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Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front

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Abstract Neonate sea turtles disperse from nesting beaches into the open ocean and develop during a multi-year growth period at sea, but data that characterize their behavior, feeding, and habitat during this developmental period have been few. Limited information has suggested that neonate sea turtles associate with lines of floating debris and biota at areas of surface downwelling. Data from the present study come from measurements of habitat, turtle behavior, and apparent foraging preferences in areas where neonate (post-hatchling) loggerhead turtles (*Caretta caretta*) were observed and captured. Turtles were observed ($n=293$) and captured ($n=241$ of the 293 observed) in downwelling lines that had formed in the slope water near the Gulf Stream front off east-central Florida, USA. Catch-per-unit-effort averaged 12.4 turtles/h from a vessel moving at 2.5 knots. Turtles were largely inactive and were closely associated with floating material, especially pelagic species of *Sargassum*. Turtles captured along with samples of floating material and given a gastric-esophageal lavage showed a preference for animal material (35.5% of volume in habitat, 70.9% in lavage) over plant material (60.3% of volume in habitat, 22.5% in lavage). Ingested anthropogenic debris included tar (20% of turtles) and plastics (15% of turtles). Ingested animals were principally small (most < 1 mm) and were typically slow-moving or non-motile species or stages. Ingested plants were most commonly *Sargassum* fragments or seagrasses that bore epiphytic animals. Preferred or commonly ingested animals were hydroids,

copepods, and pleuston such as *Janthina*, *Creseis*, *Porpita*, and *Halobates*. Data support a hypothesis describing post-hatchling loggerheads as facultatively active but principally low-energy float-and-wait foragers both within and outside of downwelling lines. Pelagic dispersal of turtles may be best predicted by a “smart” drifter analogy wherein turtle buoyancy, surface advection, and minimal oriented movement determine their distribution at sea. Conservation implications of plastic and tar ingestion are discussed.

Introduction

Hatchling sea turtles emerge from nests on oceanic beaches, crawl to the sea, and swim away from land. This offshore dispersal begins an extended pelagic phase of development for six of the seven sea turtle species. The pelagic phase has been referred to as the “lost year,” although the time period involved may be closer to a decade in some species (Bolten and Balazs 1995). It remains the least understood stage of sea turtle life history.

Most information on the pelagic phase has come from the loggerhead turtle (*Caretta caretta*). For loggerhead turtles inhabiting the North Atlantic Ocean, there is sufficient information for a model describing how pelagic turtles are distributed relative to later, benthic life-history stages. A widely accepted model was proposed by Carr (1986, 1987a), who hypothesized that hatchling loggerheads from western Atlantic beaches (principally eastern Florida) disperse from land, become entrained in the Gulf Stream, and are transported by the North Atlantic Gyre during a multi-year period of growth at sea. In this model, the end of the pelagic phase is marked by entry into the shallow coastal waters of the western Atlantic, where larger (10–100 kg), immature loggerheads forage within benthic habitats.

Support of Carr’s loggerhead pelagic dispersal model is robust. Records of loggerheads from the eastern North Atlantic (principally the Azores and Madeira;

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Brongersma 1971; Carr 1986) fill a gap in the size-frequency distribution of western North Atlantic loggerheads (subadult and adult loggerheads found in coastal Florida; Carr 1986). Moreover, studies of pelagic loggerhead turtles around the Azores and Madeira demonstrate both genetic similarities between the eastern and western Atlantic (Bolten et al. 1998) and movements of individuals between the eastern and western Atlantic (Eckert and Martins 1989; Bolten et al. 1992a, b; Bjørndal et al. 1994) that are predicted by Carr's model. Genetic and size-frequency information from loggerhead turtles captured from the Pacific Ocean suggests that Pacific loggerheads also have an extended pelagic development within an oceanic gyre (Bowen et al. 1995).

Growth and size data suggest that loggerheads spend approximately 10 years in pelagia (Bolten and Balazs 1995). Despite this lengthy period of development at sea and the confidence researchers have in how young loggerheads are distributed throughout the North Atlantic, little specific information exists on the nature of the surface waters that pelagic loggerheads inhabit, on turtles' ecological relationships with other organisms there, or on turtles' behavior within this developmental habitat. These ecological data have been lacking because of the difficulties of access to the open ocean, of data collection there, and in locating specific areas where young pelagic turtles can be studied.

Post-hatchling loggerheads have provided useful data from which to form hypotheses about the pelagic ecology of loggerheads. [I use the term "post-hatchling" henceforth to describe neonate sea turtles that have matured beyond the period of frenzied swimming as hatchlings (Wyneken and Salmon 1992). Pelagic post-hatchlings become pelagic juveniles as they depart neritic waters near their natal beach. Juvenile loggerheads (> 200 g) are seldom observed near the Florida coast.] Post-hatchlings are occasionally washed ashore during storm events (Caldwell 1968; Brongersma 1972; Hughes

1974; Fletemeyer 1978; Carr and Meylan 1980; Carr 1987a; Limpus et al. 1994), are found in the stomachs of pelagic fishes (Caldwell et al. 1959; Hughes 1974; Witham 1974; Carr 1987a; Limpus et al. 1994), and are observed at sea (Smith 1968; Brongersma 1982; Carr 1987a; Schwartz 1988; Limpus et al. 1994). These records, although not detailed, suggest that post-hatchling loggerheads disperse into the open ocean and may have an association with *Sargassum* and other floating material collected within areas of surface downwelling [see a presentation of this hypothesis by Carr (1986) and a review by Walker (1994)].

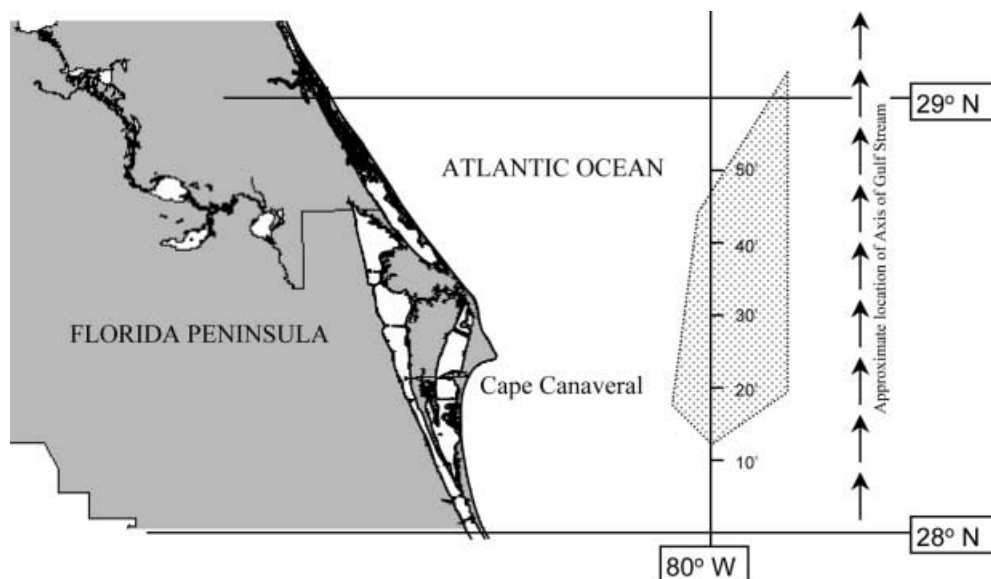
A principal purpose of the present study was to test hypotheses that describe post-hatchling sea turtles as pelagic drifters having a strong association with *Sargassum* and with lines of floating material at areas of downwelling. Specific goals of this study were (1) to locate pelagic post-hatchling sea turtles, (2) to provide a description of habitats where post-hatchling sea turtles are found, (3) to describe abundance and seasonality of post-hatchling sea turtles in the Atlantic Ocean off Florida, (4) to describe the behavior and food choice of post-hatchling sea turtles, and (5) to describe threats to turtles from anthropogenic debris such as plastics and tar.

Materials and methods

Study area and study period

I made 18 trips to a region of the Atlantic approximately 20–40 nautical miles east of Cape Canaveral, Florida, near the 40-fathom depth contour and the western wall of the Gulf Stream at approximately 28.5°N and 80.0°W (Fig. 1). The trips were made between 22 July and 2 October 1997, the period during which hatchlings exit nearby nesting beaches. All observations of pelagic turtles were made in daylight between 0800 and 1800 hours.

Fig. 1 The shaded polygon represents the study area, where lines of floating material were searched for post-hatchling sea turtles, 22 July through 1 October 1997



The study area is down-current from nesting beaches from which large numbers of loggerhead hatchlings enter the Atlantic and is near a permanent frontal boundary in the slope water at the western boundary of the Gulf Stream. During the study period, approximately 33,000 loggerhead hatchlings per day leave the beaches immediately "upstream" from the study site ("upstream" refers to the Florida coast between Cape Florida and Cape Canaveral; hatchling numbers are based on an assumption of 70,000 nests/year, 115 eggs/nest, 50% success in survivorship from egg to hatchling, and 120 days of hatchling emergence activity; Ehrhart and Witherington 1987; Meylan et al. 1995).

Habitat surveys and physical oceanographic measurements

Habitat was surveyed from a low-freeboard, 6.5-m, outboard vessel (R.V. "Excellent Fishe II"). Within the study area, I targeted lines of floating material at regions of surface-water downwelling. I determined the latitude and longitude of these areas of potential neonate sea turtle habitat, and at points 0.1 nautical miles on either side of each downwelling line, I measured water-surface temperature and conductivity (depth=1.0 m), and current speed and direction. Temperature and conductivity were measured with a YSI model 30 meter and current measurements were made by tracking a current drogue with a Garman global positioning receiver. I made additional notes describing density of *Sargassum* and other floating material, width of the downwelling line, orientation of the downwelling line relative to wind direction, and weather and sea conditions.

Turtle capture

After the initial physical oceanographic measurements were made, timed searches for turtles were conducted by observers on the bow of the research vessel (elevation was approximately 3 m above the surface) as it moved at idle speed (approximately 2.5 knots) through the center of each downwelling line. When a turtle was observed, the observer noted the time of the observation, and the geographic position, species, and behavior of the turtle. Observed turtles fell into four categories:

1. Turtles observed but not captured ($n=49$). Data from these turtles were used in addition to data from captured turtles to calculate catch-per-unit-effort and species frequency.
2. Turtles captured by dip net and released ($n=175$). In addition to gathering time, position, and species data, researchers weighed these turtles with a spring scale, measured them for straight-line carapace length (SCL, nuchal to pygal tip), and examined their mouths for the presence of tar.
3. Turtles captured with a habitat sampler, lavaged, and released ($n=66$). This capture technique (described below) was used to collect turtles along with nearby floating material. These turtles were weighed, measured, and examined as in (2) and were given gastric-esophageal lavages to sample recently ingested items.
4. Turtles found dead and collected ($n=3$). These turtles were weighed, measured, and examined as in (2) and were necropsied so that gut contents could be examined.

All captured turtles were marked with a red grease pencil to identify the turtle should it be recaptured (none were recaptured). Turtles were released into habitat similar to their capture site within 2 h of their capture.

Paired habitat samples and lavage samples

The device used for capturing turtles and nearby material was a modified dip net. In this habitat sampler, the net mesh was replaced with a funnel of 500- μ m stainless-steel mesh that connected to a 300- μ m-mesh removable sample bag. The net opening was circular, 70 cm in diameter, and sampled a radius of approximately 30–40 cm around the turtle.

Turtles chosen for paired habitat and gastric-esophageal samples were the first five turtles encountered each day of sampling that were judged to be undisturbed and ahead of the vessel's path. When the vessel reached these turtles, the habitat sampler was placed into the water for a 2-s count in order to collect both the turtle and nearby material in the mesh sample bag. After the turtle was removed from the sample bag, the bag and the remaining contents were sealed in an airtight plastic bag and placed on ice for later examination.

Each turtle captured with a habitat sample was also given a gastric-esophageal lavage. In the lavage procedure, the turtle was inverted and its mouth opened to receive a 3-mm outside-diameter flexible vinyl tube. A reference point on the tube aided in its insertion and indicated that the tip of the tube had reached the stomach (but it is not certain whether samples represented items from both esophagus and stomach). Filtered sea water was introduced into the stomach and esophagus by hand-pumping a rubber ear-wash bulb connected to the tube. Items flushed from the turtle were caught in a 500- μ m-mesh sieve. There were no detectable adverse effects from the procedure. Lavage samples were washed with filtered seawater into glass vials and stored on ice for later examination.

I examined the mouths of all captured turtles and sampled any loose or adhering items. Suspected tar was scraped from the tomia and inner beak using a wooden toothpick and placed with the toothpick into a glass vial for later analysis.

Volume approximation for habitat samples, lavage samples, and gut contents

I approximated indices of volume for the items found in lavage and habitat samples by measuring the spatial proportion of each individual item to the rest of the sample in which it was found. Spatial proportions were assessed by counts at microscopically viewed intercept points (microstereology). The theoretical basis for deriving indices of volume from these counts is discussed by Schaefer (1970).

After samples were weighed they were reduced in size by randomly dividing them and discarding portions selected by coin toss. I reduced samples in size until they fit onto an 8.4 cm² grid (6 \times 6) of filter paper. After samples were drained on the filter paper, a clear acrylic plate with a 6 \times 6 grid etched into it was placed over the sample on the filter paper. One-centimeter posts supporting the acrylic plate kept the plate from crushing the sample.

The sample was then placed on the stage of a binocular dissecting microscope that had a 10 \times 10 square graticule in one eyepiece. I surveyed the sample by matching the outer margin of the graticule grid to each of the 36 squares of the etched acrylic plate overlying the sample. Item descriptions to the lowest possible taxon were made for four graticule intercept points at each of the 36 overlying grid squares.

Analysis of tar samples

Suspected tar samples from loggerhead post-hatchlings were collected from lavage washings or from jaw scrapings and placed into 4-dram glass vials. A subsample of 20 suspected tar samples from 19 turtles was sent for gas chromatography to the petroleum chemistry laboratory, University of South Florida. There, samples were dissolved in approximately 1 ml of dichloromethane (DCM) and later evaporated under nitrogen to approximately 100–200 μ l. Each sample solution was injected into a Shimadzu GC-14A high-resolution gas chromatograph (GC) equipped with a 30-m \times 0.2-mm internal-diameter fused silica column and flame ionization detector. Hydrogen was used as the carrier gas. Oven temperature was programmed to increase from 50°C to 280°C at a rate of 6°C per minute and was held at 280°C for 10 min. All GC peak identifications were based on comparison of sample retention times to those of authentic standards. Peak identifications of selected samples were confirmed by combined gas chromatography-mass spectrometry (GCMS). GCMS and GC conditions were the same

except that helium was used as the carrier gas for GCMS. I verified the presence of tar in the remainder of the samples by observing solubility in DCM under a binocular microscope.

Capture probability based on proportion of species at the nesting beach

The probability of encountering the proportion of loggerhead and green turtle post-hatchlings observed in this study was calculated given the proportion of each species leaving nearby nesting beaches as hatchlings during the study period. The hypothesis tested was that loggerhead turtles and green turtles disperse in a similar way, occupy the same pelagic habitat, and are equally observable in the habitat surveyed.

I calculated the binomial probability for the frequency of loggerhead and green turtle captures as

$$p(x) = \binom{n!}{x!(n-x)!} (p^x q^{n-x})$$

where p is the probability that a captured post-hatchling would be a green turtle if the hypothesis were true, q is the probability that a captured post-hatchling would be a loggerhead if the hypothesis were true, n is the total number of post-hatchling captures, and x is the number of green turtles in n captures. I based both p and q on the proportion of green turtle and loggerhead eggs [(nests) × (clutch size)] on adjacent Florida beaches in 1997 (two tests were made, one on species proportions from Brevard County, Florida, 27.8°–28.8°N, and one on proportions from the entire Atlantic coast of Florida, 24.5°–30.7°N; Florida Marine Research Institute, unpublished data).

Results

Description of habitat

Each habitat sampled had evidence of downwelling and floating material in long (to 5 nautical miles) contiguous lines or in smaller (0.05–0.5 nautical miles), multiple, closely set, parallel lines. Evidence of downwelling commonly included positively buoyant items, such as *Sargassum* and plastics, submerged below the line of surface material. Often, masses of submerged medusae were observed to be swimming against an apparent downward current.

Three habitat types (categories of downwelling lines) were surveyed, and all were found to contain neonate turtles. The first type of habitat occurred where there was evidence of an oceanic front. Fronts were evident as shear boundaries between two water masses having different temperatures, conductivities, and/or current characteristics and a profound degree of downwelling (numerous buoyant objects submerged below a line of floating material). Downwelling lines along fronts were oriented north–south (parallel to the axis of the Gulf Stream), had slightly turbulent surface water, and often divided two areas of distinctly different water color.

A second type of habitat occurred at slicks. Slicks are produced by the downwelling above and behind the crests of large, slow-moving, internal waves and in this study were evident as approximately north–south-oriented lines of foam and other material adjacent to or within an area of calm surface water. There was little

or no difference between measures of temperature, conductivity, and current on either side of lines of material thought to be brought together by slicks. No slicks were observed when the wind was greater than 10 knots.

A third type of habitat occurred at aligned, multiple windrows. Windrows are produced by wind-generated Langmuir circulation cells and, in this study, were evident as closely aligned (within 20 m), offset, parallel rows of material. Windrows were individually oriented approximately parallel with wind direction. Most were collectively oriented approximately north–south, indicating that the windrows may have been fragmented lines of material from slicks or fronts. Windrows were evident when winds were greater than approximately 10 knots.

These three identified habitat types were not analyzed separately because most of the sampling and the majority of the post-hatchling captures were made in slicks. In addition, habitat types were often in transition during the time they were sampled. For instance, fronts and slicks were commonly observed to break up into windrows when the wind became greater than 10 knots.

Direction of the current both east ($\bar{\theta}=003$, $r=0.76$) and west ($\bar{\theta}=013$, $r=0.59$) of the downwelling lines sampled was generally north (and significantly directed, according to a Rayleigh test of uniformity, $P<0.01$) and did not differ statistically (according to a Watson's F test for two circular means, $F=1.06$, $P=0.31$, $df=26$). However, current speeds east ($\bar{x}=1.8$ knots, $SD=1.1$ knots) and west ($\bar{x}=1.4$ knots, $SD=1.0$ knots) of the downwelling lines sampled were different (t -test for dependent samples, $P<0.001$, $n=14$). Although there were individual cases in which temperature and/or salinity differed east and west of the downwelling lines sampled, mean water temperatures and salinities of the two sides were not different at $\alpha=0.05$ (t -test for dependent samples; for water temperature, $P=0.25$, for salinity, $P=0.26$; $n=14$ for each).

Captures and catch-per-unit-effort

A total of 293 post-hatchling loggerheads were observed. Of these, 241 were captured. Gastric-esophageal samples were taken from 66 loggerheads that were collected along with associated material. Forty-nine loggerheads were observed but not captured, and 3 were found dead in fresh condition and were collected.

The seasonal trend in observations of post-hatchling loggerheads in downwelling lines (Fig. 2) appeared similar to the trend in numbers of hatchlings leaving nearby nesting beaches. The period of hatchling emergence and dispersal in Florida is July through October with a peak in August (Ehrhart and Witherington 1987). Mean post-hatchling catch-per-unit-effort (CPUE) in six biweekly periods between 15 July and 15 October ranged from 31.4 turtles/hour (in early August) to 0.0 turtles/hour (in early October). The mean CPUE for the study period was 12.4 turtles/hour.

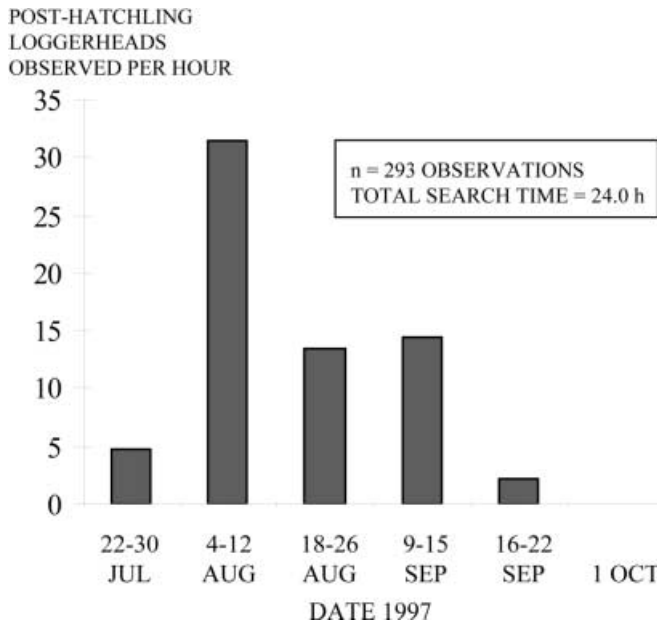


Fig. 2 Catch per unit effort based on hours spent searching for post-hatchling sea turtles in lines of floating material off eastern Florida

No neonate green turtles (*Chelonia mydas*) were observed. I conducted a test of binomial probability to determine whether the number of turtle observations was large enough to allow for the probability that at least one green turtle would be captured. With the number of green turtle encounters (x) equal to zero, the binomial probability equation described in Methods simplifies to

$$p(x) = q^n$$

The proportion of loggerhead turtles expected to have departed the nearby Brevard County coast was 0.9898 and the proportion of loggerheads departing the entire Atlantic coast of Florida was 0.9874 (Florida Marine Research Institute, unpublished data; these proportions represent q in the equation). The probability $p(x)$ that 293 loggerheads and no green turtles would be captured from an assemblage of neonate sea turtles with species proportions equal to the proportions of the two species leaving the Brevard County coast and the entire Atlantic coast of Florida was 0.05 and 0.02, respectively. Thus, the hypothesis that neonate loggerhead turtles and green turtles disperse in a similar way, occupy the same pelagic habitat, and are equally observable in the habitat surveyed is rejected (note that only one condition need be false to reject the hypothesis).

Association with floating material

I captured 66 post-hatchling loggerheads in such a manner that the floating material surrounding them was collected with the turtle. All but one of the 66 turtles had

measurable amounts of material collected with the turtle (Fig. 3). The median wet weight of the surrounding material was 30.3 g (0.0–490.1 g, mean = 79.6 g, SD = 117.7 g). The nature of the material sampled from around captured turtles is described below.

Comparisons of paired habitat and lavage samples

All but 1 of the 66 turtles collected with habitat samples had measurable material in their lavage samples. Most of the material collected in the habitat and lavage samples could be placed into seven principal categories (Table 1). The first, plants and cyanobacteria, included seagrasses (mostly *Syringodium*), *Sargassum* (mostly *Sargassum natans*), algae other than *Sargassum*, and the filamentous cyanobacterium *Rivularia*. The second category, animals endemic to or closely associated with the *Sargassum* community (as described by Butler et al. 1983; principally sessile animals or meiofaunal associates), included hydroids (principally thecate hydroids), copepods (principally harpacticoid copepods), *Spirorbis* (a tubicolous polychaete), *Membranipora* (a bryozoan), fishes, crabs (principally *Portunus*), and shrimps (principally *Latreutes*). The third category included winged insects. The fourth was made up of pelagic animals not closely associated with the *Sargassum* community (largely pleustonic, wind-dispersed animals), such as *Janthina* and *Creseis* (planktonic shelled gastropods), *Porpita* (a siphonophore), *Halobates* (a pelagic hemipteran insect), and *Pelagia* (a medusa). The fifth category included anthropogenic debris, the sixth category included unidentified material, and a seventh category

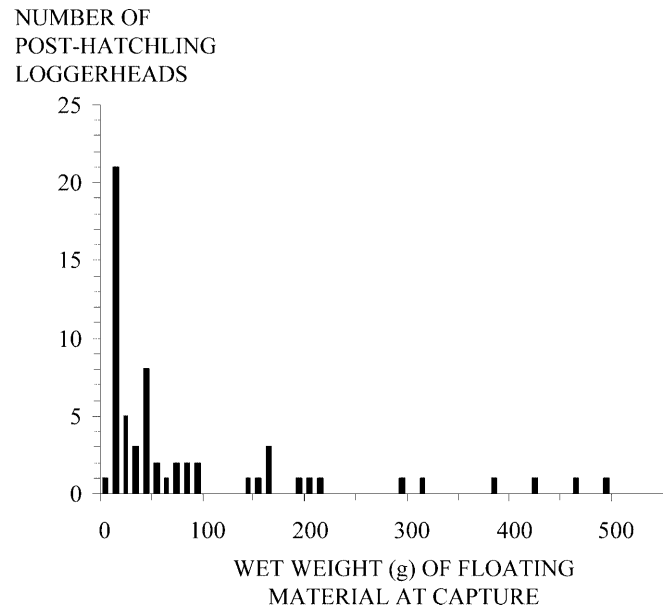


Fig. 3 The association of captured post-hatchling loggerheads with floating material. These habitat samples contained material from approximately 30–40 cm around each turtle at the time of capture

Table 1 Mean proportions of items recovered from the water surrounding 65 post-hatchling loggerhead turtles (*habitat samples*) and from gastric-esophageal lavage samples (*lavage samples*) from the same group of turtles. Percent of sample is represented by the proportion of individual and total-sample identifications made at intercept points of an overlaying grid (3,479 identifications in habitat samples, 1,006 in lavage samples) as each sample was examined under a dissecting microscope. The difference in mean proportions between 65 paired habitat and lavage samples was tested with a *t*-test for dependent samples run on transformed ($y_i = \arcsin \sqrt{y}$) proportions

	Mean % of sample	
	Habitat samples	Lavage samples
Plants and cyanobacteria		
Seagrasses ^a	19	5.0
<i>Sargassum</i> ^a	33	11
Other algae and cyanobacteria ^a	8.0	4.5
Animals commonly associated with <i>Sargassum</i>		
Hydroids	19	21
Copepods ^a	0.042	5.1
<i>Spirorbis</i> ^a	1.8	0.57
<i>Membranipora</i> ^a	7.6	2.0
Fishes, crabs, shrimp ^a	2.1	0.85
Winged insects	1.1	1.0
Pelagic animals not commonly associated with <i>Sargassum</i> ^a	0	2.8
Anthropogenic debris		
Plastics	2.8	2.8
Tar	0.21	4.4
Minor items	5.0	12
Unknown material and unidentified tissues ^a	0.19	27

^a Paired samples significantly different ($\alpha=0.05$)

included the remaining infrequently observed components.

A *t*-test for dependent samples was run on the transformed ($y_i = \arcsin \sqrt{y}$) mean proportion of volume representing 14 item groups within the seven categories described above (Table 1). Tests on an item's proportion were made between the 65 paired samples (1 sample-pair of 66 was excluded because no measurable lavage sample was obtained). In the 65 pairs of measurable samples, mean proportion of plant material was higher in habitat samples (61%) than in lavage samples (24%), and mean proportion of animal material was higher in lavage samples (66%) than in habitat samples (33%) (*t*-test for dependent samples, $\alpha=0.05$).

Size and activity

Loggerhead post-hatchlings in the present study ($\bar{x}=46.9$ mm SCL, SD = 3.2 mm, range = 40.9–78.4 mm, $n=244$; $\bar{x}=23$ g in weight, SD = 3.4 g, range = 18–50 g, $n=241$) were on average slightly larger (*t*-tests on SCL and weight, $P<0.01$) than loggerhead hatchlings from nearby nesting beaches ($\bar{x}=44.5$ g SCL, $n=79$, Witherington 1994b). Two turtles were not weighed because of rough sea conditions, and one turtle was not weighed because it exceeded the scale's capacity.

The modal behavior of post-hatchling loggerheads when first observed was a tuck (41 of 67 observations). I observed turtles in a tuck to float motionless with the ventral surface of the front flippers in full contact with and pressed flat against the lateral carapace margin and with the distal webs of the rear flippers overlapping, thereby concealing the tail (described by Witherington 1994b, 1995). The second most common behavior was a rear-flipper kick pattern (16 of 67 observations). Turtles showing this behavior were in a position similar to the

tuck except that the rear flippers moved with a rhythmic, simultaneous stroke to propel the turtle forward at the surface (described by Davenport and Clough 1986). I considered similar movements – employing single rear flippers and occasional extensions of a single front flipper (as might be expected from steering movements) – to be part of the rear-flipper kick pattern. The third most frequent behavior was the dog paddle (9 of 67 observations). Turtles in a dog paddle moved all four flippers in an alternating pattern similar to exaggerated crawling movements. During a dog paddle the head was raised above the surface, and among turtles that were observed closely, there were buccal-pharyngeal indications that a breath was taken. Dog paddling resulted in little forward movement. Only one turtle was observed in the fourth behavior recorded, a dive. When this turtle was first observed, it was actively swimming beneath the surface using its flippers.

Prevalence of plastic and tar

Of 66 post-hatchling loggerheads sampled, the lavage samples of 8 (12%), and either the lavage or mouth samples of 13 (20%) contained tar. The lavage samples of 8 turtles (12%), and either the lavage or mouth samples of 10 (15%) contained plastic. These frequencies are lower than the 63% incidence of tar and the 17% incidence of plastic recorded in either mouth or lavage samples of loggerheads ($n=103$) captured in 1993 (Witherington 1994a). All three of the loggerheads that were found dead and were later necropsied had tar and plastic in their gut.

The ten samples of suspected tar collected from turtle mouths and the one sample collected from an associated habitat sample were analyzed by GC and/or GCMS (Table 2) and gave chromatograms indicating a variety

of sources and ages. Tar samples had n-alkane profiles in keeping either with fresh to moderately weathered crude oil or with moderately weathered refined oil such as bunker C fuel oil.

Discussion and conclusions

Habitat description

Numerous features make the area sampled (Fig. 1) likely to contain habitat for post-hatchling sea turtles. The most important of these features is the continental edge of the Gulf Stream, where a persistent front collects lines of floating material. Off the central Florida peninsula, the front occurs in an area where water depth changes sharply from approximately 50 m to 200 m within a distance of 5 nautical miles. This bathymetric feature may cause internal waves to refract and slow, thereby creating an area where north-south-oriented slicks frequently occur. Formation of slicks east of central Florida may be more profound during the late-summer sea turtle hatching season when sea conditions are often calm and the local thermocline (in which internal waves travel) is distinct. Each of these phenomena creates lines of downwelling where debris and biota collect (Ashjian et al. 1994) within frenzied-swimming distance of the hatchlings that leave eastern Florida nesting beaches.

The material collected at these downwelling areas appears to originate from both land and sea and was transported by movements of both water and air (Table 1). Terrestrial plants likely originated from continental or island sources and made up only a small fraction ($\bar{x}=0.56\%$, $SD=2.3\%$) of the downwelling lines sampled. Oceanic biota such as *Sargassum* species (*S. natans* and *S. fluitans*), their associates, and the various pelagic animals recorded were most common. Winged insects, especially those smaller than a few millimeters in length, were likely members of the aerial plankton that had fallen to the ocean's surface. The abundant plastics and tar observed may have had both

terrestrial and oceanic sources. Inscriptions on many plastic items collected from downwelling lines indicated that they had a distant origin (Arabia, Asia, Europe, Latin America, etc.) and probably had been discarded from ships. Similarly, analyses of tar samples indicated that oil-transport ships may be a principal origin of the hydrocarbons collected in downwelling lines (Table 2).

In addition to creating lines of floating material, currents are also important in transporting neonate turtles that are within these lines. Most of the turtles I observed were being transported north at approximately 10–80 nautical miles/day. This observation is in keeping with the hypothesis that loggerheads from Florida become entrained in the North Atlantic Gyre soon after leaving the nesting beach.

Weather conditions in the survey area and during the survey period greatly affected the researcher's abilities to find downwelling-line habitat and the turtles within it. In this area during the summer, winds are usually light (< 10 knots) and variable – conditions that make downwelling lines longer, more distinct, and easier to search for turtles. In winds greater than 10 knots, lines of floating material were observed to break up into more widely separated and difficult-to-survey windrows. It is not known how this fragmentation of habitat may affect the dispersal of neonate turtles and their ability to forage.

Abundance, species composition, and seasonality

Post-hatchling loggerheads were common in the downwelling lines surveyed within the study area, with as many as 30 turtles observed within a 50-m² area of floating material. Using the average capture rate of approximately 12 turtles/h, a survey speed of 2.5 knots, and an estimated 10-m width of the downwelling line surveyed (the approximate sighting limit of observers), I determined the approximate density of post-hatchling loggerheads in downwelling lines to be 9,000 turtles per square nautical mile. It is not known how great a con-

Table 2 Results of gas chromatography of suspected tar from mouth, lavage, and associated habitat samples from post-hatchling loggerhead turtles captured near the western Gulf Stream in 1997

Date	Origin	Indications from gas chromatography			
		Tar source	Weathering/age	n-Alkane range	n-Alkane maximum
29 July	Mouth	Crude oil	Several weeks	nC ₁₈ –nC ₃₂	nC ₂₂
30 July	Mouth	Crude oil	Days–weeks	nC ₁₅ –nC ₃₂	nC ₂₂
11 August	Mouth	Crude oil	Weeks	nC ₁₅ –nC ₃₂	nC ₂₇
18 August	Lavage	Crude oil	Days–weeks	nC ₁₇ –nC ₃₂	nC ₂₉
	Mouth	Crude oil	Several weeks	nC ₁₇ –nC ₂₈	nC ₂₀
15 Sept.	Mouth	Crude oil	Weeks	nC ₁₅ –nC ₃₂	nC ₂₂
	Mouth	Crude oil	Days–weeks	nC ₁₅ –nC ₃₂	nC ₂₇
	Mouth	Crude oil	Weeks	nC ₁₅ –nC ₃₂	nC ₁₉ and nC ₂₉
16 Sept.	Habitat	Refined oil ^a	Days–weeks	nC ₁₇ –nC ₃₂	nC ₂₇
	Lavage	Refined oil ^b	Uncertain ^b	nC ₂₄ –nC ₃₂	nC ₂₉
22 Sept.	Mouth	Crude oil	Days	nC ₁₂ –nC ₃₂	nC ₂₀

^a Likely bunker C fuel oil

^b Possibly also crude oil aged weeks

centration this is in comparison to the surrounding surface water.

As was found in a study of post-hatchling loggerheads captured in 1993 (Witherington 1994b), captured post-hatchling loggerheads were slightly larger than hatchlings leaving the nesting beach. Because feeding and growth occur after the initial swimming frenzy and not during the few days that yolk reserves are retained (Kraemer and Bennett 1981) and because observed turtles did not display frenzied swimming, I estimate that the post-hatchlings in downwelling lines were approximately 5–30 days old. Sizes of some turtles indicated that they had been feeding and growing for weeks (surmised from growth rates of young, captive loggerheads, Caldwell 1962; some turtles in the present study had doubled in weight). Other indications of time at sea came from the growth of epizoa (algae, hydroids, cirripeds, etc.) on turtles. I reason that the captured turtles were within 1 or 2 days of their entrainment in the Gulf Stream (given the approximate transport time from the southern reach of the nesting range). If true, larger post-hatchlings probably swam out their frenzy period, began foraging, and grew substantially in the area of ocean between the western Gulf Stream and the Florida peninsula during a period of days or weeks. The similarity of loggerhead-capture seasonality (Fig. 2) to the July–October hatching season indicates that the average lag time between hatchling emergence from nests and entrainment in the Gulf Stream is less than 1 month.

No neonate green turtles were captured despite the expectation that approximately 2% of the hatchlings dispersing from nearby beaches were green turtles. Because this lack of captures was not likely due to chance alone, neonate green turtles may differ from loggerheads in the areas they inhabit, in how they are distributed in this habitat, in their behavior (e.g., greater activity than loggerheads), in their ability to conceal themselves from observers, or in any combination of these.

Behavior and diet of pelagic post-hatchling loggerheads

Evidence from the present study suggests that post-hatchling loggerheads within collections of floating material at pelagic surface downwellings are low-energy, float-and-wait foragers. The most common behaviors among captured loggerheads appeared to be those requiring minimal energy: the tuck, in which there is little or no movement, and the rear-flipper-kick pattern, in which there is relatively limited movement of the rear flippers only. Limiting activity may function both to conserve energy for growth and to conceal turtles from predators.

A post-hatchling's positive buoyancy and minimal activity help explain the observed association between turtles and floating material (principally *Sargassum*) at downwelling lines (Fig. 3). Following capture and release, however, many turtles were observed to orient and move toward nearby floating objects such as *Sargassum*

(others remained in a tuck position until the research vessel left the area). Thus, the observed association with floating material may be both active and passive.

Whether the association with floating material is passive or active, it is clear that post-hatchling loggerheads forage within floating material because a large proportion of the food items they consume are biota that are closely, if not obligately, associated with floating pelagic substrates (i.e., associates of the *Sargassum* community, Table 1). Of the identifiable biota within lavage samples from post-hatchlings, 70% were organisms commonly associated with the *Sargassum* community (Butler et al. 1983).

The pairing of lavage with habitat samples allowed an assessment of the turtles' preference for items relative to their occurrence where the turtles were foraging (Table 1). A comparison of lavage and habitat samples showed that post-hatchlings had fed upon a wide variety (approximately 100 categorized items) of principally small items (often < 1 mm) and that animal material was preferred over plant material. Ingested animals were typically species or stages that were generally slow moving, meiofaunal, or sessile. Plants were most commonly fragments of *Sargassum* or seagrasses that bore epiphytic animals such as hydroids. Other ingested material included small inanimate items such as carrion (e.g., insects that must have been dead when eaten) and anthropogenic debris.

Animals that were apparently preferred or easily obtained by post-hatchlings included copepods and some pelagic animals that are not commonly associated with the *Sargassum* community (Table 1). Post-hatchlings showed a strong preference for small, pleustonic, pelagic animals (*Janthina*, *Creseis*, *Porpita*, *Halobates*) that are not common (or in this study, recorded at all) in *Sargassum* or in downwelling lines. These pleustonic animals are probably more susceptible to wind dispersal than are most members of the *Sargassum* community. Because turtles were minimally active and pleuston appeared recently eaten (fresh condition in gastric and esophageal lavage samples), it is likely that turtles fed on pleustonic animals as they "blew through" the downwelling lines. Pleuston may make up the principal forage of post-hatchlings that are outside of downwelling lines.

Animals apparently not preferred or not easily obtained by loggerheads included *Spirorbis*, *Membranipora*, and a group that includes fishes, crabs, and shrimp. The latter group includes motile animals that tend to be larger than 1 cm and that may be difficult or energetically expensive for post-hatchlings to capture. Hydroids apparently make up a large part of the diet of loggerhead post-hatchlings although paired comparisons indicate they are no more common in the diet than they are in the surrounding habitat (Table 1). Insects also made up similar proportions of habitat and lavage samples.

Previous reports of items ingested by neonate loggerheads involved relatively small numbers of turtles and varied with respect to the types of items found.

Richardson and McGillivray (1991) reported that 2 turtles from the Atlantic off Florida had ingested insects, *Sargassum* associates, and tar; Hughes (1974) reported that stranded turtles from southeast Africa beaches had ingested small buoyant objects and pelagic animals; Van Nierop and Den Hartog (1984) reported that 5 turtles from the southeast Atlantic had ingested mostly pelagic coelenterates and other pelagic animals; and Carr and Meylan (1980) reported that 15 stranded turtles found after a hurricane struck eastern Florida had ingested *Sargassum* associates. All of the items reported in these four accounts were generally represented in samples in the present study.

Consequences of living in downwelling lines

Living amid the material concentrated at downwellings must have its tradeoffs. Food appears to be readily available to turtles in downwelling lines, especially food items that do not require diving or chasing for their capture, and that may be concentrated at densities much greater than would occur elsewhere at the ocean's surface (Barstow 1983). Yet this biotic assemblage concentrates predatory fishes and birds as well. During this study, I commonly observed predators in downwelling lines such as fishes (especially dolphins *Coryphaena* spp.) and birds (e.g., gulls, *Larus* spp., and terns, *Sterna* spp.) that are known to take small sea turtles (Stancyk 1995). Rates of mortality from predation are not known for pelagic turtles.

An additional consequence of living in downwelling lines is dispersal. The current that creates shear boundaries that assemble masses of floating material also transports this material, and turtles, around the North Atlantic. Although living at the edge of an oceanic current may facilitate passive collection of turtles into downwelling lines, it also necessitates that they travel around an entire ocean basin and, occasionally, into regions that are inhospitable to them (as might result from transport within the North Atlantic Drift to northern Europe).

There is insufficient evidence to wholly accept or reject hypotheses either that downwelling lines at downwellings are pelagic-turtle refugia (Carr 1986) or that downwellings create hazardous habitats that turtles need not inhabit in order to forage (Collard 1990). However, the present study does show that the number of post-hatchlings inhabiting downwelling lines is high, that the behavior of these turtles would not result in turtles moving far from downwelling lines, and that these turtles consume enough food there to grow.

I propose a hypothesis that is a modification of the one proposed by Carr (1986) and that describes pelagic loggerheads as facultatively active or "smart" drifters. Expectations from this model are that (1) small loggerheads are largely inactive; (2) they forage and grow within downwelling zones but are able to feed

opportunistically on pleuston when they are not in downwelling lines; (3) they take part in short periods of oriented swimming when floating material becomes fragmented or widely spaced; (4) they are regularly incorporated into downwelling lines principally as a function of passive transport (following their initial swimming frenzy); and (5) they may take part in extensive oriented swimming when there is a risk of transport onshore or into cold waters. The first two expectations of the model are strongly supported by the present study. The third expectation is partially supported by field observations of released post-hatchling loggerheads swimming toward *Sargassum* patches and stopping within them. The fourth expectation is based on speculation about the benefits of energy conservation, on the regular and common assembly of material at downwellings, and on the benefits of association with floating material both for foraging and for concealment from predators. The fifth expectation is supported by the work of Lohmann and Lohmann (1994) showing that neonate loggerheads from Atlantic Florida beaches adjust their swimming bearing predictably (i.e., orient in directions that would be away from the continental edges of the North Atlantic Gyre) when the laboratory-induced magnetic field around them is altered to imitate inclination angles at different latitudes around the North Atlantic.

In addition to consequences that may have selected for specific foraging strategies in sea turtles, there are two recent consequences that have had little time to shape behavioral adaptations in turtles and are important threats to their conservation: threats of mortality from anthropogenic debris and from *Sargassum* harvesting. Ingestion of plastics and tar by sea turtles is common and is believed to contribute to their mortality (Carr 1987b). Young pelagic loggerheads seem to be especially susceptible to anthropogenic-debris ingestion, perhaps because loggerheads forage on novel items that stand out most against the backdrop of *Sargassum* and because floating plastics and tar concentrate within the downwellings inhabited by turtles (Barstow 1983). Given that the post-hatchlings in this study had been exposed to anthropogenic debris for only a few weeks at most, and that the technique for sampling stomach contents probably missed some material, young pelagic turtles as a whole may ingest even more plastic and tar than was revealed by this study. This ingestion is likely to have both lethal and sublethal effects (McCauley and Bjorndal 1999). High mortality to small sea turtles could occur in the open ocean without leaving much detectable evidence. Additional study is needed.

The concentration of turtles in lines of *Sargassum* and other material also makes turtles susceptible to incidental harvest along with the *Sargassum* that is collected by surface trawlers. The seasonal *Sargassum* harvest that occurs near the Gulf Stream off the outer banks of North Carolina is known to take neonate loggerheads (Schwartz 1988) and is anticipated to involve the collection of 180 metric tons of *Sargassum* annually over

the next few years (unpublished report, South Atlantic Fishery Council, 1998).

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References

- Ashjian CJ, Smith SL, Flag CN, Mariano AJ, Behrens WJ, Lane PVZ (1994) The influence of a Gulf Stream meander on the distribution of zooplankton biomass in the slope water, the Gulf Stream, and the Sargasso Sea, described using a shipboard acoustic Doppler current profiler. *Deep Sea Res Oceanogr Res Pap* 41:23–50
- Barstow SF (1983) The ecology of Langmuir circulation: a review. *Mar Environ Res* 9:211–236
- Bjorndal KA, Bolten AB, Gordon J, Caminas JA (1994) Natural history notes: *Caretta caretta* (loggerhead). Growth and pelagic movement. *Herpetol Rev* 25:23–24
- Bolten AB, Balazs GH (1995) Biology of the early pelagic stage – the “lost year.” In: Bjorndal K (ed) *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington D.C., pp 579–581
- Bolten AB, Martins HR, Bjorndal KA, Cocco M, Gerosa G (1992) Life history notes: *Caretta caretta* (loggerhead). Pelagic movement and growth. *Herpetol Rev* 23:116
- Bolten AB, Santana JC, Bjorndal KA (1992b) Transatlantic crossing by a loggerhead turtle. *Mar Turtle Newsl* 59:7–8
- Bolten AB, Bjorndal KA, Martins HR, Dellinger T, Biscoito MJ, Encalada SE, Bowen BW (1998) Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. *Ecol Appl* 8:1–7
- Bowen BW, Abreu-Grobois FA, Balazs GH, Kamezaki N, Limpus CJ, Ferl RJ (1995) Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proc Natl Acad Sci U S A* 92:3731–3734
- Brongersma LD (1971) Ocean records of turtles (North Atlantic Ocean). IUCN – The World Conservation Union Publication (new series), suppl paper no 31:103–108
- Brongersma LD (1972) European Atlantic turtles. *Zool Verh Leiden* 121
- Brongersma LD (1982) Marine turtles of the eastern Atlantic Ocean. In: Bjorndal K (ed) *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington D.C., pp 407–416
- Butler JN, Morris BF, Cadwallader J, Stoner AW (1983) Studies of *Sargassum* and the *Sargassum* community. (Special publication 22) Bermuda Biological Station, St. Georges West, Bermuda
- Caldwell DK (1962) Growth measurements of young captive Atlantic sea turtles in temperate waters. *LA Co Mus Contrib Sci* 50:1–8
- Caldwell DK (1968) Baby loggerhead turtles associated with *Sargassum* weed. *Q J Fla Acad Sci* 31:271–272
- Caldwell DK, Carr A, Ogren LH (1959) Nesting and migration of the Atlantic loggerhead turtle. *Bull Fla St Mus Biol Sci* 4:295–308
- Carr AF (1986) Rips, FADS, and little loggerheads. *Bioscience* 36:92–100
- Carr AF (1987a) New perspectives on the pelagic stage of sea turtle development. *Conserv Biol* 1:103–121
- Carr AF (1987b) The impact of nondegradable marine debris on the ecology and survival outlook of sea turtles. *Mar Pollut Bull* 18:352–356
- Carr AF, Meylan AB (1980) Evidence of passive migration of green turtle hatchlings in *Sargassum*. *Copeia* 1980:366–368
- Collard SB (1990) Speculation on the distribution of oceanic-stage sea turtles, with emphasis on Kemp's ridley in the Gulf of Mexico. *Mar Turtle Newsl* 48:6–8
- Davenport J, Clough W (1986) Swimming and diving in young loggerhead sea turtles (*Caretta caretta* L). *Copeia* 1986: 53–57
- Eckert SA, Martins HR (1989) Transatlantic travel by juvenile loggerhead turtle. *Mar Turtle Newsl* 45:15
- Ehrhart LM, Witherington BE (1987) Human and natural causes of marine turtle nest and hatchling mortality and their relationship to hatchling production on an important Florida nesting beach. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Tech Rep No 1
- Fletemeyer J (1978) Underwater tracking evidence of neonate loggerhead sea turtles seeking shelter in drifting *Sargassum*. *Copeia* 1978:148–149
- Hughes GR (1974) The sea turtles of south-east Africa II. The biology of the Tongaland loggerhead turtle *Caretta caretta* L with comments on the leatherback turtle *Dermochelys coriacea* L and the green turtle *Chelonia mydas* L in the study region. *Ocean Res Inst Invest Rep* 36
- Kraemer JE, Bennett SH (1981) Utilization of posthatching yolk in loggerhead sea turtles, *Caretta caretta*. *Copeia* 1981:406–411
- Limpus CJ, Walker TA, West J (1994) Post-hatchling sea turtle specimens and records from the Australian region. In: James R (comp) *Proceedings of the Australian Marine Turtle Conservation Workshop*. Queensland Department of Environment and Heritage, and Australian Nature Conservation Agency, Canberra, pp 95–100
- Lohmann KJ, Lohmann CMF (1994) Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *J Exp Biol* 194:23–32
- McCauley SJ, Bjorndal KA (1999) Conservation implications of dietary dilution from debris ingestion: sublethal effects in post-hatchling loggerhead sea turtles. *Conserv Biol* 13: 925–929
- Meylan AB, Schroeder BA, Mosier A (1995) Sea turtle nesting activity in the state of Florida 1979–1992. *Fla Mar Res Publ* 52:1–51
- Richardson JJ, McGillivray P (1991) Post-hatching loggerhead turtles eat insects in *Sargassum* community. *Mar Turtle Newsl* 55:2–5
- Schaefer A (1970) The mathematical basis of sterology. *Microscopion* 7:3–16
- Schwartz FJ (1988) Aggregations of young hatchling loggerhead sea turtles in the *Sargassum* off North Carolina. *Mar Turtle Newsl* 42:9–10
- Smith WG (1968) A neonate Atlantic loggerhead turtle, *Caretta caretta caretta*, captured at sea. *Copeia* 1968:880–881
- Stancyk SE (1995) Non-human predators of sea turtles and their control. In: Bjorndal K (ed) *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington D.C., pp 139–152
- Van Nierop MM, Den Hartog JC (1984) A study of the gut contents of five juvenile loggerhead turtles, *Caretta caretta* (Linnaeus) (Reptilia, Cheloniidae), from the south-eastern part of the north Atlantic Ocean, with emphasis on coelenterate identification. *Zool Meded Leiden* 59:35–54
- Walker TA (1994) Post-hatchling dispersal of sea turtles. In: James R (comp) *Proceedings of the Australian Marine Turtle Conservation Workshop*. Queensland Department of Environment and Heritage, and Australian Nature Conservation Agency, Canberra, pp 79–94

- Witham R (1974) Neonate sea turtles from the stomach of a pelagic fish. *Copeia* 1974:548
- Witherington BE (1994a) Flotsam, jetsam, post-hatchling loggerheads, and the advecting surface smorgasbord. In: Bjorndal KA, Bolten AB, Johnson, DA, Eliazar PJ (comps) Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech Memo NMFS-SEFSC-351:166–168
- Witherington BE (1994b) Some “lost-year” turtles found. In: Schroeder BA, Witherington BE (comps) Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech Memo NMFS-SEFSC-341:194–196
- Witherington BE (1995) Observations of hatchling loggerheads during the first few days of the lost year(s). In: Richardson JI, Richardson TH (comps) Proceedings of the Twelfth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech Memo NMFS-SEFSC-361:154–157
- Wyneken J, Salmon M (1992) Frenzy and postfrenzy swimming activity in loggerhead, green, and leatherback hatchling sea turtles. *Copeia* 1992:478–484