A review of environmental conditions along the coastal range of the Diamondback terrapin, *Malaclemys terrapin*

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ABSTRACT — The Diamondback terrapin, *Malaclemys terrapin*, is distributed along the east coast of North America from Cape Cod, Massachusetts to Corpus Christi Bay, Texas. Six characteristic sections occur along this narrow coastal range, and the individual ranges of the seven subspecies of *M. terrapin* correspond closely to them. From north to south and west these are the Embayed Section (*M. t. terrapin*), Sea Island Section (*M. t. centrata*), Floridian Section (*M. t. tequesta* in the north, *M. t. rhizophorarum* in the mangrove thickets of the Florida Keys), East Gulf Coast Section (*M. t. macrospilota*), Mississippi Alluvial Plain Section (*M. t. pileata*), and West Gulf Plain Section (*M. t. littoralis*). Each section is described using the following environmental factors: the underlying geology and geological history, beach conditions, major inflowing rivers, inshore and beach vegetation, ocean currents, tides and wave action, and air and water temperatures. A discussion is presented of the most important of these, in regards to possible influence on subspeciation (geological features and history, environmental temperatures, tidal ranges, and the mangrove vegetation of southern Florida and the Florida Keys).

THE Diamondback terrapin, *Malaclemys terrapin* (Testudines: Emydidae) occupies a narrow North American coastal range that extends from Cape Cod, Massachusetts, to Corpus Christi Bay, Texas, and includes the Florida Keys (Conant and Collins, 1998; Ernst and Bury, 1982; Ernst et al., 1994). It occupies various habitats along the edge of the coastal plain, such as salt marshes, brackish estuaries and lagoons, tidal creeks and flats, and sounds behind barrier islands (Ernst et al., 1994; Palmer and Cordes, 1988).

Within this range, seven subspecies are currently recognized (Ernst and Bury, 1982): the Northern diamondback terrapin, *Malaclemys terrapin terrapin*, ranges along the Atlantic Coast from Cape Cod, Massachusetts to Cape Hatteras, North Carolina; the Carolina diamondback terrapin, *M. t. centrata*, is found on the Atlantic Coast from Cape Hatteras to northern Florida; the Florida East Coast diamondback terrapin, *M. t. tequesta*, occupies the Atlantic Coast of Florida to the Keys; the Mangrove diamondback terrapin, *M. t. rhizophorarum*, lives on the Florida Keys; the Ornate diamondback terrapin, *M. t. macrospilota*, ranges north from Florida Bay in the south along the Gulf Coast to Mobile Bay; the Mississippi diamondback terrapin, *M. t. pileata*, is found from Mobile Bay west along the Gulf Coast to western Louisiana; and the Texas diamondback terrapin, *M. t. littoralis*, ranges from western Louisiana to Corpus Christi Bay, Texas. Zones of intergradation occur where the various subspecific ranges meet (Ernst and Bury, 1982; Ernst et al., 1994).

It is interesting that the subspecific ranges correspond closely to the six characteristic sections of the North American Coastal Plain described by Thornbury (1965). From north to south and west these are the Embayed Section, Sea Island Section, Floridian Section, East Gulf Coast Section, Mississippi Alluvial Plain Section, and West Gulf Plain Section. The six sections exhibit somewhat different biological, geological and oceanographic characters, which possibly played roles in the evolution of the observed subspecific ranges within *M. terrapin*.

METHODS

In this paper we examine and describe the characteristics of each of Thornbury's six sections as presented in Duncan & Duncan (1987), Kumpf et al. (1999), Myers & Ewel (1990), and Thornbury (1965), and several primary sources. The major environmental factors examined for each section are those that probably play major roles in shaping the biology of the species. These are as follows:

Underlying Geology and Geological History. Geology provides the topographic features of the coastal range of *M. terrapin*. As such, it affects the path of ocean currents, tidal range, beach depth, and the plants present.

Beach Conditions. Beaches provide nesting habitat for the turtle. Sand beaches are preferred, although some beaches contain gravel, and others are almost nonexistent due to rocky outcrops. The beaches near Cape Cod are generally narrower than those farther south.

Major Rivers. The major watersheds entering the section provide varying amounts of freshwater, depending on the upland area drained, season and local storms. *M. terrapin* and some of its prey species depend on freshwater inflow to lower the salinity of the coastal waters. The salinity of ocean water, approximately 35 parts per thousand, varies according to the temperature, degree of evaporation, and the amount of freshwater influx (Zottoli, 1978). The turtle will acclimate to high salinity concentrations, but can not withstand, especially hatchlings, permanent exposure to seawater (Bels et al., 1995; Bentley et al., 1967; Cowan, 1981; Davenport & Macedo, 1990; Dunson, 1970, 1985; Gilles-Baillien, 1973a, 1973b, 1973c; Robinson & Dunson, 1976). Rivers also provide the nutrients and trace elements necessary for many of the prey species of *M. terrapin*, and molluscan and crustacean breeding areas are more intense in estuaries or near the mouths of major rivers (Kumpf et al., 1999).

Inshore and Beach Vegetation. Inshore vegetation provides foraging areas for all life stages and hiding places for hatchlings and juveniles. Beach vegetation provides nesting habitat and protection from the sun and predators during nesting.

Ocean Currents. These currents, depending on the source and direction of flow, are largely responsible for the temperature of the water along the shore. The rapidity of inshore currents may make it dangerous for *M. terrapin* to move along the shoreline.

Tides and Wave Action. Malaclemys terrapin must nest above the high tide line, and extreme high tides and severe wave action can erode nesting beaches, destroy established nests, or alter foraging habitat. Waves also cause turbidity, the amount of which may affect prey species. Presented tidal data are from the United States Department of Commerce (1987).

Air and Water Temperatures. Both temperatures vary with season and with latitude. Generally, temperatures average cooler in the north and warmer in the south, and may cause northern populations to hibernate in the winter (Lawler & Musick, 1972; Yearicks et al., 1981). These affect both daily and annual cycles of activity and have a profound effect on successful nesting. Incubation temperatures may also affect the sex ratio of hatchlings. *Malaclemys terrapin* practices temperature-dependent sex determination; incubation temperatures of 24–29°C produce almost all males, eggs incubated at 30°C produce only females (Ewert & Nelson, 1991; Sachsse, 1984). Seasonal temperature data were obtained from two websites:

www.nws.noaa.gov/climatex.html, and
www.usatoday.com/weather/climate/usa.

RESULTS

Section Descriptions

The Embayed Section. Thornbury's (1965) Embayed Section, ranging from Cape Cod, Massachusetts, to a little south of the Neuse River in North Carolina, contains many estuarine embayments that divide the Atlantic Coastal Plain into several peninsular tracts, and an inner lowland on lower Cretaceous Raritan clays. Offshore sandbars are particularly common in the north. This section corresponds to the range of *M. t. terrapin*. Its most outstanding geomorphic characteristics are related directly or indirectly to the most recent submergence of the Atlantic Coastal Plain (greater in the north than in the south) caused by the weighing down of northeastern North America by Pleistocene glaciation, and to the subsequent postglacial rise in sea level upon return of large volumes of melted ice runoff to the oceans. Beaches in New England and around Cape Hatteras are rather narrow, but all others are fairly broad.

The major freshwater drainages entering the section from north to south are the Narragansett Bay complex; Connecticut River; Hudson River; Delaware River and Bay; Chesapeake Bay complex, including the Susquehanna, Potomac and James rivers; Chowan River emptying into Albemarle Sound; Pamlico River and Sound; and Neuse and Cape Fear rivers. These waterways, depending on upland rainfall, may add much freshwater to the coastal Atlantic Ocean, and their mouths and estuaries are very productive zones for the important mollusk and crustacean prey of *M. t. terrapin*.

Algae cling to the more rocky shores of New England; these are productive areas for snails (*Littorina* sp.), an important food source. Farther south offshore seagrass (*Cymodocea filiforme, Halodule wrightii, Thalassia testudinum*) beds are more numerous, providing habitat for crabs (*Callinectes* sp., *Gelasimus* sp., *Sesarma* sp., *Uca* sp.), small bivalves (*Anomalocardia cuneimens, Gemma gemma, Macoma* sp., *Mya arenaria, Mytilus edulis, Tagelus* sp.), snails (*Littorina* sp., *Melampus* sp., *Nassarius obsoletus*), and marine annelids (*Nereis* sp.) (Allen & Littleford, 1955; Coker, 1906; Ernst et al., 1994; Mitchell, 1994; Palmer & Cordes, 1988; Roosenburg, 1994; Roosenburg et al., 1999; Whitelaw & Zajac, 2002). Most populations of *M. terrapin* are associated with saltmarshes, in which the predominate vegetation is Cordgrass (*Spartina alterniflora*). Beach vegetation often includes *Ammophila breviligulata, Myrica pensylvanica* and *Phragmites* sp. (Duncan & Duncan, 1987; Palmer & Cordes, 1988).

The New England coast from Cape Cod, Massachusetts, to about the eastern tip of Long Island, New York is influenced by the cold Labrador Current which originates in the Arctic (Thurman, 1994). From Long Island south to Florida, the Atlantic coast is bathed by the warm Gulf Stream that originates in the Caribbean Sea as the Caribbean Current. Mean water temperatures in January vary from 4.4°C at Boston Harbor, Massachusetts, to 9.4°C at Cape Hatteras, North Carolina, and from 18.9°C and 25.0°C in July for the two sites, respectively. Northern coastal waters become cold enough in winter to stun marine turtles, often with fatal results (Morreale et al., 1982). Mean air temperature corresponds accordingly from north to south, and may be so cold as to force *M. terrapin* to hibernate as far south as Virginia (Lawler & Musick, 1972; Yearicks et al., 1981).

Tides, and subsequent wave action, vary within the section. Average tide ranges on 15th June (the turtle's nesting season) for the section vary from a high of 2.9 m at Boston, Massachusetts, to a low of 0.7 m at Hampton Roads, Virginia. The entire section is subject to occasional hurricane events during the summer and fall which may cause much beach erosion and damage to tidal marshes.

The Sea Island Section. This region covers the youthful to mature terraced coastal plain from about the Neuse River, North Carolina, south to northern Florida. It contains fewer estuaries than the Embayed Section but has a low border of barrier islands. It covers most of the range of *M. t. centrata*. The amount of submergence is less than that north, and the drowned mouths of its rivers are shallower. Beaches are narrow around Cape Hatteras but broad south of there. Offshore sandbars are less common and are replaced by a series of coastal sea (barrier) islands. The underlying geology is similar to the Embayed Section, but the Miocene rocks of the sea islands do not extend to the inner margin of the Coastal Plain, where they are replaced by Eocene and Cretaceous rocks. Near the beaches is a tract of young terraces, largely unmodified by stream erosion, with extensive swamps on them. The chain of sea islands is separated from the parallel mainland by salt marshes, passes, tidal creeks ('guts'), sounds or lagoons which are good feeding areas for the turtles. Three types of islands are present along the coast (Zeigler, 1959): erosion remnant islands, marsh islands, and beach ridge islands; and the islands serve as important nesting sites for the turtles.

The prevailing rivers can be dated to either the pre-Wisconsinian (Santee, Edisto, Savannah, Saltilla) which drain from the Piedmont across the coastal plain, or the post-Wisconsinian (Midway, Newport, Turtle) which head near the escarpment and form the inner boundary of the Pamlico terrace (Zeigler, 1959).

Some seagrass beds (*Thalassia testudinum*) occur offshore. Beach vegetation is similar to that of the Embayed Section, but palmetto (*Sabal* sp.) is present on some barrier islands and inshore borders of continental beaches. Animals reportly consumed by this section's *M. terrapin* include most of those invertebrates previously listed for the Embayed Section, and the bivalves (*Geukensia demissa*), crabs (*Uca pugnax*), and small adult fishes (Atlantic Silversides, *Menidia menidia*) (Middaugh, 1981; Tucker et al., 1997).

Fed by the Gulf Stream, the offshore waters are relatively warm. Mean January water temperatures vary from 9.4°C at Cape Hatteras to 10.6°C at Savannah, Georgia; mean July water temperatures at these two sites are 25.0°C and 28.3°C, respectively. Mean air temperatures in January and July at these two sites are 7.1°C and 9.4°C and 25.8°C and 27.8°C, respectively. Summer and fall hurricanes are not infrequent in this section. Normally, however, the tidal range is from about 1.3–2.3 m.

The Floridian Section. This coastal region extends along the Atlantic coast of Florida. Its northern boundary blends into the southern Sea Island Section; however, it has certain distinctive features of its own. It is comprised of a recently emerged (Eocene to Pleistocene) terrace with carbonate rocks and extensively developed karst features. Its sandy beaches are usually broad. Offshore sandbars or limestone keys (small islands) border much of the coast, and its southernmost area is a series of Atlantic Coastal Ridge limestone keys. Lagoons lie behind the sandbars. Prominent tidal marshes and swamps are present, and extensive marine terraces occur on the east and south around the higher central peninsula of Florida (Thornbury, 1965). The edge of the continental shelf is only a few miles east off the coast. Major freshwater drainages of the region are the St. Johns and Indian rivers and the Everglades. This section corresponds closely with the ranges of *M. t. tequesta* and *M. t. rhizophorarum*.

Vast tidal saltmarshes of Cordgrass (*Spartina alterniflora*, *S. patens*), Eelgrass (*Zostera* sp.), Saltwort (*Salicornia* sp.), brown algae (*Ascophyllum nodosum*, *Fucus vesiculosus*), and mats of green algae (*Cladophora* sp., *Enteromorpha* sp.) and blue-green Algae (*Calothrix* sp., *Lyngbya* sp.) may be present (Duncan & Duncan, 1987; Zottoli, 1978). These create important crab (*Callinectes*, sp., *Sesarma* sp., *Uca* sp.), snail (*Littorina* sp., *Melampus*, sp., *Nassarius* sp.), bivalve (*Macoma* sp., *Mytilus* sp.) and annelid worm (*Nereis* sp.) habitat (Montague & Wiegert, 1990; Zottoli, 1978).

The predominant vegetation changes in the southernmost parts, especially the Florida Keys, where extensive stands of mangrove occur; *Rhizophora mangle* is the most common species, but *Avicennia germinans* and *Laguncularia racemosa* may also be present along the shoreline. The mangroves create a new habitat, and their rich invertebrate and vertebrate faunas are much different than those of the more northern portion of the Floridian Section (Odum & McIvor, 1990; Zottoli, 1978). This is the habitat of *M. t. rhizophorarum*. Unfortunately, prey reports for this subspecies are generalized, small bivalves (possibly, *Anomalocardia cunimeris*, *Mya* sp. and *Mytilus* sp.) and snails (possibly *Littorina* sp., *Melampus* sp. and *Nassarius* sp.), but one was observed feeding on a small dead fish (Red snapper, *Lutjanus compectanus*; Wood, 1992). Immediately north and west of the Florida Keys, *M. t. rhizophorarum* intergrades with *M. t. tequesta* and *M. t. macrospilota*, respectively (Ernst, pers. obs.).

Climate of the entire Floridian Section is influenced by the warm Gulf stream which flows offshore. January mean water temperatures vary from 10–11°C in the north to 21.7°C at Miami, Florida and 20.6°C at Key West, Florida. Correspondingly, mean January air temperatures at these sites are 9–10°C, 19.6°C and 15.6°C, respectively. July mean water and air temperatures at these three sites are 27–28°C and 27–28°C;

30.6°C and 28.2°C; and 30.0°C and 29.4°C, respectively.

Frequent hurricanes and tropical storms affect the section during the summer and fall. Tidal ranges in the north are 2–3 m, and at Key West, 0.4 m.

The East Gulf Coastal Plain Section. The range of *M. t. macrospilota*, is found in this region, from southwestern Florida to Mobile Bay, Alabama. Intergradation with at least *M. t. rhizophorarum* occurs in southwestern Florida (Ernst, pers. observ.). It is a youthful to maturely dissected, belted coastal plain with a series of alternating cuestas (formations with a cliff on one side and a gentle slope on the other) and lowlands. Coastwise terraces are present along the outer margin (Thornbury, 1965). There is an increase westward in number and thickness of the Cretaceous and Eocene formations, resulting in a widening of the coastal plain, causing a sharp contrast with the inland Piedmont. The 'Fall Line' is distinct on its rivers. The greater part of this section consists of belted Pleistocene coastal plain, including a series of lowlands on weak rock, usually limestone or clay shales, bordered seaward by cuesta scarps and dip slopes on stronger, commonly sandstone, rocks. Inland, adjacent to this is a narrow stripe of coastwise terraces. The major rivers of this region, from south to north, include the Caloosahatche, Peace, Withlacoochee, Waccasassa, Suwannee, Auchilla, Ochlackonee, Apalachicola, Choctawhatchee, Escambia, Tensaw, and Mobile.

The vegetation is rich and grades from mangroves in the south to more herbaceous plants as the coastal dunes are transversed northward. Forbs and grasses present include *Alternanthera ramosissima, Ambrosia hispida, Aristida patula, Chloris petraea, Croton glandulosus (var. floridanus), Flaveria floridana, Muhlenbergia capillaris*, and *Schizachyrium semiherbe* (Johnson & Barbour, 1990). Sea oat (*Uniola paniculata*) and *Phragmites* sp. also occur on the dunes, and *Spartina* sp. is ever present in the tidal marshes (Duncan & Duncan, 1987). Stable dunes are dominated by either small palms (*Sabel* sp.) or Gramma grass (*Bouteloua hirsuta*). The only report on the diet of *M. t. macrospilota* was that of Carr (1952) who noted that one had fed on a Pointed venus clam, *Anomalocardia cuneimeris*, but the snail genera *Littorina* and *Nassarius*, and the bivalve genera *Macoma* and *Mytilus* are also present.

The predominate offshore current is the warm Gulf Stream. Air temperatures in January average 9–10°C and in July 27–28°C; January and July water temperatures average 10–11°C and 28.5–30.0°C, respectively. The turtles seldom, if ever, are forced to hibernate in the winter. Normal tidal ranges are 0.7–1.0 m, but this section frequently experiences tropical storms and hurricanes with high wave action.

The Mississippi Alluvial Plain Section. This coastal region consists of alluvial and deltaic plains, with alluvial terraces inland and coastwise deltaic terraces along the seaside. It covers most of the range of *M. t. pileata*. Most of the deltaic area is composed of meandering branches of the Mississippi/Atchafalaya River complex, mostly formed in the last 2,000 years, but the Pascagoula and Sabine rivers contribute freshwater in the east and west, respectively. Saltmarsh and dune plants are similar to those of the preceding section; barrier islands may contain *Juncus* sp. (Duncan & Duncan, 1987; Johnson & Barbour, 1990). Cagle (1952) reported the intestinal contents of *M. t. pileata* from this section contained only 'fragments of small clams and snails'. Present are the bivalve genera *Macoma* and *Mytilus*, and the snail genera *Anomalocardia*, *Littorina* and *Nassarius*, popular prey of *M. terrapin* elsewhere.

The Gulf Stream keeps the section warm, allowing the turtles to remain active all year long. January and July mean air and water temperatures are, respectively: 9.5–15.0°C, 27.5–28.0°C; 10.6–16.0°C, 28.7–30.0°C. The normal tide range is 0.7–1.0 m, but the coast is subject to severe tropical storms and hurricanes each year.

The West Gulf Coastal Plain. This is Thornbury's (1965) most western section, and it is here that *M. t. littoralis* is found. The section's inner portion comprises a wide belted coastal plain with inconspicuous cuestas; the seaward margin is a deltaic coastal plain. This Quaternary coastal plain consists of a series of coalescing deltaic and alluvial Pleistocene terraces built by rivers; from east to west, the Sabine, Neches, Trinity, Brazos, Colorado, Lavaca Guadalupe, Nueces, and Rio Grande. These terraces decrease in age and elevation toward the sea, and each is thought to have developed during a high sea level. The western end of the section contains a series of fault systems, with the westernmost quite pronounced. Many igneous intrusions are found within the fault zone, and salt domes are more plentiful than in Thornbury's more eastern sections. Coastal vegetation resembles those of the last two sections. No specific data relating to the diet of *M. t. littoralis* has been published, but the common prey genera of bivalves and snails are present in this region.

Once again, the warm Gulf Stream bathes the region; air temperatures in January average 11–13°C and in July 28–30°C. The coastal water averages 12–14°C in January and 29–30°C in July. The region experiences several tropical storms or hurricanes each year, but normally the tidal range is 3.1–1.2 m.

DISCUSSION

The section descriptions above clearly indicate that core environmental conditions vary along the coastal range of *Malaclemys terrapin*. The most variable are geological morphology (including beach conditions), air and water temperatures, and tidal range. All sections have large rivers contributing freshwater, and the beach and tidal marsh vegetation are relatively constant regarding the major plants, with the exception of the mangrove area of southern Florida.

Diversification based on geology is supported by studies of other western Atlantic and Gulf of Mexico marine and coastal animals continuously distributed throughout the range of *M. terrapin*: Horseshoe crab (*Limulus polyphemus*; Saunders et al., 1986), Stone crab (*Menippe* sp.; Bert, 1986), Virginia oyster (*Crassostrea virginica*; Reeb & Avise, 1990), Black sea bass (*Centropristis striata*; Bowen & Avise, 1990), Menhaden (*Brevoortia tyranus, B. patronus*; Bowen & Avise, 1990), Atlantic sturgeon (*Acipenser oxyrhynchus*; Bowen & Avise, 1990), the Dusky seaside sparrow (*Ammodramus maritimus*; Lamb & Avise, 1992), and *M. terrapin* (Avise, 1992). Most of these studies used mtDNA as the primary marker of diversity within species.

Two clear clades appeared in *M. terrapin*, north and south of approximately Cape Canaveral, Florida (28° 27'N; Avise, 1992). Avise (1992) did not speculate about which geological features may have led to such distinctions, but Lamb and Avise (1992) suggested that Atlantic and Gulf Coast Diamondback terrapins may have been isolated during the late Pleistocene glaciation. However, five other species with the same split (Toadfish, *Opsanus* sp.; American oyster; Horseshoe crab; Dusky seaside sparrow; and Black sea bass) showed much higher genetic diversity, leading to the theory that the various populations of *Malaclemys* may have had more recent evolutionary contact than the other five animals (Avise et al., 1992). Because of the correlation between geological features and subspecies ranges (Thornbury, 1965), strengthened by genetic evidence, underlying geologic history may have played a role in the subspeciation within *M. terrapin*.

The air and water temperature regimes experienced by *M. terrapin* within the various geological sections may also have played some role in subspeciation. The greatest differences occur between the New England populations, adapted to the cold waters of the Labrador Current, and the southern Florida and the Gulf of Mexico populations that are adapted to the warm waters of the Gulf Stream. However, although these differences may affect the sex ratios of clutches or possibly the number of clutches a female produces each year, no pressure for subspeciation is readily apparent. Populations of *M. t. terrapin* bridge the gap between the cold New England waters and those of the warm Gulf Stream without apparent significant changes in phenotypic characters. Nevertheless, along the Gulf Coast from the Florida Panhandle to southern Texas two subspecies, *M. t. pileata* and *M. t. littoralis*, are different in both pattern and morphology (Ernst et al., 1994), although they experience almost identical temperature variation during the year.

Practically no research has been done on the effects of tides on *M. terrapin*. Females prefer to nest above the high tide line (Auger and Giovannone, 1979; Burger and Montevecchi, 1975), but how this would affect subspeciation is unknown. However, the tidal regimes, like the underlying geology, have a correlation with the subspecies ranges. Three, *M. t. macrospilota, M. t. pileata* and *M. t. littoralis*, experience noncontiguous tidal periods. Because of limited data on the tidal activity of *Malaclemys*, no firm conclusions can be made about the tide's potential effect on subspeciation. The correspondence of the three Gulf of Mexico subspecies with tidal periods mark tidal activity as a promising prospect for further study.

As noted, the only major difference in vegetation type within the ranges of the subspecies of *M. terrapin* is that of the mangrove habitat of *M. t. rhizophorarum*. The mangrove habitat may have encouraged the development of both the solid black adult carapace and bulbous keel knobs of *M. t. rhizophorarum* as camouflage; the dark monocoloration to hide it among the mangrove roots, and the knobs as mimics of the breathing pneumatophores (air roots) of the mangroves.

REFERENCES

Allen, J. F. & Littleford, R. A. (1955). Observations on the feeding habits and growth of immature Diamondback Terrapins. *Herpetologica* **11**, 77–80.

Auger, P. J. & Giovannone, P. (1979). On the fringe of existence: Diamondback Terrapins at Sandy Neck. *The Cape Naturalist* **8**, 44–58.

Avise, J. C. (1992). Molecular structure and the biogeographic history of a regional fauna: A case history with lessons for conservation biology. *Oikos* **63**, 62–75.

Avise, J. C., Bowan, B. W., Lamb, T., Meylan, A. B. & Bermingham, E. (1992). Mitochondrial DNA evolution at a turtle's pace: Evidence for low genetic variability and reduced microevolutionary rate in the Testudines. *Molec. Biol. Evol.* **9**, 457–473.

Bels, V. L., Davenport, J. & Renous, S. (1995). Drinking and water expulsion in the Diamondback Terrapin *Malaclemys terrapin*. *J. Zool., Lond.* **236**, 483–497.

Bentley, P. J., Bretz, W. L. & Schmidt-Nielson, K. (1967). Osmoregulation in the Diamondback Terrapin, *Malaclemys terrapin centrata*. *J. Exp. Biol.* **46**, 161–167.

Bert, T. M. (1986). Speciation in the Western Atlantic Stone Crabs (genus *Menippe*): The role of geological processes and climatic events in the formation and distribution of species. *Mar. Biol. Berlin* **93**, 157–170.

Bowen, B. W. & Avise, J. C. (1990). Genetic structure of Atlantic and Gulf of Mexico populations of Sea Bass, Menhaden, and Sturgeon: Influence of zoogeographic factors and life-history patterns. *Mar. Biol. Berlin* **107**, 371–381.

Burger, J. & Montevecchi, W. A. (1975). Nest site selection in the terrapin *Malaclemys terrapin*. *Copeia* **1975**, 113–119.

Cagle, F. R. 1952. A Louisiana Terrapin population (*Malaclemys*). *Copeia* **1952**, 74–76.

Carr, A. F., Jr. 1952. *Handbook of Turtles. The Turtles of the United States, Canada, and Baja California*. Ithaca, New York: Comstock Publishing Associates, Cornell University Press.

Coker, R. E. 1906. The natural history and cultivation of the Diamond-back Terrapin. *Bull. N. Carol. Geol. Econ. Surv.* **14**, 1–69.

Conant, R. & Collins, J. T. (1998). *A Field Guide to Reptiles & Amphibians: Eastern and Central North America*. 3rd ed., Expanded. Boston, Massachusetts: Houghton Mifflin Company.

Cowan, F. B. M. (1981). Short term acclimation of *Malaclemys terrapin* to saltwater. *Comp. Biochem. Physiol.* **68A**, 55–59.

Davenport, J. & Macedo, E.-A. (1990). Behavioural osmotic control in the euryhaline Diamondback Terrapin *Malaclemys terrapin*: Responses to low salinity and rainfall. *J. Zool., Lond.* **220**, 487–496.

Duncan, W. H. & Duncan, M. B. (1987). *Seaside Plants of the Gulf and Atlantic Coasts*. Washington, D.C.: Smithsonian Institution Press.

Dunson, W. A. (1970). Some aspects of electrolyte and water balance in three estuarine reptiles, the Diamondback Terrapin, American and 'Salt Water' crocodiles. *Comp. Biochem. Physiol.* **32**, 161–174.

Dunson, W. A. (1985). Effect of water salinity and food salt content on growth and sodium efflux of hatchling Diamondback Terrapins (*Malaclemys*). *Physiol. Zool.* **58**, 736–747.

Ernst, C. H. & Bury, R. B. (1982). *Malaclemys, M. terrapin.Cat. Amer. Amph. Rept.* **299**, 1–4.

Ernst, C. H., Lovich, J. E. & Barbour, R. W. (1994). *Turtles of the United States and Canada*. Washington, D.C.: Smithsonian Institution Press.

Ewert, M. A. & Nelson, C. E. (1991). Sex determination in turtles: Diverse patterns and some possible adaptive values. *Copeia* **1991**, 50–69.

Gilles-Baillien, M. (1973a). Hibernation and osmoregulation in the Diamondback Terrapin, *Malaclemys centrata centrata* (Latreille). *J. Exp. Biol.* **59**, 45–51.

Gilles-Baillien, M. (1973b). Seasonal changes in organic ions in red blood cells of terrestrial and aquatic chelonia. *Biochem. Syst.* **1**, 123–125.

Gilles-Baillien, M. (1973c). Seasonal variations and osmoregulation in the red blood cells of the Diamondback Terrapin *Malaclemys centrata centrata* (Latreille). *Comp. Biochem. Physiol.* **46A**, 505–512.

Johnson, A.F. & Barbour, M. G. 1990. Dunes and maritime forests. In *Ecosystems of Florida*, pp. 429–480. Myers, R. L. & Ewel, J. J. (Eds.). Orlando: University of Central Florida Press.

Kumpf, H., Steidinger, K. & Sherman, K. (Eds.). (1999). *The Gulf of Mexico Large Marine Ecosystem. Assessment, Sustainability, and Management.* London: Blackwell Science.

Lamb, T., & Avise, J. C. (1992). Molecular and population genetic aspects of mitochondrial DNA variability in the Diamondback Terrapin, *Malaclemys terrapin. J. Herpetol.* **83**, 262–269.

Lawler, A. R. & Musick, J. A. (1972). Sand beach hibernation by a Northern Diamondback Terrapin, *Malaclemys terrapin terrapin* (Schoepff). *Copeia* **1972**, 389–390.

Middaugh, D. P. (1981). Reproductive ecology and spawning periodicity of the Atlantic Silverside, *Menidia menidia* (Pisces): Atherinidae). *Copeia* **1981**, 766–776.

Mitchell, J. C. (1994). *The Reptiles of Virginia*. ashington, D.C.: Smithsonian Institution Press.

Montaque, C. L. & Wiegert, R. G. 1990. Salt marshes. In *Ecosystems of Florida*, pp. 481–516. Myers, R. L. & Ewel, J. J. (Eds.). Orlando, Florida: University of Central Florida Press.

Morreale, S. J., Meylan, A. B., Sandove, S. S. & Standora, E. A. (1982). Annual occurrence and winter mortality of marine turtles in New York waters. *J. Herpetol.* **26**, 301–308.

Myers, R. L. & Ewel, J. J. (Eds.). (1990). *Ecosystems of Florida*. Orlando: University of Central Florida Press.

Odum, W. E. & McIvor, C. C. (1990). Mangroves. In *Ecosystems of Florida*, pp. 517–548. Myers, R. L. & Ewel, J. J. (Eds.). Orlando, Florida: University of Central Florida Press.

Palmer, W. M. & Cordes, C. L. (1988). Habitat suitability index models: Diamondback Terrapin (nesting)–Atlantic Coast. *U.S. Fish & Wildlife Serv. Biological Report* **82**(10.151), 1–18.

Reeb, C. A. & Avise, J. C. (1990). A genetic discontinuity in a continuously distributed species: Mitochondrial DNA in the American Oyster, *Crassostrea virginica. Genetics* **124**, 397–406.

Robinson, G. D. & Dunson, W. A. (1976). Water and sodium balance in the estuarine Diamondback Terrapin (*Malaclemys*). *J. Comp. Physiol.* **105**, 129-152.

Roosenburg, W. M. (1994). Nesting habitat requirements of the Diamondback Terrapin: A geographic comparison. *Wetl. J.* **6**, 8–11.

Roosenburg, W. M., Haley, K. L. & McGuire, S. (1999). Habitat selection and movements of Diamondback Terrapins, *Malaclemys terrapin*, in a Maryland estuary. *Chelonian Conserv. Biol.* **3**, 425–429.

Sachsse, W. (1984). Long term studies of the reproduction of *Malaclemys terrapin centrata*. In *Maintenance and Reproduction of Reptiles in Captivity 1*, pp. 297–308. Bels, M. V. L. & Van den Sande, A. P. (Eds.). *Acta Zool. Path. Antverp.* **78**.

Saunders, N. C., Kessler, L. G. & Avise, J. C. (1986). Genetic variation and geographic differentiation in mitochondrial DNA of the Horseshoe Crab, *Limulus polyphemus*. *Genetics* **112**, 613–627.

Thornbury, W. D. (1965). *Regional Geomorphology of the United States*. New York: John Wiley & Sons.

Thurman, H. V. (1994). *Introductory Oceanography*. New York: MacMillan Publishing Company.

Tucker, A. D., Yeomans, R. & Gibbons, J. W. (1997). Shell strength of mud snails (*Hyanassa obsoleta*) may deter foraging by Diamondback terrapins (*Malaclemys terrapin*). *Am. Midl. Nat.* **138**, 224–229.

United States Department of Commerce. (1987). *Tide Tables 1988: High and Low Water Predictions. East Coast of North and South America Including Greenland*. National Oceanographic and Atmospheric Administration. Washington, D.C.: U.S. Government Printing Office.

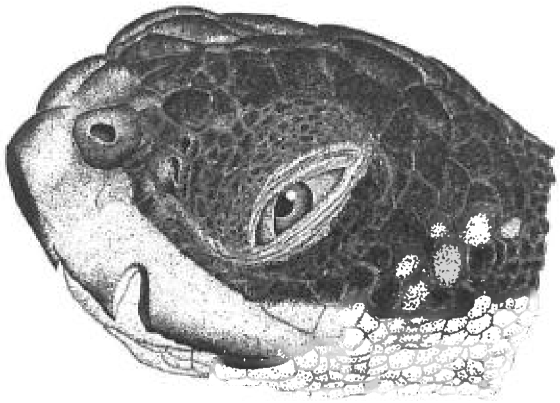
Whitelaw, D. M. & Zajac, R. N. (2002). Assessment of prey availability for Diamondback Terrapins in a Connecticutt salt marsh. *NEast. Nat.* **9**, 407–418.

Wood, R. C. (1992). Mangrove Terrapin, *Malaclemys terrapin rhizophorarum* Fowler, Family Emydidae, Order Testudines. In *Rare and Endangered Biota of Florida. Volume III. Amphibians and Reptiles*, pp. 204–299. Moler, P. E. (Ed.). Gainesville, Florida: University Press of Florida.

Yearicks, E. F., Wood, R. C. & Johnson, W. S. (1981). Hibernation of the Northern Diamondback Terrapin, *Malaclemys terrapin terrapin*. *Estuaries* **4**, 78–80.

Zeigler, J. M. (1959). Origin of the sea islands of the southeastern United States. *Geographic Review* **49**, 222–237.

Zottoli, R. (1978). *Introduction to Marine Environments*. 2nd ed. Saint Louis, Missouri: C. V. Mosby Company.



Head detail of hatchling Leatherback sea turtle, *Dermochelys coriacea*. Reproduced with kind permission of the artist/author, Julian C. Lee, from *The Amphibians and Reptiles of the Yucatán Peninsula* (Cornell University Press, 1996).