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ORIGINAL ARTICLE

Artificial nesting habitats as a conservation strategy for turtle populations experiencing global change

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Abstract

Diamondback terrapins (*Malaclemys terrapin*) inhabit estuaries in eastern USA and may tolerate salinity of seawater for short durations. Many North American estuaries are adversely affected by anthropogenic impacts, such as pollution, dredging and invasion by non-native plants. Many nesting areas have been altered or destroyed, causing terrapins to nest on roadsides and artificial islands made of dredged substrate from bottom sediments. Shading by non-native plants may suppress development and reduce survival of embryos. In Barnegat Bay, New Jersey, USA, there is a mosaic of natural and degraded terrapin nesting habitats. We investigated the effects of dredge soil and shade on the hatching success of diamondback terrapins to determine whether nesting habitat could be increased by using dredged bottom sediments. In year 1, unshaded nests in natural loamy-sand had the highest hatching success (55.2%), while nests in dredge soil produced no hatchlings. In year 2, nests in unshaded loamy-sand had a hatching success of 85.3%, whereas those in dredge soil, aged 1 year, had a hatching success of 59.4%. Dredge soil improved as an incubation substrate after aging 1 year by the washout of salt. Nest temperatures were generally cool and produced mostly male hatchlings. Uncontaminated dredge soil may provide suitable nesting substrates for diamondback terrapins if used after one year, and may be particularly beneficial if used for constructing islands that provide new nesting sites with reduced access of mammalian predators.

Key words: dredge, estuarine turtles, hatching success, *Malaclemys terrapin*, nesting ecology, nest temperature, nest substrate, shade

INTRODUCTION

The biological consequences of global change occur at levels ranging from biomes and ecosystems to local populations of species and the reproductive success of individual organisms. Timeframes for recovery from anthropogenic changes vary greatly. For example, the invasion of islands by rats destroys seabird colonies, and restoration of these colonies and island ecosystems requires decades after rat eradication (Jones 2010). However, removal of invasive plants restores habitat function for crabs in saltwater estuaries within a few years (Holsman *et al*. 2010). Invasion by alien plants destroys nesting habitat of Nile crocodiles (*Crocodylus niloti-*

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cus Laurenti, 1768) resulting in a reduction in reproductive success. Removal of the plants can restore nesting habitat within 1 year (Leslie & Spotila 2001). Pollution of aquatic systems results in deformities in individual snapping turtle hatchlings (*Chelydra serpentina* Linnaeus, 1758) (Bell *et al*. 2005) and highlights the sensitive role of reproduction in the maintenance of turtle populations. Thus, understanding and remedying the effects of global change on individual species requires detailed knowledge of the limiting factors controlling the size of their populations, including nesting ecology and impacts to nest habitats.

Reproductive success of reptiles depends on genetic, maternal and environmental factors (Ernst *et al.* 1994). In turtles, temperature, soil composition and moisture affect the hatching success of eggs (Packard *et al*. 1993; Feinberg & Burke 2003; Butler *et al*. 2004) and hatchling survivorship in nests (Nagle *et al*. 2000). In addition, the location of the egg within a clutch, coupled with microenvironmental conditions within a nest affect the growth of an embryo and development, as seen in leatherback turtles (Wallace *et al*. 2004). Habitat quality is also important to the survival of local populations of species of numerous taxa (reviewed in Hanski 1996; McKinney 2002). Turtles face human threats that impact their habitat (Gibbons *et al*. 2000; Hartig *et al*. 2002), including destruction and fragmentation of foraging and nesting areas (Joyal *et al.* 2001).

Diamondback terrapins (*Malaclemys terrapin* Schoepff, 1793) are estuarine emydid turtles, endemic to the USA, with a geographic range from Cape Cod, Massachusetts to the Gulf Coast of Texas (Ernst *et al*. 1994). This species has been greatly reduced in numbers throughout most of its range as a result of a long history of commercial harvesting (Carr 1952). In addition, habitat fragmentation due to development and filling of estuaries has resulted in limited foraging areas and eliminated nesting areas (Burger & Montevecchi 1975; Wood & Herlands 1997). Throughout their range, diamondback terrapins have failed to recover to their levels of abundance in the 1800s despite conservation efforts and attempts to farm them by the US Fish Commission and Bureau of Fisheries in the 1900s (Carr 1952).

Loss of nesting habitat and increased mammalian predation by raccoons, dogs and foxes, especially in areas near human development, continue to restrict population growth of diamondback terrapins. Therefore, it is important to determine whether reproductive success can be improved by creating new nesting habitat that has reduced mammalian predation. Because many freshwater and sea turtle species face similar reproductive problems (Klemens 2000; Moll & Moll 2004; Spotila 2004) the diamondback terrapin provides a model for addressing the conservation problems of many turtle species.

Barnegat Bay Estuary in New Jersey contains a mosaic of natural nesting habitats for diamondback terrapins, including sand dunes and bay beach areas, as well as altered habitats filled with dredged sediment taken from the bottom of the bay. Many terrapin nesting areas have been destroyed or altered by development. Over the past century, Barnegat Bay has lost over 30% of its salt marsh habitat, and over 36% of its shoreline now includes bulkheading, which are vertical walls constructed of metal, vinyl, concrete or wood, which reduce shoreline erosion (BBEP 2001). These shoreline structures may prevent or impede diamondback terrapins from coming ashore to nest. Houses and other structures have been built over other historic nesting areas. Raccoons, dogs, foxes and other mammalian predators destroy up to 98% of clutches on nesting beaches accessible to the mainland (H. Avery, unpubl. data). Over the past 50 years, dredge soils have been dumped within the estuary to build dredge-fill islands or to fill upland sites (Brown 2001). Diamondback terrapins nest on some of these islands but nesting success is not known. These areas are potentially important to the survival of the diamondback terrapin in Barnegat Bay and other estuaries in North America. Dredge-filled areas are also used by nesting female diamondback terrapins in the Patuxent River, Maryland (Roosenburg *et al*. 2003; Roosenburg & Kendall 2004) and Jamaica Bay, New York (Feinberg & Burke 2003).

Dredge soil is composed of unconsolidated, randomly mixed sediments, including: rock, soil, sand and/or shell materials extracted and deposited during dredging and dumping activities (Schoeneberger & Wysocki 2005). Dredge soil may contain high concentrations of organic solids (Newell *et al.* 1999; Brown 2001), and in estuarine areas may also have high salt content, which could impact embryo survival, by altering soil moisture content and desiccating embryos (Brooks *et al*. 1991; Miller & Dinkelacker 2008).

The composition of the dredge soil can also affect nest temperature. Diamondback terrapins have temperature-dependent sex determination, with the pivotal temperature at 29 °C. Eggs incubated below 28 °C develop

as males, while eggs incubated at or above 30 °C develop as females (Jeyasuria & Place 1997). Incubation temperature also affects duration of incubation in diamondback terrapins (Jeyasuria *et al*. 1994; Roosenburg & Kelley 1996). Nests incubated above 31 °C hatch in 45 days while those incubated below 27 °C hatch in 60–104 days (Burger 1976, 1977). Soil composition in both natural and artificial nesting areas affects microenvironmental conditions (e.g. temperature, CO_2, O_2 and soil moisture) within the nest chamber, which affects water exchange, metabolism and development of turtle embryos (Packard *et al.* 1987; Cagle *et al.* 1993; Wilson 1998).

Vegetation cover reduces nest temperature (Jeyasuria *et al*. 1994). Diamondback terrapins in New Jersey usually select nesting locations with less than 20% cover (Burger & Montevecchi 1975) and terrapins in South Carolina do not produce successful clutches if cover is greater than 75% (Palmer & Cordes 1988). Therefore, interaction of vegetation cover with soil composition plays an important role in determining the success of terrapin clutches. At Barnegat Bay, terrapin nesting areas may be shaded by non-native plant species, such as *Phragmites australis*. Vegetation may also produce thick root systems, making it difficult for adult terrapins to dig nests and for hatchlings to emerge in vegetated areas.

The objective of the present study was to determine whether nesting habitat along Barnegat Bay could be increased by the use of sediment dredged from the bottom of the bay. We conducted experiments to test the effects of dredge soil and shade on the hatching success of diamondback terrapin eggs. We measured nest temperature, incubation time and egg survivorship in nests with different soil characteristics (i.e. sand, loamy-sand and dredge soil) with full sun exposure and 50% shade. The 50% shade was chosen to model the percentage of shading caused by *Phragmites australis* and cover of *Spartina* grasses at terrapin nesting sites at North Sedge Island, where there has been an annual increase in the amount of vegetation of both native and non-native vegetation types, resulting in fewer nesting areas with 25% or less vegetative cover and shading.

We also determined whether the age of dredge soil affected hatching success. From these findings we were able to define the conditions under which dredge soil may be used to create artificial nesting habitats for the diamondback terrapin.

MATERIALS AND METHODS

Study area

The present study took place on North Sedge Island in Barnegat Bay, New Jersey, USA (39°47′48″N, 74°07′07″W) (Fig. 1). North Sedge Island is managed by the New Jersey Division of Fish and Wildlife within a Marine Conservation Zone established in 2003. A portion of North Sedge Island was formed with sediment from Barnegat Bay in the early 1900s to build hunting and fishing shacks (Miller 1994). The island is covered predominantly with native salt marsh grass, *Spartina* sp., and the non-native common reed *Phragmites australis*, at nesting beaches on the north and east sides of the island. The soil is predominately loamy-sand.

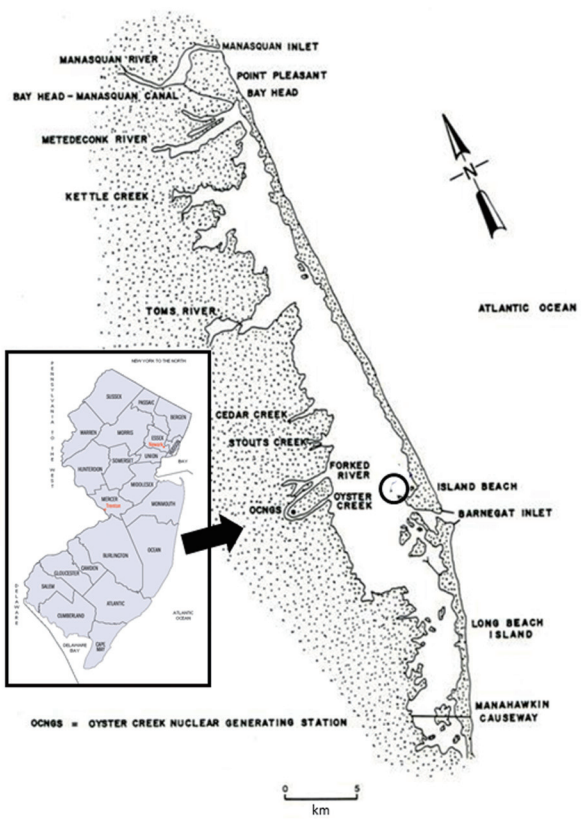

Figure 1 Barnegat Bay, New Jersey, USA showing the study area. North Sedge Island is within the open circle adjacent to Island Beach (State Park). The insert shows the State of New Jersey. Map courtesy of Dr Michael Kennish, Rutgers University, New Jersey, USA.

Female diamondback terrapins nested on the beaches and adjacent uplands of North Sedge Island in Jun and Jul. Island Beach State Park comprises 16 km of undeveloped peninsula consisting of bay and ocean beach with primary and secondary sand dunes. It is approximately 1 km east of North Sedge Island and provides additional contiguous nesting habitat for the diamondback terrapin population (Fig. 1).

Experimental design

We established 3 experimental areas that were large enough to allow several clutches of eggs to incubate without affecting neighboring nests. Each plot contained 1 of the experimental nesting substrates (sand, loamy-sand or dredge soil). The size of experimental areas was based on our experience with incubation of olive ridley turtle (*Lepidochelys olivacea* Eschscholtz, 1829) clutches in a prior study (Honarvar *et al*. 2008). Because olive ridley turtles lay larger clutches of larger eggs than terrapins, we were confident that diamondback terrapin nests would not affect each other in these experimental plots and, therefore, would be statistically independent. Measurements of gas exchange during the experiment confirmed our assumption (Wnek 2010). We also used natural nests laid on the island as controls. Conducting the experiment over 2 years, we measured differences due to the age of the dredged soil and the effects of normal variation in weather conditions.

Experimental soils

We collected sand from terrapin nesting sites at Island Beach State Park, loamy-sand from a natural terrapin nesting area on Sedge Island, and dredge soil from a nearby channel east of the island. Dredge soil consisted of unsorted sediments from the bottom of the bay and was dried outside 2 months prior to the nesting season. The type of dredge soil used in this study is representative of dredge soil throughout the study area that was found at nest sites used by terrapins.

We analyzed soils for percent composition of sand, silt and clay particles using the Bouyoucos soil texture method (Wilson 1998). We dried soils at 100 °C for 24 h (Theocharopoulos *et al.* 2004), then dry-sieved and separated them. We used the dry mass fragments remaining in each sieve to calculate particle size distribution, which we normalized with respect to the total dry mass (Diaz-Zorita *et al*. 2007). We then classified soil types according to the US Department of Agriculture soil texture system. The dredge soil was sandy-loam. Natural nests on Sedge Island were oviposited in loamy-sand.

Experimental plots

We constructed 3 experimental plots (2.25 m^2) on North Sedge Island, with the same solar orientation where diamondback terrapins nest. Natural nests on the island served as reference nests and were oviposited by wild terrapins near experimental plots.

We filled experimental plots with 45 cm of soil after measuring the salt content of the soils. All soils were analyzed for salt composition by washing the soil with equal volumes of distilled water and determining the electrical conductivity (deciSiemens [dS] per meter; Rhoades 1996) using a YSI 85 model meter (± 0.1 dS/m). The composition of the soil below the plots was 85% sand. We covered half of each plot with a 50% landscape shade cloth (Gempler) 15 cm above the plot. The other half of each plot was open to full sun. A standard photometer (± 100 lux) measured 49 200 lux in the shaded plots and 100 000 lux in the unshaded treatments at midday. The sides of the plots were open for ventilation. Natural nests were in full sun, but had up to 25% vegetative cover within 10 cm of the nests. The vegetation around the natural nests was composed of *Spartina* sp. and other grasses that grew no more than 12 cm in height and did not provide significant shade for the nests. The experimental plots were kept free of vegetation, so that there were no effects of root growth on the nests and they were not shaded. Borders (1 m) between experimental plots provided drainage and space between treatment types to ensure statistical independence.

Experimental nests

We separated nests >0.25 m to provide a boundary between nest chambers, which was chosen based on diamondback terrapin nest densities found on North Sedge Island. We collected clutches laid on North Sedge Island in areas where there was high human activity and placed clutches in each plot type in order of clutch deposition. In 2006, we used 5 nests in each treatment and 5 natural nests as controls or reference nests. In 2007, we used 6 nests in each treatment and 8 natural nests as controls. We dug experimental nests at the mean nest depths of clutches laid by female diamondback terrapins on North Sedge Island in previous years: 8 cm (top of the nest), 12 cm (middle of the nest) and 16 cm (bottom of the nest).

We marked and transported eggs ≤100 m from their original nest to experimental plots in an insulated container in vermiculite without changing egg orientation (Packard & Packard 2000). We used predator excluder devices made of 7 mm hardware cloth that covered all

individual nests, and retained emerged hatchlings. All procedures were approved by the Animal Care and Use Committee of Drexel University. Permits to Avery and Wnek were obtained from the New Jersey Division of Fish and Wildlife.

Monitoring temperatures and nests

A Campbell CR-10X datalogger with a AM32 multiplexer (Campbell Scientific, USA) recorded temperatures (0.05 °C) daily at 1200 hours within each experimental plot treatment and within 3 natural nests using Type T 24 gauge copper–constantan thermocouples. Thermocouples were set at the surface above a nest, and at 8, 12 and 16 cm below the surface within the nest. Temperatures were monitored within plots at the same depths in areas without nests for comparison, which were referred to as 'control treatment temperatures'. Air temperatures were recorded using 2 shaded thermocouples. We used a one-way analysis of variance (ANOVA) and a Tukey honestly significant difference (HSD) post-hoc test to compare temperatures between treatments.

We carefully excavated all nests after 60 days of incubation to determine egg condition, egg development stage and, finally, hatching success. We excavated nests daily when the eggs were close to hatching, and we allowed hatchlings to emerge from the nest cavity without removing them. We also excavated nests and examined unhatched eggs to determine stage of development and possible causes of embryo death. We used a one-way ANOVA and a Tukey HSD post-hoc test to compare arcsine-transformed percent hatched eggs between soil types and shading treatments. Due to the decomposition of some dead terrapin embryos within eggs, especially within the dredge treatments, we could only classify the embryos into early, middle and late development (*sensu* Bell *et al.* 2004). We used a one-way ANOVA to test for differences in incubation time between soil types and shading treatments. Data are reported as means ± SE.

RESULTS

In year 1 (2006), soil conductivity (SC) in sand and loamy-sand treatments was 0.3 dS/m, which was weakly saline, while SC of dredge soil was 7.9 dS/m, which was strongly saline. In year 2, SC in the 1-year aged dredge soil treatment was 0.4 dS/m, which was weakly saline. SC of natural reference nests on the island was 0.4 dS/m. For comparison, the conductivity of water where the new dredge was taken was 40.0 dS/m.

Nest temperatures

Year 1

There were no statistically significant differences between mean nest temperatures for all treatments at all depths in year 1 (2006). Nests were the same temperatures as the surrounding soil. Nests in unshaded loamy-sand had the highest mean temperature (26.4 ± 0.7 °C), whereas nests in the shaded dredge soil had the lowest mean temperatures (23.9 ± 0.4 °C; Table 1). However, there were no significant differences in nest temperatures between soil treatments and/or shade treatments at the 16 cm (bottom) nest depths. There were no significant differences in mean nest temperatures between all shaded, unshaded and natural reference nests for all depths combined (Fig. 2).

Nest temperatures varied on a daily basis (Fig. 3). At noon, temperatures at the upper levels of the nest were always higher than at the lower levels. At night, these differences were undoubtedly reversed, although we did not measure them. Rainfall events lowered all temperatures and reduced differences between depths and treatments (Fig. 3).

Year 2

There were no statistically significant differences between mean nest temperatures for control and treatment nests at all depths in year 2 (2007). Nests were generally the same temperature as the surrounding soil. Nests in unshaded dredge soil had the highest mean temperature (25.8 ± 0.5 °C; Fig. 2), and nests in shaded dredge soil (23.3 ± 0.4 °C) and shaded loamy-sand (23.4 ± 0.4 °C) had the lowest temperatures (Fig. 2). At the 8 cm depth (top), nests in unshaded dredge soil (Fig. 3d) had significantly higher temperatures than nests in all other shaded treatments (Fig. 3; Table 2). Nests in unshaded loamy-sand had significantly higher temperatures than nests in shaded loamy-sand. At the 12 cm depth (middle) and 16 cm depth (bottom), nests in unshaded dredge soil had significantly higher mean temperatures than nests in shaded dredge soil. Mean nest temperatures in unshaded soils were significantly higher (24.6 ± 0.2 °C) than mean nest temperatures in shaded soils (23.5 ± 0.2 °C; ANOVA, $F = 1.07$, $P < 0.01$). Mean air temperature from Jul through Sep was 26.0 °C in 2006 and 26.3 °C in 2007.

Table 1 Comparison of mean nest temperatures (°C ± SE) in year 1 (2006) incubation experiment for diamondback terrapin nests on North Sedge Island, New Jersey

Depth	Treatment						
	Natural reference (°C)	Unshaded loamy-sand (°C)	Shaded loamy-sand (°C)	Unshaded sand (°C)	Shaded sand (°C)	Unshaded dredge (°C)	Shaded dredge (°C)
8 cm	27.3 ± 0.6	28.4 ± 1.1[a]	25.6 ± 0.5	26.6 ± 0.7	25.2 ± 0.6[a]	26.7 ± 0.6	24.6 ± 0.5[b]
12 cm	25.5 ± 0.6	26.1 ± 0.6[a]	24.9 ± 0.5	25.5 ± 0.6	24.6 ± 0.5	25.1 ± 0.5	23.7 ± 0.4[c]
16 cm	25.0 ± 0.5	24.8 ± 0.5	24.5 ± 0.5	24.7 ± 0.6	24.1 ± 0.5	24.3 ± 0.5	23.4 ± 0.4
Mean	25.9 ± 0.6	26.4 ± 0.7	25.0 ± 0.5	25.6 ± 0.6	24.7 ± 0.5	25.4 ± 0.5	23.9 ± 0.4

All temperatures were compared using one-way analysis of variance and a Tukey honestly significant difference post-hoc test ($P \leq 0.05$). At 8 cm depth, mean nest temperature in unshaded loamy-sand[a] was significantly higher ($P \leq 0.05$) than mean nest temperatures in shaded sand[b] and shaded dredge soil.[b] At 12 cm depth, mean nest temperature in unshaded loamy-sand[a] was significantly higher ($P < 0.05$) than mean nest temperature in the shaded dredge soil.

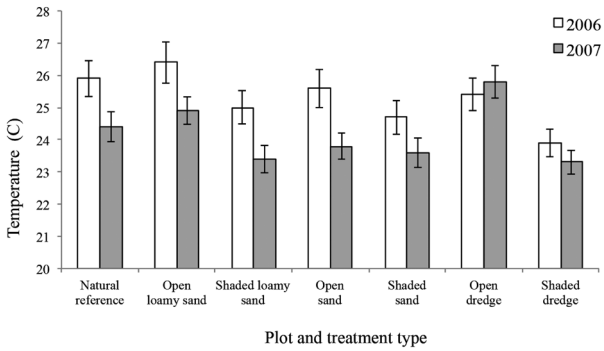

Figure 2 Mean temperatures (± SE) in all diamondback terrapin experimental and natural reference nests on North Sedge Island, New Jersey in 2006 and 2007. Temperatures were recorded at 1200 hours each day at the top of the nest (8 cm), the middle of the nest (12 cm) and the bottom of the nest (16 cm). Data are overall means for each nest.

Hatching success and incubation time

Year 1

In year 1 (2006), 13 of 35 diamondback terrapin nests (30 experimental and 5 natural reference nests) produced hatchlings (Table 3). Nests in unshaded loamy-sand (mean = 55.2%) and natural reference nests (mean = 53.6%) had significantly higher hatching percentages than nests in unshaded dredge, shaded dredge and shaded sand treatments, which produced no hatchlings (one-way ANOVA, $F = 4.04$, $P = 0.048$). There was a significantly higher percentage of hatching in natural reference nests and unshaded treatments than in shaded nests (one-way ANOVA, $F = 5.80$, $P = 0.01$).

Development of embryos in both dredge treatments ceased during the first third stage of development and a majority of eggs were desiccated. All 5 nests in unshaded loamy-sand produced hatchlings, while only 2 of 5 nests in shaded loamy-sand produced hatchlings. In 3 nests in the shaded loamy-sand with no hatching, embryo development ceased during the middle third of development. Embryos died after a major rainfall event in late Jul that flooded the nests. Flooding may have also killed embryos in other nests in loamy-sand substrate, because hatching success in these nests ranged from 13.0 to 100%.

Of 5 nests in the unshaded sand, 3 produced hatchlings, but no nests in the shaded sand produced hatchlings. Unhatched embryos in sand substrate were in the final third stage of development but died after a ma-

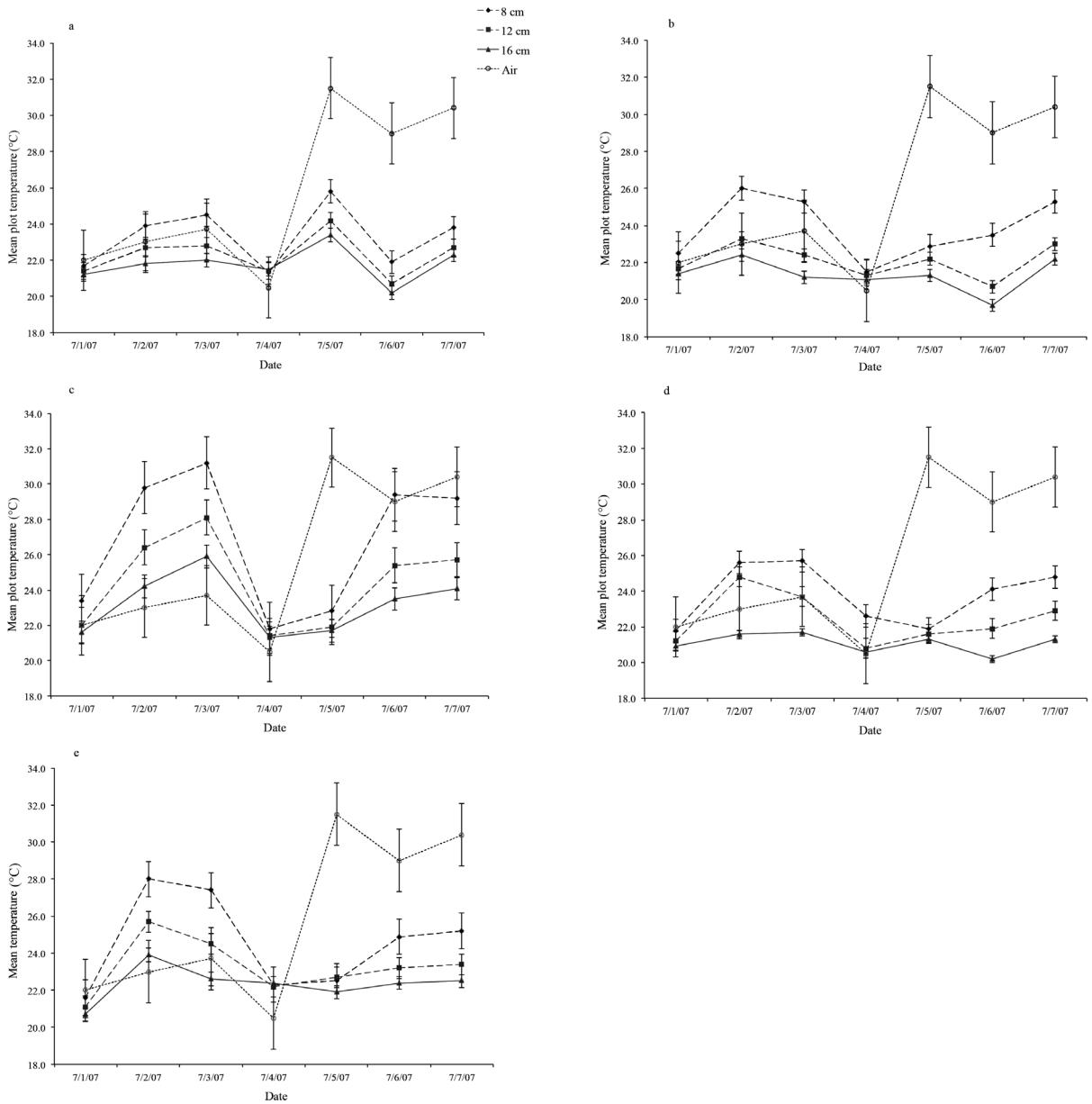

Figure 3 One week (1–7 Jul 2007) mean temperature profiles within diamondback terrapin nests in each experimental treatment and natural reference nests on North Sedge Island, New Jersey: (a) open sand treatment, (b) shaded sand treatment, (c) open dredge treatment, (d) shaded dredge treatment and (e) natural reference nest. Nest temperatures were recorded at the top of the nest (8 cm), the middle of the nest (12 cm) and the bottom of the nest (16 cm) at 1200 hours EST. Temperature variation on 4 Jul 2007 was due to a precipitation event. Bars indicate SE values of the mean (°C). (Loamy-sand temperatures are not shown because they are intermediate values to those provided.)

jor rainfall event (15 cm of rain in 6 h) in early Sep that flooded the island. Outside of this major rainfall event, there were no significant differences in mean monthly rainfall amounts between years from Jun through Aug. Of 5 natural reference nests, 3 produced hatchlings, with the other 2 also affected by flooding. There was no sig-

Table 2 Comparison of mean nest temperatures (°C ± SE) in year 2 (2007) incubation experiment for diamondback terrapin nests on North Sedge Island, New Jersey

Depth	Treatment						
	Natural reference (°C)	Unshaded loamy-sand (°C)	Shaded loamy-sand (°C)	Unshaded sand (°C)	Shaded sand (°C)	Unshaded aged dredge (°C)	Shaded aged dredge (°C)
8 cm	25.9 ± 0.6	26.6 ± 0.6[f]	24.3 ± 0.4[b,g]	25.2 ± 0.4	24.5 ± 0.5[b]	27.7 ± 0.7[a]	24.9 ± 0.4[b]
12 cm	24.2 ± 0.5	24.9 ± 0.4	23.2 ± 0.4[c]	23.5 ± 0.4[c]	23.4 ± 0.5[c]	25.4 ± 0.5[a]	23.5 ± 0.4[c]
16 cm	23.2 ± 0.5	23.1 ± 0.5	22.5 ± 0.5	22.8 ± 0.5	22.9 ± 0.5	24.3 ± 0.4[a]	22.4 ± 0.4[d]
Mean	24.4 ± 0.5	24.9 ± 0.4	23.4 ± 0.4[e]	23.8 ± 0.4	23.6 ± 0.5	25.8 ± 0.5[g]	23.3 ± 0.4[e]

All temperatures were compared using one-way analysis of variance and a Tukey honestly significant difference post-hoc test ($P \leq 0.05$). There were significant differences in mean temperatures of nests between the unshaded aged dredge soil[a] and the shaded aged dredge soil[b,c,d] at all depths, the shaded sand and shaded loamy-sand at 8 and 12 cm and the unshaded sand at 12 cm ($P \leq 0.05$). Nests in unshaded loamy-sand[f] had significantly higher mean temperatures than nests in shaded loamy-sand at 8 cm ($P < 0.05$). [g] Overall mean nest temperature in unshaded aged dredge soil[g] was significantly higher than mean nest temperature in shaded aged dredge soil and shaded loamy-sand[e] ($P \leq 0.05$).

nificant difference in the incubation time of reference or experimental nests in year 1 (one-way ANOVA; Table 3). The range of incubation was 67 days in unshaded loamy-sand plot to 102 days in the shaded loamy-sand plot.

Year 2

In year 2 (2007), 5 diamondback terrapin nests were predated, 2 in shaded sand and 3 in shaded loamy-sand. Of the remaining 39 nests (31 experimental and 8 natural reference nests), 36 nests produced hatchlings (Table 3). Hatching success was higher in all treatments and in natural nests in year 2 as compared to the same categories of nests in year 1. Nests in dredge soils and shaded sand produced hatchlings with mean hatching success ranging from 41.4 to 59.4%.

All non-predated nests in loamy-sand, unshaded sand and unshaded dredge soil produced hatchlings. All 8 natural reference nests also produced hatchlings. Hatching percentage in nests in unshaded loamy-sand (85.3 ± 6.3%) was significantly higher than hatching percentage in the shaded sand treatment (41.4 ± 9.4%; one-way ANOVA, $F = 0.84$, $P = 0.04$).

Mean incubation time was significantly shorter in nests that hatched in unshaded loamy-sand (mean = 80.0 days) versus shaded dredge soil (mean = 99.3 days; one-way ANOVA, $F = 11.3$, $P < 0.01$). There was also a significant difference in mean incubation time between natural reference nests (mean = 86.4 days) and nests in shaded dredge soil (99.3 days; one-way ANOVA, $F = 12.9$, $P = 0.049$). The range of incubation time was 58 days for nests in unshaded loamy-sand to 106 days in shaded dredge soil.

DISCUSSION

Dredge soil improved as an incubation substrate for diamondback terrapin eggs after it aged 1 year, likely a result of a decrease in salt content due to percolation of water from rain and snow. In year 1, embryos in dredge soil died during the first third of development and were desiccated. This was probably because the soil was strongly saline. In year 2, mean hatching success of eggs oviposited in unshaded clutches in the aged dredge soil was 59.4%, which was not significantly different from those in sand (65.4%), but was significantly lower than those in loamy-sand (85.3%). Some nests were very successful while others had very low hatching success. A longer period of time may be needed to establish

Table 3 Hatching success of diamondback terrapin clutches in 2006 and 2007 on North Sedge Island, Barnegat Bay, New Jersey

Nest plot type and treatment and number of nests	Number of nests that hatched	Percent eggs that hatched in each treatment	Hatching percentage (range)	Incubation time in days
2006				
Unshaded loamy-sand (5)	5	55.2 ± 7.0	13.0–100	71.8 ± 2.4
Shaded loamy-sand (5)	2	11.1 ± 10.2	0–31.7	83.5 ± 15.5
Unshaded sand (5)	3	30.6 ± 20.2	0–100	84.3 ± 8.8
Shaded sand (5)	0	0	—	—
Unshaded dredge (5)	0	0[b]	—	—
Shaded dredge (5)	0	0[b]	—	—
Natural reference (5)	3	53.6 ± 17.1[a]	0–100	81.3 ± 0.7
All unshaded treatments (15)	8	26.6 ± 12.2	0–100	75.0 ± 5.1
All shaded treatments (15)	2	3.4 ± 1.3	0–31.7	84.3 ± 8.8
2006 total (35)	13	21.6 ± 10.7	0–100	78.9 ± 3.3
2007				
Unshaded loamy-sand (6)	6	85.3 ± 6.3	66.7–100	80.0 ± 4.5
Shaded loamy-sand (6)	3[d]	63.4 ± 8.4	26.7–60.0	88.0 ± 1.7
Unshaded sand (6)	6	65.4 ± 13.2	7.1–88.6	86.5 ± 2.7
Shaded sand (6)	3[d]	41.4 ± 9.4	0–88.9	88.6 ± 2.9
Unshaded dredge (aged) (6)	6	59.4 ± 10.2	18.2–75.0	90.3 ± 2.8
Shaded dredge (aged)[c] (6)	4	41.6 ± 11.3	0–100	99.3 ± 2.5
Natural reference nests (8)	8	70.4 ± 12.1	30.8–100	86.4 ± 3.1
All unshaded treatments (18)	18	70.1 ± 8.4	7.1–100	85.6 ± 2.1[a]
All shaded treatments (18)	10	47.6 ± 11.3	0–100	92.2 ± 1.8
2007 total (44)	36	55.6 ± 9.7	0–100	88.4 ± 1.3

All nest treatments types were analyzed using a single factor ANOVA ($P < 0.05$) and Tukey HSD post-hoc test. In 2006 there were 5 nests in each treatment and 5 natural nests as references or controls. In 2007 there were 6 nests in each treatment and 8 natural nests. Data are presented as means (± SE). Natural nests[a] had a significantly higher hatching percentage (ANOVA, $F = 5.80$, $P = 0.01$) than all shaded nest treatments combined in 2006. All combined unshaded nest treatments in 2007[a] had a significantly lower incubation time (days) than all combined shaded nest treatments (ANOVA, $F = 6.57$, $P = 0.03$). [b]Both treatments produced no embryo development past the first third stage of development. [c]Dredge soil was aged 1 year at the study site and used in 2007. [d]Two nests in the shaded sand treatment and 3 nests in the shaded loamy-sand treatment were predated and not used as part of the analysis.

dredge soil as a nesting substrate equivalent to that of natural sand or loamy-sand for diamondback terrapins.

In the 50 years since North Sedge Island was created from deposited sediments from Barnegat Bay, the soil has aged to become a very successful substrate for nesting diamondback terrapins. Similarly, diamondback terrapins in Jamaica Bay on Long Island New York nest primarily on dredge-filled locations (Feinberg & Burke 2003). Terrapins in the Patuxent River on Chesapeake Bay, Maryland also nest on old dredge-filled areas (Roosenburg *et al*. 2003; Roosenburg & Kendall 2004). It is not known how long a dredge soil must age before it is able to support successful nesting. However, it appears that this time is much closer to 1 year than 50 years.

In addition to salinity, another problem with early nesting on sediments may be the presence of contaminants in the dredge soil. There is little information on the levels of organic and inorganic contamination of sediments in Barnegat Bay. However, snapping turtles eggs are sensitive to organic contaminants (Bell *et al*. 2005; Van Meter *et al*. 2005) and we found that both diamondback terrapins and their eggs are contaminated with flame retardants (polybrominated diphenyl ethers), polychlorinated biphenyls and other persistent organic chemicals in Barnegat Bay (Basile *et al*. 2010). There-

fore, some of the variation in hatching success could be due to contamination of the sediments or the eggs themselves. Other factors may include variations in environmental temperature and rainfall.

Our experiments were constrained by the availability of space on the island to install artificial incubation plots and the availability of clutches of diamondback terrapin eggs as experimental units. Ideally, we would have had several plots for each treatment and several clutches in each plot to ensure replication. However, neither the space available nor the number of clutches we could collect allowed this. We were cognizant of the danger of pseudoreplication, as discussed by Hurlbert (1984), and the need to limit 'nondemonic intrusion' in our experiment. However, we were also aware of the concerns of Oksanen (2001) that hypothesis testing may often lack desired levels of replication but is still valid for addressing questions involving large-scale systems, and the subsequent arguments between Hurlbert (2004) and Oksanen (2004) on this subject.

Nest temperatures

Nest temperatures were lower in year 2 (2007) than in year 1 (2006). Nests did not heat up higher than the surrounding soil, as occurs in sea turtle nests (Wallace *et al*. 2004). In both years, nests in shaded dredge soil had the lowest mean temperatures (Fig. 2). Lower temperatures in shaded nests caused significantly longer incubation times than those in reference nests in 2006 and unshaded nests in 2007. In 2006, nests in unshaded loamy-sand had the highest mean temperatures, while nests in unshaded dredge soil had the highest mean temperatures in 2007.

In general, nest temperatures in all treatments were below the pivotal temperature in both years so that most or all hatchlings were males in each nest. Only the eggs at the top of the unshaded nests had temperatures at or above the pivotal temperature to produce female hatchlings (Fig. 3a–e). There was a greater difference in nest temperatures between treatments at the 8 cm depth with less variation between treatments at the bottom 16 cm nest depth (Fig. 3a–d). Unshaded loamy-sand nest temperatures were higher than all other treatments at all depths and significantly higher than the shaded sand and shaded dredge soil at the 12 cm nest depth, and shaded sand at the 16 cm nest depth. Similar variation in nest temperatures occurs in snapping turtle nests in New Jersey, although temperatures are generally higher in those nests, which are laid inland at the Great Swamp Wildlife Refuge (Wilhoft *et al*. 1983). We also found an inverse relation between mean nest temperature and incubation time, which generally occurs with turtles (Packard *et al.* 1987; Packard & Packard 2000; Miller & Dinkelaker 2008).

Hatching success and incubation time

Hatching success was higher in all types of incubation soils in year 2 (2007) than in year 1 (2006). The nests in dredge soil that had aged 1 year (i.e. in year 2) now produced hatchlings, and those in unshaded sand also produced hatchlings. There were no flood events in 2007, which enabled embryos developing slowly in cool shaded nests to survive until hatching. Incubation times were generally longer in 2007 than 2006. It is not surprising that there were differences in hatching success and incubation time between the 2 years because climatic differences are common between years and differences in hatching success between years has been reported for other turtles (Santidrián Tomillo *et al*. 2009).

The inclusion of natural reference nests as controls allowed us to determine that differences in hatching success between years was due to a difference in natural conditions between years, wetter conditions and cooler temperatures, as opposed to treatment effects of soil differences and shading. Data from these nests suggest that the aging of the dredge soil was important in making it a more suitable substrate for diamondback terrapin egg incubation.

The 50% shade treatment reduced hatching success by lowering temperatures, which lengthened incubation time and exposed the developing embryos to environmental conditions, such as flooding, which killed them. In addition, hatching success in some natural reference nests were reduced because of root growth into the nests from surrounding vegetation. Nests in treatment plots did not have this problem because roots were prevented from growing into these nests. These data support the habitat suitability model of Palmer and Cordes (1988) that states that excessive shade reduces the nest success of diamondback terrapins. With the introduction of *Phragmites* sp. in many coastal areas, along with continued rebuilding of structures adjacent to locations that serve as terrapin nesting sites, shade will continue to play a role in incubation time and hatching success.

CONCLUSIONS

Uncontaminated dredge soil may provide suitable nesting substrate for diamondback terrapins after allow-

ing washout of salts. If used to construct islands, dredge soil can provide new nesting sites with reduced access to mammalian predators compared to mainland sites. Any substrate used to create nesting areas for estuarine turtles should be first analyzed for contaminants and allowed to age for 1 or more years to remove salt.

Unshaded loamy-sand soil is the most suitable nesting substrate for diamondback terrapins in Barnegat Bay. Nest sites need to be kept unshaded in New Jersey to avoid low incubation temperatures that will delay development, increase risks of embryo death and skew sex ratios of hatchlings in favor of males. Delayed emergence may also result in increased death due to exposure to flooded soil conditions because Barnegat Bay is prone to northeastern storm patterns, which cause flooding of bay beach areas.

The experimental approach used in this study will be useful for assessing whether other mitigation efforts, such as beach renourishment (i.e. restoration of nesting beaches with sand taken from the ocean bottom), will be successful for sea turtles.

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