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# Site fidelity and homing behavior in juvenile loggerhead sea turtles (*Caretta caretta*)

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**Abstract** To investigate site fidelity and homing behavior in juvenile loggerheads (*Caretta caretta*, L.), a mark-recapture study spanning four years (1998–2001) was conducted in Core Sound, N.C., USA. Each year of the study, approximately half of the turtles captured were tagged and released near the capture sites ($n = 207$), while the remaining turtles were displaced 15–20 km and released ($n = 198$). Loggerheads in both groups were recaptured in equal proportions near the original capture sites and many individuals were also recaptured in subsequent years. These data imply that juvenile loggerheads often returned to their capture sites following displacement, because if turtles dispersed randomly or remained near their release sites, then fewer displaced turtles should have been caught again. Moreover, because turtles migrate out of North Carolina sounds each winter, turtles recaptured at the same locations in different years evidently returned to specific sites following long migrations. To further investigate homing behavior, a small number of displaced turtles ($n = 28$) were tracked using radio telemetry following their release. Although transmitters detached from most turtles within a few days, analyses of initial headings showed strong orientation in the direction of the capture site. In addition, four turtles successfully tracked for longer periods of time all returned rapidly to the vicinity of the capture location and remained in the area. Taken together, the results of this study indicate that juvenile loggerheads exhibit fidelity to specific areas during summer months and possess the navigational abilities to home to these areas following forced displacements and long-distance migrations.
**Electronic Supplementary Material** is available for this article if you access the article at http://dx.doi.org/10.1007/s00227-003-1085-9. A link in the frame on the left on that page takes you directly to the supplementary material.

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## Introduction

After emerging from their nests, hatchling loggerheads originating from the east coast of the United States migrate offshore from their natal beaches to reach the open ocean (Salmon and Wyneken 1987). The turtles spend approximately the first decade of their lives inhabiting the North Atlantic Gyre, a circular current system that encircles the Sargasso Sea (Carr 1986,1987; Musick and Limpus 1997; Bolten et al. 1998).

After residing in the pelagic environment for a period of years, the turtles return to the east coast of the United States. Juvenile loggerheads ranging from about 50 to 80 cm standard straight-line carapace length inhabit foraging areas in inshore waters such as sounds, bays, and estuaries in sub-tropical to temperate regions (reviewed by Musick and Limpus 1997). Sea turtles occupying areas where water temperatures fall below lethal levels during the winter undertake seasonal migrations, moving to warmer, southern waters in the fall and returning to northern foraging grounds in the spring (Shoop and Kenney 1992; Keinath 1993; Epperly et al. 1995a, 1995b; Morreale and Standora 1995). Little is known about the patterns of residence, habitat utilization, or movements of juvenile loggerheads occupying foraging areas in inshore waters. Limited data and anecdotal reports suggest that juvenile loggerheads exhibit site fidelity within preferred areas and that the turtles sometimes return to specific sites after having completed seasonal migrations or after being displaced (Mendonca and Ehrhart 1982; Lutcavage and

Musick 1985; Henwood 1987; Byles 1988; Dickerson et al. 1995). However, to date these issues have not been systematically studied.

To investigate site fidelity in juvenile loggerheads, mark-recapture data spanning a 4-year period were examined to determine if turtles caught at specific locations were recaptured at those same sites during the year of their initial capture, as well as during subsequent years. In addition, recapture data for turtles released at the capture site and those released at sites 15–20 km distant were analyzed to ascertain whether the turtles exhibited homing behavior. Several displaced turtles were also followed using radio telemetry to more closely monitor homing.

## Materials and methods

### Study area

The study was conducted in Core Sound, N.C., USA. (Fig. 1). Core Sound is relatively shallow (2–3 m deep), and is separated from the Atlantic Ocean by a series of barrier islands (Ferguson et al. 1993). Juvenile loggerhead turtles (*Caretta caretta*, L.) ranging from 42 to 87 cm SCL (NMFS, Beaufort Laboratory, unpublished data) reside in the sound during the spring, summer, and early fall, leaving inshore waters when water temperatures begin to decrease in mid- to late fall and returning again in the spring (Epperly et al. 1995a, 1995b). The study was therefore carried out between May and December of each year from 1998 to 2001.

### Turtle capture and tagging

Juvenile loggerheads were obtained through the cooperation of commercial fishermen and were incidentally captured in pound nets, a type of passive, stationary, fishing gear that retains turtles but allows them to surface to breathe (see Fig. 1 for capture locations). Because the pound net fishery is most active during the fall, the number of nets set in the study area varied seasonally, with 5–6 nets being active during the summer and up to 15 nets being set during the autumn months. Pound nets in the study location were fished twice a week from mid-May until the first week in December (as weather allowed) during each year of the study. The geographic coordinates of capture locations were determined using a hand-held global positioning system (GPS) unit.

Turtles were marked with two Inconel Style 681 flipper tags (National Band and Tag, Newport, Ky., USA); one on the trailing margin of each rear flipper. In addition, a 125 kHz unencrypted passive integrated transponder (PIT) tag (Destron-Fearing Corp., South St. Paul, Minn., USA) was injected subcutaneously above the second most proximal scale of the trailing margin of the left front flipper. Standard straight-line carapace lengths (SCL) were taken to the nearest 0.1 cm.

### Mark-recapture

Each year from 1998 to 2001, approximately half of the loggerheads captured were tagged, measured, and released near their capture sites. The other turtles were displaced either approximately 20 km southwest to Shell Point or approximately 15 km northeast to Cedar Island Point (Fig. 1) and released. Turtles subjected to displacements were first transported by boat from the pound nets to shore along convoluted routes. They were then driven in a covered vehicle along winding, coastal roads to the National Oceanic and Atmospheric Administration (NOAA) laboratory in Beaufort, N.C., about 30 km southwest of the capture area (Fig. 1). For logistical reasons, turtles were held at the NOAA laboratory for 48–72 h before again being transported in a covered vehicle along winding roads to the release sites at Shell Point or Cedar Island Point. Although turtles might occasionally have glimpsed the sky while on the fishing vessel, they were seldom, if ever, able to view their surroundings or the sky during transport on land.

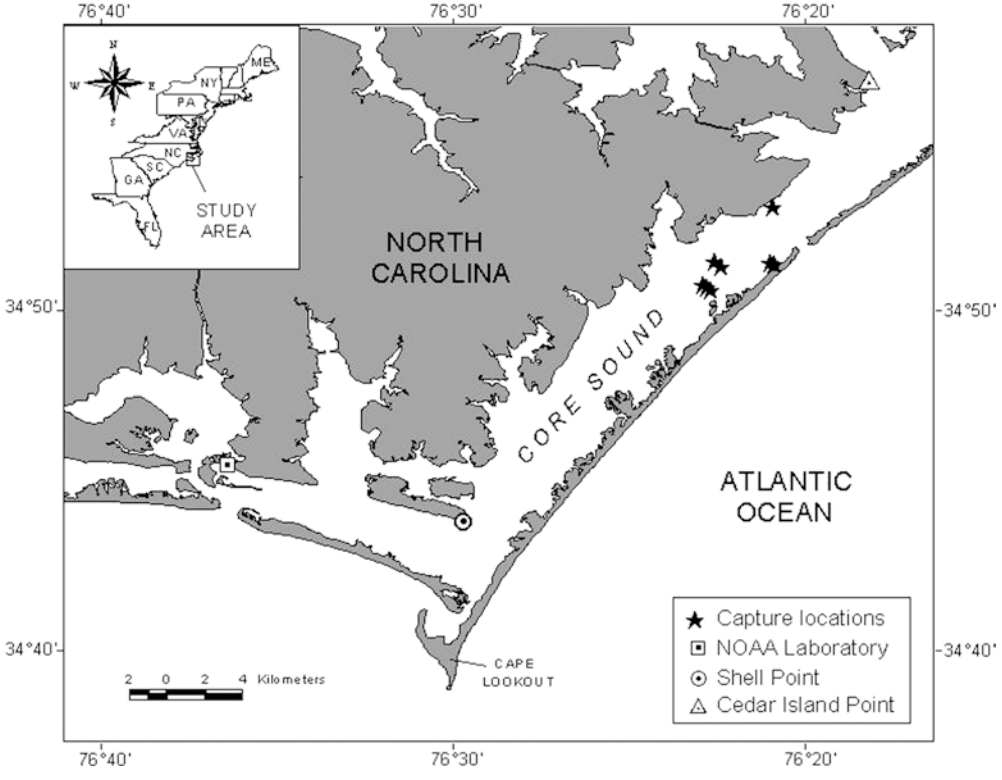


**Fig. 1** Map of Core Sound, N.C., USA. Turtles were captured at locations denoted by *stars* on map and were either released near the capture site or displaced. The NOAA laboratory, where displaced turtles were held, is shown as a *square* on the map. Displaced turtles were released either at Shell Point (location indicated by *circle*), approximately 20 km southeast of the capture sites or Cedar Island Point (location indicated by *triangle*), located about 15 km northeast of the capture area

Only turtles caught and displaced between May and September were used in the homing study because turtles begin to migrate out of inshore waters in October or November (Epperly et al. 1995a). The tag numbers and capture locations of recaptured turtles were recorded for later analysis.

### Radio telemetry

To monitor potential homing behavior more closely, 18 of the loggerheads displaced to Shell Point and 10 of the turtles displaced to Cedar Island Point during 1998, 1999, and 2000 were outfitted with MOD-050 radio transmitters (164–165 MHz) with TA-6L antennas (Telonics, Ariz.). Four of these loggerheads were tracked during two separate years. To attach the transmitters, a 0.5-cm-diameter hole was first drilled through one of the turtle's pygal bones at the posterior margin of the carapace, as well as the overlying scutes, using a drill bit scrubbed with Betadine disinfectant. A plastic electrician's tie was then passed through the hole and secured. Transmitters were housed in bullet-shaped buoys (approximately 10 cm diameter and 10 cm in height) secured to one end of a 0.5-m tether (0.1-cm-diameter stainless steel fishing leader). The tether was then connected to the plastic tie in the turtle's shell using a ball-bearing swivel and two short lengths of either 30 lb. spiderwire or 30 lb. test monofilament fishing line. This configuration allowed the turtles to break free if either the buoy or tether became entangled in submerged or floating debris, or on a bottom structure.

Tracking was accomplished using a Telonics (Mesa, Ariz.) TR-2 Receiver (164/166 MHz) with a TS-1 Scanner/Programmer, in combination with a 4-element, hand-held, Yagi antenna (AVM Instrument Company, Colfax, Calif.). Beginning 12–24 h after release, each turtle was tracked daily from the western shoreline of Core Sound. When a transmitter signal was detected, the bearings at which the signal could no longer be heard were determined and the direction of the transmitter was taken as the line bisecting those bearings (Kenward 2001). A compass bearing was then taken along that line using a hand-held, digital compass (Autohelm, Portsmouth, England). Because radio waves do not transmit well through sea water and transmitters were generally submerged when turtles were not at the surface, transmitter signals were only detected when turtles surfaced to breathe. Therefore, if a constant signal was detected this signified that the transmitter had become detached.

During tracking, a single observer sequentially obtained between two and four bearings for each turtle's position and those bearings were then plotted on a nautical chart. On a given day, a turtle's location was taken to be either the point where all bearings intersected or the center of the polygon formed when three or four bearings did not precisely intersect one another (Byles 1988). True positional error is not reported here because bearings were not obtained simultaneously and therefore a turtle's movements between the times at which bearings were taken made it impossible to precisely determine its location. However, the sizes of the polygons formed when 3–4 bearings were plotted to determine a turtle's position were generally $< 1$ km$^2$; thus, the location data obtained using this method were sufficient to determine whether turtles had returned to the vicinity of their capture area.

For those turtles that retained their transmitters longer than 1 day but were not successfully followed long enough to obtain homing data, the location at which a turtle was last detected still bearing its radio transmitter was used to obtain information regarding direction of movement. The final positional fix obtained for a turtle was plotted on a nautical chart and the compass bearing between the release site and that location was then measured.

### Data analysis

Recapture data were analyzed: (1) to test for differences between the proportion of turtles recaptured after being displaced versus the proportion recaptured after being released near their capture locations, and (2) to determine whether there was a difference between the proportion of turtles recaptured after being displaced 20 km south to Shell Point and the proportion recaptured after being displaced 15 km north to Cedar Island Point. Chi-square analysis was used to make these comparisons except when recapture numbers were too small to appropriately do so; in these cases, the Fisher Exact test was used (Zar 1996). Although turtles were occasionally displaced more than once, only a turtle's first displacement was included in the analysis of homing data to avoid problems with statistical independence. The Kolmogorov-Smirnov Two-Sample test (Sokal and Rohlf 1981) was used to determine whether there was a difference between the sizes of recaptured turtles and those that were not recaptured.

The initial headings obtained during the radio telemetry part of this study were analyzed using standard procedures for circular statistics (Batschelet 1981). The V-test was applied to determine whether these initial headings were significantly oriented.

## Results

Between 1998 and 2001, 405 loggerheads ranging from 42.3 to 86.8 cm SCL (mean = 61.7 cm; $\pm$0.38 cm SE) were captured. Of these, 207 turtles were tagged and released near their capture sites (Figs. 1, 2). Throughout the study, 21% of these turtles were recaptured in the same year they were tagged (see Fig. 2 for data from individual years). In addition, 198 loggerheads were displaced to locations either 20 km south or 15 km north and released (Figs. 1, 2). Over the course of the study, 17% of all displaced turtles were recaptured in the same year they were released (see Fig. 2 for data during individual years). The proportions of turtles recaptured after being released near the capture location and after being displaced were not significantly different over the entire study ($\chi^2$: $P = 0.33$), as well as for each separate year ($\chi^2$: 1998 $P = 0.64$, 1999 $p = 0.27$; Fisher Exact Test: 2000 $P = 0.65$, 2001 $P = 0.12$) (Fig. 2).

From 1998 to 2001, 36% of the non-displaced turtles that were recaptured were caught in the same net as in their original capture and 30% were recaptured more than once; ten turtles were recaptured twice and three turtles recaptured three times each. Similarly, 32% of the turtles recaptured after being displaced were caught in the same net as in their original capture and 29% were recaptured more than once. Five turtles were recaptured twice, three were recaptured three times, and two were recaptured five times over periods of several months.

Throughout the study, 20% of turtles displaced to the southwest and 10% of the turtles displaced to the northeast were recaptured during the year they were displaced (see Fig. 3 for data from individual years). The proportions of turtles recaptured after being displaced southwest versus northeast were not significantly different over the course of the study ($\chi^2$: $P = 0.11$), as well as for each year turtles were displaced to both locations (Fisher Exact Test: 1999 $P = 0.63$, 2000 $P = 0.13$, 2001 $P = 0.66$) (Fig. 3). Intervals between release of displaced turtles and their recapture ranged from 1 to 95 days (mean = 26 days; $\pm$24 days SD). Of the turtles recaptured after displacement, 26% were caught less than 1 week after being released and 45% were caught in less than 2 weeks.

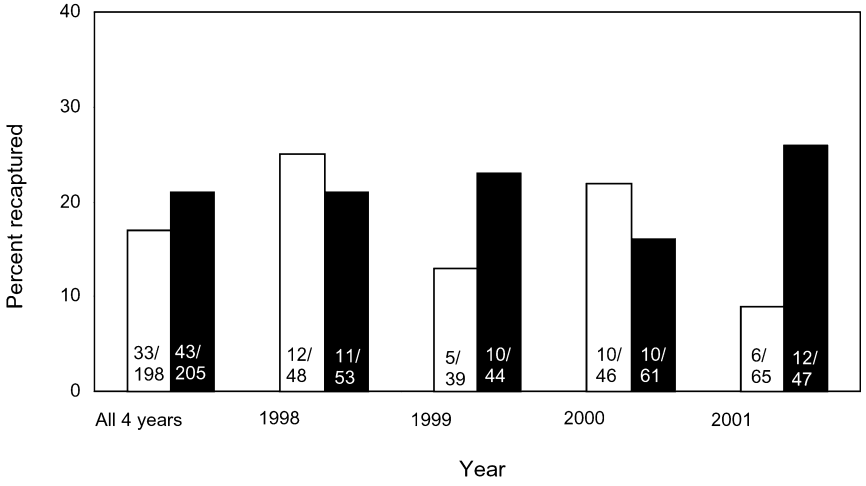


**Fig. 2** *Caretta caretta.* Recapture percentages of displaced (*white bar*) and non-displaced (*black bar*) juvenile loggerheads. Proportions of displaced and non-displaced turtles recaptured within a given year and over all 4 years of the study were not significantly different from one another (see text for details)

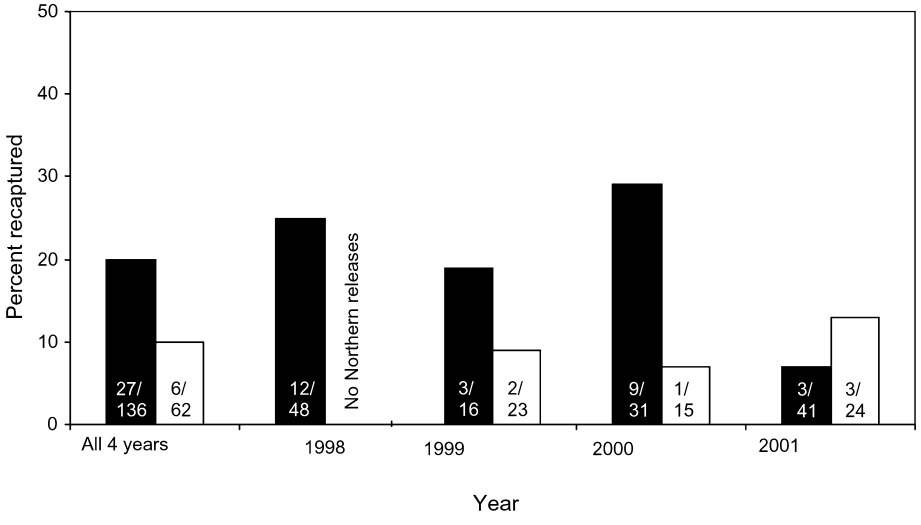


**Fig. 3** *Caretta caretta.* Recapture percentages of juvenile loggerheads displaced 20 km southwest (*black bars*) or 15 km northeast (*white bars*) of their capture area. Proportions of turtles recaptured from the two sites within a given year and over all 4 years of the study were not significantly different from one another (see text for details)

In addition to those turtles recaptured during the year in which they were first tagged, a number of both displaced and non-displaced turtles were recaptured at least once in subsequent years (Tables 1, 2). Many turtles were caught multiple times during subsequent years (Appendix 1, Electronic Supplementary Material; Avens 2003); 53% of those in the same net in which they were originally captured. There was no significant difference between the sizes of the turtles recaptured and those not recaptured throughout the course of the study ($P = 0.20$, Kolmogorov-Smirnov two-sample test).

Homing data were obtained from four telemetered turtles, one of which was tracked during two separate years. Of the four turtles that were successfully tracked using radio telemetry, all four returned to the vicinity of their capture locations within 3–5 days of release (Figs. 4, 5, 6, 7). While one turtle (Cc73) was recaptured multiple times following its release at Shell Point (Fig. 4), the other three telemetered turtles were not recaptured despite having returned to the capture area.

For those turtles that retained their transmitters for 1 day or more but were not continuously tracked due to logistical difficulties, the final positional fixes obtained for each turtle were used to plot directional headings. Thirteen headings were obtained for turtles released at Shell Point and these individuals were significantly oriented with a mean angle that coincided closely with the most direct route back to the capture site (Fig. 8). Only

**Table 1** *Caretta caretta.* Summary of displaced loggerheads recaptured throughout the study

| Year of displacement | Number displaced | Number recaptured in 1998 | Number recaptured in 1999 | Number recaptured in 2000 | Number recaptured in 2001 |
|---|---|---|---|---|---|
| 1998 | 48 | 12 (25%) | 6 (13%) | 7 (15%) | 7 (15%) |
| 1999 | 39 | – | 5 (13%) | 8 (21%) | 2 (7%) |
| 2000 | 46 | – | – | 10 (22%) | 3 (7%) |
| 2001 | 65 | – | – | – | 6 (9%) |

**Table 2** *Caretta caretta*. Summary of non-displaced loggerheads recaptured throughout the study

| Year of capture | Number not displaced | Number recaptured in 1998 | Number recaptured in 1999 | Number recaptured in 2000 | Number recaptured in 2001 |
|---|---|---|---|---|---|
| 1998 | 53 | 11 (21%) | 2 (4%) | 6 (11%) | 4 (7%) |
| 1999 | 44 | – | 10 (23%) | 5 (11%) | 3 (7%) |
| 2000 | 61 | – | – | 10 (16%) | 7 (11%) |
| 2001 | 47 | – | – | – | 12 (26%) |

two of the turtles released at Cedar Island Point retained their transmitters for 1 day or longer. The initial headings of these individuals were 152° and 185°, yielding a mean angle of 169° (direction of capture site = 224°). However, the sample size was too small to permit a statistical analysis.

Apart from the five successful tracks, during the remaining 28 telemetry attempts 16 turtles lost their transmitters in 1 day or less, 7 turtles lost their transmitters after 2–3 days, and 5 turtles lost their transmitters after 4–7 days of intermittently successful tracking efforts. Recovery of lost transmitters showed that attachment failed both when the breakaway links were severed as well as when the electrician's tie secured

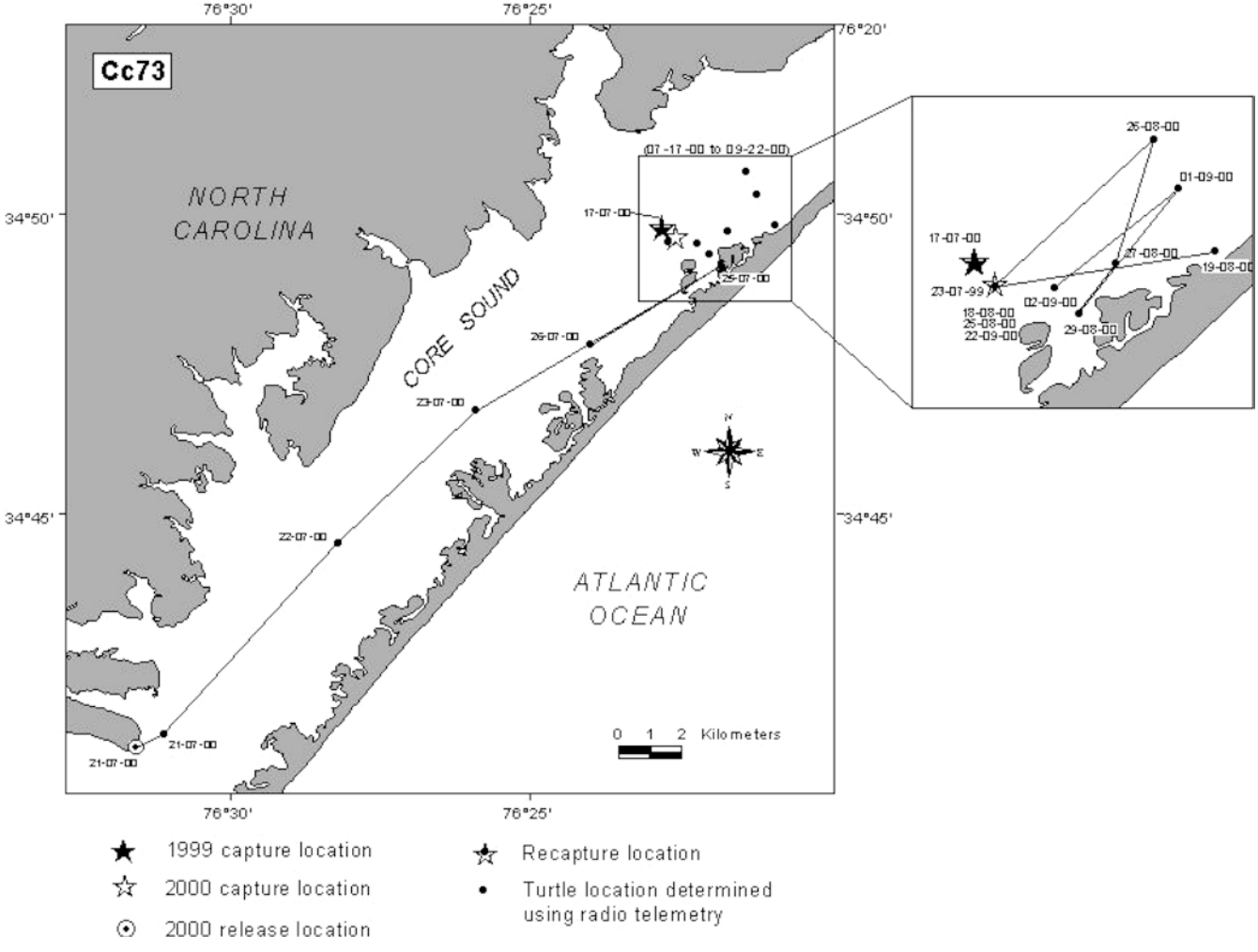


**Fig. 4** *Caretta caretta*. Radio track of turtle displaced to Shell Point. Cc73 was caught for the first time 23 July 1999 and was recaptured 17 July 2000. After being outfitted with a transmitter and released at Shell Point; Cc73 returned to capture area in 4 days, swam back southwest, and then lost its transmitter. Turtle was recaptured again three times in the same location several hundred meters east of the 1999 and original 2000 capture site. These recapture events made it possible to re-outfit Cc73 with a transmitter twice and release the turtle near the capture site. Brief tracks subsequently obtained before the turtle again entered a pound net and lost its transmitter combined with the turtle's recaptures showed that Cc73 remained close to the capture location, suggesting that it probably stayed in the area for several months. *Inset* Close-up of 1999 and 2000 capture locations, with two additional short tracks obtained after the turtle was recaptured and subsequently released after attachment of radio transmitter

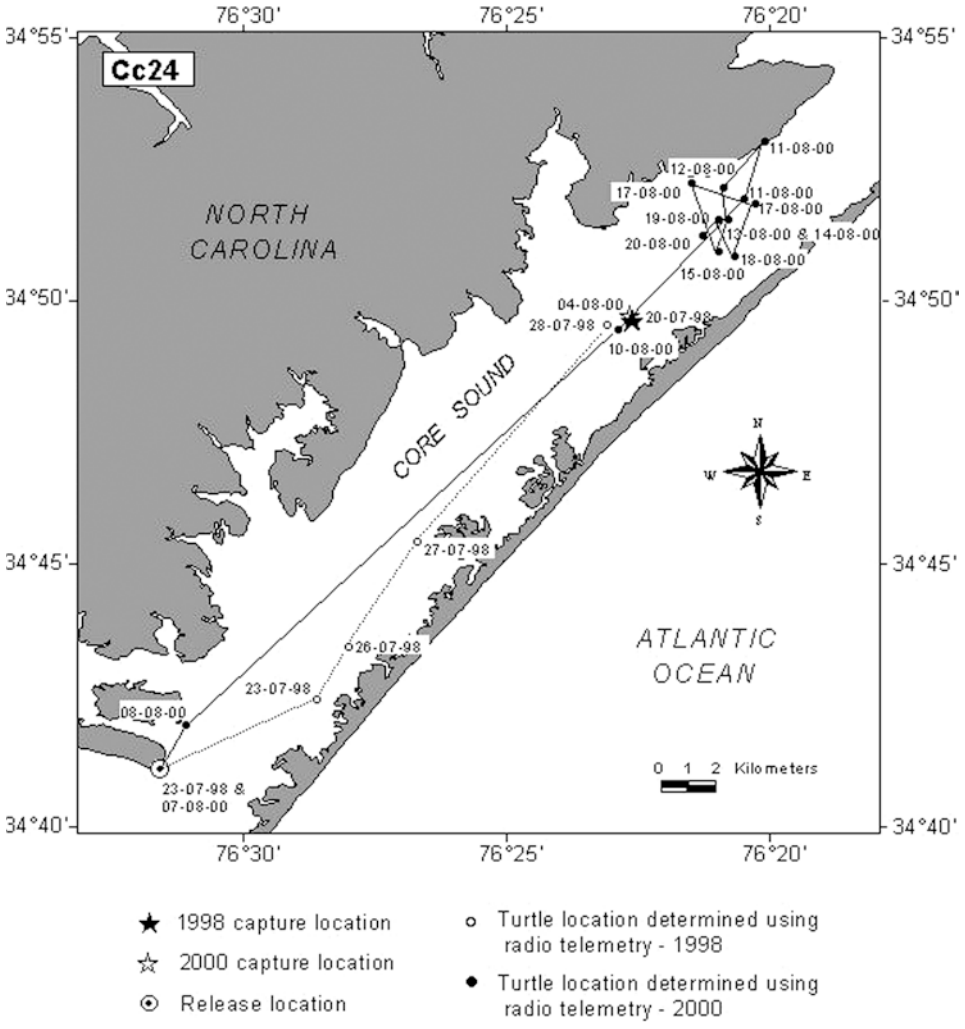


**Fig. 5** *Caretta caretta*. Cc24 was initially captured 20 July 1998 and released 20 km southwest of the capture site at Shell Point on 23 July 1998. It was tracked to the capture location within 5 days of release, when it lost the transmitter. Cc24 was recaptured 4 August 2000 at the same location as in 1998 and was again displaced to Shell Point, outfitted with a transmitter, and released 7 August 2000. Turtle returned to capture site in 3 days, but continued moving until it reached a location 5 km northeast of capture site, and remained there for approximately 7 days before it lost its transmitter

through a hole in the carapace snapped. Furthermore, on several occasions, recovered transmitters were found either entwined in or adjacent to structures associated with pound nets. This suggests that the transmitter attachment method used in this study is not optimal in shallow, inshore waters where benthic structures, fishing gear, and abundant debris often entangle transmitters and tethers.

## Discussion

Over the course of the study, the proportions of displaced and non-displaced turtles recaptured in the vicinity of their original capture sites were not significantly different. These data imply that displaced turtles frequently homed to the locations where they were captured, because if turtles dispersed randomly or remained where they were released, then fewer displaced turtles than non-displaced turtles should have been recaptured. Thus, the results indicate that juvenile loggerheads exhibit site fidelity and that individuals displaced from their capture locations possess the ability to navigate back to particular sites.

In addition to the recaptures observed within a given year, a number of turtles were recaptured in the vicinity of their original capture sites in following years. Inshore water temperatures in the sounds of North Carolina drop below lethal levels ($< 10°C$; Schwartz 1978) for sea turtles during the winter months (Epperly et al. 1995c). Juvenile loggerheads migrate offshore and/or south to warmer waters during the winter and subsequently return to their feeding areas in the spring when water temperatures rise. Thus, the turtles recaptured during more than 1 year of the study evidently returned to specific locations following seasonal migrations that sometimes span hundreds or even thousands of kilometers (Keinath 1993; Morreale and Standora 1995).

The navigational mechanisms underlying this ability are unknown. However, the directional headings and homing tracks obtained from telemetered turtles imply that displaced loggerheads were able to rapidly assess their position and then move toward the capture area. Turtles were apparently able to determine their position even after being transported along convoluted routes under conditions in which they could not view the sky or their surroundings. Thus, it is doubtful that the turtles determined the direction to travel using inertial (Etienne

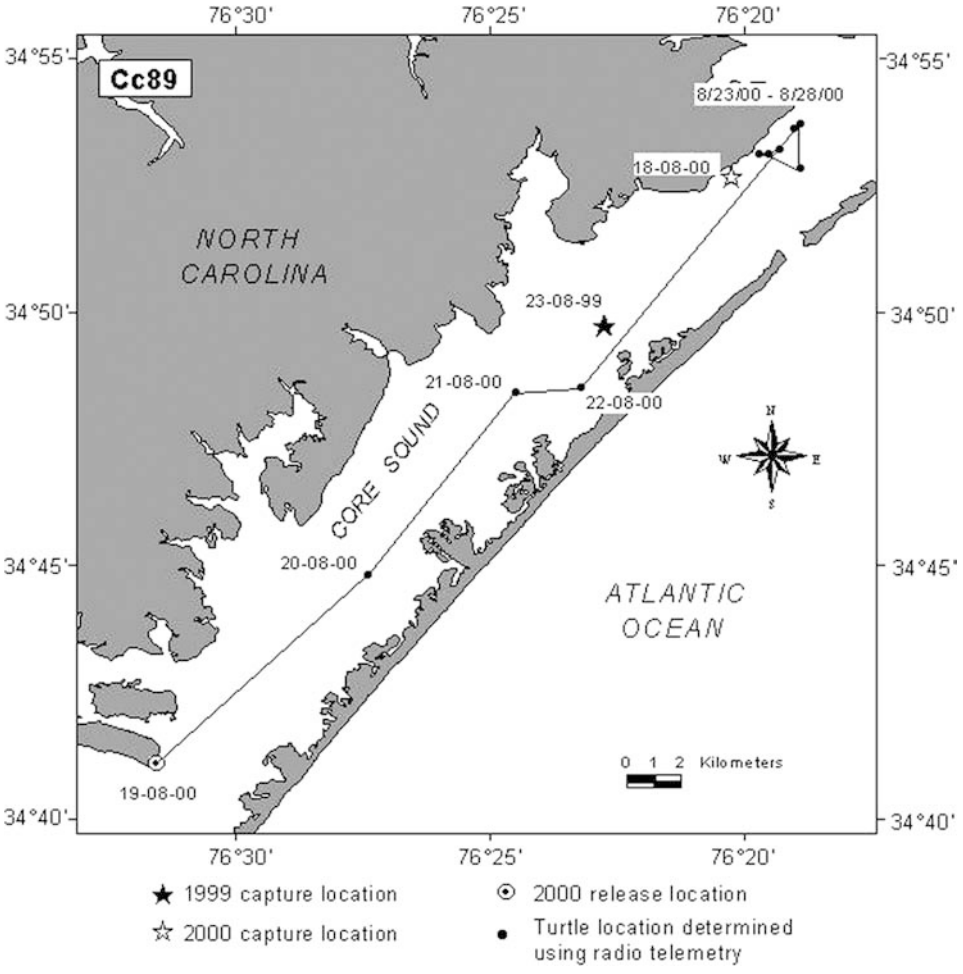


**Fig. 6** *Caretta caretta*. Cc89 was caught 23 August 1999 and again on 18 August 2000, 6.5 km northeast of the 1999 capture site. After being displaced to Shell Point and released with a transmitter 19 August 2000, the turtle returned to the vicinity of the 1999 capture location in 3 days and continued to move north until it reached a location slightly northeast of the 2000 capture site. Turtle remained there for 6 days and then lost its transmitter

et al. 1996), landmark (Papi 1992), or compass (Wiltschko and Wiltschko 1978; Wehner et al. 1996) cues that were detected during displacement. Instead, it appears likely that the turtles determined their position relative to the capture area by relying on information available at the release site, an ability that fulfills the definition of map-based navigation (Able 2000). Although precisely how the turtles determined position cannot be inferred from this study, potential sources of positional information include chemical cues (Grassman et al. 1984), familiar landmarks (Wallraff et al. 1994), and magnetic field information (Lohmann and Lohmann 1996, 1998; Lohmann et al. 2001).

The recapture data were used to ascertain whether there was a difference between the sizes of turtles that were recaptured and those that were not. Turtles of a wide range of sizes coexist in the same habitat in Core Sound and it is possible that turtles of different sizes might exhibit different degrees of site fidelity, as is the case in some fishes (Gerking 1953; Parker and Hasler 1959; Yoshiyama et al. 1992; Huntingford et al. 1998) and snakes (Fraker 1970). In this study, however, no relationship was found between the size of loggerhead turtles and their tendency to home, or their tendency to remain in the capture area.

The recapture percentages observed for both displaced and non-displaced turtles are similar to those obtained for non-displaced loggerheads in Florida inshore waters (22%; Mendonca and Ehrhart 1982). In addition, the recapture rates are comparable to those of other experimentally displaced aquatic or semiaquatic vertebrates such as spotted turtles, *Clemmys guttata* (28%; Ernst 1968), English sole, *Parophrys vetulus* (15%; Day 1976), senorita fish, *Oxyjulis californica* (13–26%; Hartney 1996), and brown trout, *Salmo trutta* (18–21%; Halvorsen and Stabell 1990). However, while all four of the telemetered turtles in this study returned to the vicinity of their capture location within 3–5 days after release, only one was subsequently recaptured. These results suggest that the recapture rates obtained by sampling with pound nets probably underestimated the homing activity that actually occurred, as many turtles that return to the area may not enter the nets a second time.

Several other factors might also have decreased the number of individuals recaptured, yielding a conservative estimate of homing tendency. Some animal populations are known to consist of individuals that exhibit either resident or transient behavior (Eifler and Eifler 1998). Thus, some of the turtles captured only once might have been transients or recent recruits that were

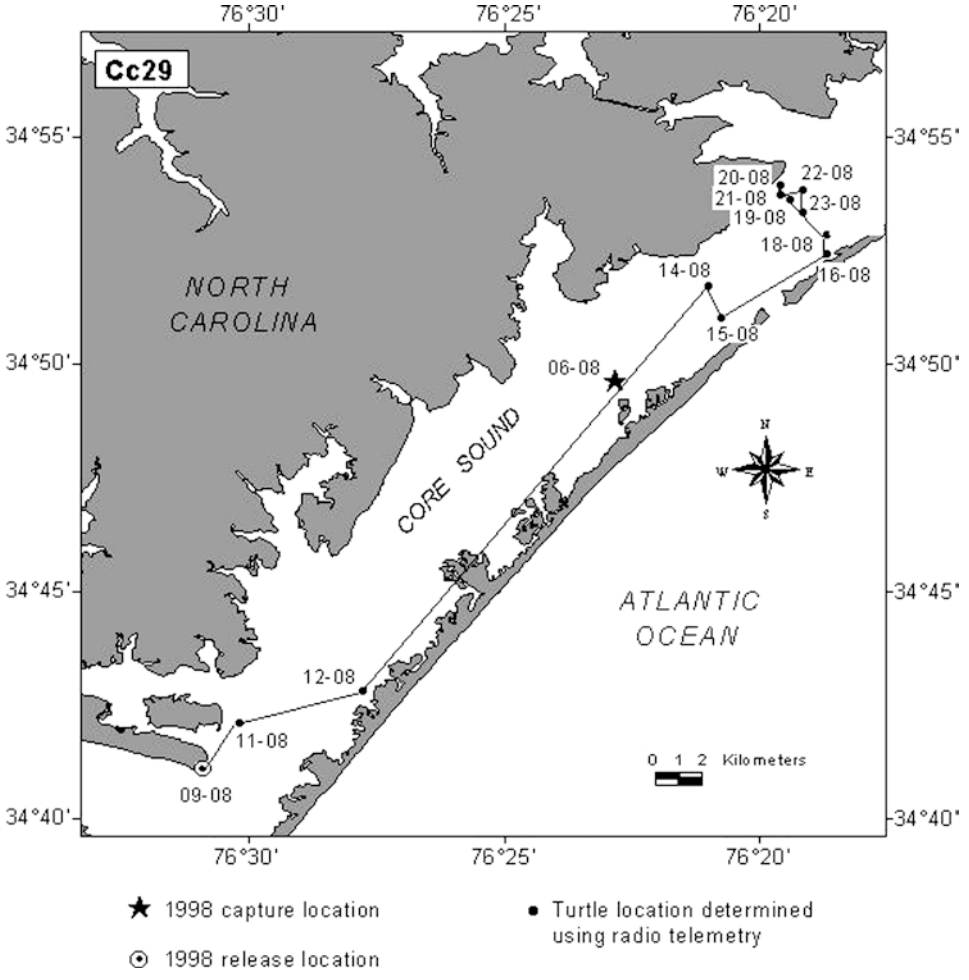


**Fig. 7** *Caretta caretta*. Cc29 was captured 6 August 1998, displaced to Shell Point, and released 9 August 1998. Turtle reached a location approximately 5 km northeast of capture location 5 days after release. Cc29 continued to move until it reached a location about 10 km northeast of capture site and remained in this area until it lost its transmitter 7 days later

not in an established home area, but instead were passing through the study location on their way to other destinations. Seasonal migrations might also temporarily increase the number of transient turtles. For example, during 1999 and 2000, there was a tendency for more turtles to be recaptured after having been displaced south versus north (Fig. 3). This tendency may reflect the recapture of turtles migrating through the inshore waters of North Carolina on their way to feeding areas further north such as Pamlico Sound, Chesapeake Bay, or Long Island Sound (Lutcavage and Musick 1985; Epperly et al. 1995a).

Because loggerheads feed opportunistically on many types of invertebrates, including patchily distributed mollusks and mobile, widely dispersed prey such as crustaceans and horseshoe crabs (Lutcavage and Musick 1985; Burke et al. 1993; Plotkin et al. 1993; Youngkin 2001), there is no obvious reason for a loggerhead to restrict its foraging activity to a small, localized area. Aerial survey data obtained during summer months (Epperly et al. 1995b) indicate that juvenile loggerheads are found throughout Core Sound, including areas near both the Shell Island Point and Cedar Island Point release sites (F. Gaskill, personal communication; NOAA Beaufort Laboratory, unpublished data). The presence of loggerheads in these areas suggests that suitable benthic foraging habitat exists near both locations where displaced turtles were released. Why then did many turtles return to their specific capture locations? While this study did not address the specific reasons for the turtles' return, it is possible that loggerhead distribution within Core Sound has been modified to some extent by the presence of pound nets, which enable the turtles to obtain prey such as fish that they cannot otherwise capture. Thus, one possibility is that turtles are strongly motivated to return to the pound nets even after displacements because these areas represent locations that are unusually rich in resources (Stanley 1998).

The finding that juvenile loggerheads often exhibit homing behavior has implications for dredging operations in which turtles are displaced short to moderate distances from dredging equipment in an attempt to reduce turtle mortality (Dickerson et al. 1995). Little information is available to indicate whether turtles exhibit site fidelity to areas that are routinely dredged. However, some juvenile loggerheads captured in or near the regularly dredged shipping channel at Cape Canaveral, Fla., USA, have been recaptured in the area both within a given year and in different years (Henwood 1987). In the present study, turtles displaced 20 km often

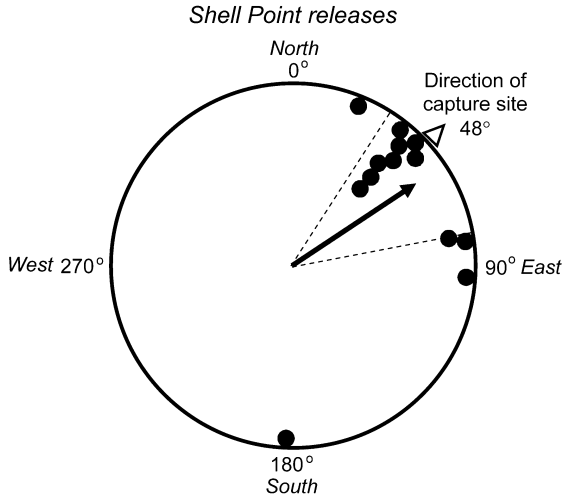


**Fig. 8** *Caretta caretta*. Initial directional headings of juvenile loggerheads released from Shell Point, 20 km southwest of their capture location (headings of turtles successfully tracked not included in this analysis). Location at which a turtle was last detected still bearing its radio transmitter was plotted on a nautical chart, and angle between release site and location was then determined as the turtle's vanishing bearing. Each *dot* within circular diagram corresponds to initial heading for an individual turtle and the *triangle* on the outside of the *circle* corresponds to the direction of the capture area (48°). *Dotted lines* represent boundaries of the 95% confidence interval. Turtles were significantly oriented with a mean angle of 56° ($n = 13$, $r = 0.82$, $P < 0.005$ V-test, 95% confidence interval $\pm 23°$)

returned to their capture locations within 3–5 days, and sometimes in as little as 24 h. Thus, if turtles captured at dredge sites display the same homing behavior as those in our study, then displacing them short distances is unlikely to be an effective means of reducing the likelihood that the turtles will interact with dredging equipment.

The present study provides evidence that juvenile loggerheads occupying inshore waters exhibit site fidelity to preferred areas and often home to those locations after displacement. In addition, the results demonstrate that some turtles returned repeatedly to specific sites during subsequent years after having migrated away from the area. However, further research is needed to determine the mechanisms underlying such homing behavior, as well as the manner in which loggerheads use available foraging habitat.

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## References

Able KP (2000) The concepts and terminology of bird navigation. J Avian Biol 32:174–183

Avens L (2003) Homing behavior, navigation, and orientation of juvenile sea turtles. PhD thesis, University of North Carolina–Chapel Hill, Chapel Hill, NC

Batschelet E (1981) Circular statistics in biology. Academic Press, London

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

Burke VJ, Standora EA, Morreale SJ (1993) Diet of juvenile Kemp's ridley and loggerhead sea turtles from Long Island, New York. Copeia 1993:1176–1180

Byles R (1988) Behavior and ecology of sea turtles from Chesapeake Bay, Virginia. PhD thesis, College of William and Mary, Williamsburg, Va.

Carr A (1986) Rips, FADS, and little loggerheads. Bioscience 36:92–100

Carr A (1987) New perspectives on the pelagic stage of sea turtle development. Conserv Biol 1:103–121

Ciofi C, Chelazzi G (1994) Analysis of homing pattern in the colubrid snake *Coluber viridiflavus*. J Herpetol 28:477–484

Day D (1976) Homing behavior and population stratification in Central Puget Sound English sole (*Parophrys vetulus*). J Fish Res Bd Can 33:278–282

Dickerson DD, Reine KJ, Nelson DA, Dickerson CE Jr (1995) Assessment of sea turtle abundance in six south Atlantic U.S. channels. Miscellaneous paper EL-95–5, U.S. Army Engineer Waterways Experiment Station, Vicksburg, Miss.

Eifler DA, Eifler MA (1998) Foraging behavior and spacing patterns of the lizard *Cnemidophorus uniparens*. J Herpetol 32:24–33

Epperly SP, Braun J, Veishlow A (1995a) Sea turtles in North Carolina waters. Conserv Biol 9:384–394

Epperly SP, Braun J, Chester AJ (1995b) Aerial surveys for sea turtles in North Carolina inshore waters. Fish Bull 93:254–261

Epperly SP, Braun J, Chester AJ, Cross FA, Merriner JV, Tester PA (1995c) Winter distribution of sea turtles in the vicinity of Cape Hatteras and their interactions with the summer flounder trawl fishery. Bull Mar Sci 56:547–568

Ernst CH (1968) Homing ability in the spotted turtle, *Clemmys guttata* (Schneider). Herpetologica 24:77–78

Etienne AS, Maurer R, Seguinot V (1996) Path integration in mammals and its interaction with visual landmarks. J Exp Biol 199:201–209

Ferguson RL, Wood LL, Graham DB (1993) Monitoring spatial change in seagrass habitat with aerial photography. Photogr Eng Remote Sensing 59:1033–1038

Fraker MA (1970) Home range and homing in the watersnake, *Natrix sipedon sipedon*. Copeia 1970:665–673

Gerking SD (1953) Evidence for the concepts of home range and territory in stream fishes. Ecology 34:347–365

Grassman MA, Owens DW, McVey JP, Marquez RM (1984) Olfactory-based orientation in artificially imprinted sea turtles. Science 224:83–84

Halvorsen M, Stabell OB (1990) Homing behaviour of displaced stream-dwelling brown trout. Anim Behav 39:1089–1097

Hartney KB (1996) Site fidelity and homing behaviour of some kelp-bed fishes. J Fish Biol 49:1062–1069

Henwood TA (1987) Movements and seasonal changes in loggerhead turtle *Caretta caretta* aggregations in the vicinity of Cape Canaveral, Florida (1978–84). Biol Conserv 40:191–202

Huntingford FA, Braithwaite VA, Armstrong JD, Aird D, Thorpe KE, Joiner P (1998) Social status and growth rates as determinants of site attachment in juvenile Atlantic salmon. J Fish Biol 53:314–321

Keinath JA (1993) Movements and behavior of wild and head-started sea turtles. PhD thesis, College of William and Mary, Williamsburg, Va.

Kenward RE (2001) A manual for wildlife radio tagging. Academic Press, New York
Kramer G (1961) Long-distance orientation. In: Marshall, AJ (ed) Biology and comparative physiology of birds. Academic Press, New York, pp 341–371
Lohmann KJ, Lohmann CMF (1996) Detection of magnetic field intensity by sea turtles. Nature 380:59–61
Lohmann KJ, Lohmann CMF (1998) Migratory guidance mechanisms in marine turtles. J Avian Biol 29:585–596
Lohmann KJ, Cain SD, Dodge SA, Lohmann CMF (2001) Regional magnetic fields as navigational markers for sea turtles. Science 294:364–366
Lutcavage M, Musick JA (1985) Aspects of the biology of sea turtles in Virginia. Copeia 1985:449–456
Mendonça MT, Ehrhart LM (1982) Activity, population size, and structure of immature *Chelonia mydas* and *Caretta caretta* in Mosquito Lagoon, Florida. Copeia 1982:161–167
Morreale SL, Standora EA (1995) Cumulative evidence of southward migration of juvenile sea turtles from temperate northeastern waters. NOAA Technical Memorandum NMFS-SEFSC-36. National Marine Fisheries Service, Miami, Fla
Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, New York, pp 137–163
Papi F (1992) General aspects. In: Papi F (ed) Animal homing. Chapman & Hall, London, pp 1–18
Parker RA, Hasler AD (1959) Movements of some displaced centrarchids. Copeia 1959:11–18
Plotkin PT, Wicksten MK, Amos AF (1993) Feeding ecology of the loggerhead sea turtle *Caretta caretta* in the Northwestern Gulf of Mexico. Mar Biol 115:1–5
Salmon M, Wyneken J (1987) Orientation and swimming behavior of hatchling loggerhead turtles (*Caretta caretta* L.) during their offshore migration. J Exp Mar Biol Ecol 109:137–153
Schwartz FJ (1978) Behavioral tolerance responses to cold water temperatures by three species of sea turtles (*Reptilia, Cheloniidae*) in North Carolina. Fla Dept Nat Res 33:16–18
Shoop CR, Kenney RD (1992) Seasonal distributions and abundances of loggerhead and leatherback sea turtles in waters of the northeastern United States. Herpetol Monogr 6:43–67
Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, New York
Stanley MC (1998) Homing in the skink, *Oligosoma grande*, within a fragmented habitat. J Herpetol 32:461–464
Wallraff HG, Kiepenheuer J, Streng A (1994) The role of visual familiarity with the landscape in pigeon homing. Ethology 97:1–25
Wehner R, Michel B, Antonsen P (1996) Visual navigation in insects: coupling of egocentric and geocentric information. J Exp Biol 199:129–140
Wiltschko R, Wiltschko W (1978) Evidence for the use of magnetic outward-journey information in homing pigeons. Naturwissenschaften 65:112–114
Yoshiyama RM, Gaylord KB, Philippart MT, Moore TR, Jordan JR, Coon CC, Schalk LL, Valpey CJ, Tosques I (1992) Homing behavior and site fidelity in intertidal sculpinds (*Pisces: Cottidae*). J Exp Mar Biol Ecol 160:113–130
Youngkin DA (2001) A long-term dietary analysis of loggerhead sea turtles (*Caretta caretta*) based on strandings from Cumberland Island, Georgia. Master's thesis, Florida Atlantic University, Boca Raton, Fla.
Zar JH (1996) Biostatistical Analysis: 3rd edn. Prentice Hall, New Jersey

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