6 Habitat Utilization and Migration in Juvenile Sea Turtles

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CONTENT

6.1 INTRODUCTION

Sea turtles are basically creatures that spend their entire lives in marine or estuarine habitats. Their only remaining reptilian ties to terrestrial habitats are for nesting and restricted cases of basking. Consequently, physiological, anatomical, and behavioral adaptations have evolved largely in response to selection in the aquatic environment,

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and sea turtles share many common elements with larger fishes and cetaceans in their habitat utilization and migrations. A generalized habitat model may be constructed for sea turtles based on ontogenetic stages (Figure 6.1):

1. Early juvenile nursery habitat (usually pelagic and oceanic).
2. Later juvenile developmental habitat (usually demersal and neritic).
3. Adult foraging habitat.
4. Adult inter-nesting and/or breeding habitat.

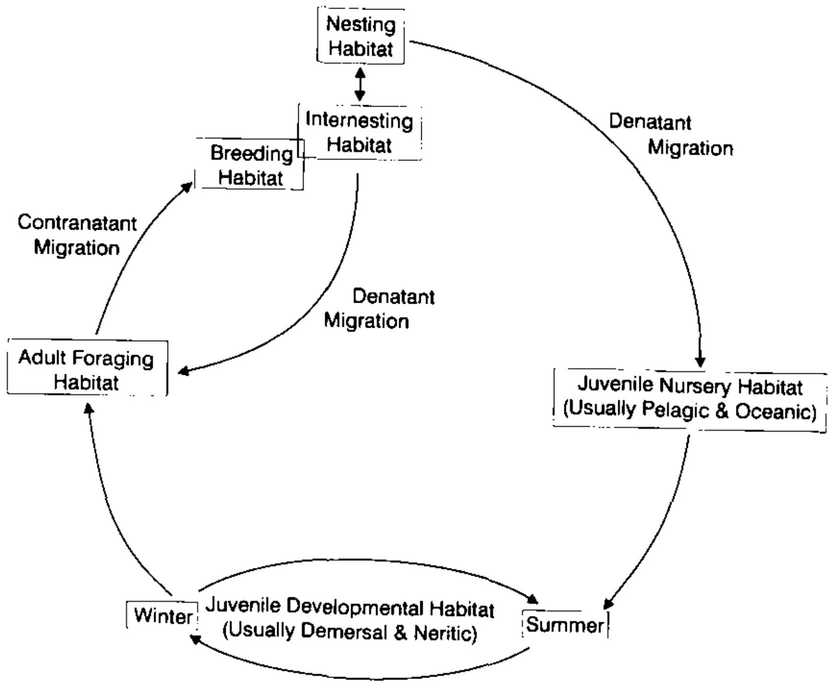

FIGURE 6.1 Conceptual model of ontogenetic habitat stages in sea turtles.

All sea turtles move immediately to the sea after hatching, usually after dark, and swim actively offshore. Most then undertake a mostly passive, denatant (sensu Jones)[1] migration drifting pelagically in oceanic gyre systems. Subsequently, after a period of years, these now larger and older juveniles actively recruit to demersal neritic developmental habitats in the tropical and temperate zones. Demersal juveniles in some temperate zone populations make seasonal migrations to foraging areas at higher latitudes in summer and lower latitudes in winter (see below) while those in tropical areas are more localized in their movements. When approaching maturity, pubescent turtles move into adult foraging habitats. In some populations adult habitats are geographically distinct from juvenile developmental habitats;[2-4] in others they may overlap or coincide.[5,6] Upon maturity as the nesting season approaches adults make a contranatant migration toward the nesting beaches. Most mating occurs at poorly defined courtship areas that are close to the nesting beaches relative to the distant foraging areas. After mating the females move to their respective nesting beaches.[7,8] Courtship areas may be directly off the nesting beaches,[9] or remote from the beaches,[10] depending on the population. During the nesting season, females usually become resident in the internesting habitat in the vicinity of the nesting beach.[11] The focus of the present paper is habitat utilization and migration of juvenile sea turtles and nursery and developmental habitats.

6.2 METHODS

Although some authors have attempted to define objective size catagories of sea turtles by ontogenetic stages,[12] terminology for juvenile life history stages has been varied and often imprecise. The words hatchling and neonate have been widely used and clearly refer to animals that have quite recently hatched. The term post-hatchling obviously refers to individuals that are larger and older than a hatchling, but the size (or age) at which a hatchling becomes a post-hatchling varies by author and is ill defined. Even less well defined is the size or age when a post-hatchling becomes a juvenile or an "immature" or a "yearling", and when this stage becomes the subadult stage. Many authors have used the term subadult to refer to all juvenile turtles that have recruited to demersal, neritic habitats. This term is a misnomer for animals that may not mature for 15 to 45 years. Critical ontogenetic habitat shifts such as that from the pelagic nursery to the demersal developmental habitats occur in different species or even populations at different ages and sizes. For instance, *Eretmochelys imbricata* and *Lepidochelys kempi* usually make this shift at a smaller size (and younger age) than *Chelonia mydas*, which in turn makes this shift at a smaller size (and younger age), than does *Caretta caretta* (see below). Even within *C. caretta*, western North Atlantic populations make the shift from the juvenile pelagic habitat to demersal habitat at a smaller size (and younger age) than do western South Pacific populations (see below). The adult stage would seem to be easily defined (i.e., minimum size of nesting females and clearly mature males with large dimorphic tails); however, large numbers of *Chelonia mydas*, *Caretta caretta*, and *E. imbricata* that are larger than the minimum breeding size of the nesting females recorded on the beaches are still sexually immature and hence incapable of breeding.[5,6,13] Sexually immature turtles that are within the size of breeding turtles also occur with *L. kempii* and *Dermochelys coriacea*.[14] The average female commences to breed at a size only slightly smaller than the average size of the entire nesting population.[15] Consequently, the size and age range for transition from the juvenile to the adult stage is usually broad within most populations. In order to avoid further confusion concerning ontogenetic stages, we have restricted our use to the terms hatchling (or neonate), juvenile, and adult. Hatchlings refer to sea turtles that have quite recently hatched and are still on the nesting beach or at sea only until they commence to feed (i.e., while they are dependent on the internalized yolk sac).[16] The at-sea period for the hatchling is short (days), so that size is still essentially similar to that at hatching. Juveniles include turtles that have commenced feeding, but have not attained sexual maturity. The term adult will be used to describe all turtles that have attained adult size, i.e., that are larger than minimum breeding size. Adult-sized turtles within feeding areas will include a mixture of sexually immature and mature animals, unless maturity is assessed via direct observation of the gonads and associated ducts or from a past breeding history. We will reference other terms when used by other authors. The size of sea turtles is usually given as curved carapace length (ccl, length measured with tape over the curvature of the back) or straight carapace length (scl, straight line length of the carapace measured with calipers). When the type of measurement has not been designated in the literature we have referenced it as undesignated length (ul).

6.3 EARLY JUVENILE NURSERY HABITATS

After emerging from the nest, neonate sea turtles crawl down the beach, swim into the waves, and disappear offshore, not to reappear in the neritic habitat until they have grown to be much larger juveniles.[17] This largely unknown stage of sea turtle life history became known as the "lost year". Carr[18] noted that the lost year puzzle was the "most substantial of all obstacles to understanding the ecology of sea turtles", but he also suggested that the lost year was spent in pelagic, oceanic habitats. Evidence for that hypothesis has been slowly, but steadily accumulating.

6.3.1 LOGGERHEAD, *CARETTA CARETTA*

The early juvenile nursery habitat of the loggerhead has been best documented of all sea turtle species. The occurrence of small loggerheads far at sea often in close association with drifting *Sargassum* within the North Atlantic Ocean has been known for several years.[19,20] Several authors have noted the potential importance of oceanic convergence zones and major gyre systems in the distribution and local concentration of juvenile loggerheads.[21-24] Recent studies have provided strong support for these hypotheses. Witherington[25] has documented substantial numbers of neonate loggerheads along the western edge of the Gulf Stream in convergence zones actively feeding among *Sargassum*. Similarly, Richardson and McGilivary[26] recorded post-hatchling loggerheads actively feeding (on aeolian transported insects) in *Sargassum*. Behavioral studies in the laboratory[27,28] have shown that neonate loggerheads are attracted to floating seaweed and hide in the weed motionless for long periods of time. (The hatchlings' basic brown and tan coloration renders them cryptic in the *Sargassum* habitat.) Carr et al.[21] hypothesized that neonate loggerheads from the southeastern U.S. swam offshore and entered the Florida current (subsequently the Gulf Stream) where they became entrained and were passively transported across the North Atlantic to the eastern Atlantic. Then they drifted south in the North Atlantic gyre past the Azores and the Canary Islands and subsequently returned with the North Equatorial Current back into the western Atlantic (Figure 6.2). He based this hypothesis on the small size classes (≤40 cm scl) of loggerheads recorded stranded in the eastern Atlantic.[29] (These "lost year" size classes are rare in the western Atlantic). Witham[23] had estimated that a young sea turtle could make this trip in about a year, but other evidence suggests it lasts longer. Several recent papers[30-33] have shown that young loggerheads successfully make trans-Atlantic cross-

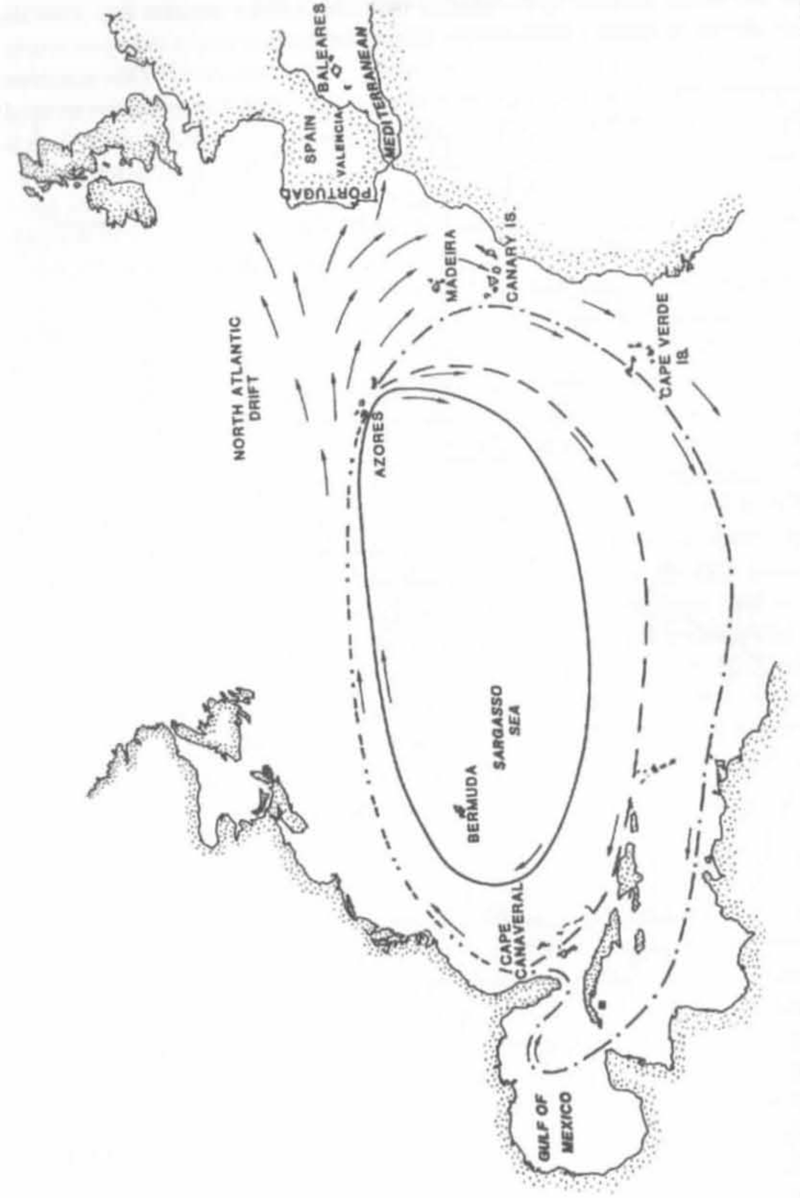

FIGURE 6.2 North Atlantic gyre showing potential oceanic transport routes for pelagic juvenile sea turtles. (After Carr, 1987.)

ings. Juvenile loggerheads have been reported to be common and often captured incidentally in longline fisheries around the Azores and Madeira.[29,34-36] Lohmann et al.[37] (see Chapter 5) showed that juvenile loggerheads could use the magnetic field of the earth for navigation, and could make midcourse corrections to maintain their position in the North Atlantic gyre. Studies near the Azores suggest that juvenile loggerheads appear to spend a much longer time in the oceanic realm than previously supposed, the "lost year" more likely representing a "lost decade".[38] This assertion is supported by skeletochronological studies of pelagic juvenile loggerheads captured incidentally in oceanic driftnets in the North Pacific.[39] These turtles were 2 to 8 years old and probably originated from nesting beaches in Japan. In addition, a large pelagic feeding aggregation of juvenile loggerheads (20 to 30 cm ul) has been documented off Baja California.[10] Genetic studies have shown that these animals originated in Japanese and Australian rookeries.[40] Within the Indian Ocean, Hughes[41] has successfully plotted the dispersal of "tagged" juvenile *C. caretta* from the South African (Natal) nesting beaches by the Agulhas Current into the Indian Ocean gyre. Thus, much evidence has accumulated that loggerhead turtle populations nesting in the northwest Atlantic, West Indian, and West Pacific oceans utilize oceanic, pelagic nursery grounds, and migrate with the predominant ocean gyres from west to east for several years before returning to their western neritic foraging and nesting habitats. The duration of the pelagic stage is highly variable and probably ranges from three to at least ten years or longer, depending on the individual and ocean basin. Loggerheads as small as 25 to 35 cm (ccl) have been recorded stranded in the Chesapeake Bay (U.S.) developmental habitat.[3] These animals were probably about two to four years of age.[42] In addition, Keinath,[43] using satellite telemetry, found that head-started loggerheads released at two years of age off Virginia still exhibited the same epipelagic surfacing behavior as neonates and migrated east to the Gulf Stream. However, a head-started loggerhead released at three years of age became demersal and followed the same autumn migration pattern to the south as that followed by wild demersal juveniles from Chesapeake Bay. Thus, the ontogenetic behavioral shift from epipelagic to demersal had taken place in this individual.

6.3.2 Kemp's Ridley, *Lepidochelys kempi*

Neonate Kemp's ridleys disappear into the sea and do not reappear in the neritic zone until they have reached a length of about 20 to 25 cm (scl)[44] or at about an age of two years.[45] As their somber coloration would predict, juvenile Kemp's ridleys have also been reported in floating mats of vegetation.[46] Kemp's ridleys only nest on one restricted beach area (Rancho Nuevo) in Tamaulipas, Mexico. Thus, pelagic, oceanic transport of neonates must be initially controlled by the hydrography in the western Gulf of Mexico.[47,48] After initial entrainment in the anticyclonic Mexican Current off the nesting beach, pelagic *L. kempi* should be swept into the northern Gulf of Mexico, then eastward. Some juveniles are probably retained in the northern Gulf until they migrate inshore and become demersal. Others may be swept south into the Loop current, and then into the Florida Current and north into the Gulf Stream[49] (Figure 6.3). Most of these have grown sufficiently large to migrate inshore and to adopt a demersal life-style by the time they reach the latitude of Long Island,

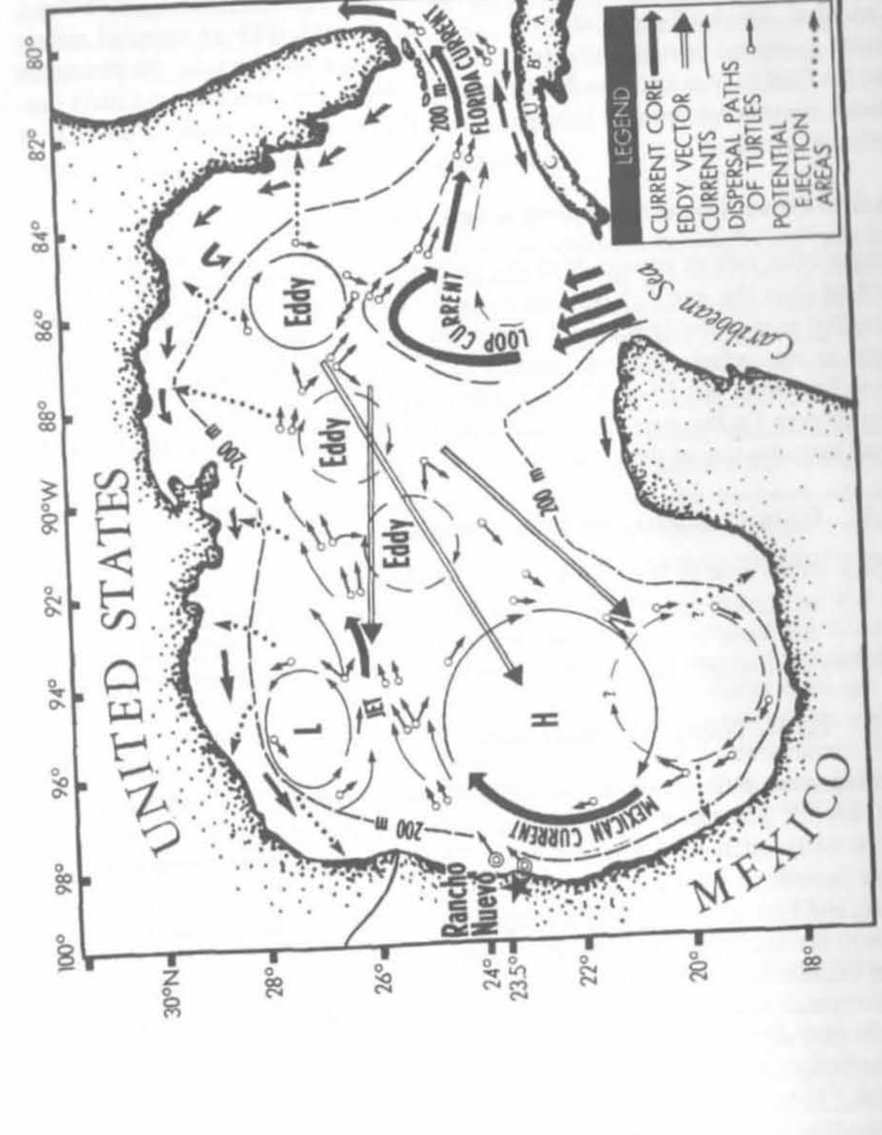

FIGURE 6.3 Major hydrographic features in the Gulf of Mexico that may effect transport of pelagic juvenile Kemp's ridley's. (After Collard 1990.)

NY, or southern New England.[50,51] Others are carried by the Gulf Stream and North Atlantic gyre into the eastern Atlantic[34,54] (see review in Marquéz).[55] The fate of these pelagic juveniles expatriated from the Gulf of Mexico has been conjectural, some authors suggesting that they are lost to the breeding population.[22,47] Conversely, there is no reason to assume that Kemp's ridleys do not have navigational abilities equal to those of loggerheads and, therefore, probably are able to find their way back to the Gulf of Mexico. Mounting evidence on the behavior of demersal juveniles in neritic developmental habitats strongly supports the latter hypothesis (see below). In addition, Meylan[56] reported that from 1980 to 1985, 29% of stranded ridleys (mostly juveniles) were reported from the Atlantic coast of the U.S.; the remainder from the Gulf of Mexico. If such a large proportion of the population regularly uses Atlantic coast developmental habitats, it is likely that they can return to the Gulf of Mexico to breed.

6.3.3 Olive Ridley, *Lepidochelys olivacea*

Neonate olive ridleys emerge from the nest at night and rapidly crawl across the beach to enter the surf.[57,58] Nothing is known of the early juvenile nursery area, although it most probably is pelagic and oceanic. Even the adults of some populations appear to use pelagic, oceanic feeding areas when not breeding or nesting.[59,60] Pitman[10] reported that 26 of 247 olive ridleys sighted at sea by shipboard observers in the eastern Pacific were associated with floating *Sargassum*. Unfortunately, he did not note the size of these animals.

6.3.4 Flatback Turtle, *Natator depressus*

Flatback turtles emerge from the nest and rapidly enter the sea at night.[61] Evidently they lack an oceanic stage[62,63] and use neritic nursery areas while still feeding near the top of the water column. Hatchling flatbacks are larger (5.7 to 6.2 cm scl) than most other cheloniids[64] and thus may have higher survivorship in the neritic habitat.

6.3.5 Green Turtle, *Chelonia mydas*

Hatchling green turtles enter the sea and continue to swim actively offshore for at least 24 h.[65-67] Thereafter, the hatchlings apparently rest at night, but continue to swim actively offshore during the day.[37,67,68] Carr[22] documented several pelagic, oceanic records of *Chelonia* neonates or post-hatchlings (≤20 cm scl) both in the Atlantic and Pacific.[69] Many of these were in the vicinity of *Sargassum* driftlines.[70] However, the occurrence of juvenile *Chelonia* in or near *Sargassum* might be fortuitous because both the animals and the weed could be brought together passively in convergence zones.[18] The strong counter-coloration of neonate green sea turtles suggests they are open-water animals, and experiments in the laboratory[27,28] showed that hatchling *Chelonia* avoided floating weed and spent a greater amount of time swimming in open water than did *Caretta* or *Eretmochelys*. Carr and Meylan[70] have speculated on the most probable routes of transport for early juvenile *Chelonia* hatched at Tortuguero, Costa Rica, based on major oceanographic circulation patterns in the Caribbean. Witham[23] provided a model for the transport of neonate green turtles from the east coast of Florida in the Gulf Stream, around the North Atlantic Basin in the North Atlantic gyre, with return to the Caribbean and Florida in the North Equatorial Current (the same model presented for loggerheads above) (Figure 6.2). He also provided tagging records of yearling green turtles released in Florida and recovered in the Azores and Madeira. Oceanic records of juvenile *Chelonia* are not as common as those for *Caretta*. In addition, the recruitment of *Chelonia* to neritic developmental habitats in general occurs at smaller sizes (≅30 to 40 cm ccl)[13,71-74] than those for *Caretta* (≅50 to 70 cm ccl).[3,6] Therefore, *Chelonia* must spend a shorter time in the oceanic nursery and recruits to demersal developmental habitats at a younger age than does *Caretta*, or it has a much slower pelagic growth rate.

6.3.6 Hawksbill, *Eretmochelys imbricata*

Upon hatching, neonate hawksbill behavior is much like that reported for other sea turtles with emergence at night and immediate movement to the sea.[75] Carr[22] provided several pelagic records of early juvenile hawksbills (5 to 21 cm scl) many of which were found in association with *Sargassum*. Other recent records have been provided by Redfoot et al.,[76] Limpus et al.,[63] and Parker.[77] Unfortunately, other than the one original record Parker provided (≅23 cm ccl), most of the others he cited were based on beach strandings, and many of the animals might have been neritic and demersal prior to death. At least one of his records[77] was based on a benthic hawksbill captured in clam tongs inside Chesapeake Bay. In the laboratory, neonate hawksbills were attracted to floating weed and used it for cover where they remained motionless for long periods.[27,28] Apparently at least some hatchlings may remain on reefs close to their natal beaches.[79,80] However, Boulon[81] reported that juvenile hawksbills recruit to the demersal coral reef habitat in the Virgin Islands at 20 to 25 cm (scl). This range complements the largest verified pelagic records (21 cm scl, 23 cm ccl) noted above. Thus hawksbills in the Atlantic recruit to the neritic developmental habitat at a smaller size than either the loggerhead or green turtle, probably at an age of 1 to 3 years. Age and growth have not been determined in pelagic hawksbills, and this tentative age estimate is based on growth rates in demersal juvenile hawksbills,[81] and pelagic juvenile loggerheads[39] and juvenile Kemp's ridleys.[45] In the Indo-Pacific region hawksbills recruit to inhabit coral reefs at a larger size (usually >35 cm [ccl])[7] and presumably at a greater age.

6.3.7 Leatherback, *Dermochelys coriacea*

Hatchling leatherbacks move immediately to the sea and swim actively offshore.[82] Leatherbacks are pelagic even as adults, and it is not surprising that neonates are more active than other species of sea turtles, swimming offshore both day and night for at least six d after entering the sea.[67] The fate of pelagic juvenile leatherbacks after leaving the nesting beach is one of the great mysteries of sea turtle biology. Other than neonates, there are very few records of leatherbacks ≤110 cm ccl.[41,84-87] If Zug and Parham's[88] age estimates are correct, and leatherbacks grow rapidly, then juveniles virtually disappear for four years. Lutcavage and Lutz[89] noted that small leatherbacks need to consume gelatinous prey (the low-energy food upon which they specialize) equal to their biomass every day in order to support routine metabolism. Their food requirements must even be higher to promote rapid growth. In the oceanic realm, production necessary to support high biomass of gelatinous (and other) animals is found primarily in areas of major upwelling such as those along the eastern sides of the major ocean basins or perhaps in the Equatorial Convergence Zones.[90] These areas may provide nursery grounds for leatherbacks.

6.4 LATER JUVENILE DEVELOPMENTAL HABITATS

6.4.1 Loggerhead

In the western Atlantic, juveniles recruit from oceanic pelagic to neritic demersal habitats when as small as 25 to 30 cm ccl[3] (Figure 6.4), but most are ≥50 cm (ccl)[3] at an age of about 7 to 10 years.[42] Limpus et al.[6] reported that loggerheads in Australia do not recruit to demersal habitats until 70 cm (ccl) or greater (Figure 6.5). Larger size may be in keeping with the much more expansive gyre system in the Pacific (thus requiring more time for pelagic juveniles to make the transit), or to slower growth in pelagic juveniles in the Pacific or both. This is supported by recaptures of large juvenile loggerhead turtles which had originally been "tagged" at south Queensland nesting beaches as hatchlings and which had recently recruited to residency in shallow inshore habitats in eastern Australia at 15 years of age or older.[6,14] Loggerheads are antitropical in distribution, and nest on subtropical and warm-temperate beaches.[91] In the western Atlantic some demersal juvenile loggerheads make strong seasonal foraging migrations into temperate latitudes, occurring commonly as far north as Long Island, NY.[92] Chesapeake Bay is a major seasonal developmental habitat in summer[2] with 5,000 to 10,000 loggerheads present each summer.[93,94] Around 95% of the loggerheads that visit Chesapeake Bay are juveniles (Figure 6.4). They usually enter the bay in late May or early June when water temperatures rise to 16 to 18°C, and depart from late September to early November.[3,94] Juveniles become resident for the summer along channel edges (5-13 m) and forage back and forth along the bottom, passively with the tide within a home range of 10 to 80 km^2 with preferred ranges (within the home range) of about 5 to 15 km^2.[93] These juveniles show strong foraging site fidelity. Animals displaced >100 km have returned to within a few kilometers of their point of origin within a few weeks.[93,95] Of 121 loggerheads tagged in Virginia, 48 were recaptured there in subsequent (but not necessarily consecutive) seasons.[43] Some were recaptured up to four seasons, showing strong foraging ground fidelity between seasons. Bowen et al[96] showed that there were two nesting populations of loggerheads in the western North Atlantic; one in Florida, and another north of there in Georgia and South Carolina. Norrgard[97] found that juvenile loggerheads from Chesapeake Bay were derived at about a 50/50 ratio from both nesting populations. Sears[98,99] found similar results for juvenile loggerheads from Charleston, SC. These data suggest that the Georgia-South Carolina turtles selectively use more northerly summer developmental habitats than do Florida turtles. The Florida nesting population is about nine times larger, and the juvenile ratios should have been heavily skewed toward the

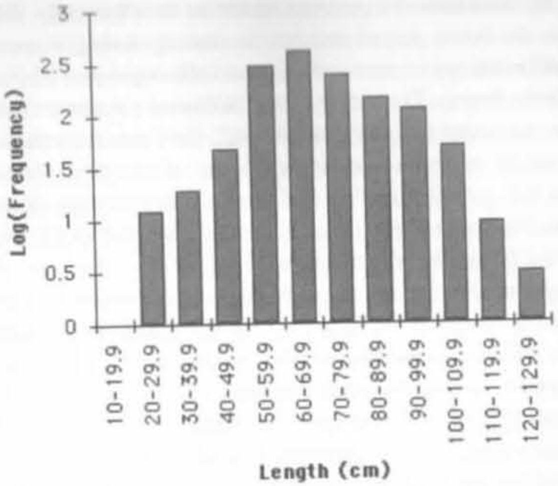

FIGURE 6.4 Length frequency distribution (ccl) for loggerheads stranded in Virginia from 1974 to 1995.

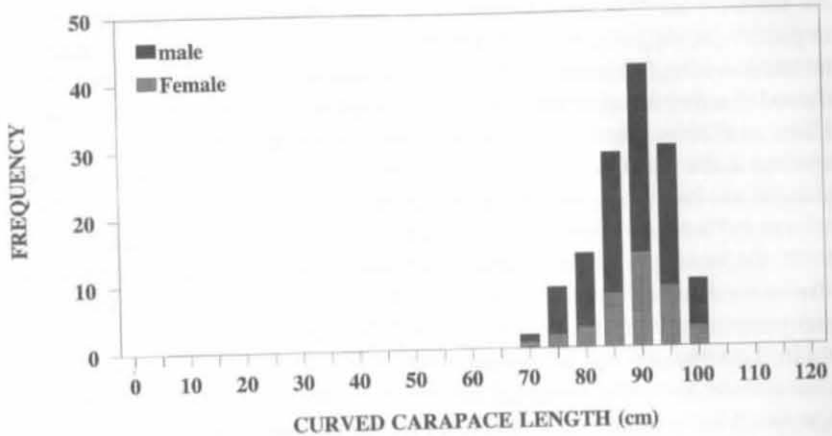

FIGURE 6.5 Length frequency distribution (ccl) for loggerheads collected in foraging habitats in Australia.

Florida population if there were a random distribution of juveniles from both groups.[99] Aerial surveys and satellite tracking studies have shown that when juvenile loggerheads migrate from Chesapeake Bay in autumn, they travel relatively close to the coast (≤20 km) and move south, rounding Cape Hatteras around December.[43,100,101] They are joined in the fall by substantial members of juvenile loggerheads from the sounds of North Carolina.[102,103] By December most loggerheads have migrated south of Oregon Inlet, NC,[101] and by January most are south of Cape Hatteras.[102] Most of the turtles that remain off North Carolina in January and February are found at the edge of the Gulf Stream.[103] Keinath[43] found that the juvenile loggerheads he tracked from Virginia wintered in two basically distinct areas: one group went down the coast, stayed inshore (hesitating during warm spells at various major inlets), and wintered inshore off southern Georgia and Florida (one traveled as far as the Florida Keys). The other group followed the same inshore route south of Cape Hatteras to about Cape Lookout, NC, then moved offshore to winter on reefs along the shelf edge on the western side of the Gulf Stream. One might hypothesize that the group wintering off North Carolina was derived from Georgia/South Carolina rookeries, and those that wintered off Florida were from Florida rookeries. Only further genetic research will tell.

Juvenile loggerheads of about the same size distribution (50 to 80 cm scl) are common during the summer in estuaries as far south as Mosquito and Indian Lagoons, Florida[104,105] and in the Gulf of Mexico.[106,107] In South Carolina and Georgia they exhibit seasonal emigration from estuaries into the ocean in the autumn, with immigration occurring in the spring.[108] In Mosquito Lagoon, Florida, juvenile *Caretta* occur year-round, but are captured in smallest numbers during February and March (the time of lowest water temperature).[104] The reason for this may be because the turtles emigrate out into the ocean, or rather they may be inactive, actually brumating in the mud during this period. Juvenile loggerheads commonly brumate in winter by digging head first into the mud in the Canaveral Ship Channel (in the ocean not far from Mosquito Lagoon).[109,110] We have never observed any evidence of brumation in Virginia, nor have Epperly et al.[103] in North Carolina where winter water temperatures fall below the lethal lower limit for loggerheads (5 to 6.5°C).[111,112] Henwood[113] noted that juvenile loggerheads reached their peak abundance in winter in Canaveral Ship Channel, and that some turtles tagged there in winter were recaptured to the north in summer. In contrast, to the well-defined seasonal foraging migrations exhibited by juvenile loggerheads along the Atlantic coast of the U.S., both large (>70 cm ccl) juvenile and adult *Caretta* were resident all year in the coral reefs of the southern Great Barrier Reef and in Moreton Bay, Australia in the southwestern Pacific.[6,114] The most southerly of these sites, Moreton Bay, has an annual water temperature range of 16 to 28°C, much more moderate than those found in estuarine and coastal waters north of Florida in the U.S. After recruitment into the eastern Australian demersal habitats, these juvenile loggerheads show strong forage site fidelity to relatively small areas, mostly remaining within a few square kilometers for the next 8 to 20 years of growth to sexual maturity.[14,15,115] Adult loggerheads, after completing their first breeding migration to distant nesting beaches, return with high fidelity to the same juvenile foraging areas in which each had completed its juvenile life.[115] They also return to the same foraging sites following subsequent breeding migrations.[116] It is strongly indicated that individual loggerheads in the southwestern Pacific occupy very localized home ranges for the decades that span their later juvenile and entire adult lives.

6.4.2 Kemp's Ridley

Initial recruitment of juveniles from pelagic oceanic to demersal neritic habitats takes place at a size of 20 to 25 cm (scl) in the northern Gulf of Mexico and in New England and New York waters.[44] Contrary to the assumption of Carr[18] and Carr et al.,[21] the juveniles carried by the Gulf Stream into the Atlantic probably make an active rather than a passive migration west from the edge of the continental shelf to find suitable shallow developmental habitats such as Long Island Sound. Although Gulf Stream gyres may impinge upon the edge of the continental shelf, they rarely cross the shelf to near coastal habitats.[117] In the Gulf of Mexico, shallow coastal habitats serve as foraging areas for Kemp's ridley throughout the year, although there is evidence for seasonal offshore movements in response to low water temperatures in winter.[44,118] Occurrence of *L. kempi* in shallow water off northwest Florida is seasonal, with no turtles captured in the coldest winter months.[119] In New York and New England, juveniles must emigrate coastally to the south or face cold stunning and death in the winter.[52,53,120]

Chesapeake Bay serves as an important developmental habitat for juvenile *L. kempi*.[2,3,94] The summer population size has been estimated to be 211 to 1083 (a minimum estimate) with a mean size of about 40 cm (ccl)[121] (Figure 6.6). Juvenile *L. kempi* preferred shallower summer habitats in Long Island Sound (<8 m)[120,122] and Chesapeake Bay (<5 m)[93] than were used by juvenile loggerheads,[93] and often foraged in submerged aquatic grass beds for *Callinectes sapidus* and other crabs.[3] The seasonal migration pattern is similar to that of the loggerhead, with immigration in May and June and emigration from September to November. Of 57 Kemp's ridleys tagged in Chesapeake Bay, 2 were recaptured there in subsequent summers.[43] Thus, site fidelity is possible for summer foraging locations. Upon leaving Chesapeake Bay in autumn, juvenile *L. kempi* migrate down the coast, passing Cape Hatteras in December and January. These larger juveniles are joined there by juveniles of the same size from the North Carolina sounds and smaller juveniles from New York and New England to form one of the densest concentrations of Kemp's ridleys outside the Gulf of Mexico.[102,103] Keinath[43] used satellite transmitters to track three juvenile Kemp's ridleys released in Virginia in October. They followed the same inshore route noted for loggerheads above, and two individuals migrated as far as Florida by mid-January. (The transmitter failed on the third turtle in November when the animal was approaching Cape Fear, NC). Henwood and Ogren[123] noted that juvenile Kemp's ridleys reached their maximum abundance off Cape Canaveral, FL in January to March, and that their tagging data suggested a northward movement in summer and a southward movement in the winter. These data complement and support the pattern of seasonal migration noted to the north.

Ogren[44] reported that the entire northern coast of the Gulf of Mexico from Port Aransas, TX to Cedar Key, FL served as demersal developmental habitat for juvenile Kemp's ridleys. Areas where significant concentrations of juvenile ridleys occurred included: the Sabine Pass area of Texas; Caillou Bay, Terrabonne Parish, LA; and Big Gulley east of Mobile Bay, AL. The smallest juveniles (20 to 25 cm scl) were found in two areas: one off western Louisiana and eastern Texas, and the other off northwest Florida.[44,124] Most juvenile *L. kempi* in the latter area were captured at depths ≤6.1 m, and all ridleys <25 cm (scl) were from <1 m. Juvenile Kemp's ridleys, then, recruit to shallow estuarine and coastal habitats in the western Gulf of Mexico and off New England and New York in summer. In winter they migrate south and/or offshore to avoid cold temperatures, but may remain resident in some areas of the

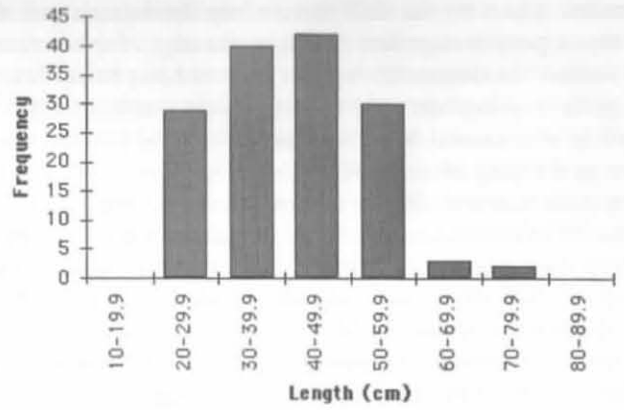

FIGURE 6.6 Length frequency distribution (ccl) for Kemp's ridley stranded in Virginia from 1979 to 1995.

Gulf of Mexico that are sufficiently warm. It is possible that some individuals may brumate at temperatures ≤15°C.[110]

6.4.3 Olive Ridley

Very little is known about the developmental habitats of older juvenile olive ridleys.[58] Adults may use coastal[58,125] or oceanic foraging habitats[10,59,126] and juveniles may be able to use either as developmental habitats, depending on food availability. In northern Australian continental shelf waters, large immature and adult-sized olive ridleys (52.0 to 72.0 cm ccl) are captured all year-round in prawn trawls over soft-bottomed habitats.[127]

6.4.4 Flatback Turtle

This species is endemic to the Australian continental shelf. Demersal juveniles have been reported frequently from the prawn trawling grounds inshore from the Great Barrier Reef and across northern Australia. The species appears to avoid reef habitats, but is common in turbid, shallow, inshore water throughout northern Australia north of 25°.[64,128] Adult flatbacks appear to live sympatricly with the larger juveniles.

6.4.5 Green Turtle

Juvenile green turtles recruit to demersal developmental habitats at about 30 to 40 cm (ccl) or larger[63,71,73,74] (Figure 6.7). In the western Atlantic the summer developmental habitat encompasses estuarine waters as far north as Long Island Sound, Chesapeake Bay, and the North Carolina Sounds south throughout the tropics. Green turtles north of Florida must migrate south in autumn or face the risk of cold stunning.[73,120,123,129] Guseman and Ehrhart[130] noted that the smallest juvenile green turtles (26.8 to 45.3 cm scl) to appear in the demersal developmental habitat off the east coast of Florida occurred on sabellarid polychaete reefs, and that as juveniles

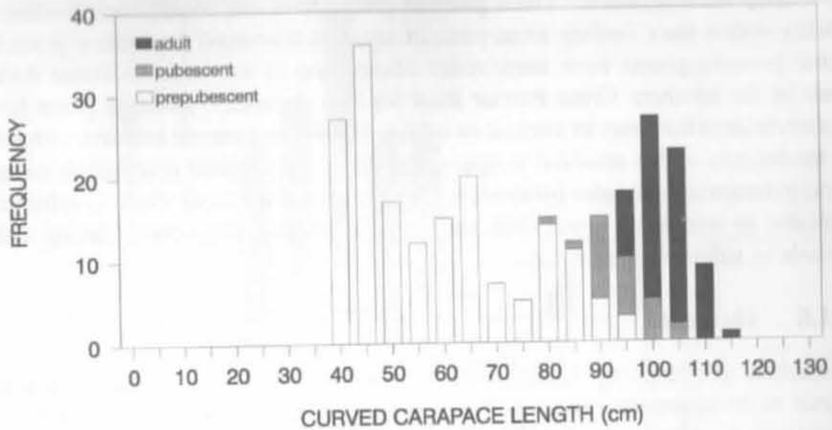

FIGURE 6.7 Length frequency distribution (ccl) for green turtles captured in Shoalwater Bay, Australia.

became larger (28.8 to 66.8 cm scl) they moved into the Indian River Lagoon seagrass beds to forage. Henwood and Ogren[123] also noted that juvenile green turtles off Cape Canaveral were smaller than those in the Mosquito Lagoon estuary.[104] Henwood and Ogren[123] suggested that these small coastal green turtles might be in early developmental stages prior to the shift to herbivory and recruitment to shallow inshore feeding pastures. Mendonca and Ehrhart[104] showed that juvenile green turtles recruited to the Mosquito Lagoon (Florida) estuarine developmental habitat at 30 to 40 cm scl and that some individuals became resident, showing foraging site fidelity. Many turtles remained in the Lagoon year-round until they approached maturity. They also noted that the catch rates of juvenile *Chelonia* were highest in the summer, but that the winter decline might be due in part to turtle inactivity (brumation?). Severe cold-stunning events in winter in 1977 and 1978 showed that green turtles were still common in the Lagoon. Felger et al.[131] reported *Chelonia* to burrow in the mud (brumate) in winter in the Gulf of California. Mendonca[132] noted that juvenile green turtles in Mosquito Lagoon wandered as far as 5 to 10 km a day when the water was cooler (11 to 18°C) but established home ranges of 1.2 to 4.1 km when temperatures were above 25°C. Bjorndal and Bolton[133] reported that tidal embayments were important developmental habitats for juvenile green turtles in the Bahamas. Their tagging studies showed that immigration occurred to other areas of the Bahamas, Colombia, Cuba, Dominican Republic, Haiti, Nicaragua, Panama, and Venezuela.

Balasz[74] and Green[134] noted that juvenile green turtles in the Pacific remained on reef habitats and consumed macroalgae. Balasz[74] also reported that almost all juvenile green turtles he tagged in the Hawaiian Islands were recaptured in the same resident areas. Similarly, all the juvenile green turtles tagged by Green[134] in the Galapagos were recaptured within the archipelago. In the southwest Pacific juvenile greens occupy the same wide range of habitats as the adults, being common on coral reefs where algae is the dominant food[5] and in inshore embayments where the main food items are seagrasses.[13] These juvenile greens have displayed strong feeding site fidelity within their feeding areas (tens of square kilometers) over many years.[13,135] Some juvenile greens have been under observation in the same localized feeding areas in the southern Great Barrier Reef for two decades.[14] Juvenile green turtles can be resident for years in tropical or subtropical developmental habitats with stable or moderately stable seasonal temperatures. They may utilize continental foraging areas in temperate latitudes (to about 40°N) in summer, but must return to subtropical latitudes in winter to avoid cold stunning. Brumation may occur during colder periods in subtropical estuaries.

6.4.6 Hawksbill

Hawksbills are restricted to the tropics more than any other sea turtle. Juveniles recruit to developmental habitats at a very small size (20 to 25 cm scl) or even as hatchlings (see above). The developmental habitat includes shallow (<20 m) coral reefs and mangrove estuaries[79] where there are abundant sponges, the principal food of this species.[136] The developmental habitat does not seem to differ from that of the adult, and juveniles and adults are taken together in the same foraging areas.[4,137] Boulon[138] tagged juvenile hawksbills in the Virgin Islands and found that many migrated to areas outside the Virgin Islands. (Nesting hawksbills from the Virgin Islands have also been found to be mostly migratory).[139] In contrast, in eastern Australia, juvenile hawksbills >35 cm (ccl) have displayed a high fidelity to localized feeding areas in coral reef habitats with some individuals being associated with the same site for over a decade.[4] In addition, juvenile hawksbills less than 30 cm ccl are uncommon in the Great Barrier Reef waters, and none have been recorded in demersal developmental habitats.[63] Very little research has been conducted on behavior and habitat utilization in juvenile hawksbills.

6.4.7 Leatherback

Although leatherbacks are pelagic, they recruit seasonally to temperate and boreal coastal habitats to feed on concentrations of jellyfish.[51,92,140] In the western Atlantic, juvenile *Dermochelys* appear in these habitats at about 110 to 120 cm (ccl), based on stranding data[85,140] (Figure 6.8). If we accept the size at maturity (based on the nesting population in St. Croix) as 137 cm (ccl) (the size of the smallest nesting female) or as 157 cm (ccl), (the approximate average size of nesting females),[141] then a substantial percentage of leatherbacks stranding along the U.S. east coast must be large juveniles. Aerial surveys have shown large numbers of leatherbacks off the northeast coast of Florida in February,[142] southern Virginia in late April,[143] and the Gulf of Maine in summer.[92] Leatherback strandings from 1980 to 1991 in Florida occurred mostly between October and April.[85] Sightings of leatherbacks off Massachusetts peak in August, with no live sightings before June or after October.[144] Although several tagging and tracking studies have been done on adult females that show long-distance oceanic migration to higher-latitude coastal feeding habitats, virtually no work of this kind has been done on juveniles. Paladino et al.[145] pointed out that leatherbacks were inertial endotherms, but that the high surface area-to-

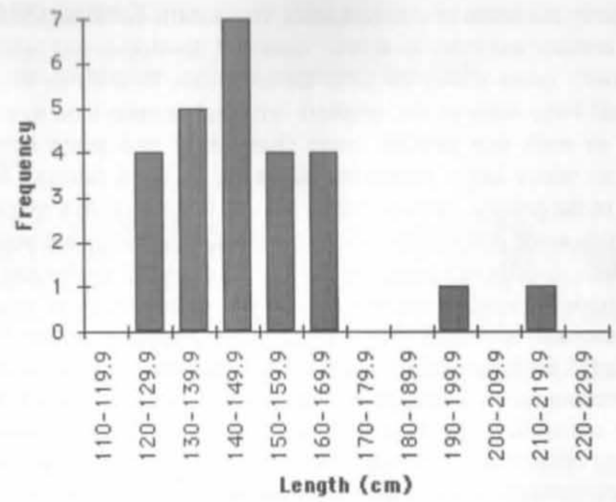

FIGURE 6.8 Length frequency distribution (ccl) for leatherbacks stranded in Virginia from 1979 to 1995.

mass ratio in juveniles precluded body temperatures significantly higher than ambient. The size range at which leatherbacks become efficient endotherms is probably the same as that when they first appear in coastal, boreal waters (110 to 120 cm ccl).

The leatherback shares many attributes with the endothermic scombroid fishes (tunas). Both reproduce in the tropics. Both have been able to expand their effective foraging ranges into higher latitudes and greater depths (into the thermocline), well beyond the normal range of their nonendothermic relatives.[146]

6.5 CONCLUSIONS

A comparison of the ontogenetic patterns of habitat utilization and migration among the seven species of sea turtles leads to the following hypotheses: natural selection will favor those nesting locations with the highest survivorship during the vulnerable early juvenile stage when predation is highest. Given all sea turtles nest in tropical, subtropical, or warm temperate latitudes, the most important determinant of nesting beach locations probably is survivorship of hatchlings and small juveniles in the nursery habitats.

In sea turtles as in fishes, the numbers and diversity of potential predators and resulting mortality rates are inversely proportional to the size of the juvenile. The advantage of pelagic, oceanic nurseries is the low density of predatory fishes and sea birds there dictated by low primary production.[90,147] (Productive-upwelling areas are exceptions.) Based on predator mouth size alone, few potential avian or fish predators, except sharks,[148] are capable of engulfing hard-bodied epipelagic prey (such as sea turtles) ≥20 to 30 cm in diameter. Marine crocodiles, which can also be significant predators of most size ranges of marine turtles, are largely restricted to tropical inshore margins of marine turtle foraging habitats. Marine mammals appear to be rarely predators of marine turtles. Hawksbills and Kemp's ridleys recruit from pelagic, oceanic nurseries to neritic, demersal developmental habitats at about 20 to 25 cm (scl); green turtles do so at about 30 cm. In order to avoid predation from sharks and large teleosts, the smallest demersal recruits tend to use structured habitats such as reefs that provide cover (hawksbills and green turtles) or very shallow habitats where larger predators cannot go (Kemp's ridleys). Juvenile loggerheads stay in the pelagic, oceanic nursery much longer and to a much larger size. Apparently, so do some populations of olive ridleys, which may use oceanic feeding grounds as adults (mostly in upwelling areas with abundant crustacean prey). Loggerheads are opportunistic carnivores utilizing a wide variety of prey, including molluscs, crustaceans, horseshoe crabs, and gelatinous macroplankton.[149] They seem to be well adapted for long periods of opportunistic foraging (mostly on gelatinous prey) in the oceanic realm, although they have relatively slow growth rates there.[39] Older juvenile and adult green, hawksbill, and Kemp's ridley turtles have specialized diets (herbivory, spongivory, and cancrivory, respectively), and might be compelled by dietary energetic constraints to seek out more productive demersal developmental habitats at smaller sizes than loggerheads. In addition, Kemp's ridley, the smallest species of sea turtle, seems to have a shorter life cycle and matures at an earlier age than other species of the Cheloniidae.[45]

Most species that primarily utilize pelagic, oceanic nurseries and have relatively long ($\geq$3-year) oceanic stages tend to have high-density nesting localities located adjacent to major oceanic currents that can maintain small juveniles passively and safely for sufficient time for them to grow large enough to lower predation risk and to have the mobility to actively swim to developmental habitats. Loggerheads, green turtles, and both Kemp's and olive ridleys seem to fit this pattern. Nesting is mostly restricted to certain sites used (or historically used) by large numbers of nesters. Small scattered nesting sites along the fringes or outside of these primary sites are probably constrained by very low survivorship of the pelagic juveniles caused by poor access to the passive hydrographic pathways that lead to the oceanic nurseries. Hawksbills do not fit this pattern well. Although some concentrated nesting areas exist[150] or existed historically, solitary nesting is widespread and frequent mostly on islands.[79] Hawksbills may have the shortest pelagic stage of all sea turtles (except the flatback), or hatchlings may recruit directly to demersal developmental habitats on coral reefs or mangrove flats. Also, they tend to occur in archipelagos where local or regional hydrographic features may be more important than major oceanic gyres during the short passive transport stage of the juveniles. Leatherbacks are pelagic during all stages of their life, and utilize oceanic habitats more than any other sea turtle.[91,151] Although there are some high-density nesting areas,[151,152] much scattered nesting occurs, and this species may have lower renesting fidelity than other sea turtles.[153,154] This apparent enigma may be explained by the larger size and faster growth rates and superior swimming ability of neonate leatherbacks. These attributes may render juvenile leatherbacks much less dependent on passive transport to the oceanic nurseries. Young leatherbacks undoubtedly use major oceanic current systems for transport, but may be more capable of actively reaching those passive pathways.

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REFERENCES

1. Jones, F. R., *Fish Migration*, Edward Arnold, London, 1968.
2. Musick, J. A., *The Sea Turtles of Virginia*, 2nd rev. ed., Virginia Sea Grant Program, Virginia Institute of Marine Science, Gloucester Point, VA, 1988.
3. Lutcavage, M. and Musick, J. A., Aspects of the biology of sea turtles in Virginia, *Copeia*, 2, 449, 1985.
4. Limpus, C. J., The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: population structure within a southern Great Barrier Reef feeding ground, *Wild. Res.*, 19, 489, 1992.
5. Limpus, C. J. and Reed, P. C., The green turtle, *Chelonia mydas*, in Queensland: a preliminary description of the population structure in a coral reef feeding ground, in *Biology of Australiasian Frogs and Reptiles*, Griggs, G., Shine, R., and Ehmann, H., Eds., Surrey Beatty and Sons, Sydney, 1985, 47.
6. Limpus, C. J., Couper, P. J., and Reed, M. A., The loggerhead turtle, *Caretta caretta*, in Queensland: population structure in a warm temperate feeding area, *Mem. Queensl. Mus.*, 37(1), 195, 1994.
7. Limpus, C. J., The green turtle, *Chelonia mydas*, in Queensland: breeding males, *Wild. Res.*, 20, 513, 1993.
8. Meylan, A. B. and Meylan, P. A., Description of a mighty fleet of green turtles, in *Proc. 13th Ann. Symp. Sea Turtle Biology and Conservation*, Schroeder, B. A. and Witherington, H. E., Compilers, NOAA Tech. Memo. NMFS-SEFSC-341, 107, 1994.
9. Balazs, G. H., Recovery records of adult green turtles observed or originally tagged at French Frigate Shoals, northwestern Hawaiian Islands, NOAA Tech. Memo. NMFS-SWFC-36, 42, 1983.
10. Pitman, R. L., Pelagic distribution and biology of sea turtles in the eastern tropical Pacific, in Proc. Tenth Annu. Workshop on Sea Turtle Biology and Conservation, Richardson, T. H., Richardson, J. I., and Donnely, M., Compilers, NOAA Tech. Memo. NMFS-SEFC-278, 143, 1990.
11. Meylan, A., Behavioral ecology of the west Carribean green turtle (*Chelonia mydas*) in the internesting habitat, in *Biology and Conservation of Sea Turtles*, Bjorndal, D., Ed., Smithsonian Institution Press, Washington D.C., 1982, 67.
12. Dodd, D. C., Synopsis of the biological data on the loggerhead sea turtle, *Caretta caretta* (Linnaeus, 1758), FAO Synopsis NMFS-149, USFWS Biological Report 88(14), 110, 1988.
13. Limpus, C. J., Couper, P. J., and Reed, M. A., The green turtle *Chelonia mydas* in Queensland: Population structure in a warm temperate feeding area, *Mem. Queensl. Mus.*, 35(1), 139, 1994.
14. Limpus, C. J., unpublished data, 1966.
15. Limpus, C. J., Puberty and first breeding in *Caretta caretta*, NOAA Tech. Memo. NMFS-SEFC-278, 81-3, 1991.
16. Miller, J. D., Embryology and marine turtles, in *Biology of the Reptilia*, Gans, C., Billett, F., and Maderson, P. F. A., Eds., (14), 269, 1985.

17. Carr, A., *So Excellent a Fish*, Natural History Press, Garden City, NY, 1967, 249.
18. Carr, A., Notes on the behavioral ecology of sea turtles, in *Biology and Conservation of Sea Turtles*, Bjorndal, K. A., Ed., Smithsonian Institution Press, Washington, D.C., 1982, 19.
19. Fletmeyer, J. R., Underwater tracking evidence that neonate loggerhead sea turtles seek shelter in drifting Sargassum, *Copeia*, 1, 148, 1978.
20. Smith, W. G., A neonate Atlantic loggerhead turtle, *Caretta caretta*, captured at sea, *Copeia*, 4, 880, 1968.
21. Carr, A., Heath, H., and Ogren, L., The ecology and migrations of sea turtles: the hawksbill turtle in the Caribbean Sea, *Am. Mus. Novit*., 2248, 1, 1966.
22. Carr, A., New perspectives on the pelagic stage of sea turtle development, *Conserv. Biol*., 1(2), 103, 1987.
23. Witham, R. M., The "lost years" question in young sea turtles, *Am. Zool*., 20, 525, 1980.
24. Witham, R., On the ecology of young sea turtles, *Fl. Sci*., 54, 179, 1991.
25. Witherington, B. E., Some "lost year" turtles found, in *Proc. 13th Annu. Symp. Sea Turtle Biology and Conservation*, Schroeder, B. A. and Witherington, H. E., Compilers, NOAA Tech. Memo. NMFS-SEFSC-341, 192, 1994.
26. Richardson, J. I. and McGillivary, R., Post-hatching loggerhead turtles eat insects in *Sargassum* community, *Mar. Turtle. Newsl*., 55, 2, 1991.
27. Mellgren, J. R., Morra, M., Bushong, M., Harkins, S., and Krumke, V., Habitat selection in three species of captive sea turtle hatchlings, in *Proc. 14th Annu. Symp. Sea Turtle Biology and Conservation*, Bjorndal, K. A., Bolton, A. B., Johnson, P. A., and Eliazar, P. J., Compilers, NOAA Tech. Memo. NMFS-SEFSC-351, 259, 1994.
28. Mellgren, R. G., and Mann, M. A., Comparative behavior of hatchling sea turtles, in *Proc. 15th Annu. Symp. Sea Turtle Biology and Conservation*, Keinath, J. A., Barnard, D. E., Musick, J. A., and Bell, B. A., Compilers, NOAA Tech. Memo. NMFS-SEFSC-387, 202, 1996.
29. Brongersma, L. D., European Atlantic turtles, *Zool. Berhand. Leiden*, 121, 318, 1972.
30. Eckert, S. A. and Martins, H. R., Transatlantic travel by a juvenile loggerhead turtle, *Mar. Turtle Newsl*., 45, 15, 1989.
31. Manzella, S. A. and Fontaine, C. T., Loggerhead sea turtle travels from Padre Island, Texas to the mouth of the Adriatic Sea, *Mar. Turtle. Newsl*., 42, 7, 1988.
32. Bolten, A. B., Santana, C., and Bjorndal, K. A., Transatlantic crossing by a loggerhead turtle, *Mar. Turtle Newsl*., 59, 7, 1992.
33. Bolton, A. B., Martins, H. R., Watali, M. L., Thomas, J. C., and Marcovaldi, M. A., Loggerhead released in Brazil recaptured in Azores, *Mar. Turtle. Newsl*., 48, 24, 1990.
34. Brongersma, L. D., Marine turtles of the eastern Atlantic ocean, in *Biology and Conservation of Sea Turtles*, Bjorndal, K. A., Ed., Smithsonian Institution Press, Washington, D.C., 1982, 407.
35. Bolten, A. B., Martins, H. R., Bjorndal, K. A., and Gordon, J., Size distribution of pelagic-stage loggerhead sea turtles (*Caretta caretta*) in the waters around the Azores and Madeira, *Arquipelagic*, 11A, 49, 1993.
36. Bjorndal, K. A., Bolten, A. B., Gordon, J., and Camiñas, J. A., *Caretta caretta* (loggerhead) growth and pelagic movement, *Herptol. Rev*., 25, 23, 1994.
37. Lohmann, K. J., Witherington, B. E., Lohmann, C. M., and Salmon, M., Orientation, navigation and natal beach homing in sea turtles, in *Biology of Sea Turtles*, Lutz, P. and Musick, J. A., Eds., CRC Press, Boca Raton, FL, 1996, 109.
38. Bolton, A. B. and Balazs, G. H., Biology of the early pelagic stage — the "lost year", in *Biology and Conservation of Sea Turtles*, Bjorndal, K. A., Ed., Smithsonian Institution Press, Washington, D.C., 1995, 579.
39. Zug, G. R., Balzs, G. H., and Wetherall, J. A., Growth in juvenile loggerhead sea turtles (*Caretta caretta*) in the north Pacific pelagic habitat, *Copeia*, 484, 1995.
40. Bowen, B. W., Abreu-Grobois, F. L., Balazs, G. H., Kamezaki, N., Limpus, C. J., and Ferl, R. J., Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers, *Proc. Natl. Acad. Sci*., 92, 3731, 1995.
41. Hughes, G. R., The sea turtles of southeast Africa. I. Investigational Report No. 36, Oceanographic Research Institute, Durban, 1974.
42. Klinger, R. C. and Musick, J. A., Age and growth of loggerhead turtles (*Caretta caretta*) from Chesapeake Bay, *Copeia*, 1995(1), 204, 1995.
43. Keinath, J. A., Movements and Behavior of Wild and Head-Started Sea Turtles, Ph.D. dissertation, College of William and Mary, Williamsburg, VA, 1993.
44. Ogren, L. H., Distribution of juvenile and subadult Kemp's ridley turtles: preliminary results from the 1980–1987 surveys, in *Proc. 1st Int. Symp. Kemp's Ridley Sea Turtle Biology, Conservation and Management*, Calliouet, C. W., and Landry, A. M., Eds., Texas A & M University Sea Grant College Program Spec. Publ. -89(105), 116, 1989.
45. Zug, G. R., Kalb, H., and Luzan, S. L., Age and growth in wild Kemp's ridley sea turtles (*Lepidochelys kempi*) from skeletochronological data, *Biol. Conserv*., in press.
46. Manzella, S. A., Williams, J. A., Schroeder, B., and Teas, W., Juvenile head-started Kemp's ridleys found in floating grass mats, *Mar. Turtle Newsl*., 52, 5, 1991.
47. Collard, S. B., Guest editorial: speculation on the distribution of oceanic-stage sea turtles, with emphasis on Kemp's ridley in the Gulf of Mexico, *Mar. Turtle Newsl*., 48, 6, 1990.
48. Collard, S. B., The influence of oceanographic features in post-hatching sea turtle distribution and dispersion in the pelagic environment, in *Proc. 10th Annu. Workshop on Sea Turtle Biology and Conservation*, Richardson, T. H., Richardson, J. I., and Donnely, M., Compilers, NOAA Tech. Memo. NMFS-SEFC-278, 111, 1990b.
49. Collard, S. B. and Ogren, L. H., Dispersal scenarios for pelagic post-hatchling sea turtles, *Bull. Mar. Sci*., 47, 233, 1990.
50. Lazell, J. D., *This Broken Archipelago: Cape Cod and the Islands, Amphibians and Reptiles*, Demeter Press, New York, 1976, 260.
51. Lazell, J. D., New England waters: critical habitat for marine turtles, *Copeia*, 290–295, 1980.
52. Burke, V. J. and Standora, E., Factors affecting stranding of cold-stunned juvenile Kemp's ridley and loggerhead sea turtles in Long Island, New York, *Copeia*, 1136, 1991.
53. Morreale, S. L., Meylan, A., Sadove, S., and Standora, E., Annual occurrence and winter mortality of marine turtles in New York waters, *J. Herpetol*., 26, 301, 1992.
54. Bolten, A. B. and Martins, H. R., Kemp's ridley captured in the Azores, *Mar. Turtle Newsl*., 48, 23, 1990.
55. Marquéz, R., Synopsis of biological data on the Kemp's ridley turtle *Lepidochelys kempi* (Garman, 1880), NOAA Tech. Memo. NMFS-SEFSC-343, 91, 1994.
56. Meylan, A. B., Riddle of the ridleys, *Nat. Hist*., 95(11), 90, 1986.
57. Cornelius, S., The Sea Turtles of Santa Rosa National Park, *Fondacion de Parques Nacionales*, Costa Rica, 65, 1986.

58. Reichart, H. A., Synopsis of biological data on the Olive ridley sea turtle *Lepidochelys olivacea* (Eschsholtz, 1829) in the western Atlantic, NOAA Tech Memo. NMFS-SEFSC-336, 78, 4, 1993.
59. Plotkin, P. T., Reproductive Behavior of the Olive Ridley Turtle (*Lepidochelys olivacea*) in the Eastern Pacific Ocean, Ph.D. dissertation, Texas A & M University, College Station, TX, 1994.
60. Plotkin, P., Byles, R. A., and Owens, D. M., Ups and downs in the life of the Olive ridley turtle: breeding versus post-reproductive diving behavior, in *Proc. 15th Annu. Sea Turtle Symposium*, Keinath, J. A., Barnard, D. E., Musick, J. A., and Bell, B. A., Eds., NOAA Tech. Memo. NMFS-SEFC, 1996.
61. Limpus, C. J., The Flatback turtle, *Chelonia depressa* (Garman) in southwest Queensland, Australia, *Herpetologica*, 27, 434, 1971.
62. Walker, T. A. and Parmenter, C. J., Absence of a pelagic phase in the life cycle of the flatback turtle, *Natator depressa* (Garman), *J. Biogeogr.*, 17, 275, 1990.
63. Limpus, C. J., Walker, T. A., and West, J., Posthatchling specimens and records from the Australian region, in *Proc. Marine Turtle Conservation Workshop*, James, R., Compiler, Australian National Parks and Wildlife Service, Canberra, 1994, 86.
64. Limpus, C. J., Parmenter, C. J., Baker, V., and Fleay, A., The flatback turtle, *Chelonia depressa*, in Queensland: post-nesting migration and feeding ground distribution, *Aust. Wildl. Res.*, 10, 557, 1983.
65. Frick, J., Orientation and behavior of hatchling green turtles (*Chelonia mydas*) in the sea, *Anim. Behav.*, 24, 849, 1976.
66. Ireland, L. C., Frick, J. A., and Wingate, D. B., Nighttime orientation of hatchling green turtles (*Chelonia mydas*) in the open ocean, in *Animal Migration, Navigation, and Homing*, Schmidt-Koenig, K., and Keeton, W. J., Eds., Springer-Verlag, New York, 1978, 420.
67. Wyneken, J. and Salmon, M., Frenzy and post-frenzy swimming activity in loggerhead, green and leatherback hatchling sea turtles, *Copeia*, 478, 1992.
68. Wyneken, J., Sea turtle locomotion: mechanisms, behavior and energetics, in *Biology of Sea Turtles*, Lutz, P. and Musick, J. A., Eds., CRC Press, Boca Raton, FL, 1996, chap. 7.
69. Caldwell, D. K., Hatchling green sea turtles, *Chelonia mydas* at sea in the northeastern Pacific Ocean, *Bull. So. Calif. Acad. Sci.*, 68, 113, 1969.
70. Carr, A. and Meylan, A. B., Evidence of passive migration of green turtle hatchlings in Sargassum, *Copeia*, 2, 366, 1980.
71. Bjorndal, K. A. and Bolton, A. B., Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the southern Bahamas, *Copeia*, 555, 1988.
72. Bjorndal, K. A. and Bolton, A. B., Comparison of length-frequency analyses for estimation of growth parameter for a population of green turtles, *Herpetologica*, 51(2), 160, 1995
73. Keinath, J. A. and Musick, J. A., Atlantic green turtle *Chelonia mydas* (Linnaeus), in *Virginia's Endangered Species*, Terwilliger, K., Coord., McDonald and Woodward, Blacksburg, VA, 1991, 448.
74. Balazs, G. H., Growth rates of immature green turtles in the Hawaiian Archipelago, in *Biology and Conservation of Sea Turtles*, Bjorndal, K. A., Ed., Smithsonian Institution Press, Washington, D.C., 1982, 117.
75. Carr, A., Heath, H., and Ogren, L., The ecology and migrations of sea turtles: the hawksbill turtle in the Caribbean Sea, *Am. Mus. Novit.*, 2248, 1, 1966.
76. Redfoot, W. E., Ehrhart, L. M., and Raymond, P. W., A juvenile Atlantic hawksbill turtle *Eretmochelys imbricata* from Brevard County, Florida, *Fl. Sci.*, 48, 193, 1985.
77. Parker, L. G., Encounter with a juvenile hawksbill turtle offshore Sapelo Island, Georgia, *Mar. Turtle Newsl.*, 71, 119, 1995.
78. Keinath, J. A., Musick, J. A., and Swingle, W. M., First verified record of the hawksbill sea turtle (*Eretmochelys imbricata*) in Virginia waters, *Catesbeina*, 11(2), 37, 1991.
79. Witzell, W. N., Synopsis of the biological data on the Hawksbill turtle *Eretmochelys imbricata* (Linnaeus, 1766), *FAO Fish. Synop.*, 137, 78, 1983.
80. Witzell, W. and Banner, A., The hawksbill turtle, *Eretmochelys imbricata*, in western Samoa, *Bull. Mar. Sci.*, 30(3), 571, 1980.
81. Boulon, R. H., Growth rates of wild juvenile hawksbill turtles *Eretmochelys imbricata* in St. Thomas, United States, Virgin Islands, *Copeia*, 811, 1994.
82. Carr, A. and Ogren, L., The ecology and migrations of sea turtles. 3: *Dermochelys* in Costa Rica, *Am. Mus. Novit.*, 1958, 1, 1959.
83. Caldwell, D. K., On the status of the Atlantic leatherback turtle, *Dermochelys coriacea coriacea* as a visitant to Florida mating beaches, with natural history notes, *Q. J. Fla. Acad. Sci.*, 21(3), 285-291, 1959.
84. Brongersma, L. D., Miscellaneous notes on turtles. III, *K. Ned. Akad. Wet. Amsterdam Ser. C*, 73(4), 323, 1970.
85. National Marine Fisheries Service and U.S. Fish and Wildlife Service, Recovery Plan for Leatherback Turtles in the U.S., Caribbean, Atlantic and Gulf of Mexico, National Marine Fisheries Service, Washington, D.C., 65, 1992.
86. Grant, G. S., Juvenile leatherback turtle caught by longline fishing in American Samoa, *Mar. Turtle Newsl.*, 66, 5, 1994.
87. Horrocks, J. A., Leatherbacks in Barbados, *Mar. Turtle Newsl.*, 41, 7, 1987.
88. Zug, G. R. and Parham, J. F., Age and growth in leatherback sea turtles, *Dermochelys coriacea* (Reptilia, Dermochelyidae), *Biol. Bull.*, in press.
89. Lutcavage, M., and Lutz, P. L., Metabolic rate and food energy requirements of the leatherback sea turtle, *Dermochelys coriacea*, *Copeia*, 1986, 796, 1986.
90. Koblentz-Mishke, O. J., Volkovinsky, V. V., and Kaloanova, J. G., Plankton primary production of the world oceans, in *Scientific Exploration of the South Pacific*, Wooster, W. S., Ed., National Academy of Sciences, Washington, D.C., 1970, 183.
91. Ernst, C. H., Lovich, J. E., and Barbour, R. W., *Turtles of the United States and Canada*, Smithsonian Institution Press, Washington, D.C., 1944.
92. Shoop C. R. and Kenney, R. D., Seasonal distribution and abundances of loggerhead and leatherback sea turtles in waters of the northeastern United States, *Herpetol. Monogr.*, 6, 43, 1992.
93. Byles, R. A., Behavior and Ecology of Sea Turtles from Chesapeake Bay, VA, Ph.D. dissertation, College of William and Mary, Williamsburg, VA, 1988.
94. Keinath, J. A., Musick, J. A., and Byles, R. A., Aspects of the biology of Virginia's sea turtles: 1979–1986, *Va. J. Sci.*, 38(4), 329, 1987.
95. Musick, J. A. and Keinath, J. A., unpublished, 1988.
96. Bowen, B. W., Richardson, J. I., Meylan, A. B., Margaritoulis, D., Hopkins-Murphy, S. R., and Avise, J. C., Population structure of loggerhead turtles (*Caretta caretta*) in the west Atlantic ocean and Mediterranean Sea, *Conserv. Biol.*, 7, 834–844, 1993.
97. Norrgard, J., Determination of Stock Composition and Natal Origin of a Juvenile Loggerhead Turtle Population (*Caretta caretta*) in Chesapeake Bay Using Mitochondrial DNA Analysis, Master's thesis, College of William and Mary, School of Marine Science, Williamsburg, VA, 1995.
98. Sears, C. J., Genetic Structure of a Local Loggerhead Sea Turtle Population Based on Mitochodrial DNA Analysis, Masters thesis, University of Charleston, SC, 1993.

99. Sears, C. J., Preliminary genetic analysis of the population structure of Georgia loggerhead sea turtles, in *Proc. 14th Annu. Symp. Sea Turtle Biology and Conservation*, Bjorndal, K., Bolton, A. B., Johnson, D. A., and Elizar, P. J., Compilers, NOAA Tech. Memo. NMFS-SEFSC-351, 135, 1994.
100. Keinath, J. A., Musick, J. A., and Barnard, D. E., Abundance and distribution of sea turtles off North Carolina, Mineral Management Service, OCS Study, Virginia Institute of Marine Science, Gloucester Point, VA, MMS 95-0024, 1, 1996.
101. Musick, J. A., Barnard, D., and Keinath, J. A., Aerial estimates of seasonal distribution and abundance of sea turtles near the Cape Hatteras faunal barrier, in *Proc. 13th Annu. Symp. Sea Turtle Biology and Conservation*, Schroeder, B. A. and Witherington, H. E., Compilers, NOAA Tech. Memo. NMFS-SEFSC-341, 121, 1994.
102. Epperly, S. P., Braun, J., and Chester, A. J., Aerial surveys for sea turtles in North Carolina inshore waters, *Fish. Bull.*, 93, 254, 1995.
103. Epperly, S. P., Braun, J., Chester, A. J., Cross, F. A., Merriner, J. W., and Tester, P. A., Winter distribution of sea turtles in the vicinity of Cape Hatteras and their interaction with the summer flounder trawl fishery, *Bull. Mar. Sci.*, 56(2), 547, 1995.
104. Mendonca, M. T. and Ehrhart, L. M., Activity, population size and structure of immature *Chelonia mydas* and *Caretta caretta* in Mosquito Lagoon, Florida, *Copeia*, 1, 161, 1982.
105. Ehrhart, L. M., Marine turtles of the Indian River Lagoon System, *Fl. Sci.*, 46, 337, 1983.
106. LeBuff, C. R., *The loggerhead turtle in the eastern Gulf of Mexico, Caretta*, Research Inc., Sanibel, Florida, 216, 1990.
107. Hildebrand, H. H., A historical review of the status of sea turtle populations in the western Gulf of Mexico, in *Biology and Conservation of Sea Turtles*, Bjorndal, K., Ed., Smithsonian Institution Press, Washington, D.C., 447, 1982.
108. Keinath, J. A., Barnard, D. E., and Musick, J. A., Behavior of loggerhead sea turtles in Savannah, Georgia, and Charleston, South Carolina shipping channels, Final report to the U.S. Army Corps of Engineers, Vicksburg, MI, Contract Report FACW39-93-C-0016, 75 pp. + appendices, 1995.
109. Carr, A., Ogren, L., and McVea, C., Apparent hibernation by the Atlantic loggerhead turtle *Caretta caretta* off Cape Canaveral, Florida, *Biol. Conserv.*, 19, 7–14, 1980.
110. Ogren, L. and McVea, C., Apparent hibernation by sea turtles in North American waters, in *Biology and Conservation of Sea Turtles*, Bjorndal, K., Ed., Smithsonian Institution Press, Washington, D.C., 127, 1982, 127.
111. Schwartz, F. J., Behaviorial and tolerance responses to cold water temperatures by three species of sea turtles (Reptilia, Cheloniidae) in North Carolina, *Fla. Mar. Rec. Publ.*, 13, 16–18, 1978.
112. Lutz, P. L., Bergy, A., and Bergy, M., Effects of temperature on gas exchange and acid-base balance in the sea turtle *Caretta caretta* at rest and during routine activity, *J. Exp. Biol.*, 144, 155–169, 1989.
113. Henwood, T. A., Movements and seasonal changes in loggerhead turtle, *Caretta caretta*, aggregations in the vicinity of Cape Canaveral, Florida, *Biol. Conserv.*, 40, 191, 1987.
114. Limpus, C. J., Fleay, A., and Guinea, M., Sea turtles of the Capricornia Section, Barrier Reef, in *The Capricornia Section of the Great Barrier Reef: Past, Present and Future*, Ward, W. T. and Saeger, P., Eds., Royal Society of Queensland and Australian Coral Reef Society, Brisbane, 61, 1984.
115. Limpus, C. J., The loggerhead turtle, *Caretta caretta*, in Queensland: feeding ground selection following her first breeding season, NOAA Tech. Memo. NMFS-SEFC-351, 78, 1994.
116. Limpus, C. J., The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: population structure within a southern Great Barrier Reef feeding ground, *Wildl. Res.*, 19, 489, 1992.
117. Beardsly, R. C., Boycourt, W. C., and Hanson, D. Z., Physical oceanography of the Middle Atlantic Bight, *Am. Soc. Limnol. Oceanogr. Spec. Symp.*, 2, 20, 1976.
118. Rudloe, A., Rudloe, J., and Ogren, L., Populations of Atlantic ridley sea turtles (*Lepidochelys kempi*) in Apalachee Bay, Florida, costal waters, in *Proc. 9th Annu. Workshop on Sea Turtle Conservation and Biology*, Eckert, S. A., Eckert, K. L., and Richardson, T. H., Eds., NOAA Tech. Mem. NMFS-SEFC-232, 151, 1989.
119. Schmid, J. R. and Ogren, L.H., Subadult Kemp's ridley sea turtles in the southeastern U.S.: results of long-term tagging studies, in *Proc. 11th Annu. Workshop on Sea Turtle Biology and Conservation*, Salmon, M. and Wyneken, J., Compilers, NOAA Tech. Memo. NMFS-SEFSC 302, 14, 1992.
120. Morreale, S. J. and Standora, E. A., Occurrence, movement and behavior of the Kemp's ridley and other sea turtles in New York waters, *J. Herpetol.*, 26, 301, 1992.
121. Keinath, J. A., Barnard, D. E., Musick, J. A., and Bell, B. A., Kemp's ridley sea turtles from Virginia waters, in *Proc. 14th Annu. Symp. Sea Turtle Biology and Conservation*, Bjorndal, K.A., Bolton, A. B., Johnson, P. A., and Eliazar, P. J., Compilers, NOAA Tech. Memo. NMFS-SEFSC-351, 70, 1994.
122. Standora, E. A., Morreale, S. J., Thompson, R. D., and Burke, V. S., Telemetric monitoring of diving behavior and movements of juvenile Kemp's ridleys, in *Proc. 10th Annu. Workshop on Sea Turtle Biology and Conservation*, Richardson, T. H., Richardson, J. I., and Donnely, M., Compilers, NOAA Tech. Memo. NMFS-SEFC-278, 133, 1990.
123. Henwood, T. A. and Ogren, L. H., Distribution ann migration of immature Kemp's ridley turtles (*Lepidochelys kempi*) and green turtles (*Chelonia mydas*) off Florida, Georgia and South Carolina, *Northeast Gulf Sci.*, 9(2), 153, 1987.
124. Rudloe, A., Rudloe, J., and Ogren, L., Ocurrence of immature Kemp's ridley turtles, *Lepidochelys kempi*, in coastal waters of northwest Florida, *Northeast Gulf Sci.*, 12(1), 49, 1992.
125. Pritchard, P. C. H., Post-nesting movement of marine turtles (Cheloniidae and Dermochelidae) tagged in the Guianas, *Copeia*, 1976, 749, 1976.
126. Byles, R. and Plotkin, P., Comparison of the migratory behavior of the congeneric sea turtles *Lepidochelys olivacea* and *L. kempi*, in *Proc. 13th Annu. Symp. Sea Turtle Biology and Conservation*, Schroeder, B. A. and Witherington, H. E., Compilers, NOAA Tech. Memo. NMFS-SEFSC-341, 39, 1994.
127. Harris, A., Species review: olive ridleys, in Proc. Marine Turtle Conservation Workshop, James, R., Comp., Australian National Parks and Wildlife Service, Canberra, 1994, 58.
128. Poiner, I. R. and Harris, A. N. M., The incidental capture and mortality of sea turtles in Australia's northern prawn fishery, in *Proc. Marine Turtle Conservation Workshop*, James, R., Comp., Australian National Parks and Wildlife Service, Canberra, 1994, 115.
129. Epperly, S. A., Braun, J., and Veishlow, A., Sea turtles in North Carolina waters, *Conserv. Biol.*, 2, 384, 1994.

130. Guseman, J. L. and Ehrhart, L. M., Green turtles on sabellariid worm reefs: initial results from studies on the Florida Atlantic coast, in *Proc. 10th Annu. Workshop on Sea Turtle Biology and Conservation*, Richardson, T. H., Richardson, J. I., and Donnely, M., Compilers, NOAA Tech. Memo. NMFS-SEFC-278, 125, 1990.
131. Felger, R. S., Clifton, S. K., and Regal, P. S., Winter dormancy in sea turtles: independent discovery and exploitation in the Gulf of California by two local cultures, *Science*, 191, 283, 1976.
132. Mendonca, M. T., Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon, *Copeia*, 4, 1013, 1983.
133. Bjorndal, K. A. and Bolton, A. B., Developmental migrations of juvenile green turtles in the Bahamas, in *Proc. 15th Annu. Symp. Sea Turtle Biology and Conservation*, Keinath, J. A., Barnard, D. E., Musick, J. A., and Bell, B. A., Compilers, NOAA Tech. Memo. NMFS-SEFSC-387, 38, 1996.
134. Green, D., Growth rates of wild immature green turtles in the Galapagos Islands, Ecuador, *J. Herpetol.*, 27(3), 338, 1993.
135. Limpus, C. J. and Walter, D. G., The growth of immature green turtles (*Chelonia mydas*) under natural conditions, *Herpetologica*, 36, 162, 1980.
136. Meylan, A. B., Spongivory in hawksbill turtles: a diet of glass, *Science*, 239, 393, 1988.
137. Broderick, D., Moritz, C., Miller, J. D., Guinea, M., Prince, R., and Limpus, C. J., Genetic studies of the Hawksbill turtle *Eretmochelys imbricata*: evidence for multiple stocks in Australian waters, *Pac. Conserv. Biol.*, 4, 124, 1994.
138. Boulon, R. H., Virgin Island turtle tag recoveries outside the U.S. Virgin Islands, in *Proc. 9th Annu. Workshop on Sea Turtle Conservation and Biology*, Eckert, S. A., Eckert, K. L., and Richardson, T. H., Compilers, NOAA Tech. Memo. NMFS-SEFC-232, 215, 1989.
139. Hillis, Z. M., The hawksbill turtles of Buck Island Reef National Monument: a shared resource of the Caribean, *Proc. 14th Annu. Symp. Sea Turtle Biology and Conservation*, Bjorndal, K.A., Bolton, A. B., Johnson, P. A., and Eliazar, P. J., Compilers, NOAA Tech. Memo. NMFS-SEFSC-351, 59, 1994.
140. Barnard, D. E., Keinath, J. A., and Musick, J. A., Distribution of ridley, green and leatherback turtles in Chesapeake Bay and adjacent waters, in *Proc. 9th Annu. Workshop on Sea Turtle Conservation and Biology*, Eckert, S. A., Eckert, K. L., and Richardson, T. H., Compilers, NOAA Tech. Memo. NMFS-SEFC-232, 201, 1989.
141. Boulon, R., Leatherback turtle (*Dermochelys coriacea*) nesting biolgy Sandy Point, St. Croix: 1981–1990, in *Proc. 11th Annu. Workshop on Sea Turtle Biology and Conservation*, Salmon, M. and Wynhken, J., Compilers, NOAA Tech. Memo. NMFS-SEFC 302, 14, 1992.
142. Knowlton, A. R. and Weigle, B., A note on the distribution of leatherback turtles (*Dermochelys coriacea*) along the Florida Coast in February 1988, in *Proc. 9th Annu. Workshop on Sea Turtle Conservation and Biology*, Eckert, S. A., Eckert, K. L., and Richardson, T. H., Compilers, NOAA Tech. Memo. NMFS-SEFC-232, 83, 1989.
143. Musick, J. A., unpublished, 1989.
144. Prescott, R. L., Leatherbacks in Cape Cod Bay, Massachusetts 1977–1987, in *Proc. 8th Annu. Workshop on Sea Turtle Conservation and Biology*, NOAA Tech. Memo. NMFS-SCFC-214, 83, 1988.
145. Paladino, F. V., O'Connor, M. P., and Spotila, J. R., Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs, *Nature*, 344, 959, 1990.
146. Block, D. A., Finnerty, J. R., Stewart, A. F. R., and Kidd, J., Evolution of endothermy in fish: Mapping physiological traits on a molecular phylogeny, *Science*, 260, 210, 1993.
147. Ryther, J. H., Photosynthesis and fish production in the sea, *Science*, 166, 72, 1969.
148. Stancyk, S. E., Non-human predators of sea turtles and their control, in *Biology and Conservatioin of Sea Turtles*, Bjorndal, K., Ed., Smithsonian Institution Press, Washington, D.C., 139, 1982.
149. Bjorndal, K. A., Foraging, ecology and nutrition in sea turtles, in *Biology of Sea Turtles*, Lutz, P. and Musick, J. A., Eds. CRC Press, chap. 8.
150. Loop, K., Miller, J. D., and Limpus, C. J., Hawksbill turtle nesting on Milman Island, Great Barrier Reef, Australia, *Wild. Res.*, 22, 241, 1995.
151. Pritchard, P. C. H., Nesting of the leatherback turtle *Dermochelys coriacea* in Pacific Mexico, with a new estimate of the world population status, *Copeia*, 3, 741, 1982.
152. Sternberg, J., The Worldwide Distribution of Sea Turtle Nesting Beaches, Center for Environmental Conservation, Washington, D.C., 1981.
153. Pritchard, P. C. H., International migrations of South American sea turtles Chloniidae and Dermochelidae, *Am. Behav.*, 21, 18, 1973.
154. Keinath, J. A. and Musick, J. A., Movements and diving behavior of a leatherback sea turtle, *Dermochelys coriacea*, *Copeia*, 4, 1010, 1993.