bay (OLSEN and BODGE, 1991). Before any large scale use of oolitic aragonite is permitted it must first be established that any significant physical and chemical differences will cause no environmental harm on Florida beaches.

Questions in particular have been raised about the suitability of aragonite sand as a nesting substrate for sea turtles. Of the four species of sea turtle which nest in southeast Florida, the green (*Chelonia mydas*), leatherback (*Dermochelys coriacea*), and hawksbill turtle (*Eretmochelys imbricata*) are listed as endangered, while the loggerhead sea turtle (*Caretta caretta*) is considered a threatened species. Moreover, the southeastern shores of the United States serve as the nesting grounds for the second largest aggregation of loggerhead turtles in the world, accounting for approximately 30% of world population nesting (NATIONAL RESOURCE COUNCIL, 1990). Deleterious changes to their nesting habitat in the

United States could thus have serious consequences for the survival of the species.

While the addition of sand to a beach undoubtedly can benefit sea turtles by creating nesting habitat, questions have been raised concerning both the direct and indirect effects of beach renourishment on nesting turtles (RAYMOND, 1984a). Direct effects such as buried nests can be avoided by careful monitoring and/or by renourishing beaches outside of the turtle nesting season, however beach nourishment may indirectly affect female nest site selection, clutch viability and incubation times, and hatchling sex ratios (PACKARD *et al.*, 1987; MROSOVSKY and PIEAU, 1991). The main concern when utilizing a different sand type is that the physical properties of a sand to a large extent determine the composition of the nest environment. The sand surrounding a turtle clutch acts as a barrier through which water vapor, oxygen, carbon dioxide and heat must diffuse; different sands can thus produce different nest environments.

The purpose of this study was to examine the suitability of oolitic aragonite as a nesting substrate for sea turtles in Florida. The first large scale renourishment project utilizing aragonite, on Fisher Island, Dade County, Florida, provided an ideal opportunity to examine the impact of aragonite on nesting success utilizing a controlled experimental design. In the spring of 1991, 60,000 cubic yards of aragonite were spread along 2,030 linear feet of the eastern shoreline of Fisher Island. Hatcheries were constructed containing aragonite or the original Fisher Island sand, permitting us to examine the two sand types for differences in temperature, hydric potential, and grain size distribution, and to relate physical characteristics to differences in loggerhead turtle incubation period, nesting and hatching success, and hatchling fitness.

## MATERIALS AND METHODS

In 1991, two 12 by 12 meter, 60 cm (24 inch) deep hatcheries were excavated by Fisher Island Developers, Inc. approximately 23 m from the shoreline on the eastern side of Fisher Island between Government and Norris Cuts. Hatcheries were surrounded by 1 m high heavy nylon mesh to provide security while minimizing shading. The south hatchery was filled with washed oolitic aragonite imported from Ocean Cay, Bahamas by Marcona Ocean Industries. The north hatchery was filled with silicate sand from the original Fisher Island Beach; the hatcheries were separated by 12 m of renourished beach. As Fisher Island is a private beach, space for replicate hatcheries was not provided; replicate testing following the original relocation was attempted in 1992 (August), but these nests were destroyed by Hurricane Andrew (MILTON *et al.*, 1994).

Ten newly laid loggerhead nests were collected from Juno Beach, Jupiter, Florida and relocated within 12 hrs to the hatcheries. Nests were collected the same night to eliminate differences such as variable weather conditions; nest relocation occurred during peak nesting. Clutches averaging 113 eggs were placed 8–11 m apart (to minimize nest-nest interactions, ACKERMAN, *Personal Communication*) in the center and 1 m in from the 4 corners of each hatchery (to minimize edge effects). Nest cavities were flask-shaped, 46 cm (18 inch-

es) deep and 15–23 cm (6–9 inches) in diameter. The top of each clutch was 23 cm below the beach surface.

Nest temperatures were recorded hourly using copper-constantin thermocouples placed in each nest at the bottom, center (30 cm) and top (23 cm depth) of each clutch. One dummy nest (sand only) in each sand type was constructed by placing thermocouples at identical depths approximately 4 m from the nearest nest.

Grain size and water potential measurements were performed on each sand type by R. Ackerman, Iowa State University, College of Agriculture, according to his previously published methods (ACKERMAN *et al.*, 1991). SEM micrographs were prepared by M. Lutz, University of Miami, RSMAS Department of Marine Geology. Samples were mounted on aluminum studs and sputter coated with palladium. Photomicrographs were produced on an ISI-TS130 dual stage scanning electron microscope at 21 kv to a resolution of  $\times 96$ .

As each nest hatched, a random subsample of 20 hatchlings was weighed on a digital scale; straight line carapace lengths and widths were measured with Vernier calipers. The entire clutch was counted, and 48 hr after mass emergence the nest cavities excavated to count eggshells, infertile and unhatched eggs, and dead or premature hatchlings. Transplanted hatchlings were released at Juno Beach on the night of emergence.

Incubation periods were measured as extending from the date each nest was laid to its night of mass emergence.

Most data were collected in 1992 following a preliminary study in 1991; additional temperature and hatchling data were collected in 1993.

Statistical analysis was done using the SAS Institute program JMP. Analysis of variance (ANOVA) was done to determine significant differences between control and nest data at 23, 30, and 46 cm and between sand types at all three depths. Comparisons were made utilizing a single time point (1200 hr) over six (6) days (2nd week of data shown, below) to eliminate variability due to diurnal and seasonal fluctuations. Student's T-test was used to compare incubation times and hatchling sizes.  $P < 0.05$  was considered significant.

## RESULTS

### Temperature

The most significant result of this study with implications for sea turtle reproductive success was that the aragonite sand was consistently significantly cooler than the native Florida (silicate) sand (Figure 1). This trend was evident at all three sand depths and remained despite diurnal fluctuations in dummy and turtle nests, and despite nest warming due to metabolic heat production by the developing embryos.

### Control Temperatures

Sand temperatures under field conditions were neither stable nor uniform, but showed clear diurnal cycles throughout the incubation period in both silicate and aragonite sands, at all three depths (Figure 2). These diurnal fluctuations were larger in the native silicate-based sand than in aragonite, and in both sands decreased in amplitude as depth increased.

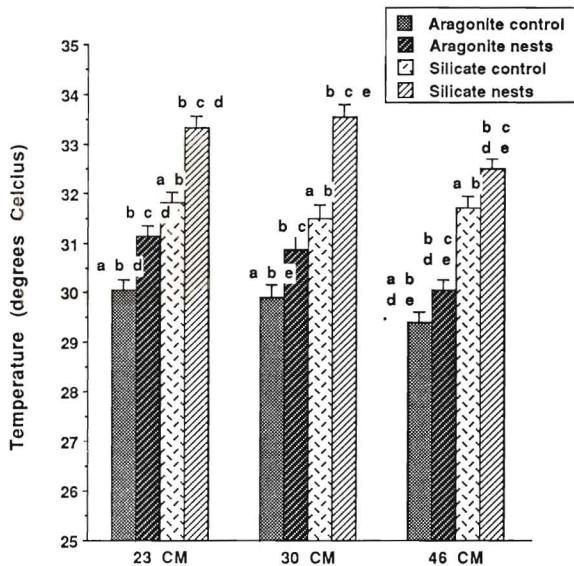


Figure 1. Fourteen day mean temperatures (with SEM) of control sand and nests in silicate and aragonite sand at three depths: 46, 30, and 23 cm below the beach surface. Temperatures are means of hourly readings over a 2-week period, June 29-July 13, 1992. Controls: 1 probe at each depth/sand type. Nests: N = 5 probes at each depth per sand type. Key to statistics as follows: a = controls significantly different (s.d., p < .05) between sand types at same depth. b = controls s.d. from nests, same sand type, same depth. c = nests s.d. between sands at same depth. d = 23 cm depth s.d. from 30 and/or 46 cm depth, same category. e = 30 cm is s.d. from 46 cm depth, same category.

Over the two week period shown here (only 2 weeks of control data are shown to simplify presentation while still demonstrating relevant trends), average daily temperature changes ranged from  $0.41 \pm 0.03$  °C at 46 cm to  $1.85 \pm 0.09$  °C at 23 cm depth in aragonite. Daily temperature fluctuations in Florida sand were approximately twice as large, ranging from an average of  $0.90 \pm 0.05$  °C at 46 cm depth to  $2.67 \pm 0.12$  °C at 23 cm. Peak temperatures at 23 cm depth in aragonite during this period were significantly cooler than peak temperatures at the same depth in silicate sand; aragonite sand temperatures at 23 cm were closer instead to peak temperatures at 46 cm depth in the Florida silicate (Figure 2).

These diurnal temperature changes were staggered at each depth, as heat diffused between the surface and subsurface (MALONEY *et al.*, 1990). In each sand type, peak temperatures at 30 cm depth were reached approximately 1–2 hr after peak temperatures at 23 cm depth, with peak temperatures at 46 cm depth following one to several hours later. Maximum and minimum temperatures even at 23 cm depth did not correspond to maximum and minimum daily environmental (air) temperatures, but were delayed by as much as 7 hrs (Figure 3). The delays in reaching maximum and minimum temperatures at each depth were greater in aragonite than in silicate sand. Temperature maxima at 46 cm depth in aragonite, in fact, were reached only 2–4 hours prior to temperature minima at 23 cm depth (Figure 2), which together with small-

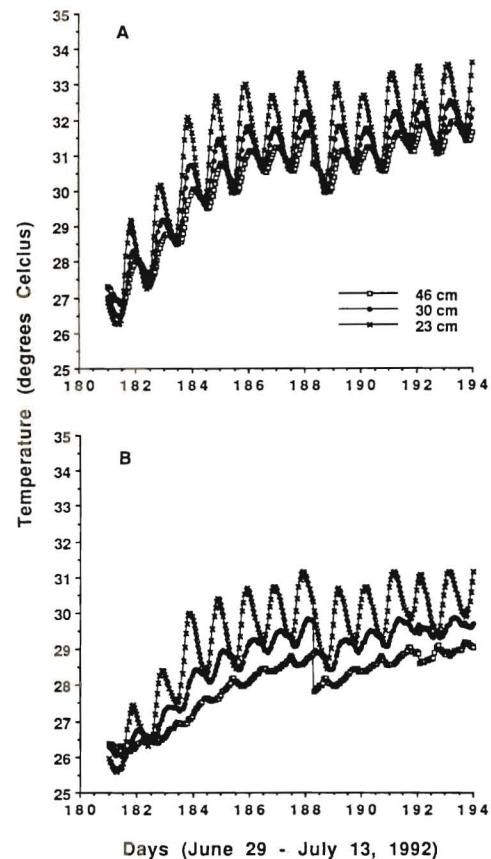


Figure 2. Diurnal temperature cycles at three depths (46 cm, 30 cm, and 23 cm from the beach surface) in native Florida silicate (A) and oolitic aragonite (B) sand over a two-week period, Fisher Island, Dade County, Florida. Temperatures were recorded hourly.

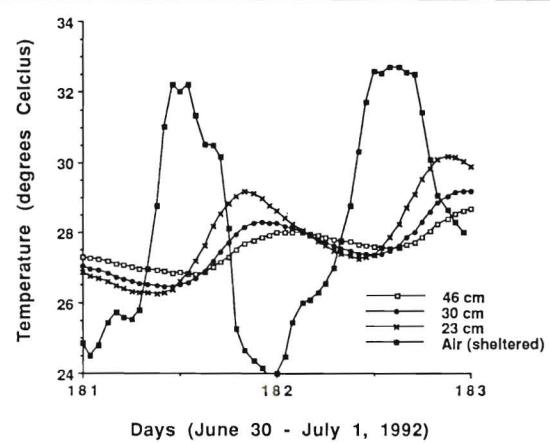


Figure 3. Hourly temperatures at three depths in silicate sand versus environmental (air) temperature over one 48-hr period. Daily air temperature extremes are increasingly buffered at greater depths.

Table 1. Four-day average sand temperatures at 30 cm depth. (Final week, middle-third of incubation period) \* = means s.d. at  $p < 0.05$ .

Period	1991		1992		
	Aragonite	Silica	Aragonite	Silica	
1	Mean (S.E.)	29.6 (0.04)	31.6 (0.11)	26.4* (0.13)	27.3* (0.14)
	Minimum	29.1	29.3	21.8	22.8
	Maximum	30.4	32.8	28.0	29.5
	N	77	77	87	87
	Actual dates	Jul 23–Jul 26	Jul 23–Jul 26	June 24–June 27	June 24–June 27
2	Mean (S.E.)	29.5 (0.04)	30.2 (0.10)	26.5 (0.03)	27.6 (0.06)
	Minimum	28.7	27.9	26.0	26.5
	Maximum	30.2	32.7	27.2	29.2
	N	95	95	96	96
	Actual dates	Jul 27–Jul 30	Jul 27–Jul 30	June 28–Jul 1	June 28–Jul 1

er temperature fluctuations at depth in aragonite vs. silica, indicates a lower thermal conductivity for aragonite.

A seasonal temperature increase as summer progressed was also evident in both sand types, as was noted by MALONEY *et al.* (1990); this increase was superimposed over daily temperature fluctuations (Figure 2). Between June 29 and July 12, 1992, the average daily sand temperature at 30 cm depth increased from a mean of 26.5 °C in aragonite (Range 26.2°–26.8 °C) and 27.3 °C in silica (Range 26.9°–28.0 °C) to 30.0 °C (Range 26.5°–30.4 °C) and 32.5 °C (Range 28.0°–33.4 °C), respectively.

Of greatest importance, however, was the discovery that aragonite sand was consistently significantly cooler over the course of this study than Florida silicate sand (Figures 1 and 2). This difference at any given point in time ranged from less than one degree Celsius at all three depths early in the nesting season to as high as 3.4 °C (23 cm depth) by mid-July. These temperature differences were greater at depth; over the two week period presented in Figure 2, the temperature difference between the sand types at each depth averaged  $1.81 \pm 0.03$  °C at 23 cm,  $2.01 \pm 1.04$  °C at 30 cm, and  $2.36 \pm 0.04$  °C at 46 cm depth. The temperature differences were greatest at each depth during the warmest part of the diurnal cycle at that depth (approximately 2 p.m. to 4 p.m.); differences were smallest at approximately 6 a.m. to 8 a.m. Such differences could impact hatchling development and hatchling sex ratios (PACKARD *et al.*, 1987; MROSOVSKY and PIEAU, 1991).

Table 1 shows the temperature differences between silicate and aragonite sand over a one week period during the middle third of the incubation period. The middle third of the incubation period has been determined to be most significant in the differentiation of hatchling sex ratios (YNTEMA and MROSOVSKY, 1982). While minimum temperatures in both sand types were similar ( $< 1$  °C) over 4 day increments, both mean and maximum temperatures at 30 cm depth (dummy nest center) are consistently higher in silica than in aragonite. While between-year temperature comparisons are not valid due to the dependence of sand temperature on environmental temperatures, it is significant that sand temperatures early in the nesting season (May and June) are significantly cooler than sand temperatures later in the year (July), seen in Table

1 as the temperature differential between sand types in 1991 (July data) verses 1992 (June data). Mean temperatures at 30 cm depth in both sand types in June (1992) were well below the 29.1 °C pivotal point for sex determination in *C. caretta* (YNTEMA and MROSOVSKY, 1982), and in fact are below the temperature (28 °C) which should produce all male hatchlings. Temperatures at greater depths and earlier in the season (but still within the critical developmental stage for sex-determination) were even lower (see Table 3, below). In aragonite, mean and minimum temperatures at 30 cm depth (nest centers) were still close to or below the pivotal temperature for sex determination even in July (1991 data).

### Nest Temperatures

Temperature trends in nests in aragonite and silicate sand were similar to controls, with several significant differences. While diurnal temperature fluctuations were still evident, the amplitude of each daily oscillation was smaller than at the corresponding depth in dummy nests (Figure 4). Between June 29 and July 13, 1992, mean daily temperatures changes ranged from  $0.36 \pm 0.03$  degrees Celsius in aragonite sand (at 46 cm) to  $1.47 \pm 0.11$  degrees at 23 cm (top of nests). In Florida sand, diurnal fluctuations averaged  $0.48 \pm 0.06$  degrees Celsius at 46 cm and  $1.56 \pm 0.11$  degrees at 23 cm depth. The amplitude of daily changes was thus 12–21% lower in nests buried in aragonite than for controls at the same depths, while in silicate sand daily fluctuations were 42–47% lower than in controls. Diurnal fluctuations in nests, as in controls, were staggered, with shallower layers warming and cooling more quickly than each succeeding depth.

While seasonal warming of the beach was also evident in nests incubating in both sand types, this temperature increase was overshadowed during the final third of the incubation period by metabolic warming of the nest. From June 29–July 13, 1992, the slopes of the temperature increases between nest and control data during the first 5 days (at 30 cm) were similar for both sand types (Table 2), however, control temperatures level off (slopes decrease significantly) during the second week (as seasonal temperature increases slow), while nest temperatures continue to increase at approximately twice the mean rate of dummy nest temperatures (Ta-

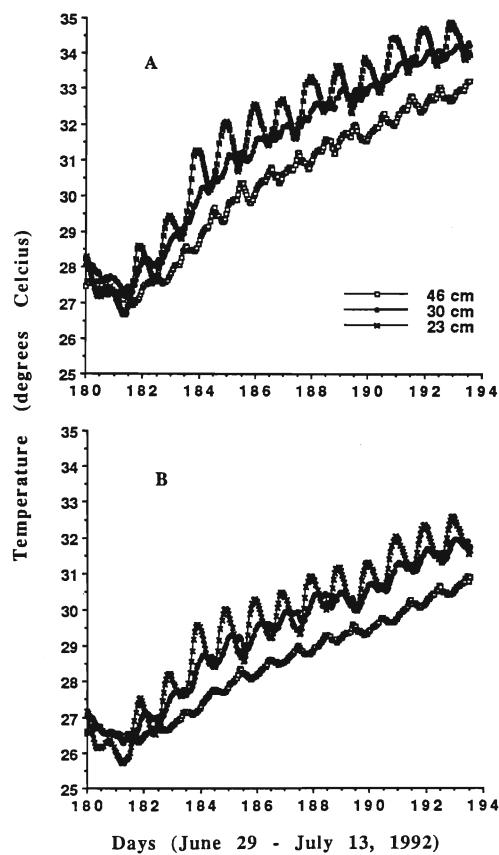


Figure 4. Diurnal temperature cycles at three depths (46 cm, 30 cm, and 23 cm from the beach surface) in nests buried in native Florida silicate (A) and oolitic aragonite (B) sand over a two-week period, Fisher Island, Dade County, Florida. Temperatures were recorded hourly.

ble 2, Figures 2 and 5). It should also be noted that silica sand is once again seen to warm significantly more quickly than aragonite as summer temperatures rise; this difference is only partially obviated by metabolic heat production later in the incubation period.

Figure 5 shows this increase in nest temperature versus sand alone at the same depth (only nest centers are shown for clarity). While both sand types show similar temperatures at 30 cm depth prior to seasonal warming (approx. 1 °C difference), in silica sand, dummy and actual nest temperatures increase more rapidly than in aragonite, so that by the second period shown the temperature difference between the sand types is approximately 3 °C. In both sands nest temperatures continue to increase more rapidly than controls, indicating that the additional heat provided by embryonic metabolism is raising nest temperatures beyond environmental influences alone. Metabolic heat production, however, is approximately equal in nests buried in each sand, and thus does not erase the temperature differential imposed by environmental forces. Only by day 188 (approx. 3 weeks prior to hatch) is metabolic heat production in aragonite nests sufficient to raise mean temperatures at the center of the nest above the pivotal temperature for loggerhead sea turtle sex determina-

Table 2. Change in nest warming rates vs. warming of sand alone over a two-week period (June 29–July 13, 1992).

Sand Type	Days	Slope*	R <sup>2</sup>
Aragonite	181–185	0.64 <sup>a,f</sup>	0.900
Control	188–194	0.16 <sup>a,f</sup>	0.867
Silicate	181–185	0.97 <sup>a,g</sup>	0.906
Control	188–194	0.26 <sup>e,g</sup>	0.499
Aragonite	182–185	0.65 <sup>b,h</sup>	0.946
Nests	188–193	0.34 <sup>c,d,h</sup>	0.982
Silica	182–185	0.88 <sup>b,i</sup>	0.943
Nests	188–193	0.38 <sup>e,i</sup>	0.969

\* Pairs of letters indicate slopes that are significantly different from each other, p < 0.05.

nation. Average nest temperatures at 46 cm (nest bottom) do not increase beyond the pivotal temperature for several days afterwards, well after the critical stage for sex determination.

Whether nest temperatures rise above the pivotal temperatures for sex determination during the critical period is of course dependent on when each nest is laid, at what depth, and on overall environmental temperatures (Table 3). During the final week of the middle third of incubation in 1992 (June), average and minimum temperatures in both sand types were below the 29.1 °C pivotal temperature (Table 4). Over the same relative period of incubation in 1991, however (July), nest temperatures were at or above the pivotal temperature, with silicate sand 1–2 degrees higher than aragonite nests (30 cm depth), reflecting both overall warmer summer temperatures as well as the more rapid warming of silicate sand as the summer progressed. Minimum and maximum as well as mean temperatures are provided because it

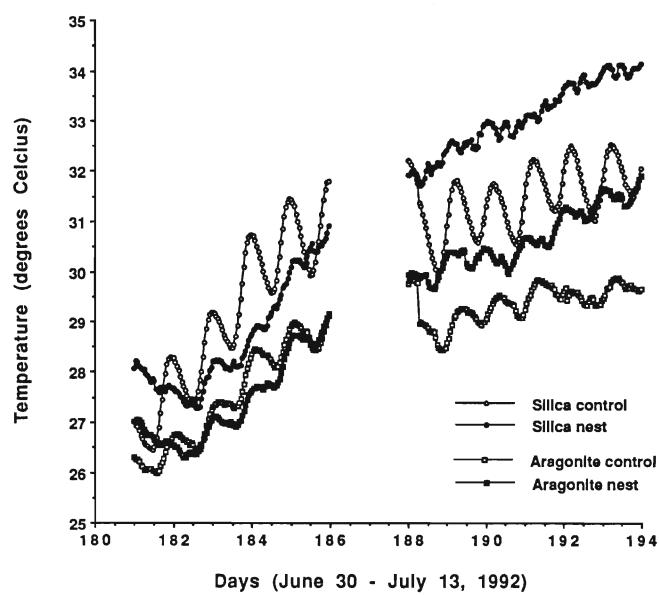


Figure 5. Mean control and nest temperatures at 30 cm depth in silicate and aragonite sand over two, 5-day segments. Metabolic heat is insufficient to raise nest temperatures beyond controls until approximately 2 weeks prior to hatching. N = 5 for each nest mean.

Table 3. Mean control and nest temperatures in aragonite and silicate sand over a two week period: June 30–July 13, 1992 (Mean  $\pm$  S.E., N = 168, \* = means s.d. at  $p < 0.05$ ).

Depth	Week	Control		Nests	
		Aragonite	Silica	Aragonite	Silica
Bottom (46 cm)	1	27.5 (0.07)	29.5 (0.11)	27.6 (0.03)	29.1 (0.05)
	2	28.6* (0.17)	32.1* (0.04)	29.8* (0.09)	32.2* (0.06)
Center (30 cm)	1	28.0 (0.09)	29.7 (0.13)	26.8* (0.05)	30.0* (0.08)
	2	29.3* (0.16)	32.3* (0.05)	30.8* (0.09)	33.4* (0.06)
Top (23 cm)	1	28.7 (0.12)	30.3 (0.15)	28.6 (0.05)	30.4 (0.08)
	2	30.8 (0.05)	33.0 (0.07)	31.3* (0.07)	33.8* (0.06)

is yet unknown what temperature regime induces temperature dependent sex-determination. For example, mean temperatures in aragonite and silicate are not significantly different during the second four-day period shown in 1991, while both minimum and maximum temperatures are approximately one degree warmer in Florida sand compared to Bahamian. It has not yet been demonstrated if mean, maximum, or minimum temperatures to which eggs are exposed determines hatchling sex, or if a minimum amount of time at a particular temperature is required.

This study thus showed that the thermal capacity and heat output of the nest egg mass not only increases nest temperature above environmental (sand) values, but also serves to buffer temperature changes. While sand alone greatly buffers the extreme diurnal temperature fluctuations which occur at the beach surface, daily oscillations are compressed further yet in nests at the same depth. Thus, while describing the thermal régime at various depths on a beach may provide some indication of nest temperatures, sand temperatures alone do not present a complete picture of the nest thermal environment (Figure 6).

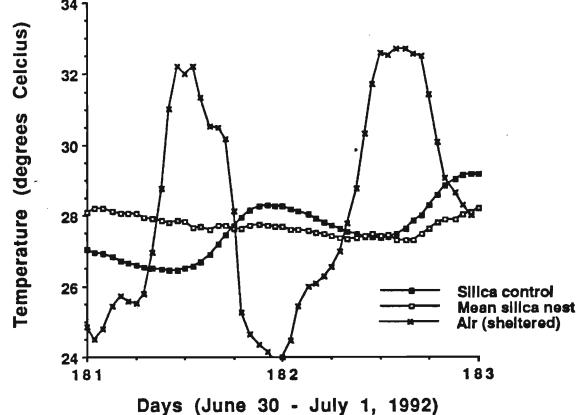


Figure 6. Mean nest temperature (30 cm) versus control (30 cm) and environmental (air) temperatures over a 48-hr period. Nest egg mass buffers temperature changes more than sand alone.

### Grain Size Distribution and Water Potential

Grain size distribution of the two sands was similar. Particle sizes ranged from 0.106 mm in diameter to more than 2.0 mm, with the native Florida sand having a slightly higher percentage of larger diameter sand (silica: 21%  $>$  2 mm vs. 9%  $>$  2 mm in aragonite).

Sand grain shape, however, which may affect packing and thus water potential, gas exchange, and nest integrity, was quite different. While silica sand is rough edged and angular, photomicrographs of aragonite clearly show its characteristic ovoid particles (Figures 7 and 8).

Despite shape and temperature differences, however, water potential was nearly identical in the two sand types, ranging from zero to +40 over a water content range of 0.05 g/g to 0.45 g/g (one measurement only, May, 1991). Both sands have higher potentials at the dry end than sands from other Florida locations (ACKERMAN, *personal communication*, 1991).

Table 4. Mean nest temperatures in aragonite and silicate sand during the final week (two 4-day periods) of the middle third of incubation, 1991 and 1992. \* = means s.d. at  $p < 0.05$ .

Period	1991			1992	
		Aragonite	Silica	Aragonite	Silica
1	Mean	29.2	31.3	26.7	27.9
	(S.E.)	(0.02)	(0.05)	(0.04)	(0.06)
	Minimum	28.9	30.5	24.9	25.1
	Maximum	29.6	32.2	28.1	29.7
	N	390	390	435	348
	Actual dates	Jul 23–Jul 26	Jul 23–Jul 26	June 24–June 27	June 24–June 27
2	Mean	29.3	29.8	26.8*	27.9*
	(S.E.)	(0.05)	(0.04)	(0.02)	(0.04)
	Minimum	28.9	29.7	26.3	27.3
	Maximum	29.6	30.9	27.6	28.7
	N	390	480	480	480
	Actual dates	Jul 27–Jul 30	Jul 27–Jul 30	June 28–Jul 1	June 28–Jul 1

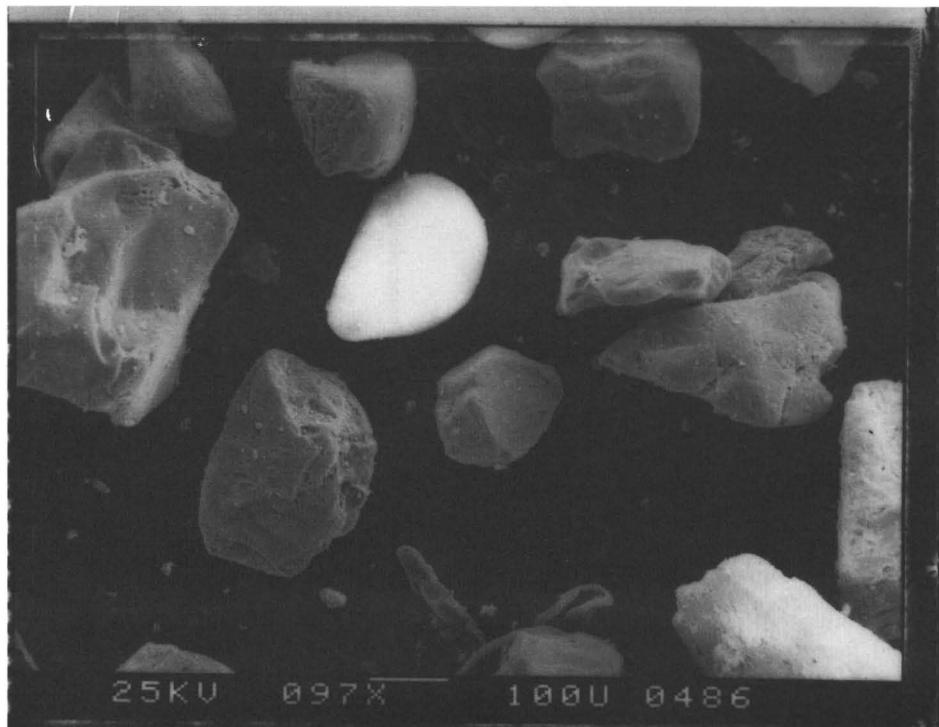


Figure 7. Scanning electron photomicrograph of aragonite sand particles from the Bahamian aragonite sand hatchery, Fisher Island, Dade County, Florida.

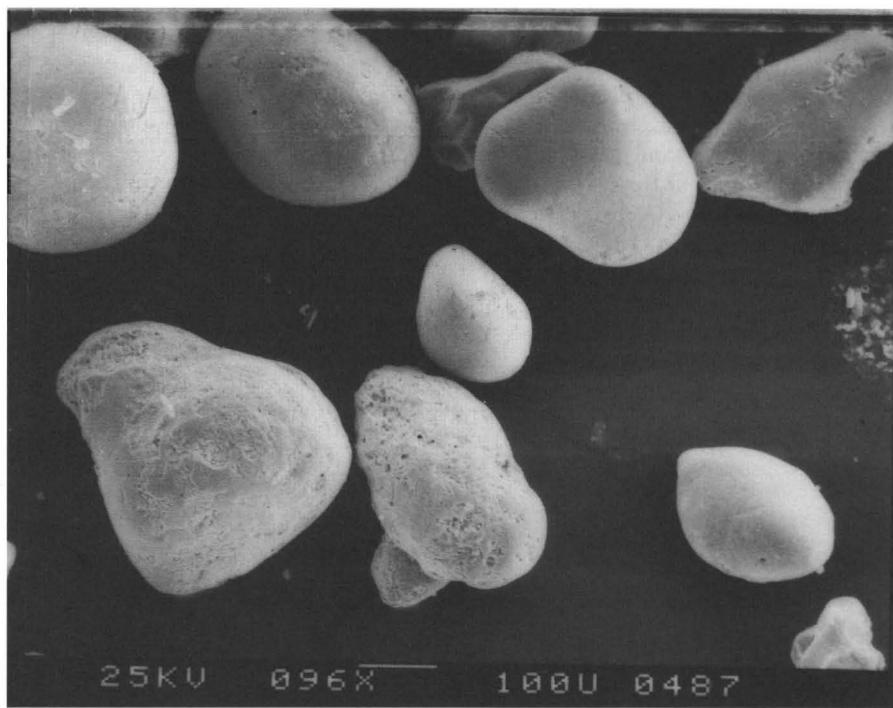


Figure 8. Scanning electron photomicrograph of silicate sand particles from the native Florida sand hatchery, Fisher Island, Dade County, Florida.

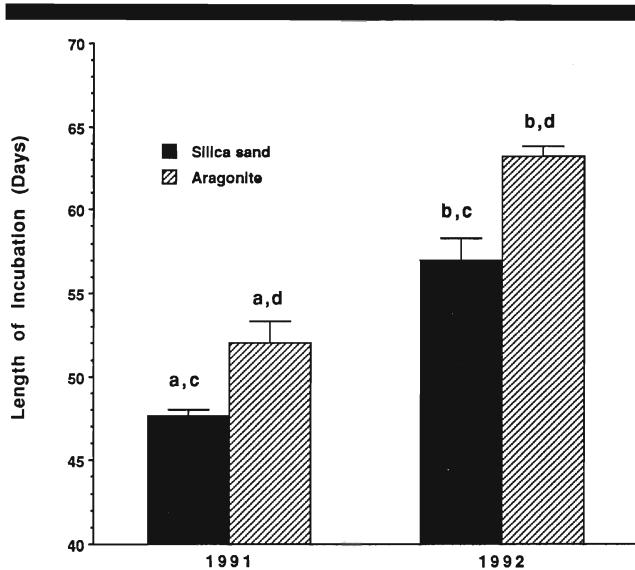


Figure 9. Incubation period for loggerhead sea turtles (*Caretta caretta*) nests in silicate versus aragonite sands, Fisher Island, Dade County, Florida.

### Incubation Period

Aragonite sand was not only cooler than silica sand, but nests incubated in aragonite had significantly longer incubation periods compared to nests incubated in silica sand (Figure 9). As with nest temperatures, incubation times were also affected by overall environmental temperatures; nests incubated earlier in the year (1992) had significantly longer incubation periods (of  $63.2 \pm 0.6$  days and  $57.0 \pm 1.3$  days in aragonite and silica, respectively,  $p < 0.05$ ) compared to nests incubated later in the summer (1991).

It was also noted in 1992 that nests laid on the Fisher Island beach and left *in situ* had a significantly longer mean incubation period ( $67.8 \pm 1.1$  days) than even those nests relocated to the aragonite hatchery. Since natural nests tend to be laid deeper than 46 cm and consequently could be expected to be cooler, in 1993 several such nests were monitored *in situ* with a BAT 12 temperature probe (Physitemp, Inc.) and copper-constantin thermocouples (placed at nest bottoms the morning after the nest was laid). These nests, which averaged 56 cm in depth, in fact averaged  $0.3^{\circ}\text{C}$  cooler at nest bottom during their first week of incubation and were  $1.2^{\circ}\text{C}$  cooler during the third week of incubation, when compared to aragonite hatchery nest temperatures recorded at the same time point (10:00 am). Further data could not be gathered due to vandalism of the BAT 12 probes. Thus it is likely that the cooler temperatures in the deeper *in situ* nests in the aragonite beach caused the average 10 day greater incubation period vs. nests relocated to 46 cm depth in the aragonite hatchery. *In situ* nests in 1993 emerged after 62 days average incubation, nine days later than nests relocated to the aragonite hatchery and 13 days later than silicate hatchery nests.

Table 5. Hatching and emergence success from aragonite and silicate sand hatcheries and *in situ* nests (aragonite) on Fisher Island, Dade County, Florida. Data shown are percent success  $\pm$  SEM.

Year		Silica Sand Hatchery	Aragonite Hatchery	In Situ (Aragonite)
1991	hatch	95.7 (0.8)	95.3 (2.2)	95.1 (2.5)
	emerge	89.1 (3.2)	90.5 (1.4)	76.7 (17.2) <sup>1</sup>
1992	hatch	96.7 (1.0)	88.0 (4.5)	94.2 (1.6)
	emerge	92.8 (2.8)	87.8 (4.5)	93.2 (1.4)
1993	hatch	83.8 (9.5) <sup>2</sup>	96.2 (0.6)	96.6 (0.2)
	emerge	82.2 (10.2)	89.4 (4.4)	94.6 (0.2)

<sup>1</sup> Includes 1 nest with unusually high mortality. If this nest is excluded emergence success rises to  $95.9 \pm 0.3\%$ .

<sup>2</sup> Includes 1 nest with a very high number of infertile eggs. If this nest is excluded hatching success rises  $93.8 \pm 0.1\%$  and emergence rises to  $86.5 \pm 5.2\%$ .

### Hatching Success and Hatchling Fitness

Hatching success, defined as the total number of hatchlings which escaped their shells, though not necessarily from the nest, was high in both *in situ* and relocated nests each year of the study, ranging in general from 94%–97% success. There was no significant differences between nests relocated to the aragonite hatchery and nests placed in Florida sand, except for a slightly lower hatching success of  $88.0 \pm 4.5\%$  in aragonite in 1992, vs. 95–96% success in 1991 and 1993 (Table 5). The average hatching success in Florida sand over the three year test period was 92.6%, vs. an average 93.2% hatching success in aragonite sand hatchery nests and 94.2% for *in situ* nests. Clearly even with inter-year variability in each sand type as well as between the two sands, hatching success is essentially identical in Florida silicate and aragonite sand.

Emergence success (defined as the number of hatchlings which escaped the nest alive on their own/total number of eggs) was also very high in the majority of nests, ranging on average from  $76.7 \pm 17.2\%$  to a high of 97%. Low emergence success in both relocated and *in situ* nests was apparently correlated with overly wet sand, from nests accidentally watered by the landscaping sprinkler system or which were laid too close to the high tide line (personal observation). Again, three year averages of emergence success, at  $86.0\% \pm$  in silicate sand and  $86.6\% \pm$  in aragonite hatchery nests, demonstrate that despite between year variability, emergence success does not depend on sand type.

Despite differences in temperature and incubation period, hatchlings from both sand types, and from both *in situ* and relocated nests, were nearly identical in size over the three year study. There were no significant differences in hatchling mass, straight carapace length or straight carapace width between years or between sand types (Table 6). Hatchling sizes were similar to those found by previous researchers for *C. caretta* hatchlings on other beaches (CALDWELL *et al.*, 1955; WORTH and SMITH, 1976; EHRHART, 1977; EHRHART, 1979a) The average mass of the loggerhead hatchlings over the three year study was  $19.2 \pm 0.2$  g for aragonite nest hatchlings and  $19.5 \pm 0.2$  g for animals from Florida sand nests. Carapace lengths and widths varied by no more than 2–3 mm over the study period, indicating that loggerhead embryos may grow

Table 6. Size of *Caretta caretta* hatchlings relocated to Florida silicate and Bahamian aragonite hatcheries, Fisher Island, Dade County, Florida. Data shown are mean ( $\pm$  SEM).

	Year	Silicate Sand	Aragonite Sand	N
Mass	1991	20.10 (0.16)	19.40 (0.10)	100
	1992	19.40 (0.10)	18.20 (0.20)	100
	1993	19.00 (0.15)	20.10 (0.20)	100
Straight-line carapace length	1991	43.30 (0.13)	43.20 (0.12)	100
	1992	45.00 (0.01)	44.00 (0.14)	100
	1993	43.80 (0.16)	45.50 (0.16)	100
Straight-line carapace width	1991	31.50 (0.20)	31.10 (0.01)	100
	1992	33.70 (0.12)	34.00 (0.11)	100
	1993	33.04 (0.14)	33.90 (0.12)	100

to a standard size before hatching regardless of substrate, incubation temperature, or duration of incubation.

## DISCUSSION

The very high hatching and emergence successes obtained in this study in both the Florida silicate and Bahamian aragonite sand hatcheries indicate that in these aspects, at least, the imported sand provides a suitable nesting substrate for loggerhead sea turtles. Hatching and emergence rates are comparable to or higher than rates previously reported for both *in situ* and relocated nests (GUSEMAN and EHRHART, 1989; WYNEKEN *et al.*, 1988; HIRTH and OGREN, 1987; HORTON, 1990; BURNETT and MARGOLIS, 1993).

The similarly high hatching and emergence successes most likely reflect the similar grain size distribution and hydric potential of the two sand types. While sand grain size apparently does not affect the choice of nesting beaches by adult female turtles (MORTIMER, 1982), there is an optimal range of grain sizes for nest hatching success (MORTIMER, 1981). Nests may fail in sands that are too coarse or too fine (MORTIMER, 1982). Beach compaction resulting from a shift to finely grained sands may inhibit nest excavation by females as well as prevent hatchling emergence. Nest collapse in very coarse sands may also deter hatchling emergence; MORTIMER (1990) reported lower hatching success in more coarsely grained beaches on Ascension Island. Despite a slightly higher percentage of coarser grained particles in silicate, however, there was no significant difference in emergence success between the two sands.

Besides affecting hatching or emergence success, sand grain distribution on a nesting beach can impact nesting success indirectly by affecting water and gas exchange. Temperature, humidity, and respiratory gas exchange are considered the most important physical variables affecting the survival of reptilian embryos (PACKARD and PACKARD, 1988), and are influenced by the sand surrounding a clutch of sea turtle eggs. Sand acts as a barrier through which water vapor, carbon dioxide, and oxygen must diffuse and which forms a blanket for heat dissipation. Altering grain size distribution on a beach can affect sand packing and therefore the pore space through which gases and water vapor must move. Preliminary data on O<sub>2</sub> and CO<sub>2</sub> exchange (not shown) and on water potential indicated no significant differences between arago-

nite and silicate sand, however, and both were clearly sufficient to induce high hatching rates.

It is generally accepted that sea turtle eggs take up water early in incubation and become more turgid (BUSTARD and GREENHAM, 1968, *personal observation*). Higher water potentials are positively correlated with hatchling growth and hatching success in reptiles (SWINGLAND and COE, 1979), although recent studies by Rimkus and Ackerman (*personal communication*) indicate that embryonic growth rates in *Caretta caretta* are independent of water exchange over a range of -10% to +30%. Water exchange is the net movement of water between the egg and its environment, and is influenced by the type of medium in which incubation occurs (PACKARD *et al.*, 1987) as well as by temperature (ACKERMAN *et al.*, 1985; KAM and ACKERMAN, 1990). While actual water exchange was not quantified in this study, water in the sand surrounding a sea turtle clutch with a water potential of approximately -5 kPa to -50 kPa, as was seen in both the aragonite and silicate sands, will result in a net inward movement of water. While this study detected no significant differences in grain size distribution, hydric potential, or hatching and emergence success which would indicate a negative impact by aragonite on loggerhead turtle nesting success, questions concerning the effect of nest temperature differences on hatchling sex ratios need to be considered before permitting the widespread use of aragonite sand on Florida beaches. The most significant finding of this study was that aragonite sand and nests buried in aragonite were consistently cooler than those buried in silicate sand. Sexual differentiation in sea turtles, as in many reptiles, is determined by nest temperature during a critical window of time in incubation (MROSOVSKY and YNTEMA, 1980). During this period, which in *Caretta caretta* occurs during the middle third of incubation (YNTEMA and MROSOVSKY, 1982), a change of only 1–2 °C is sufficient to significantly affect hatchling sex ratios (MROSOVSKY and YNTEMA, 1980). The pivotal temperature, which generates a 50:50 ratio of males to females, is 29.1 °C for loggerhead sea turtles in the southeastern United States. Above this temperature, mostly females will be produced, below 29 °C primarily males are produced (MROSOVSKY, 1988). Eggs maintained continuously at 28 °C or below will produce male hatchlings exclusively (YNTEMA and MROSOVSKY, 1982). Consequently, natural sex ratios on a beach may be altered by a variety of factors which influence the incubation temperature, such as beach shading (MARCUS and MALEY, 1987), relocation of eggs to a different area of the beach (MROSOVSKY and PROVANCHA, 1989), or beach nourishment utilizing sand of a color and/or consistency different from the original (NELSON and HUDSON, 1987).

In this study, sand temperatures in aragonite ranged from less than one degree to as much as 3.4 °C cooler than silicate sand at identical depths. While temperature differences were smaller in nests than in sand alone (Table 3), mean temperatures of nests buried in silicate sand during the critical period were still 1.1 ° to 1.2 °C warmer than nests in aragonite. Data collected in 1991 during the critical period show a difference between the sand types of 0.5 °C to nearly 2 °C at the nest center (Table 4). Temperatures in silicate control (dum-

my) and true nests were significantly warmer at all three depths than aragonite sand and nests at the same depths.

While temperatures increased in both sand types as the season progressed and environmental temperatures increased overall, the slope of the increase in aragonite was only 66.0% that of the silicate sand, indicating a lower thermal capacity for the Bahamian sand. Over a one week period in 1992, nest temperatures in aragonite increased with a slope equal to only 73.9% that of the temperature increase for silicate nests (Table 2). Once external temperatures had stabilized (July vs. June, 1992), the effects of additional heat provided by embryonic metabolism could be detected. While temperatures continued to increase slightly in dummy nests, and at similar rates in both sand types, nest temperatures increased at rates 47.1% greater than control temperature in aragonite, and 131.6% over control rates in silicate sand nests. Since absolute temperature increases due to metabolic heat production were similar in aragonite and silicate sands, however, metabolic heat output by aragonite nests was insufficient to erase the temperature difference between the two sands, which persisted to some degree throughout the incubation period. Metabolic warming of the nest was seen to occur primarily after the critical period, as has been previously suggested (MROSOVSKY and YNTEMA, 1980; MAXWELL *et al.*, 1988) thus the metabolic influence on nest temperature would occur too late to affect hatchling sex ratios.

With such a narrow range (4 °C) of temperatures which produce both male and female sea turtle hatchlings, then, the temperature difference between nests buried in aragonite and those incubated in silicate is clearly large enough to alter natural hatchling sex ratios.

The temperature difference would be biologically insignificant, of course, if temperatures in both sands fell clearly above or below the pivotal temperature for loggerhead sea turtles, as occurred during the critical period in 1992 (for nests laid in late May). For nests incubating later in the season, or in warmer years (1991 and 1993), however, the observed temperature differences placed mean temperatures in aragonite nests at or below the pivotal temperature while silicate sand temperatures were generally above the pivotal temperature. Nests buried in aragonite sand, then, could produce predominantly if not exclusively male hatchlings. Such a situation could significantly impact future populations by seriously reducing populations of breeding females.

A trend to produce all male hatchlings is even more likely considering that nest and sand temperatures decreased with increasing depth (Table 3). In sand alone, temperatures decreased at 0.09–0.24 degrees per inch; changes in nest temperature with depth were slightly less at 0.07 to 0.17 degrees/inch. As female turtles tend to dig their nests deeper than was possible in our hatcheries, temperatures for nests laid naturally on an aragonite beach are likely to be even cooler than temperatures reported here. Nests laid on the aragonite Fisher Island beach during the course of this study, and left *in situ*, were in fact approximately 53–56 cm deep at nest bottom. These nests hatched in 1992 and 1993, respectively, an average of 5 days and 10 days later than nests relocated to the aragonite hatchery (11 and 10 days later in 1992 and 1993 than nest buried in the silicate sand hatchery). In-

creased incubation times with decreasing nest temperature have been previously reported (BUSTARD and GREENHAM, 1968; ACKERMAN and PRANGE, 1972; YNTEMA and MROSOVSKY, 1979). The relationship was calculated by Mrosovsky and Yntema (1980) to be a 5 day increase in incubation time for each 1 °C decrease in temperature, which agrees well with the results of this study (see below). According to this relationship, the depth at which *in situ* nest were buried, which resulted in 5–10 day longer incubation times, indicates temperatures 1–2 °C lower than nests buried only 7–10 cm closer to the surface. This 1–2 °C difference could place the nests below the pivotal temperature throughout the entire incubation period, significantly skewing sex ratios to produce male hatchlings.

Such speculations, of course, assume that female hatchlings are currently produced in significant numbers on Florida beaches. While data on natural sex ratios for sea turtles are sparse, estimates range from approximately 50% female (for *Chelonia mydas* and *Dermochelys coriacea* in Suriname) to as high as 90% female for *C. caretta* hatchlings in Florida. (MROSOVSKY *et al.*, 1984b; MROSOVSKY and PROVANCHA, 1989; WIBBELS *et al.*, 1991; MROSOVSKY and PROVANCHA, 1992). Data on reptilian sex ratios is insufficient to determine whether a 1:1 sex ratio or a female-biased one is the normal pattern (MROSOVSKY *et al.*, 1992), or whether different species or populations can have different sex ratios. A 1:1 sex ratio could be achieved not only at the pivotal temperature but also (within a population) by an appropriate mix of male- and female-biased ratios. Such a mix would be produced when different nests are exposed to a variety of temperature regimes including variation in nest depth and temperature variations across a single season. While sand temperatures on Florida dunes were determined by MROSOVSKY and PROVANCHA (1989, 1992) to remain at or above 30.5 °C for much of the nesting season, nests may be heavily male biased at the beginning and end of a nesting season when environmental temperatures are cooler (MROSOVSKY *et al.*, 1984), leading to a nearly 1:1 sex ratio.

It thus appears that a 1:1 or female-biased hatchling sex ratio is the norm for loggerhead sea turtles on Florida beaches, at least, and that renourishment projects utilizing aragonite could significantly alter natural sex ratios by producing male-biased hatchling sex ratios. This could be true not only for loggerhead sea turtles but for other species as well. Pivotal temperatures for the leatherback (*D. coriacea*), hawksbill (*Eretmochelys imbricata*), and green turtles (*C. mydas*) are reported to lie in the 28–30 °C range as well (MROSOVSKY *et al.*, 1984b; STANDORA and SPOTILA, 1985; RIMBLOT-BALY *et al.*, 1987; MROSOVSKY *et al.*, 1992), and both *C. mydas* and *D. coriacea* nest in Florida in significant numbers. It should be determined if the sex ratio of hatchlings incubated in the field in aragonite sand differs significantly from hatchling sex ratios of nests incubated in Florida sands, prior to any extensive renourishment projects utilizing Bahamian aragonite.

#### ACKNOWLEDGEMENTS

We would like to acknowledge the support of Fisher Island Developers, Inc. and Olsen and Associates which enabled us

to carry out this study. Our thanks also to R. Ackerman and M. Lutz for providing valuable data, to the Fisher Island Landscaping Department for their help and to A. Milton and S. Leone-Kabler for their technical assistance.

## LITERATURE CITED

- ACKERMAN, R.A., 1977. The respiratory gas exchange of sea turtle nests. *Respiratory Physiology*, 31, 19–38.
- ACKERMAN, R.A., 1980. Physiological and ecological aspects of gas exchange by sea turtle eggs. *American Zoologist*, 20, 575–583.
- ACKERMAN, R.A., 1981. Growth and gas exchange of embryonic sea turtles (*Chelonia, Caretta*). *Copeia*, 1981(4), 757–765.
- ACKERMAN, R.A. and PRANGE, H.D., 1972. Oxygen diffusion across a sea turtle (*Caretta caretta*) egg shell. *Comp. Biochemistry Physiology*, 43A, 905–909.
- ACKERMAN, R.A.; RIMKUS, T., and HORTON, R., 1991. The hydric structure and climate of natural and renourished sea turtle nesting beaches along the Atlantic coast of Florida. *Annual Report, Florida Department of Natural Resources Contract #6407*, 60p.
- ACKERMAN, R.A.; SEAGRAVE, R.C.; DMI'EL, R., and AR, A., 1985. Water and heat exchange between parchment-shelled reptile eggs and their surroundings. *Copeia*, 1985, 703–711.
- BURNET, C. and MARGOLIS, W., 1993. Sea Turtle Conservation Program, Broward County, Florida, 1993 Report. *Technical Report 93-09*.
- BUSTARD, H.R. and GREENHAM, P., 1968. Physical and chemical factors affecting hatching in the green turtle *Chelonia mydas* (L.). *Ecology*, 49, 269–276.
- CALDWELL, D.K.; CARR, A., and HELLIER, T.R., JR., 1955. Natural History notes on the Atlantic loggerhead turtle, *Caretta caretta*. *Quarterly Journal Florida Academy Science*, 18, 292–302.
- EHRHART, L.M., 1977. Threatened and endangered species of the Kennedy Space Center. *Semi-annual report to the National Aeronautics and Space Administration, John F. Kennedy Space Center, Biomedical Office*. Code: MD-B. Pp. 1–214.
- EHRHART, L.M., 1979a. Threatened and endangered species of the Kennedy Space Center. *Semi-annual report to the National Aeronautics and Space Administration, John F. Kennedy Space Center, Biomedical Office*. Code: MD-B, pp. 1–214.
- GUSEMAN, J.L. and EHRHART, L.M., 1989. A comparative analysis of marine turtle reproductive success at Patrick Air Force Base, Florida, 1987–1988. Abstract. In: ECKERT, S.A.; ECKERT, K.L., and RICHARDSON, T.H. (compilers), Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Technical Memorandum NMFS-SEFC-232.
- HIRTH, H.F. and OGREN, L.H., 1987. Some aspects of the ecology of the leatherback turtle (*Dermochelys coriacea*) at Laguna Jalova, Costa Rica. *NOAA Technical Report NMFS 56*.
- HORTON, M., 1990. Factors affecting loggerhead sea turtle (*Caretta caretta*) production on Wabasso Beach, Florida. Abstract. In: RICHARDSON, T.H.; RICHARDSON, J.I., and DONNELLY, M. (compilers), Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFC-278.
- KAM, Y.C. and ACKERMAN, R.A., 1990. The effect of incubation media on the water exchange of snapping turtle (*Chelydra serpentina*) eggs and hatchlings. *Journal Comparative Physiology B* 160, 317–324.
- MALONEY, J.E.; DARIAN-SMITH, C.; TAKAHASHI, Y., and LIMPUS, C.J., 1990. The environment for development of the embryonic loggerhead turtle (*Caretta caretta*) in Queensland. *Copeia*, 1990(2), 378–387.
- MARCUS, S.J. and MALEY, C.G., 1987. Comparison of sand temperatures between a shaded and unshaded turtle nesting beach in South Florida. In: *Abstracts of the Seventh Annual Workshop on Sea Turtle Biology and Conservation, Wekiwa Springs, Florida*.
- MAXWELL, J.A.; MOTARA, M.A., and FRANK, G.H., 1988. A micro-environmental study of the effect of temperature on the sex ratios of the loggerhead turtle, *Caretta caretta*, from Tongaland, Natal. *S. Afr. Tydskr. Dierk.*, 23, 342–350.
- MILTON, S.L.; LEONE-KABLER, S.; SCHULMAN, A.A., and LUTZ, P.L., 1994. Effects of Hurricane Andrew on the sea turtle nesting beaches of South Florida. *Bulletin Marine Science*, 54(3), 974–981.
- MORTIMER, J.A., 1981. Reproductive Ecology of the Green Turtle, *Chelonia mydas*, at Ascension Island. Ph.D. dissertation, University of Florida.
- MORTIMER, J.A., 1982. Factors affecting beach selection by nesting sea turtles. In: BJORNDAHL, K.A. (ed.), *Biology and Conservation of Sea Turtles. Proceedings of the World Conference on Sea Turtle Conservation, Washington, D.C.*, 1979, p. 45–52.
- MORTIMER, J.A., 1990. The influence of beach sand characteristics on the nesting behavior and clutch survival of green turtles (*Chelonia mydas*). *Copeia*, 1990, 802–817.
- MROSOVSKY, N., 1982. Sex ratio bias in hatching sea turtles from artificially incubated eggs. *Biology Conservation*, 18, 271–280.
- MROSOVSKY, N., 1988. Pivotal temperatures for loggerhead turtles (*Caretta caretta*) from northern and southern nesting beaches. *Canadian Journal Zoology*, 66, 661–669.
- MROSOVSKY, N. and YNTEMA, C.L., 1980. Temperature dependence of sexual differentiation in sea turtles: Implications for conservation practices. *Biology Conservation*, 18, 271–280.
- MROSOVSKY, N. and PROVANCHIA, J., 1989. Sex ratio of hatchling loggerhead sea turtles hatching on a Florida beach. *Canadian Journal Zoology*, 67, 2533–2539.
- MROSOVSKY, N. and PIEAU, C., 1991. Transitional range of temperature, pivotal temperatures and thermosensitive stages for sex determination in reptiles. *Amphibia-Reptilia*, 12, 169–179.
- MROSOVSKY, N. and PROVANCHIA, J., 1992. Sex ratio of hatchling loggerhead sea turtles: Data and estimates from a 5-year study. *Canadian Journal Zoology*, 70, 530–538.
- MROSOVSKY, N.; HOPKINS-MURPHY, S.R., and RICHARDSON, J.I., 1984. Sex ratios of sea turtles: Seasonal changes. *Science*, 225, 739–741.
- MROSOVSKY, N.; DUTTON, P.H., and WHITMORE, C.P., 1984b. Sex ratios of two species of sea turtles nesting in Suriname. *Canadian Journal Zoology* 62, 2227–2239.
- MROSOVSKY, N.; BASS, A.; CORLISS, L.A.; RICHARDSON, J.I., and RICHARDSON, T.H., 1992. Pivotal and beach temperatures for hawksbill turtles nesting in Antigua. *Canadian Journal Zoology*, 70, 1920–1925.
- NATIONAL RESOURCE COUNCIL, 1990. *Decline of the Sea Turtles; Causes and Prevention*. Washington, D.C.: National Academy Press, 259 p.
- NELSON, D.A. and HUDSON, D., 1987. Sex ratios of hatchling sea turtles from Delray Beach, Florida. In: *Abstracts of the Seventh Annual Workshop on Sea Turtle Biology and Conservation, Wekiwa Springs, Florida*.
- OLSEN, E.J. and BODGE, K.R., 1991. The use of aragonite as an alternate source of beach fill in southeast Florida. In: *Proceedings, Coastal Sediments '91, American Society of Civil Engineers* (Seattle, Washington), pp. 2130–2145.
- PACKARD, G.C. and PACKARD, M.J., 1988. The physiological ecology of reptilian eggs and embryos. In: GANS, C. and HUEY, R.B. (eds.) *Biology of the Reptilia. Vol. 16, Ecology B. Defense and Life History*. New York: Alan R. Liss, pp. 523–605.
- PACKARD, G.C.; PACKARD, M.J.; MILLER, K., and BOARDMAN, T.J., 1987. Influence of moisture, temperature, and substrate on snapping turtle eggs and embryos. *Ecology*, 68(4), 983–993.
- RAYMOND, P.W., 1984a. The effects of beach restoration on marine turtle nesting in south Brevard County, Florida. M.S. Thesis, University of Central Florida, Orlando, 121p.
- RIMBLOT-BALY, F.; LESCURE, J.; FRETEY, J.J., and PIEAU, C., 1987. Sensibilité à la température de la différenciation sexuelle chez la Tortue Luth, *Dermochelys coriacea* (Vandelli, 1761); application des données de l'incubation artificielle à l'étude de la sex-ratios dans la nature. *Ann. Sci. Nat. Zool. Paris*, 8, 277–290.
- SEALEY, N.E., 1994. *Bahamian Landscapes: Introduction to the Physical Geography of the Bahamas*. Nassau, Bahamas: Media Publishing, 128p.
- STANDORA, E.A. and SPOTILA, J.R., 1985. Temperature dependent sex determination in sea turtles. *Copeia* 3, 711–722.

- STRONGE, W.B., 1994. Beaches, tourism, and economic development. *Shore and Beach*, 62(2), 6–8.
- SWINGLAND, I.R. and COE, M.J., 1979. The natural regulation of giant tortoise populations on Aldabra Atoll: Recruitment. *Philosophical Transmitter Royal Society London, Series B*, 286, 177–188.
- WIBBELS, T.; MARTIN, R.E.; OWENS, D.W., and AMOSS, M.S., 1991. Female-biased sex ratio of immature loggerhead sea turtles inhabiting the Atlantic coastal waters of Florida. *Canadian Journal Zoology*, 69, 2973–2977.
- WIEGEL, R.L. 1992. Dade County, Florida, beach nourishment and hurricane surge study. *Shore and Beach*, 60(4), 2–26.
- WORTH, D.F. and SMITH, J.B., 1976. Marine turtle nesting on Hutchinson Island, Florida, in 1973. *Florida Marine Research Publication*, 18, 1–17.
- WYNEKEN, J.; BURKE, T.J.; SALMON, M., and PETERSEN, D.K., 1988. Egg failure in natural and relocated sea turtle nests. *J. Herp.* 22(1), 88–96.
- YNTEMA, C.L. and MROSOVSKY, N., 1979. Incubation temperature and sex ratio in hatchling loggerhead turtles, a preliminary report. *Mar. Turtle Newslet.*, 11, 9–10.
- YNTEMA, C.L. and MROSOVSKY, N., 1982. Critical periods and pivotal temperatures for sexual differentiation in loggerhead sea turtles. *Can. J. Zool.*, 60, 1012–1016.