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Using telemetry to mitigate the bycatch of long-lived marine vertebrates

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Abstract. The unintended bycatch of long-lived marine species in fishing gear is an important global conservation issue. One suite of management approaches used to address this problem restricts or modifies fishing practices in areas where the probability of bycatch is believed to be high. Information on the distribution and behavior of the bycaught species is a desirable component of any such scheme, but such observations are often lacking. We describe a spatially explicit approach that combines data on the distribution of fishing effort and observations of the distribution of bycatch species derived from satellite telemetry. In a case study, we used a spatially explicit predator–prey model to investigate real-time interactions between three species of sea turtles (*Caretta caretta*, *Chelonia mydas*, and *Lepidochelys kempii*) and the fall large-mesh gill net fishery that targets southern flounder (*Paralichthys lethostigma*) in Pamlico Sound, North Carolina between 2002 and 2004. The model calculates a spatial overlap index, thereby allowing us to identify which fishing areas have the greatest risk of encountering bycatch. In this study, our telemetry deployments ($n = 50$) were designed specifically to address existing fisheries conservation measures in Pamlico Sound intended to reduce sea turtle bycatch. We were able to predict the spatial distribution of bycatch and evaluate management measures. This approach offers a powerful tool to managers faced with the need to reduce bycatch.

Key words: bycatch; Caretta caretta; Chelonia mydas; *gill net fishery;* Lepidochelys kempii; *marine vertebrates; Pamlico Sound, North Carolina, USA;* Paralichthys lethostigma; *satellite telemetry; sea turtle; southern flounder; spatial overlap index.*

Introduction

Gill net fisheries capture vast numbers of large marine vertebrates as bycatch (Read et al. 2006, Davoren 2007, Peckham et al. 2007). Current research is directed at reducing bycatch through gear modifications, but so far management that includes regional time–area closures is the most effective for reducing bycatch in gill nets (Young 2001).

In this paper we describe a method of addressing the bycatch problem from the view of the bycatch species. As a case study, we describe a spatially explicit approach that combines data on the distribution of fishing effort and observations of the distribution of bycatch species derived from satellite telemetry. By merging information on the behavior of bycatch species with fisheries data, we can determine whether there are times and areas where fishing overlaps with the habitat of the animal (i.e., assess risk). We hypothesize that bycatch is predictable because of the habitat preferences of fishers and marine vertebrates.

We suggest that much like predator–prey encounters, risk of incidental capture in fishing gear can be predicted based on the distribution and density of predators (fishing gear) and prey (bycatch species) in a given region. When both predators and prey are patchily distributed, the overall predation risk increases significantly when there is a high degree of spatial overlap (Williamson 1993). Thus, in order to predict and, therefore, avoid bycatch, we must first understand the scale-dependent patterns of how fishers and bycatch species use habitat all under the guise of a highly dynamic environment. We used a predator–prey model called the Williamson Spatial Overlap Index, SOI (Williamson 1993) to identify areas of high bycatch risk in a case study on the incidental capture of sea turtles in a gill net fishery in Pamlico Sound, North Carolina, USA. The model describes the degree to which the spatial correlation of gill nets and sea turtles deviates from a random expectation under uniform spatial distributions. The SOI, O_{ij}, is calculated as follows:

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$$O_{ij} = \frac{\sum_z (N_{iz} N_{jz}) m}{\sum_z (N_{iz}) \times \sum_z (N_{jz})}$$

where z is a sample location, m is the total number of samples, N_i is the density of species i (gill nets), and N_j is the density of species j (bycatch species). A value less than 1 indicates less than expected overlap, while a value greater than 1 indicates a greater than expected overlap, with the upper bound determined by the number of locations sampled and the lower bound theoretically zero (Williamson 1993). Although any value greater than zero indicates opportunities for bycatch, values greater than one were used in this study to identify areas with a high risk for entanglement.

Case Study

In November 1999, the North Carolina Sea Turtle Stranding Network documented a significant increase in strandings ($n = 69$) along the southeastern shore of Pamlico Sound (Boettcher 2000). Field necropsies performed on animals implicated incidental capture in fishing gear (Boettcher 2000). By December the number of strandings in this area reached 97 individuals. In response, the National Marine Fisheries Service (NMFS) and North Carolina Division of Marine Fisheries (NCDMF) investigated fishing activities in the area (shrimp trawling, large- and small-mesh gill netting) and identified the flounder gill net fishery as the likely cause of these strandings after two Kemp's ridley turtles were observed in large-mesh gear (Gearhart 2001). The fishery was closed by the NMFS on 10 December 1999 (NMFS 1999, Federal Register 1999). The decision was decidedly unpopular with flounder fishers, many of whom believed that there was not enough evidence to support a closure (Santora 2003).

In 2000, the fishery resumed in a restricted fashion under a state-held Incidental Take Permit (ITP) authorized by Section 10 of the ESA (Federal Register 2000). The initial management measures obliged the state to develop a conservation plan and to establish a zone where fishing was allowed from 1 September through 15 December each year; this zone was called the Pamlico Sound Gill Net Restricted Area (PSGNRA). The permit also established mandatory requirements for gill net fishers in the PSGNRA including: registering for a permit; using a limited length of net; weekly self-reporting of fishing activity and incidental take; and allowing an observer to accompany fishing trips. The ITP stipulated 5% observer coverage based on total effort (net length × soak time), set a goal of a 50% reduction in strandings from the previous year, and established a turtle take limit.

Many fishers opposed the restrictions included in the ITP (Santora 2003). Despite adoption of these measures, however, portions of the fishery were closed again in 2000, 2001, and in 2002 because sea turtle strandings and observed incidental takes exceeded limits set by the National Marine Fisheries Service (Proclamations M-14-2000, 27 October 2000; M-14-2001, 29 September 2001; M-12-2002, 20 October 2002). In 2002, the deepwater gill net fishery was permanently closed to large-mesh nets (>11 cm) from 1 September to 15 December (Federal Register 2002).

The three sources of data used in management of the gill net fishery have been: sea turtle strandings; fishing effort; and observed bycatch. The state, in consultation with the NMFS, has since worked to manage the Pamlico Sound gill net fishery by limiting fishing effort, making adjustments to restricted areas, and closing sections of the fishery when bycatch rates of sea turtles approach or exceed incidental take limits. An important component lacking in these management measures, however, is consideration of sea turtle habitat and behavior. The Pamlico Sound Gill Net Restricted Areas (PSGNRAs) were initially designated on the basis of spatial and temporal patterns of sea turtle strandings (Bianchi 2002). Later PSGNRAs were delineated using the distribution of traditional shallow-water fishing grounds (Gearhart 2002), which encompassed the most productive flounder habitat.

Much of the past criticism aimed at the Pamlico Sound gill net fishery management system was based on the lack of scientific information required to justify management actions and a lack of stakeholder participation (Santora 2003). We worked with fishermen to study sea turtle movements using satellite telemetry in Pamlico Sound and compared these movements to the designated management areas. We explored both pattern and variation in the movements of turtles. The data we provide here contribute to an understanding of how sea turtles use the Sound and may be used to refine or modify future management measures, such as time–area closures.

Methods

Study area

Pamlico Sound is a shallow, meso-haline estuary connected to the Atlantic Ocean by a series of small inlets (Fig. 1A). The estuary is an important nursery habitat for a wide variety of estuarine species and supports more than 90% of North Carolina's commercial finfish and shellfish catch (Copeland and Gray 1991). Sea turtles are present in the Sound on a seasonal basis (Epperly et al. 1995*a*, *b*, Avens et al. 2003).

Field sampling

We collected 50 sea turtles from commercial pound nets in and around Pamlico Sound between September 2002 and November 2004: 21 in 2002, 24 in 2003, and 5 in 2004 (Fig. 1B). Sea turtles are commonly captured in flounder pound nets, passive traps that lead turtles into a corral where they are free to swim and breathe. We tagged 36 loggerhead turtles, ranging in size from 59.2 to 82.2 cm straight carapace length (SCL); seven green turtles, ranging in size from 32.2 to 72.3 cm SCL; and

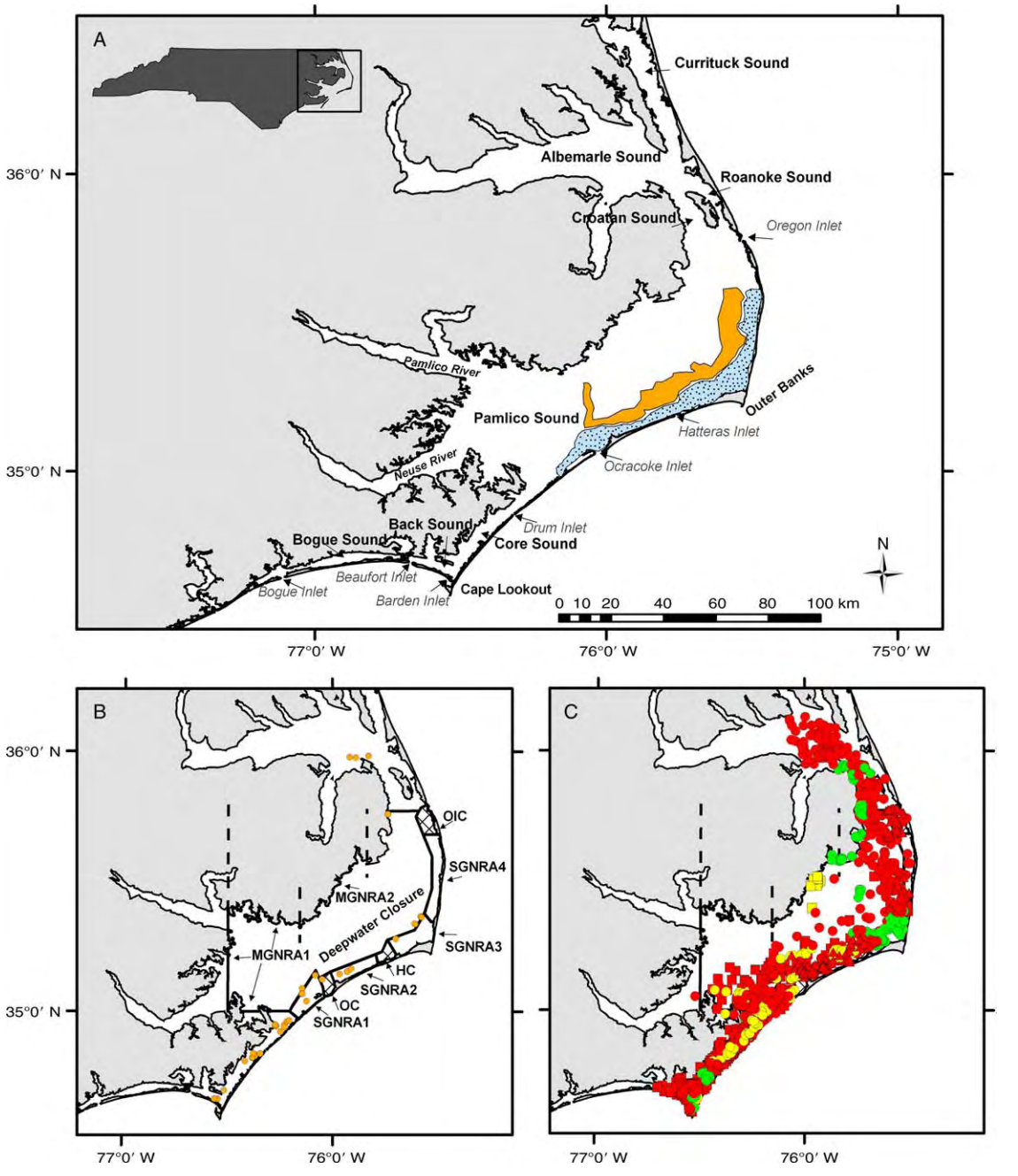

FIG. 1. (A) Map of inshore waters of North Carolina, USA, where our study was conducted. The blue stippled area indicates the traditional shallow-water gill net fishing grounds, and the orange area indicates the traditional deepwater gill net fishing grounds. In between these two lay a shallow "reef." (B) The current Pamlico Sound Gill Net Restricted Areas (PSGNRAs) with capture locations of turtles overlaid with orange circles. Key: OIC, Oregon Inlet corridor; SGNRA, southern gill net restricted areas 1, 2, 3, and 4; HC, Hatteras Inlet corridor; OC, Ocracoke Inlet corridor; Deepwater Closure, federal closure (1 September–15 December); MGNRA, mainland gill net restricted areas 1 and 2. (C) Filtered locations of sea turtles in North Carolina estuarine waters overlaid on the PSGNRAs: red, loggerhead; green, green turtle; yellow, Kemp's ridley. Circles are locations from turtles tagged in 2002, squares are from 2003, and triangles are from 2004.

seven Kemp's ridleys, ranging in size from 38.6 to 52.2 cm SCL (Table 1). Our sample is representative of sea turtles in North Carolina, both in species diversity and size (Epperly et al. 1995*b*, 2007, Sasso et al. 2006).

Fisherman participation was voluntary and we endeavored to arrange trips throughout the fishing season (September–December) and to stratify our efforts in space and time. However, no turtles were collected

TABLE 1. Satellite tagging summary of sea turtles tracked from North Carolina, 2002–2004.

Species	Size (cm SCL)	Year and no. deployed	Track duration (d)	Distance traveled (km)	No. remigrated
Loggerhead	63.9 ± 6.9	2002 (14), 2003 (17), 2004 (5)	234 ± 120	3043 ± 3471	14
Green	50.5 ± 19.6	2002 (2), 2003 (5)	80 ± 52	1753 ± 2170	0
Kemp's ridley	45.1 ± 6.1	2002 (5), 2003 (2)	33 ± 44	325 ± 611	0

Notes: Values for size, track duration, and distance traveled are means ± SD. Numbers of turtles deployed by year are indicated in parentheses. SCL is straight carapace length.

from the western side of Pamlico Sound, as no pound net fishers were operating in that area. Over our three-year study, we worked with 20 fishermen and conducted 33 sampling trips. Fishers operated from small wooden vessels ~7 m in length to fish their nets while we followed in a similar-sized research vessel. If turtles were present in their nets, they passed them to our boat.

Once turtles were brought on board our research vessel, we secured them into foam-padded plastic tubs and followed a standard NMFS sampling protocol (NMFS SEFSC 2008). We applied the satellite transmitter, antenna frontward, on the first and second vertebral scutes using a combination of PowerFast epoxy and fiberglass cloth and resin (NMFS SEFSC 2008). We used Wildlife Computers' SPOT2 ($n = 45$) and SPOT4 ($n = 5$) satellite transmitters (Wildlife Computers, Redmond, Washington, USA) in two sizes (small $73.8 \times 50.8 \times 21$ mm, 80 g; large $128 \times 49 \times 36$ mm, 185 g), to accommodate a range of sea turtle sizes. Turtles were then released into the water near their capture location.

Satellite telemetry data

Location and water temperature data were transmitted from each tagged turtle to National Ocean and Atmospheric Administration (NOAA) satellites when the animals surfaced to breathe. The satellite tags were programmed to transmit daily over an 8-h period beginning from just before dawn to near midday. A few of the smaller tags ($n = 7$) were duty-cycled to program every other day to extend the life of the transmitters.

Satellite-linked location data were converted and decoded using Wildlife Computers' (Redmond, Washington, USA) SPOT2 (2002–2003) and SATPACK (2004) software and imported into a geographic information system (GIS) for analysis (ArcView 3.2; ESRI 1992–1999, with Animal Movement (Hooge and Eichenlaub 2000), and Spatial Analyst extensions and ArcGIS 8.3; ESRI 1999–2002). These data were analyzed in Albers Equal Area projection, with a 2-km resolution (a conic, equal-area map projection that uses two standard parallels to reduce distortions in shape and linear scale, and is best suited for areas oriented east-to-west).

Estimates of the position of satellite-linked tags are coded by location accuracy classifications (LC) by Service Argos, Inc. (hereafter referred to as ARGOS). We recognize that the estimated locations of sea turtles do not represent their exact positions (Hays et al. 2001, Vincent et al. 2002). Nevertheless, we have taken great care to measure and consider the errors associated with each positional estimate. To ensure that we did not include erroneous positional estimates, we employed a three-stage filtering algorithm (McConnell et al. 1992, Austin et al. 2003) to reject implausible locations. After using this filtering method we were left with ~80% of our initial locations.

To determine how the habitat use of sea turtles in Pamlico Sound related to the active gill net fishing areas, we examined all filtered location data (including multiple locations per day) for turtles that entered the Pamlico Sound Gill Net Restricted Areas (PSGNRA) during the period of the fishery (September–December). We calculated the percentage of time each animal spent in every management area in the PSGNRA by week and over the entire season. This allowed us to assess the habitat use of sea turtles in the context of current management measures.

To examine potential interactions between sea turtles and gill nets, we calculated a density function of positions for each turtle during each week of the fishery period and corrected for the number of days without transmissions. We chose a radius of 1 km because that is the maximum error estimate provided by ARGOS. Individual densities were then added together. We were interested in relative comparisons; because the densities were extremely small, we multiplied densities times 1000.

Sea turtle movements were reconstructed by plotting the best-received location per day of the filtered location data and used to estimate distance traveled. We used these tracks to determine the points of exit the turtles used from the sounds during their fall migration. Chi-square analyses were used to test for differences in direction of movement out of the sounds. Site fidelity of loggerheads was measured by comparing distance between initial capture locations and remigration locations in the following year and using a t test.

Fisheries data

We obtained coordinates for the boundaries of the PSGNRA for each year (Fig. 1B) from DMF (North Carolina Division of Marine Fisheries 2002–2004) Proclamations (Proclamations M-10-2002, 14 August 2002; M-10-2003, 15 August 2003; M-8-2004, 20 August 2004). Management areas changed between years as DMF refined fisheries restrictions based on observed sea turtle bycatch and fishing effort. The deepwater fishing

grounds were closed to large-mesh gill nets during the entire fall flounder fishing season (September–December) in all years. Shallow-water areas were open on the mainland side (MGNRA1, MGNRA2) and along the Outer Banks (SGNRA1, SGNRA2, SGNRA3). After 2002, SGNRA3 was divided into two areas, creating a new SGNRA4. There were also three migratory corridors designated at the Oregon, Hatteras, and Ocracoke Inlets, where no fishing with large-mesh gill nets was allowed.

The NCDMF has observed a sample of the fall flounder gill net fishing trips in Pamlico Sound since 2000 (Gearhart 2001, 2002, 2003, Price 2004, 2005). Their objective is to observe 10% of the fishing effort in each restricted area (using stratified ratio sampling methods). Observer coverage is adjusted weekly based on the previous week's landings. Actual observer coverage based on logbook reports was 7.5% of fishing effort in 2002, 6.2% in 2003, and 8.5% in 2004 (Gearhart 2003, Price 2004, 2005). Observers recorded location, mesh size, net length, number of hauls, soak duration, pounds of flounder caught, and sea turtle bycatch. We obtained the large-mesh gill net observer data for 2002–2004 from DMF.

Flounder gill nets are made of monofilament, ranging from 14 to 18 cm stretched mesh set on the bottom overnight (Gearhart 2001, 2002, 2003, Steve et al. 2001, Price 2004, 2005). There is a 1829-m limit to large-mesh gill nets, but many nets are only 91 m and are typically set in a string composed of several nets set a short distance apart in a parallel fashion. Each string of nets is referred to as a "haul." We calculated fishing effort as a function of net length per haul (m) and soak duration (days). We then calculated probability density functions based on fishing effort with a 2 km radius for each week of the fishery. This distance was chosen on the basis of the maximum allowed net length; in addition, observers only recorded one end of each net hauled, so we were not able to determine the actual orientation of the set. The observed gill net densities were relatively small, so we multiplied these densities by 100. These values were later analyzed in conjunction with the observed distribution of sea turtles.

Spatial analyses

We calculated the Williamson (1993) spatial overlap index (SOI) for every PSGNRA for each week of the fishery in 2002–2004, using the probability density functions described previously for turtles and nets after Cox (2003). We used the model to evaluate the interaction potential of sea turtles and large-mesh gill nets in Pamlico Sound (i.e., SOI > 1) within 4-km^2 grid cells. We assume that our sample of sea turtle distribution was representative of the sea turtle population in the area and, furthermore, that the observed distribution of gill nets represented the distribution of fishing effort in each PSGNRA. Actual bycatches of sea turtles were then used to evaluate the performance of the model.

Sea turtle stranding data

We obtained sea turtle stranding data from the North Carolina Wildlife Resources Commission (WRC) for 1999–2004. Stranding data for Pamlico Sound are used with reservation in this assessment, as observer effort is opportunistic and spatially disjoint, due to the remoteness of the shoreline and its extensive marsh. Moreover, stranded sea turtles are widely subject to wind, tides, and currents and conclusive determination of their cause of death is rare (Epperly et al. 1996, Hart et al. 2006). We include the observations here because they have been used previously in cases of fisheries interactions (Crowder et al. 1995, Epperly et al. 1996, Lewison et al. 2003) and contributed to the instigation of the PSGNRA in the first place. These data were used to make qualitative comparisons of whether the SOI would predict strandings in the PSGNRAs in the same manner as bycatch.

Environmental data

Most of the observed sea turtle interactions with gill nets prior to our study were reported in the deepwater fishery (which ultimately led to its closure). However increasing numbers of turtle interactions were observed in shallow water when the deepwater fishery was closed (J. Gearhart, DMF, *personal communication*). We obtained a bathymetric digital elevation model (DEM) at 30-m resolution from the NOAA's National Ocean Service (NOAA NOS 1998) and sampled sea turtle locations. These analyses do not tell us the precise depths used by the turtles, because they are subject to LC (location classification) errors, but they do allow us to evaluate the general water depths occupied by the turtles.

Results

Satellite telemetry

We tracked turtles for periods ranging from 13 to 660 days as they traveled between 60 and 12 418 km (Table 1). Two transmitters failed immediately, one from a loggerhead in 2002 and the other from a Kemp's ridley in 2003. We cannot be certain about the cause of transmitter failure, but possible reasons include attachment failure, battery failure, damage to the transmitter, or death of the turtle. All but two other transmitters functioned until turtles migrated out of the Sound or until the end of the fishery period.

During September–December (the fishery period) in all years sea turtles were distributed from Albemarle Sound through Bogue Sound; these locations are presented in Fig. 1C. Our tagging efforts were restricted to the eastern side of Pamlico Sound, including the Croatan and Albemarle Sounds and in Core and Back Sounds. We tagged only nine turtles initially encountered along the Outer Banks, although a large number of estimated locations from many turtles were recorded from this area.

The directionality of turtle movements was bimodally distributed as they made their fall migration out of the

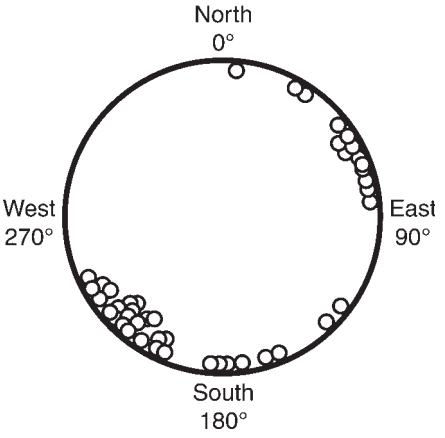

FIG. 2. Rose diagram showing a northeast–southwest bimodal distribution of turtles' migratory orientation. Direction was measured from capture location to outlet.

sounds (Fig. 2). Sea turtles tagged in Albemarle Sound, Pamlico, and Core/Back Sounds did not display a preferential migratory orientation between the northeast and southwest directions (χ^2, $0.1 < P < 0.05$). The turtles left the sounds most frequently through Barden's Inlet at Cape Lookout followed by Hatteras, Drum, Oregon, Ocracoke, and Beaufort inlets. Only 30% of the turtles left through the nearest inlet; others passed by one or more inlets before selecting a distant inlet from which to leave. We were able to determine the point of reentry for 12 of the 14 loggerheads that remigrated into the sounds in the following year. Half of these animals used the same inlets to enter and leave the estuary. In the six cases where the turtles used a different inlet, five chose an adjacent inlet to the north (1) or south (4). One animal was tracked long enough to capture its fall migration in two consecutive years, and both times this individual used Hatteras inlet; its remigration had been through Ocracoke inlet. Of the 35 loggerheads, 14 reentered the sounds in the year after capture. Core Sound turtles had significantly stronger site fidelity than those captured in Pamlico Sound ($P = 0.047$).

We calculated the percentage of time turtles spent in each PSGNRA by fishery week for 2002, 2003, and 2004 (Fig. 3). Considering only the turtles that entered the PSGNRA complex ($n = 15$ in 2002, 6 in 2003, and 5 in 2004), most time was spent in the deepwater closed area in 2002 and 2003 (64% and 70%, respectively). In 2004, the deepwater area ranked second in importance (24%) and Southern Gill Net Restricted Area (SGNRA) 2 was occupied most frequently (53%), but our tracking began late in the season (week 11 of the fishery) and all turtles left the Sound within three weeks. In 2002, all PSGNRAs were inhabited by turtles at some point during the fishery. In 2003, only the Ocracoke Corridor (OC) and Mainland Gill Net Restricted Areas (MGNRAs) were not used by sea turtles during the fishery period. On 18 September 2003, week 3 of the fishery, Hurricane Isabel passed directly over Pamlico Sound, modifying our sampling efforts, fishing effort, and probably the behavior of the turtles. In 2004, the turtles occupied all PSGNRAs except SGNRA 1 and the MGNRAs.

Fishery

The greatest large-mesh gill net fishing effort consistently occurred in SGNRA 3 followed by SGNRAs 4, 2, 1, and the MGNRAs (Fig. 4). Twelve observed takes were documented in 2002, four in 2003, and nine in 2004. Seventy-two percent of the turtles were caught in

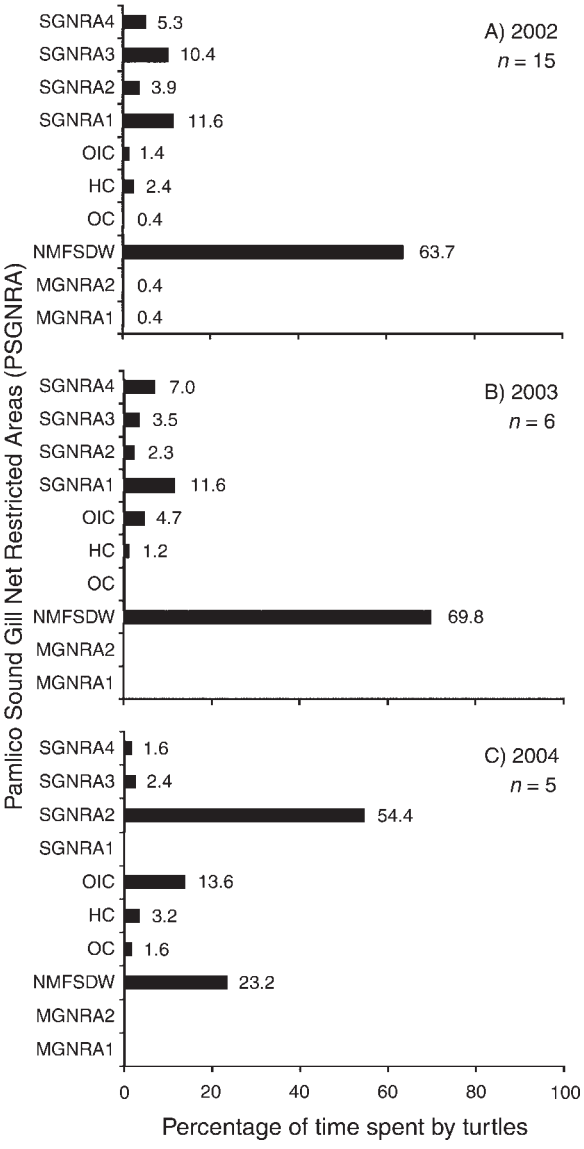

FIG. 3. Graphical summary of the percentage of time turtles spent in each Pamlico Sound Gill Net Restricted Area (PSGNRA) over all weeks in the fishery for each year (2002–2004). Turtles spent the majority of time in the NMFS deepwater closed area. The number (n) of individual satellite-tagged turtles that occupied the PSGNRAs each year is reported in the respective panels. NMFSDW indicates the National Marine Fisheries Service Deepwater Closure area; see Fig. 1 for other area codes.

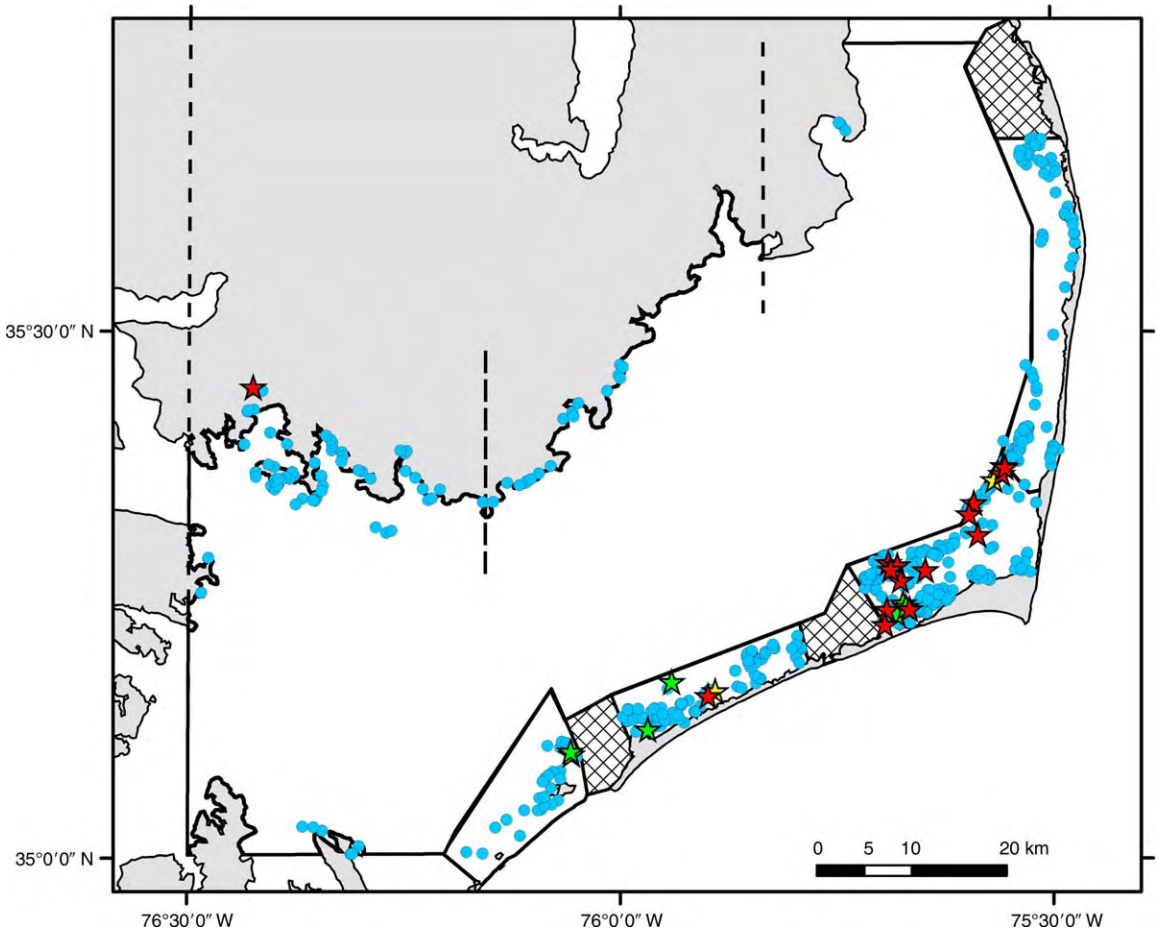

FIG. 4. Map of large-mesh gill nets (blue circles) and sea turtle bycatch (stars) observed by NCDMF (North Carolina Division of Marine Fisheries), September–December 2002–2004. Red stars are loggerheads; green stars are green turtles; yellow stars are Kemp's ridley.

SGNRA 3 (Fig. 4). Most (17) observed bycaught turtles were released alive. All three species of sea turtle were caught in gill nets, but green turtles comprised by far the largest proportion in each year. In the three years of our study, 270 turtles were estimated to be taken by this fishery (221 live, 49 lethal) (Gearhart 2003, Price 2004, 2005).

Strandings

Fourteen stranded turtles were observed in the PSGNRA in 2002, 10 in 2003, and 38 in 2004 during the fishery period (Fig. 5). Of these stranded turtles, 58% were found in the inlet corridors followed by 15% in SGNRA3, 13% in SGNRA2, 6% in SGNRA4, 5% in SGNRA1, 2% in MGNRA1, and 2% in the deepwater closure. The spatial distribution of strandings was similar to that of observed bycatch, but high percentages were located near inlets. The species dominating the strandings shifted from loggerhead (50% in 2002) to green (55% in 2004) during the three-year period. Only in two cases were large-mesh gill nets conclusively implicated in the strandings over the three-year period.

Spatial analyses

Overlap of fishing effort and satellite-tagged turtles was rare, and occurred on only a few occasions in SGNRA 2, SGNRA 3, SGNRA 4. The number of satellite-tagged turtles moving through Pamlico Sound in any given year was low and the majority occupied the deepwater area closed to fishing where overlap would have been greatest prior to the closure (Fig. 3). The SOI revealed bycatch opportunities in SGNRA2 during weeks 7 and 10 of 2002, week 8 of 2003, and weeks 11, 12, and 13 of 2004, in SGNRA3 in week 6 of 2002 and week 9 of 2003, in SGNRA4 in weeks 6, 8, 10, and 11 in 2002, week 9 in 2003, and week 11 of 2004. SOI values <1 essentially indicate that nets and turtles co-occurred, but were not clustered within the analysis unit. The SOI showed the highest potential for entanglement in SGNRA 2 during week 9 of 2002, in SGNRA 3 during week 7 of 2002 and week 11 of 2004. SGNRA 3, in particular, had the most observed bycatch (Fig. 6) as predicted the SOI. SOI values for all years, weeks, and GNRAs are available in the Appendix.

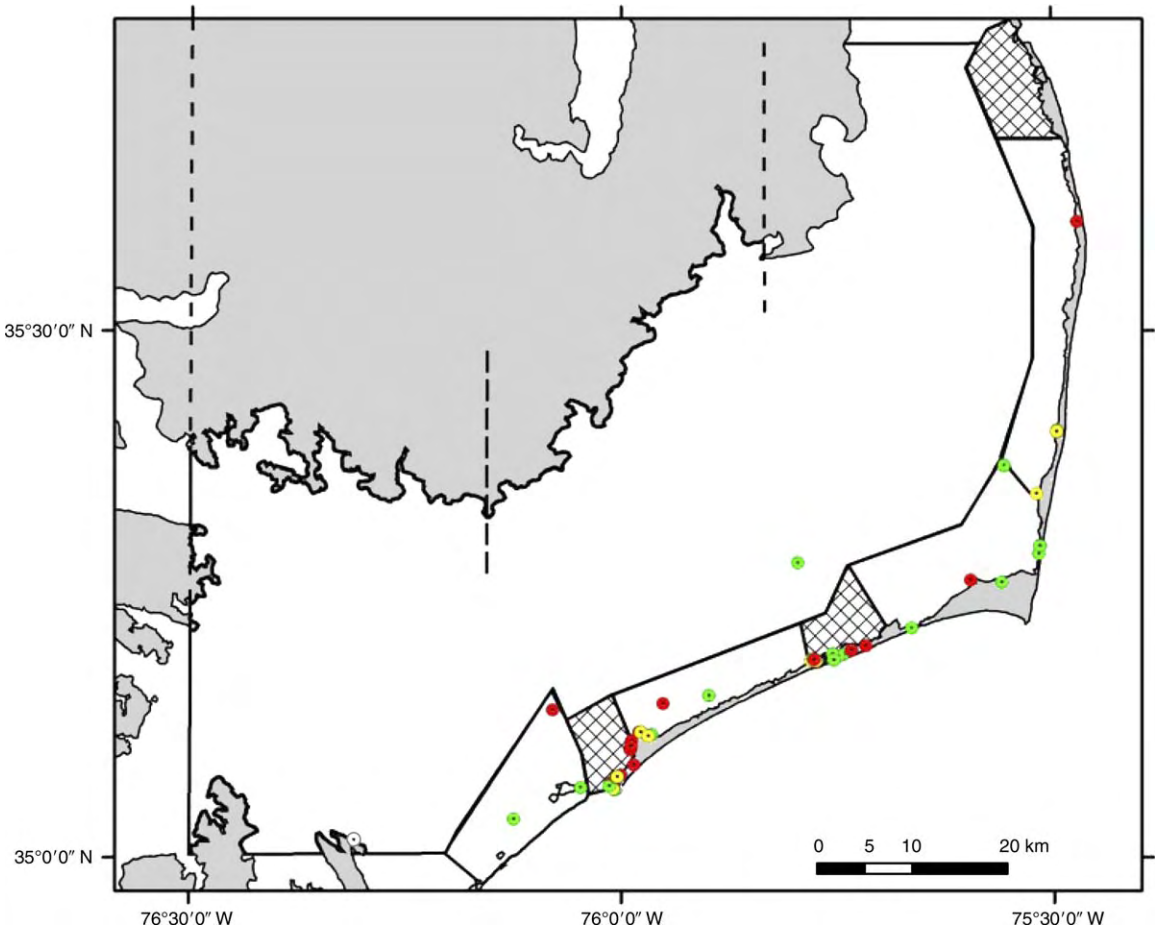

FIG. 5. Map of sea turtle strandings observed in the PSGNRA by NCWRC (North Carolina Wildlife Resources Commission), September–December 2002–2004. Turtle species are identified by circle color: red, loggerhead; green, green turtle; yellow, Kemp's ridley; white, unidentified species.

These values are conservative predictions based on the spatial and temporal scales at which we analyzed the data and because we modeled only a portion of the fishery (as available through observer coverage) and turtle locations were limited by an 8-h per day time window and foraging behavior that reduces surface intervals.

Environmental correlates

In Pamlico Sound, sea turtles were found in water depths from 0 to 6 m. Greens occurred primarily in shallow water (mean 0.5 m, range 0–5 m) while loggerheads and Kemp's ridleys occupied a wider range of depths (mean 3 m, range 0–5 m and mean 3, range 0–6 m, respectively). Most estuarine locations outside the PSGNRA occurred in Core Sound, which is shallow. Here, all turtles occupied average depths of 0.5 (range greens 0–2 m, loggerheads 0–5 m, Kemp's 0–2 m).

DISCUSSION

Our study of marine turtles in Pamlico Sound allowed us to identify areas of high use during the fall large-mesh gill net fishery period and to evaluate the current constellation of restricted areas intended to reduce turtle bycatch. The seasonal closure of the deepwater fishing grounds during the past seven years has been controversial and criticized by fishery participants (Santora 2003). Despite this criticism, we found the closure to be well placed based on the turtles' distribution in the Sound, particularly for loggerheads and Kemp's ridleys. This result concurs with the reduction in bycatch in the PSGNRA since the implementation of the closure. If the deepwater area were to reopen, it is likely that bycatches of loggerheads and Kemp's ridleys would increase as in the past (2000). Our data further suggest that many turtles use the traditional deepwater fishing grounds along the "reef" (Fig. 1A). Interactions in the shallow-water PSGNRAs may, therefore, occur along the boundaries of current management areas.

Our results were consistent with the spatial and temporal distributions reported by Epperly et al. (1995*a*, *b*) and with anecdotal reports of fishermen participating in this study, but more importantly they allowed us to determine how long individual animals remained in the PSGNRAs. We were also able to

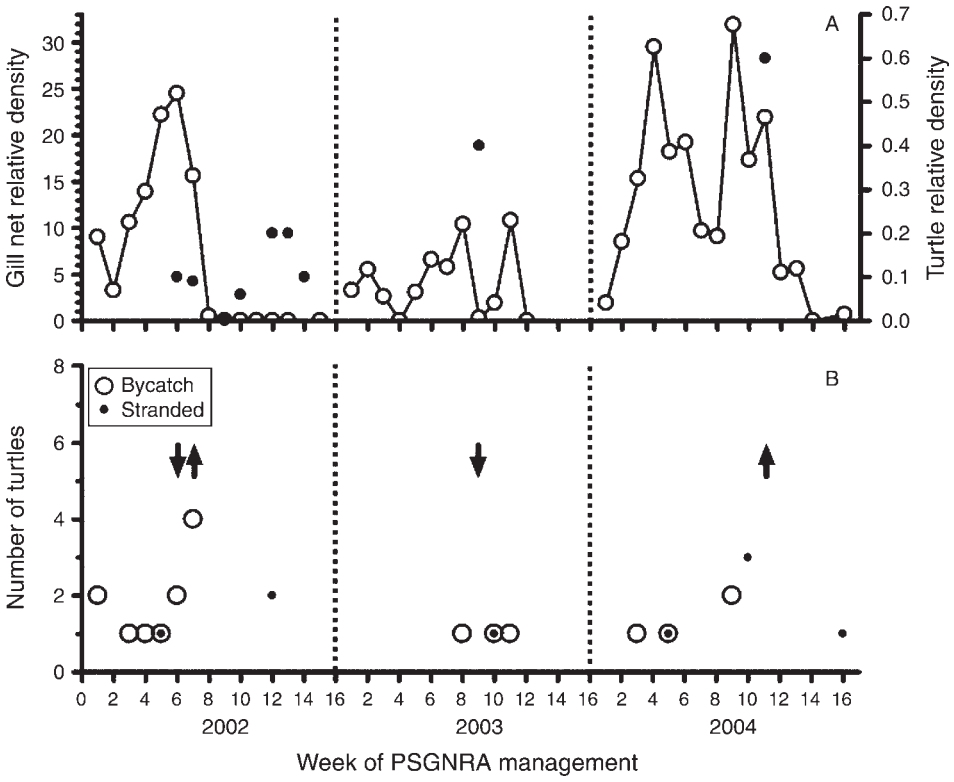

FIG. 6. Sea turtle data in relation to management week (week 1 is the first week of fishing, starting 1 September) in the Pamlico Sound Gill Net Restricted Areas for the years 2002–2004. (A) Changes in predator (gill net; open circles, left-hand axis) and prey (satellite-tagged sea turtles; solid circles, right-hand axis) relative densities in SGNRA 3 during the fishery weeks of our study. See *Methods* for density calculation. (B) Bycatch and strandings are denoted by symbol type. SOI values >1 are indicated by upward arrows, and values <1 are indicated by downward arrows. SOI, the Williamson Spatial Overlap Index, is a predator–prey model used to identify areas of high bycatch risk.

document seasonal changes in habitat use and highlight areas that have been underappreciated as turtle habitat. For example, the turtles in our study primarily used the eastern portion of Pamlico Sound, but we tracked some animals to the western side, particularly during the summer and early fall. Aerial surveys and reports from fishermen in the late 1980s and early 1990s also noted the presence of turtles in the western Pamlico during the summer and fall months (Epperly et al. 1995*a*, *b*). DMF observers documented only one Kemp's ridley in large-mesh gill nets set in the Mainland Gill Net Restricted Areas between 2002 and 2004; as a result, the state is considering reducing or eliminating observer coverage from this area. Fishing effort is currently low, but changes in regulations to other areas in the sounds could induce displacement of effort, as this region historically had much more fishing activity.

Our approach, using a spatially explicit predator–prey model (Williamson 1993), accurately predicted areas where bycatch occurred on several occasions, allowing us to independently identify high-risk fishing areas. This success is quite remarkable, given our relatively small sample of turtles (50) and limited observations (7.6%) of actual fishing effort. This technique was also successful at predicting bycatch in a post hoc analysis of harbor porpoise (*Phocoena phocoena*) telemetry data and gill net fishing in the Gulf of Maine (Cox 2003). Both studies found that the greatest risk of bycatch occurred in areas of high spatial overlap. Although this conclusion is a simple one, it demonstrates that information on habitat use and fisheries effort can predict the locations of bycatch at appropriate scales. Obviously, incidental capture is possible any time gear and turtles co-occur; therefore an understanding of behaviors that lead to entanglement would be additionally valuable.

Stranding levels in the PSGNRA have not shown the same decline as the observed bycatches and, although species composition has shifted toward green turtles, the yearly proportions are dissimilar to those of the observed bycatch. Similar to the findings of other studies on the distribution of stranded sea turtles (Epperly et al. 1996, Hart et al. 2006), we found that wind, tides, and currents probably influenced the location of strandings, which were clustered in the inlets. Strandings data remain a blunt instrument for drawing attention to potential problem areas, such as the initial suggestion of fisheries interactions in Pamlico Sound in 1999 and with regard to shrimp trawls and

Turtle Exluder Devices, TEDs (Crowder et al. 1994, 1995, Epperly and Teas 2002), but they are less useful in defining specific management areas and are unreliable indicators of actual bycatch levels. Currently, nothing can replace observer programs for monitoring bycatch.

During the period when the deepwater area remained open (2000), the bycatch consisted mostly of loggerheads and Kemp's ridleys. Recent takes, although few in number, are nearly all green turtles. This result could also be predicted by understanding the habitat preference of marine turtles and overlaying them on the habitat mosaic of Pamlico Sound. Our analysis of depth data shows that, although loggerheads and Kemp's ridleys use a wide variety of habitat, green turtles are restricted to shallow waters. These depth preferences are similar to those reported by Byles (1988) for loggerheads and Kemp's ridleys in Chesapeake Bay, Virginia and by Mendonça (1983) for green turtles in Mosquito Lagoon, Florida. Our results are also consistent with observations of the bycatches of sea turtles in Pamlico Sound; loggerheads and Kemp's ridleys in deeper water and green turtles in shallower water (Gearhart 2001, 2002, 2003, Price 2004, 2005). Green turtles are closely associated with sea grass, which is their primary diet in neritic environments (Bjorndal 1980, Mendonça 1983). Pamlico Sound is relatively turbid, so light attenuation constrains the distribution of sea grass to the shallows. Freshwater outflow from the Neuse and Tar-Pamlico rivers produces lower salinities and muddier substrates on the western side of the Sound (Woodruff et al. 1999). In contrast, the area behind the Outer Banks is adjacent to inlets that exchange clear, high-salinity sea water, and has sandy bottoms that are more favorable to sea grasses. This is also the region where the highest fishing effort now occurs. Green turtles are particularly vulnerable to entanglement in these areas. Therefore, the current management measures unwittingly selected for green turtle bycatch, albeit in small numbers.

A review of historic green turtle fisheries along the southeastern United States documents how large-mesh gill nets were very effective in catching turtles and were used widely from North Carolina to the Florida Keys (True 1887). True (1887) describes the capture technique:

> *On arriving on the grounds the boat or vessel is kept beating back and forth until signs of turtles are noticed . . . the nets are set out near them and in a straight line parallel with the course of the tide. The turtles come to surface every few minutes to breathe, and while rising and sinking near the net are very apt to become entangled in it. Only one flipper may be caught at first, but when the animal turns the other is entrapped and, shortly, the whole body is securely wrapped in the cords.*

It is not surprising that this same manner of fishing, targeting flounder, catches turtles inhabiting the same area. Fisheries observer data suggest that bycatch peaks in the first few weeks of the flounder gill net fishery. This trend has been noted in other fisheries, such as the trawl fishery off South Carolina (Crowder et al. 1995). High numbers of takes and strandings were observed coinciding with the start of the fishery. This may reflect interactions between the inaugurate fishery and turtles that have established patterns of seasonal residency.

Work by Avens et al. (2003) suggests that juvenile loggerheads exhibit strong site fidelity within Core Sound. These researchers found that turtles were recaptured multiple times within a season in the same area and that recaptures occurred between seasons in the same location. Furthermore, loggerheads displaced from the capture location and tracked with radiotelemetry displayed homing behavior and were able to navigate back to particular sites (Avens et al. 2003). The pound-net fishermen we worked with told us that they recognized particular turtles in their nets day after day. We also noted strong site fidelity, especially in Core Sound, and nearly half of the turtles in this study remigrated into the sounds in the following year, which could affect their risk to incidental capture.

Results from an experimental study on juvenile loggerheads and green turtles from North Carolina estuaries describe a southerly orientation during the autumn consistent with the onset of migration seen in the field (Avens and Lohmann 2004). However, about 30% of the turtles that we satellite-tagged did not exhibit a southern orientation in the sounds, but moved out of inlets to the northeast of their capture location. These results suggest that behavioral differences exist between turtles in North Carolina sounds. Furthermore, many turtles in our study used distant inlets to exit the sounds, suggesting that there may be individual preferences for these corridors. Clearly, more work is necessary to assess inlet fidelity. Movements within the sound affect encounters with fishing gear, especially in narrow areas such as Core Sound, where gear is highly likely to intercept the large number of animals migrating through the area.

Most bycaught sea turtles in the shallow-water fishing grounds are released alive. The average estimated lethal take of turtles based on fisheries effort in the PSGNRA between 2002 and 2004 was 16 animals: 3% of the direct harvest that took place over a century earlier. Gill netting occurs throughout North Carolina sounds at various times of the year, but so far only the Pamlico Sound fall large-mesh fishery is regulated with respect to sea turtle bycatch under a Section 10 permit. The DMF maintains proclamation authority, however, which allows establishment or modification of restrictions in areas or at times when known problems exist, such as the seasonal net attendance requirement in the lower Cape Fear River, which began in 2005 (Proclamation M-7-2005, 13 June 2005). Information on the post-release mortality and sublethal effects related to bycatch is required to fully assess fisheries-related impacts on these populations. Gill nets are only one of several gears that turtles encounter in the sounds, so identification of

turtle habitat preferences is valuable to the management of these other fisheries as well.

Catch rates of juvenile loggerheads in North Carolina have increased in the past decade, but trends on nesting beaches in other juvenile foraging grounds along the southeastern United States provide conflicting messages as to whether or not sea turtle populations are increasing, decreasing, or stable (Epperly et al. 2007). Variability in capture rates has complicated estimation of the number of turtles present in North Carolina (Sasso et al. 2007), although fishers assert that they are seeing an increasing number of turtles. The current lack of abundance estimates hinders our ability to manage fisheries and allocate take. Estuarine fisheries are declining in North Carolina. Most fishers operate alone and fish multiple gears, and an increasing number are supplementing their income with other employment (Crosson 2007). Restrictions to fisheries administer an additional toll to an already struggling heritage. Some fishers are leaving the business, while others switch to fishing more affordable gears, such as gill nets, which are cheaper to buy, require smaller boats and fewer (if any) additional crew, and allow them to move their gear as the fish move. Therefore, it is imperative that we understand and mitigate the bycatch of protected species in gill net fisheries.

Concluding Remarks

Our case study demonstrates that satellite telemetry is an excellent tool for evaluating the spatially explicit nature of fisheries interactions and for evaluating specific conservation measures. This approach could be accomplished with traditional survey data, but in our case diving behaviors of the turtles and turbid waters of the sounds limit wide applicability of this method. Satellite telemetry allows identification of important habitat without many of the biases that survey data contain and allows quantification of the time that individuals spend within particular habitats. We suggest that spatially explicit studies, such as this one, can be used to develop effective bycatch reduction measures in many situations, particularly if the telemetry studies are conducted prior to the establishment of time–area closures.

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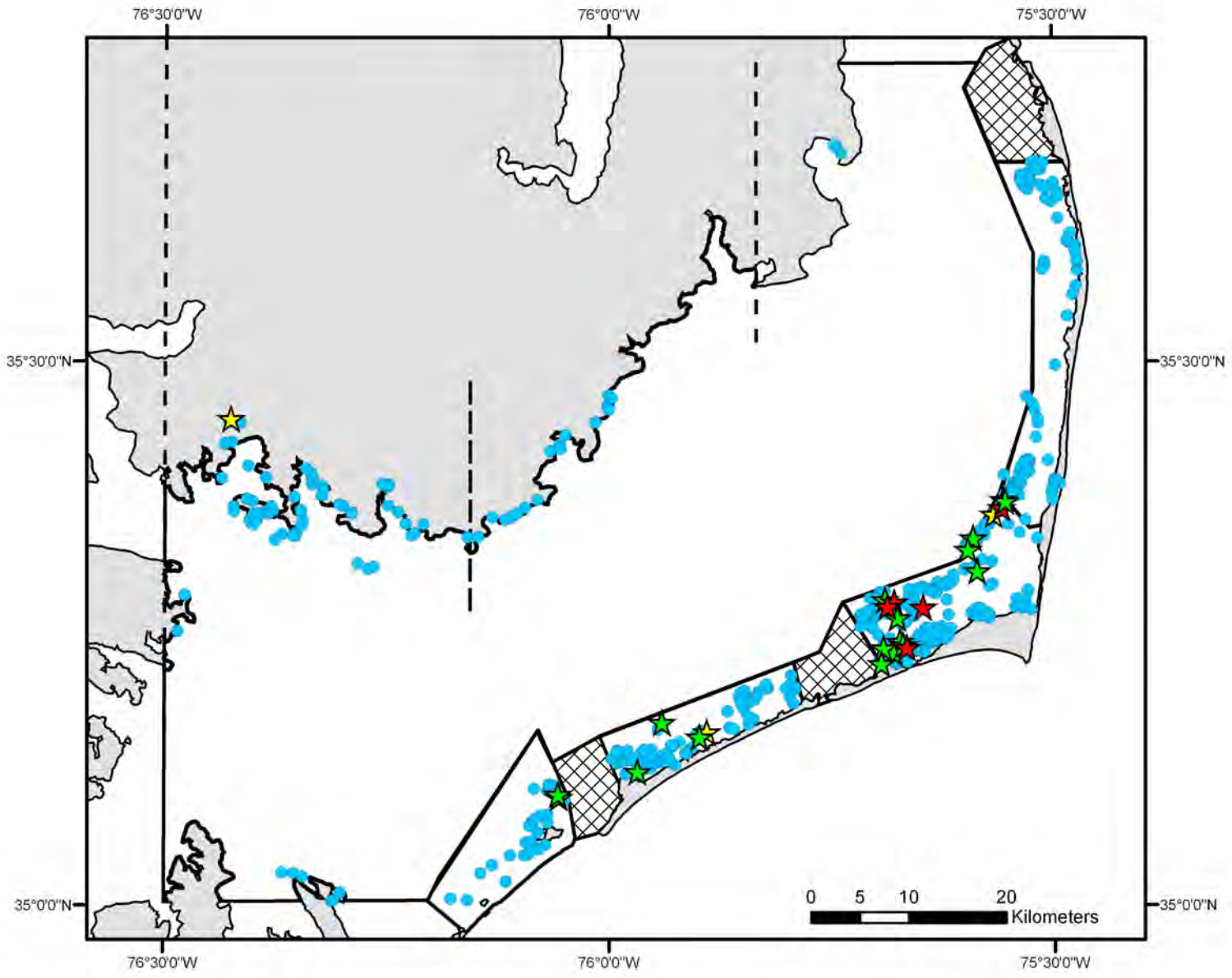
APPENDIX

Results of the Williamson spatial overlap index, sea turtle bycatch, and sea turtle strandings for each Pamlico Sound Gill Net Restricted Area (PSGNRA) by fishery week (*Ecological Archives* A019-066-A1).

PLEASE NOTE: Figure 4 was misprinted in the original publication.

The figure below is the correct version of Figure 4 (page 1666) in: McClellan et al. 2009. Using telemetry to mitigate the bycatch of long-lived marine vertebrates. *Ecological Applications* 19(6):1660-1671.