Temporal trends (2000–2011) and influences on fishery-independent catch rates for loggerhead sea turtles (*Caretta caretta*) at an important coastal foraging region in the southeastern United States

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Abstract—Seasonal trawling was conducted randomly in coastal (depths of 4.6–17 m) waters from St. Augustine, Florida, (29.9°N) to Winyah Bay, South Carolina (33.1°N), during 2000–03, 2008–09, and 2011 to assess annual trends in the relative abundance of sea turtles. A total of 1262 loggerhead sea turtles (*Caretta caretta*) were captured in 23% (951) of 4207 sampling events. Capture rates (overall and among prevalent 5-cm size classes) were analyzed through the use of a generalized linear model with log link function for the 4097 events that had complete observations for all 25 model parameters. Final models explained 6.6% (70.1–75.0 cm minimum straight-line carapace length [SCLmin]) to 14.9% (75.1–80.0 cm SCLmin) of deviance in the data set. Sampling year, geographic subregion, and distance from shore were retained as significant terms in all final models, and these terms collectively accounted for 6.2% of overall model deviance (range: 4.5–11.7% of variance among 5-cm size classes). We retained 18 parameters only in a subset of final models: 4 as exclusively significant terms, 5 as a mixture of significant or nonsignificant terms, and 9 as exclusively nonsignificant terms. Four parameters also were dropped completely from all final models. The generalized linear model proved appropriate for monitoring trends for this data set that was laden with zero values for catches and was compiled for a globally protected species. Because we could not account for much model deviance, metrics other than those examined in our study may better explain catch variability and, once elucidated, their inclusion in the generalized linear model should improve model fits.

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Analysis of temporal trends in capture rates is a significant part of conducting stock assessments (Hilborn and Walters, 1992). Capture rates generated through fishery-independent methods are ideal; however, fishery-dependent data sets are also suitable provided that historical shifts in fishing practices are accounted for (Walters, 2003). Although the value of monitoring capture rates increases with expanded temporal scope, the temporal scope of a data set often is abbreviated by economics. Consequently, resource management decisions often rely on an assortment of observations compiled across a variety of sources. Provided that heterogeneous data sets span a gamut of time and interface well, such practices are not inherently problematic. However, vast temporal gaps or intricacies that preclude the bridging of data sets can be problematic for the assessment of long-term patterns and, ultimately, for effective resource management, particularly for long-lived species.

Sea turtles (order Testudines) are long-lived marine species that have come to represent the link between anthropogenic activities and their effects on sea turtle populations (Musick, 1999). Annual monitoring of nests and eggs has generated data sets with durations that approximate the assumed generation time for some cohorts (Troëng and Rankin, 2004; Balazs and Chaloupka, 2004; Witherington et al., 2009). Conversely, challenges associated with the collection of sea turtle data in aquatic environments have resulted in less information on abundance trends for life history stages between hatchling and adult (NRC, 2010). Despite extensive characterizations of incidental capture of sea turtles in fisheries (Wallace et al., 2010a) and subsequent evaluation of mitigation measures (Brewer et al., 1998; Gilman et al., 2006; Murray, 2011), few temporal analyses of fishery-dependent captures exist. Notable exceptions include 2 assessments (both spanning 8-year periods) of loggerhead sea turtle (*Caretta caretta*) catch from pelagic longline fisheries in the southwestern Atlantic Ocean (Pons et al., 2010) and from neritic pound-net fisheries in the northwestern (NW) Atlantic Ocean (Epperly et al., 2007). Published accounts of temporal trends in fishery-independent catch rates that span one or more decades are also sparse, typically originate from spatially refined study locations, and are largely restricted to green (*Chelonia mydas*) and loggerhead sea turtles in the South Pacific and NW Atlantic Oceans (Limpus et al., 1992; Ehrhart et al., 2007; Arendt et al., 2012a).

In addition to limited spatial context, localized surveys also tend to be conducted in sea turtle aggregation areas where individuals exhibit site fidelity (Byles, 1988; Avens et al., 2003). Consequently, the statistical pitfalls attributed to monitoring fishery-dependent capture rates in areas of resource concentration (Hilborn and Walters, 1992) also apply, and they necessitate the introduction of an element of randomization to reduce bias. For example, Epperly et al. (2007) randomly selected pound nets for monitoring sea turtle catch rates, and Arendt et al. (2012a) systematically sampled among spatial blocks to monitor sea turtle catch rates within a shipping channel. Although such practices improve statistical design, they are not as robust as truly randomized sampling. Excluding random selection of aerial survey transects (Epperly et al., 1995a), which do not facilitate assessment of critical demographic parameters (Braun-McNeill et al., 2007), data on sea turtle relative abundance from random sampling on foraging grounds over large spatial expanses are not available globally.

To improve the random nature and spatial scope of in-water sea turtle data collected in the NW Atlantic Ocean, a trawl survey of sea turtle relative abundance was initiated in 2000 to address the need for "long-term, in-water indices of loggerhead abundance in coastal waters…to identify relative abundance of sea turtles over time, and to detect changes in size composition with implications regarding recruitment" (TEWG, 1998). Before mandated use of turtle excluder devices (TEDs), the decline of sea turtles in the NW Atlantic Ocean was attributed to the drowning of turtles during commercial shrimp trawling (NRC, 1990); therefore, sampling by trawling may seem odd as a sampling method. However, reduced tow times (Sasso and Epperly, 2006) enabled safe use of this accepted technique to capture sea turtles in turbid waters (Butler et al., 1987). For our study, we test the null hypotheses of no change in annual loggerhead capture rates in coastal waters from Winyah Bay, South Carolina, (33.1°N) to St. Augustine, Florida, (29.9°N) between 2000 and 2011 overall (objective 1) and for prevalent 5-cm size classes (objective 2). We also test the null hypothesis of no significant influence of 26 parameters on capture rates (objective 3) with a generalized linear model, the most powerful linear model (Hilborn and Walters, 1992).

Materials and methods

Sampling and data collection

For this study, sampling was conducted in coastal waters (at depths of 4.6–17.0 m) between Winyah Bay, South Carolina, and St. Augustine, Florida (Fig. 1). Four subregions were recognized on the basis of sampling strata established by the Southeastern Area Monitoring and Assessment Program (SEAMAP). The subregion that spanned from St. Augustine, Florida, to Brunswick, Georgia, for example, corresponded with sampling strata from the northern portions of SEAMAP strata 27–28 to strata 34. SEAMAP strata 35 to 40 approximated the subregion from Brunswick to Savannah, Georgia. SEAMAP strata 41 to 46 and 47 to 50 corresponded with the subregions from Savannah, Gerogia, to Charleston, South Carolina, and from Charleston to Winyah Bay, South Carolina, respectively. Sampling began in mid-May, roughly 6 weeks after the seasonal return of loggerhead sea turtles to nearshore coastal waters (Arendt et al., 2012b). Sampling concluded in late July in all years except 2000, when sampling had to be extended into mid-August because of a temporary shutdown that occurred (in July) when we reached the initially permitted sea turtle catch limits authorized by the National Marine Fisheries Service (NMFS), Office of Protected Resources.

At the start of each sampling year, a list of stations was randomly selected from a universe of 1500 coordinate pairs that represented the center of 3.4-km^2 grids of trawlable seafloor within the overall survey boundaries. Sampling was completed with 2–3 vessels, with a staggered north-to-south start, which primarily arose as a result of vessel availability. All vessels that participated in this study towed paired 18.3-m (head rope), 4-seam, 4-legged, 2-bridle nets with a net body that consisted of a 10.2-cm bar and 20.3-cm stretch mesh. Subregion sampling alternated weekly to the north or south of vessel homeports to reduce spatiotemporal bias. Aboard each vessel, the daily order of station sampling alternated haphazardly between stations located roughly <6 km from shore and stations located >6 km from shore to diversify longitudinal sampling with respect to time of day and tide stage while still enabling a large (~100 km of latitude) area to be sampled by each vessel weekly.

Captured sea turtles were removed from nets and examined for general health and injuries. In the event of unconscious sea turtles, project staff had been trained in veterinarian- and NMFS-approved resuscitation protocols that involved manual ventilation by a self-refilling valve-bag apparatus. Sea turtles were scanned for pre-existing tags; if none were found, each sea turtle was assigned a unique identification number when it was first encountered (and the number was used again to denote recapture events). A suite of morphometric measurements were collected, but, here, we report only minimum straight-line carapace length (SCLmin) measured with tree calipers. Sea turtles were tagged externally (2 Inconel 681[1] flipper tags, National Band and Tag Co., Newport, KY, purchased through the Archie Carr Center for Sea Turtle Research, Gainesville,

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

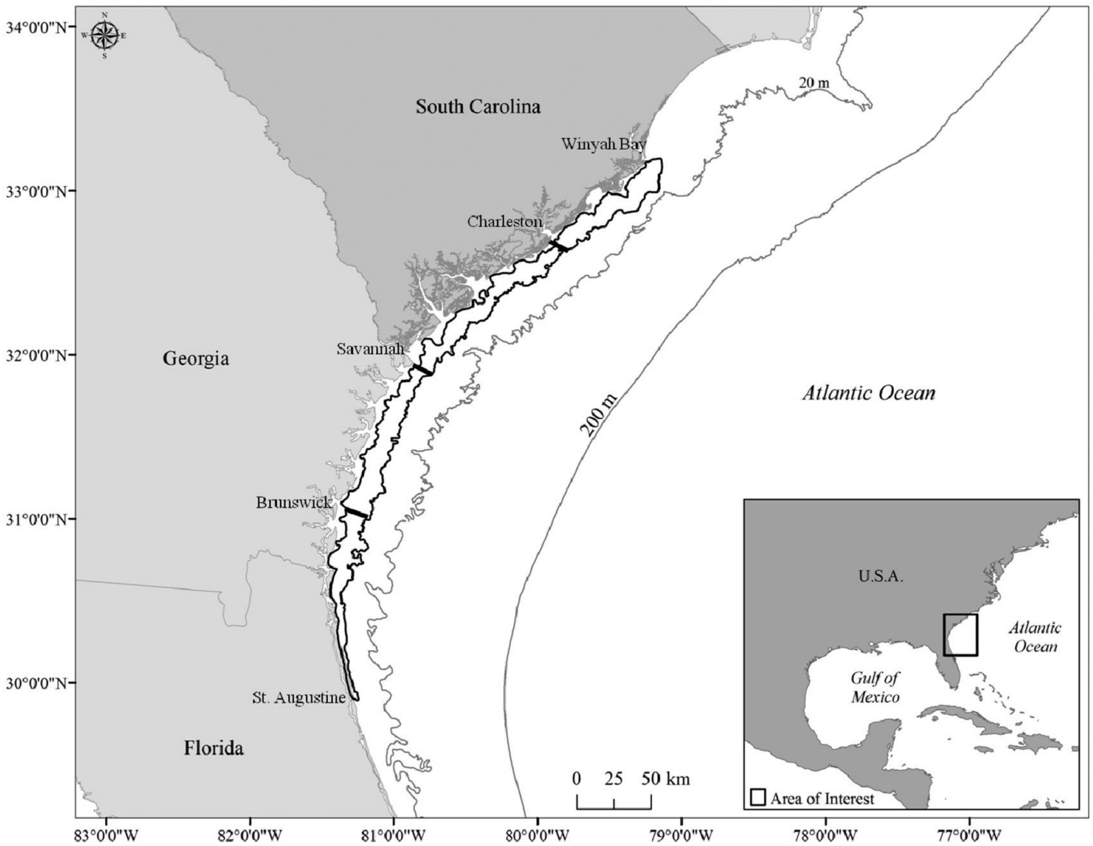

Figure 1

Map showing the location and spatial extent of the regional sea turtle trawl survey conducted in 2000–03, 2008–09, and 2011 between Winyah Bay, South Carolina, (33.1°N) and St. Augustine, Florida, (29.9°N), and the 20-m and 200-m depth contours. Thick black bars denote breaks between geographic subregions within the study area.

FL) and internally (passive integrated transponder tag TX1406L, 125 kHz, Biomark, Inc., Boise, ID) before release to assess recapture events.

Data analysis

Moran's index (ArcGIS ArcInfo Desktop, vers. 10.0; ESRI, Redlands, CA) was used to evaluate the spatial randomness of trawling events among years. Moran's index measures event similarity based on both the locations (x, y coordinates) and attribute values (year). With any set of event locations, and a single attribute, this index measures whether the location pattern is clustered, dispersed, or random on the basis of that attribute. The Moran's index value runs from +1.0 (clustering) to –1.0 (dispersion), and large or small (negative) Z scores indicate Moran's index values in the tails of the distribution and unlikely to be random.

A chi-square contingency test (significance level [α]=0.05) was performed in Minitab 15 (Minitab, Inc., State College, PA) to evaluate annual distribution among 3 types of seafloor habitat—"hard," "probably hard," and "not hard"—as determined from the co-occurrence of ≥3, 2, or ≤1 of 56 hard-bottom indicator species[2,3], respectively. Temporal trends in distribution of seafloor types were analyzed with linear regression. Sampling effort among years and subregions was also examined with chi-square analysis.

Loggerhead sea turtle catch per event (response variable) was examined with R software (vers. 2.13.0; R Development Core Team, 2011) in the context of an offset term (log of the linear distance, in kilometers, between trawl start and end locations). Catch, rather than catch rate, was analyzed given a 33% decrease in permitted bottom trawl time (and, therefore, trawl transect length) during 2008–09 relative to the other five survey

[2] Reed, J. K. 2004. General description of deep-water coral reefs of Florida, Georgia and South Carolina: A summary of current knowledge of the distribution, habitat, and associated fauna. A Report to the South Atlantic Fishery Management Council, NOAA, NMFS, 71 p

[3] VanDolah, R., P. Maier, G. Sedberry, C. Barans, F. Idris, and V. Henry. 1994. Distribution of bottom shelf habitats on the continental shelf off South Carolina and Georgia. Final Report submitted to Southeast Area Monitoring and Assessment Program South Atlantic Committee, 46 p.

years. Catch was examined annually for the overall data set and for 5-cm size classes between 40.1–45.0 cm and 100.0–105.0 cm SCLmin that had at least 100 total captured loggerhead sea turtles. For 23 turtles with posterior carapace injuries, ad hoc assignment to 5-cm size classes was made with the use of paired (SCLmin and straight-line carapace width [SCW]) measurements for loggerhead sea turtles (1230) captured in this survey. The paired measurements were used in this calculation: SCLmin=(1.42×SCW) – 10.5 (F=10,579; P<0.001; coefficient of determination [r^2]=0.90). Catch data were fitted to a negative binomial distribution and analyzed through the use of a generalized linear model with a log link function, after exclusion of 2% of attempted sampling events because of tow times (55 events) that were not ±95% of the target trawl duration (20 min in 2008–09, 30 min in all other years) or where suspect trawl start or end locations could not be resolved (42 events). Thirteen additional sampling events were excluded because data were missing for them for at least 1 of 25 model terms.

Two of the included model terms were temporal: year and time of day at the start of each trawling event (1=≤0959 h local standard time [LST]; 2=1000–1259 h; 3=1300–1559 h; 4=≥1600 h). However, two standard temporal terms (i.e., season and day of year) were not included in the model. Such temporal terms were excluded because this survey was conducted within 1 month of the summer solstice (i.e., a peak and stable photoperiod) and nearly 2 months after juvenile loggerhead sea turtles return to nearshore coastal waters in this region (Arendt et al., 2012b). Another reason for their exclusion was a spatiotemporal bias in sampling due to staggered vessel start dates.

Six spatial model terms were used. One of these parameters consisted of geographic subregions: 1=Winyah Bay to Charleston, South Carolina; 2=Charleston, South Carolina, to Savannah, Georgia; 3=Brunswick to Savannah, Georgia; 4=St. Augustine, Florida, to Brunswick, Georgia. The other spatial terms were minimum distance from shore (in kilometers) at the start of each trawling event (determined with ArcGIS ArcInfo 10.0); distance (in kilometers) and bearing (in degrees) from the closest of 31 estuary inlets within the study area; trawl transect bearing (in degrees), computed with Pythagorean theorem; and seafloor type assigned by co-occurrence of ≤1, 2, or ≥3 of 56 hard-bottom indicator species[2,3].

Six environmental parameters were measured in situ at the start of each trawling event, several of which are known to influence spatial distributions of loggerhead sea turtles in pelagic habitats (Báez et al., 2007; Mansfield et al., 2009; Kobayashi et al., 2011). Sea-surface temperature (SST, in degrees Celsius) was measured by the ship's transducer or, in 2000 and 2001, read by a digital thermometer for a bucket of surface water. Mean water depth (in meters) was recorded by a fathometer at the start and end of each trawling event, after which the relative change (in percentage) between the start and end locations was recorded. Wind velocity (in knots) and direction were recorded with a shipboard anemometer. The relative distribution of cloud cover (in percentage) across the entire dome of sky also was estimated. Wind direction was recorded as text at sea but later converted to numeric values in this manner: north (0°), north-northeast (22.5°), northeast (45°), etc. Where wind velocities were recorded as calm, wind direction was assigned to the direction recorded just before winds became calm. Hourly SST data from the buoy at Gray's Reef National Marine Sanctuary (GRNMS) (station 41008; http://www.ndbc.noaa.gov;) were used for substitutions for 539 trawling events with missing SST given ±10% agreement for 95% of 3100 paired observations from both data sets.

Seven model terms were generated through the use of external data sets and included 8-day compilations of chlorophyll-*a* (Chl-*a*, in miligrams per cubic mililiter; http://disc.sci.gsfc.nasa.gov/giovanni/overview/index.html#) at resolutions of 9 km (Sea-viewing Wide Field-of-view Sensor [SEAWIFS]; 2000–02) and 4 km (Moderate Resolution Imaging Spectroradiometer, Aqua satellite [MODIS-A]; ≥2003) for the observation closest (8.5 ±18.9 km; mean ±standard deviation [SD]) to the trawling event midpoint; daily mean and change in barometric pressure (milibars) recorded hourly at the GRNMS buoy; monthly North Atlantic Oscillation (NAO) index values from the NOAA Climate Prediction Center (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml); tide stage (0=ebb, 1=flood) and range (in meters) in water level between high and low water during the tidal event when sampling was conducted, determined from hourly data at National Ocean Service gauges near Winyah Bay, South Carolina (8662245), Charleston, South Carolina (8665530), Savannah, Georgia (8665530), and Mayport, Florida (8670870); and random scrambling of event order (H_6=2.64, P=0.852 by year) to evaluate the model (Kobayashi et al., 2011). In addition to the model and offset terms described above, null models also contained up to 4 interaction terms (mean depth vs. distance from shore; mean depth vs. distance from inlet; distance from inlet vs. distance from shore; year vs. NAO index) identified with a correlation test (Pearson's coefficient of correlation [r]>0.4) performed in R. As such, terms in the null model were analyzed in the following order: Loggerhead count=year + NAO + (*year*NAO*) + subregion + time of day + mean depth + distance from shore + trawl depth change + distance from inlet + (*mean depth*distance from shore*) + (*mean depth*distance from inlet*) + (*distance from shore*distance from inlet*) + bottom type + cloud cover + wind velocity + wind direction + daily mean barometric pressure + interdaily change in daily mean barometric pressure + bearing from inlet + tide stage + tide range + transect bearing + Chl-*a* + SST + random order + log(transect length).

Final model selection was accomplished through stepwise regression based on the lowest Akaike's information criterion (AIC) score. A chi-square analysis of deviance was performed in R to assess the statistical significance of variables retained in the final model.

Table 1

Temporal distribution of sampling effort (number of events), loggerhead sea turtle (*Caretta caretta*) captures (no. of Cc) and recaptures (by recapture year) in the sea turtle trawl survey conducted in 2000–03, 2008–09, and 2011 in a coastal foraging region in the southeastern United States.

			Recaptured							
Year	Number of events	Tagged no. of Cc	2000	2001	2002	2003	2008	2009	2011	Total
2000	621	172	0	0	1	4	0	0	0	5
2001	603	177		0	0	2	1	2	0	5
2002	684	209			1	1	0	0	2	4
2003	714	250				0	0	0	0	0
2008	589	167					0	0	0	0
2009	586	152						0	1	1
2011	410	135							1	1
Total	4207	1262	0	0	2	7	1	2	4	16

Quantile residuals (Dunn and Smyth, 1996) were then plotted against each variable to assess trends and model-assigned statistical significance of variables. Cumulative deviance attributed to all final model parameters was expressed as a percentage of null deviance to characterize the extent to which the final model accounted for catch variation. Linear regression was used to assess model fits (AIC vs. counts and SD) and annual mean modeled catch of loggerhead sea turtles. Confidence intervals ([CI], 95%) around mean catch were computed with t-statistics from Table B3 in Zar (1996).

Results

Sampling effort and catch distribution

Random sampling (Moran's Index=0.00, Z-score=0.67, P=0.501) was attempted for 4207 trawling events during 7 sampling years between 2000 and 2011. Of 1262 captured loggerhead sea turtles, 16 were captured twice during this survey (Table 1) up to 9 years later (mean ±SD=3.9 ±3.2 years). Two loggerhead sea turtles tagged during this study were recaptured by other programs (after 0.3 and 1.9 years), and 14 loggerhead sea turtles tagged by other programs (3.4 ±3.4 years earlier) also were captured in this study. No loggerhead sea turtles died during this study, and only 3 turtles required resuscitation. Six loggerhead sea turtles tagged and released in this study were subsequently (3.0 ±1.8 years later) reported as stranded dead, 5 of them on beaches adjacent to the survey area and the sixth one in the northern Gulf of Mexico.

Sampling effort was significantly different among years and subregions (χ^2_{18}=455, P<0.001). Greatest annual sampling effort occurred in 2002–03 (343–355 h; 18–19% of total) followed by 2000–01 (300–309 h; 16% of total) and then 2008–11 (194–204 h; 10–11% of total). The greatest amount of sampling effort was expended between Brunswick and Savannah, Georgia, (533 h; 28% of total), followed by Savannah, Georgia, to Charleston, South Carolina, (501 h; 26% of total), St. Augustine, Florida, to Brunswick, Georgia, (465 h; 24% of total), and Charleston to Winyah Bay, South Carolina, (404 h; 22% of total).

Loggerhead sea turtles were captured in 23% (951) of sampling events, with up to 7 individual loggerhead sea turtles captured in one sampling event. A single loggerhead sea turtle was the most common positive catch observed and accounted for 20% of sampling events in 2011 (83 of 410) to 15% of sampling events in 2009 (87 of 586); however, the ratio of zero- to single-catch events was not significantly different among years (χ^2_6=7.5, P=0.275). Double catch of loggerhead sea turtles occurred in 4% (185) of sampling events and was not significantly different among years (χ^2_6=3.1, P=0.800). Three or more loggerhead sea turtles were captured only in 1% (46) of attempted sampling events between 2000 and 2011.

Model fits

Catch rate trends were analyzed for 1227 loggerhead sea turtles captured in 4097 sampling events with complete effort and companion data. Final model AIC scores ranged from 951.0 (75.1–80.0cm SCLmin) to 5550.1 (overall; Table 2). The count of sampling events with zero turtle catches, both overall and for each of 5 prevalent 5-cm size classes, was significantly and positively associated with final model AIC ($F_{1,4}$=1123.6, r^2=1.00, P<0.001) and SD ($F_{1,4}$=1010.5, r^2=1.00, P<0.001). The overall final model explained 8.4% of deviance in the overall data set, with between 6.6% and 14.9% of deviance explained for prevalent 5-cm size classes (Table 2). In the final overall model, 12 of 25 parameters (48%) were retained, with between 6 (24%) and 12 (48%) parameters retained in the final model for prevalent 5-cm size classes (Table 3). Among parameters retained in final models, only 50% (3 of 6) to 67% (8 of 12) were deemed significant (Table 3).

Table 2

Assessment of generalized linear model fits for loggerhead sea turtle (*Caretta caretta*) catch overall and with respect to prevalent 5-cm size classes of minimum straight-line carapace length. Best model fits (12.2–14.9% of model deviance explained) were associated with the smallest and largest size classes examined, with half as much model deviance generally explained for intermediate size classes.

Model metric	Overall	55.1–60.0	60.1–65.0	65.1–70.0	70.1–75.0	75.1–80.0
AIC score, null model	5573.2	1080.7	2033.2	2285.8	1831.1	966.0
AIC score, final model	5550.1	1052.1	2004.0	2258.7	1805.5	951.0
Null model deviance	3080.8	793.6	1407.1	1514.7	1325.4	757.4
Final model deviance	2822.3	697.2	1248.8	1403.3	1238.2	644.4
Percentage of deviance explained	8.4	12.2	11.3	7.4	6.6	14.9

Catch rate influences

Geographic subregion, distance from shore, and sampling year were the only parameters retained as significant terms in all final models (Table 3). Geographic subregion was the most important parameter overall (3.9% of deviance) but was the most important observed influence on catch rates for loggerhead sea turtles that measured ≤70.0cm SCLmin, where it accounted for 3.2–7.6% of data set deviance (Table 3). Catch increased significantly ($F_{1,2}$=27.3, r^2=0.90, P=0.035; Fig. 2) between the subregion of Winyah Bay to Charleston, South Carolina, (mean ±95% CI=0.174 ±0.003 turtles per km; CV=0.24) and the subregion of Brunswick, Georgia, to St. Augustine, Florida, (0.468 ±0.013 turtles per km; CV=0.44).

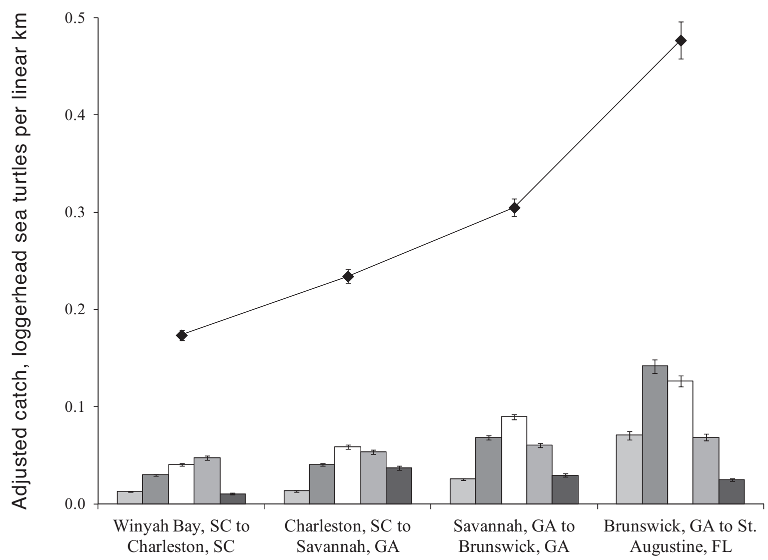

Figure 2

Spatial variability in modeled catch (mean ±95% CI) of loggerhead sea turtles (*Caretta caretta*) per linear kilometer for 4097 coastal trawling events conducted between St. Augustine, Florida, (29.9°N) and Winyah Bay, South Carolina, (33.1°N) in 2000–03, 2008–09, and 2011. The black line denotes overall catch rates. Bars denote the following 5-cm size classes of minimum straight-line carapace length: 55.1–60.0 (light gray); 60.1–65.0 (dark gray); 65.1–70.0 (white); 70.1–75.0 (medium gray); 75.1–80.0 (charcoal).

Distance from shore accounted for 1.5% of data set deviance overall, but between 0.1% and 2.5% of data set deviance among 5-cm size classes (Table 3). Catch rates decreased systematically with distance from shore (Fig. 3), with overall trends driven largely by loggerhead sea turtles that measured 60.1–70.0 cm SCLmin and captured within 5 km from shore.

Sampling year explained 0.8% of data set deviance overall and between 1.0–6.1% of data set deviance among 5-cm size classes (Table 3). Annual catch rates (sea turtles per linear kilometer) ranged from 0.256 ±0.014 (mean ±95%CI) in 2009 to 0.356 ±0.019 in 2003, but rates were not significantly different among years ($F_{1,5}$=0.0, r^2=0.00, P=0.944). Interannual differences in mean catch rates for loggerhead sea turtles that measured 55.1–75.0 cm SCLmin (Fig. 4, A and B) were not significantly different ($F_{1,5}$=0.5–4.1, r^2=0.00–0.34, P=0.098–0.500). Catch rates for loggerhead sea turtles 75.1–80.0 cm SCLmin (Fig. 4B) increased significantly ($F_{1,5}$=24.1, r^2=0.79, P=0.004) between 2000 (4, 2% of captures; CV=0.86) and 2011 (25, 19% of captures; CV=0.92).

Four terms were retained only as significant terms for a subset of all final models. The interaction between mean water depth and distance from the closest inlet was retained as a significant model term in all final models, except for the smallest (55.1–60.0 cm SCLmin) and largest (75.1–80.0 cm SCLmin) size classes evaluated, but accounted for ≤0.7% of data set deviance (Table 3). Time of day and the interaction between sampling year and the NAO index was retained as signifi-

Table 3

The influence of model terms on counts (dependent variable) of loggerhead sea turtles (*Caretta caretta*) per trawling event (offset=log[*trawl transect length*]) in the sea turtle trawl survey in a coastal foraging region in the southeastern United States. *P*-values (*=significant; chi-square) are provided for the overall data set and prevalent 5-cm size classes. The percentage (%) of explained model deviance attributed to terms retained in the final model is provided.

Model term	Overall	%	55.1–60.0	%	60.1–65.0	%	65.1–70.0	%	70.1–75.0	%	75.1 –80.0	%
Year	<0.001*	0.8	0.036*	1.7	0.798	0.2	0.022*	1.0	<0.001*	3.4	<0.001*	6.1
North Atlantic Oscillation	—	—	—	—	—	—	—	—	—	—	0.674	0.0
Year × North Atlantic Oscillation	—	—	—	—	—	—	—	—	—	—	0.018*	2.0
Subregion	<0.001*	3.9	<0.001*	7.6	<0.001*	6.3	<0.001*	3.2	0.020*	0.7	0.002*	1.9
Time of day	—	—	—	—	—	—	—	—	—	—	0.024*	1.3
Mean trawl depth	0.973	0.0	—	—	0.192	0.1	0.394	0.1	0.362	0.1	0.007*	1.0
Trawl depth change	—	—	—	—	0.129	0.2	—	—	—	—	—	—
Distance from shore	<0.001*	1.5	<0.001*	2.4	<0.001*	2.5	0.001*	0.7	0.026*	0.4	0.428	0.1
Distance from inlet	0.270	0.0	0.117	0.3	0.527	0.0	0.407	0.0	0.092	0.2	—	—
Mean depth × distance from shore	—	—	—	—	—	—	—	—	—	—	0.076	0.4
Mean depth × distance from inlet	<0.001*	0.4	—	—	0.005*	0.6	0.001*	0.7	0.003*	0.7	—	—
Distance: from shore x inlet	0.020*	0.2	—	—	—	—	0.196	0.1	—	—	—	—
Seafloor habitat type	<0.001*	0.8	—	—	0.013*	0.6	<0.001*	1.6	0.135	0.3	0.060	0.7
Cloud cover	0.113	0.1	—	—	—	—	—	—	0.123	0.2	—	—
Wind speed	—	—	—	—	—	—	—	—	—	—	0.114	0.3
Wind direction	—	—	—	—	0.134	0.2	—	—	—	—	—	—
Mean daily barometric pressure	—	—	—	—	—	—	—	—	—	—	—	—
Daily change in barometric pressure	—	—	—	—	—	—	—	—	—	—	—	—
Bearing from inlet	<0.001*	0.4	—	—	0.047*	0.3	—	—	0.003*	0.6	0.268	0.2
Tide stage	—	—	—	—	—	—	—	—	—	—	—	—
Tide range	—	—	0.699	0.0	—	—	—	—	—	—	0.008*	0.9
Transect bearing	0.021*	0.2	—	—	0.036*	0.3	—	—	—	—	—	—
Chlorophyll-a	—	—	0.216	0.2	—	—	—	—	—	—	—	—
Sea-surface temperature	0.205	0.1	—	—	—	—	—	—	—	—	—	—
Random ordering	—	—	—	—	—	—	—	—	—	—	—	—

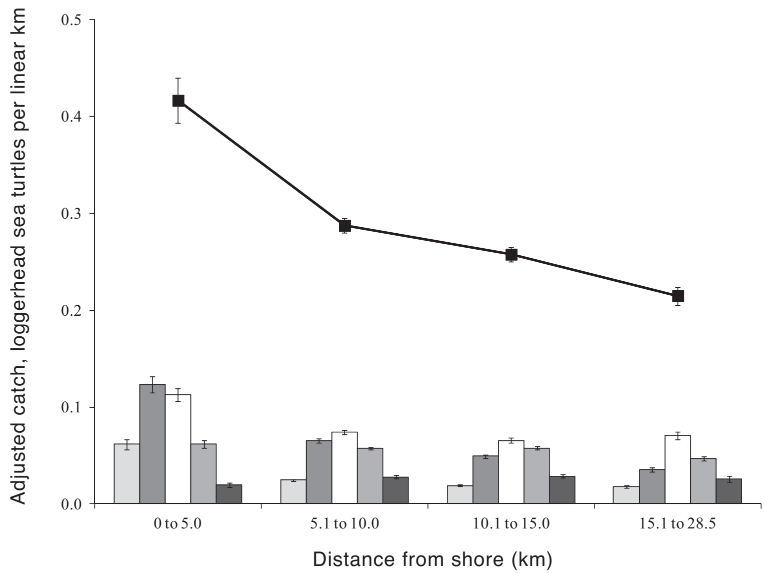

Figure 3

Modeled catch (mean ±95% CI) of loggerhead sea turtles (*Caretta caretta*) per linear kilometer with respect to incremental distances from shore during 4097 coastal trawling events conducted between St. Augustine, Florida, (29.9°N) and Winyah Bay, South Carolina, (33.1°N) in 2000–03, 2008–09, and 2011. Distance from shore was analyzed as a continuous variable, but it is plotted here as a factor for comparative purposes. The black line denotes overall catch rates. Bars denote the following 5-cm size classes of minimum straight-line carapace length: 55.1–60.0 (light gray); 60.1–65.0 (dark gray); 65.1–70.0 (white); 70.1–75.0 (medium gray); 75.1–80.0 (charcoal).

cant terms in the final model for loggerhead sea turtles 75.1–80.0 cm SCLmin and accounted for 1.3% and 2% of data set deviance, respectively (Table 3). Transect bearing was retained only as a significant model term overall and for loggerhead sea turtles that measured 60.1–65.0 cm SCLmin and accounted for ≤0.3% of data set deviance.

Seafloor type, bearing from inlet, tide range, mean trawl depth, and the interaction between distance from shore and distance from inlet were retained as a mixture of significant or nonsignificant terms in a subset of final models. Seafloor type was significant for the overall data set and for loggerhead sea turtles that measured 60.1–70.0 cm SCLmin, where it explained 0.6–1.6% of data set deviance (Table 3). Greatest catch rates were associated with habitats that were not classified as hard (Fig. 5), and these habitats represented 54 ±9% (mean ±SD) of all trawling events; probably hard and hard habitats constituted 21 ±5% and 25 ±8% of trawling events, respectively. Distributions of seafloor type differed significantly among years (χ^2_{12}=160.0, P<0.001); however, temporal trends were not detected ($F_{1,5}$=0.0, r^2=0.00, P=0.966) in the annual proportion of trawling events classified as not hard.

When retained, bearing from inlet was predominantly (3 of 4 models) significant but only accounted for 0.2–0.6% of data set deviance (Table 3). Mean trawl depth and tide range were retained only as significant terms for loggerhead sea turtles that measured 75.1–80.0 cm SCLmin, where they accounted for 1.0% and 0.9% of data set deviance, respectively (Table 3). The interaction between distance from shore and distance to inlet was significant only for the overall data set in the final model, and it accounted for 0.2% of data set deviance (Table 3). Of the remaining 13 parameters, 9 were retained only as nonsignificant terms in a subset of final models and 4 were excluded from all final models (Table 3).

Discussion

Trawling generated a large annual sample size of loggerhead sea turtles over a vast coastal expanse in a concise time frame, and this large sample size in turn enabled a reliable assessment of interannual trends. Although trawling admittedly is more expensive than other methods (Bjorndal and Bolten, 2000), it is also an effective and appropriate means for the capture of sea turtles in turbid coastal waters where sea turtles are seasonally abundant (Schmid, 1995; Casale et al., 2004). Therefore, the expense associated with collection of the data necessary to conduct stock assessments, a feat that is not possible by monitoring annual nest counts alone (Chaloupka and Limpus, 2001), is arguably an intelligent investment in the management and recovery of long-lived species. In addition to monitoring catch rates, in-water capture methods, such as trawling, enable the collection of demographic data (Roberts et al., 2005) and health assessments (Deem et al., 2009; O'Connell et al., 2010). Although such data may also be obtained from stranded animals (Monzón-Argüello et al., 2009), the opportunistic nature and reporting of stranded animals (NRC, 1990) render those data, unlike data from in-water captures, inappropriate for assessment of relative abundance trends.

A significant interannual catch trend was detected only for loggerhead sea turtles that measured 75.1–80.0 cm SCLmin, a size class that represented just 2% of loggerhead captures in 2000 but that was observed nearly 10 times as often in 2011. This size class is slightly smaller than the size at which loggerhead sea turtles reach sexual maturity in the NW Atlantic (~82 cm SCL; TEWG, 2009); therefore, increased catch rates for this size class through 2011 may not reflect mature individuals that had returned to their region of natal origin (Bowen et al., 2004). Alternatively, increased catch rates for loggerheads in this size class likely stemmed from growth of resident individuals (Mansfield et al., 2009; Arendt et al., 2012b) hatched in strong nesting years. Braun-McNeill et al. (2008) estimated that it took 17.4 years for loggerheads in the NW Atlantic to grow from 50 to 80 cm SCL, the size range associated with prevalent size classes in our study. Assuming neritic recruitment at age 11 (Conant et al., 2009) and ~50 cm SCLmin (Bjorndal et al., 2003) plus another 17.4 years (Braun-McNeill et al., 2008) to reach 80.0 cm SCL, loggerhead sea turtles of 75.1–80.0 cm SCLmin captured in 2000 likely hatched in the mid-1970s versus the mid- to late 1980s for loggerhead sea turtles in this size class captured in 2011. Given increased nest counts recorded through the 1980s (Witherington et al., 2009), increased conservation efforts in the past 3 decades, and, notably, large openings of TEDs since 2003 (Federal Register, 2003), a cohort-biased explanation seems plausible.

Stable catch rates in this study for loggerhead sea turtles that measured 55.1–75.0 cm SCLmin indicate that catch rates for loggerhead sea turtles 75.1–80.0 cm SCLmin are not likely to decline in the near term, with the assumption that high annual survival rates will continue and that catch rates observed in this study are indicative of regionwide trends. However, we also anticipate a substantial reduction in the relative abundance of the smallest loggerhead sea turtles between 2009 and 2017, consistent with a 41% decline in nest counts between 1998 and 2007 (Witherington et al., 2009) and assuming a neritic recruitment of age 11. Because a future decline in catch rates for the smallest turtles should eventually reshape future foraging ground demographic distributions, size-based monitoring is imperative. A nonsignificant decline in catch rates for loggerhead sea turtles that measured 55.1–60.0 cm SCLmin was noted between 2000 and 2003.

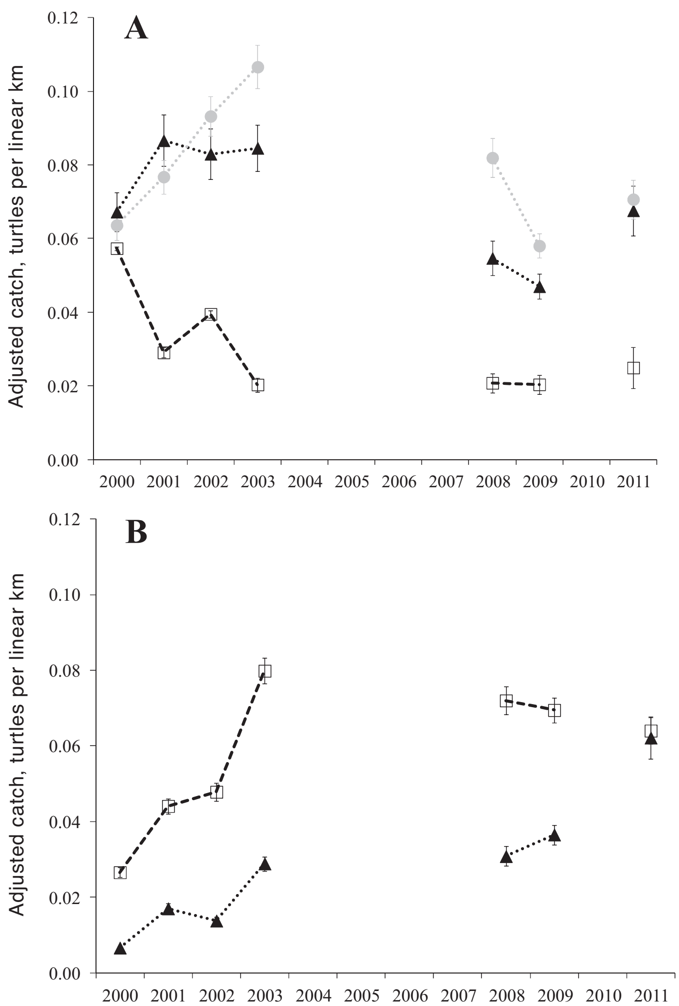

Figure 4

Annual variability in modeled catch (mean ±95% CI) of loggerhead sea turtles (*Caretta caretta*) per linear kilometer among 5 prevalent size classes recorded in a sea turtle trawl survey conducted between 2000 and 2011 in a coastal foraging region in the southeastern United States. (**A**) Interannual trends for sea turtles with minimum straight-line carapace lengths (SCLmin) ≤70.0 cm were not significantly different ($P>0.05$) for turtles 55.1–60.0 cm SCLmin (squares), 60.1–65.0 cm SCLmin (triangles), or 65.1–70.0 cm (circles). (**B**) Interannual trends for the largest loggerhead sea turtles were not significantly different ($P>0.05$) for turtles 70.1–75.0 cm SCLmin (squares) but were significantly different ($P=0.004$) for turtles 75.1–80.0 cm SCLmin (triangles).

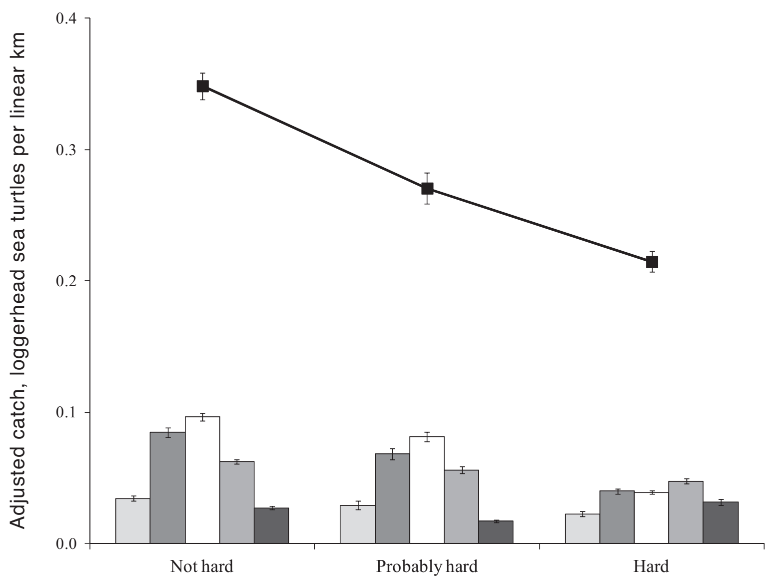

Figure 5

Modeled catch (mean ±95% CI) of loggerhead sea turtles (*Caretta caretta*) per linear kilometer with respect to type of seafloor habitat during 4097 coastal trawling events conducted between St. Augustine, Florida, (29.9°N) and Winyah Bay, South Carolina, (33.1°N) in 2000–2003, 2008–2009, and 2011. Seafloor type was classified as "hard" if ≥3 co-occurring indicator species were collected during the trawling event but classified as "probably hard" if only 1 or 2 indicator species were collected. The black line denotes overall catch rates. Bars denote the following 5-cm size classes of minimum straight-line carapace length: 55.1–60.0 (light gray); 60.1–65.0 (dark gray); 65.1–70.0 (white); 70.1–75.0 (medium gray); 75.1–80.0 (charcoal).

However, atypically high catch rates for this size class in 2000 were attributed to strong Gulf Stream intrusion across the continental shelf (evidenced by large mats of the brown macroalgae *Sargassum* and "tar ball" deposits on South Carolina beaches; senior author, pers. observ.). Between 2003 and 2011, catch rates for this size class remained relatively stable; therefore, although we remain hopeful that this trend will persist, we urge attentive monitoring of catch rates for this size class as a high priority throughout the region through at least 2017.

Even stable catch rates between 2000 and 2011 are encouraging for recovery of this species. Standardized catch rates (i.e., turtles per 30.5 net-hour) calculated by Maier et al.[4] for this study in 2003 (the year of the highest catch rates in this study) were 40 times greater than catch rates in coastal surveys in the South Atlantic Bight (SAB) from 1950 to 1976 (Bullis and Drummond, 1978) and 13 times more than rates reported for the SAB shrimp fishery in the 1970s (Henwood and Stuntz, 1987). Although historical data sets were collected by fishery-dependent means versus fishery-independent means in this study, the magnitude of increases cannot solely be explained by subtle differences in sampling gears or designs. Increased catch of loggerhead sea turtles also is reported elsewhere in this region (Ehrhart et al., 2007; Epperly et al., 2007; Arendt et al., 2012a), affirming historic increases in regional relative abundance of loggerhead sea turtles.

The inability to detect a significant overall trend generated over a span of more than a decade illustrates the long-term commitment needed to assess relative abundance trends for long-lived species, as well as the importance of size-based assessments of such trends. The inability to detect significant trends also reflects autocorrelated increases in variance and catch rates. As the ratio of catch to noncatch changes significantly in a data set laden with zero values, data set variance also increases, thereby confounding the ability to detect trends, unless catch rates decrease with time. This relationship also occurs independently of whether catch rates increase as a result of true increases in popula-

[4] Maier, P. P., A. L. Segars, M. D. Arendt, J. D. Whitaker, B. W. Stender, L. Parker, R. Vendetti, D. W. Owens, J. Quattro, and S. R. Murphy. 2004. Development of an index of sea turtle abundance based upon in-water sampling with trawl gear. Final Project Report to the National Marine Fisheries Service, National Oceanographic and Atmospheric Administration, grant no. NA07FL0499, 86 p.

tion abundance or simply from aggregation of turtles in an area at the time of sampling. Nevertheless, because in-water studies can provide more temporally refined indications of pending nesting recruitment than nesting beach surveys alone, we encourage further in-water studies. As evidenced by this study and those published by Epperly et al. (2007), Pons et al. (2010), and Murray (2011), even zero-rich data sets (for which, currently, there are no alternatives for in-water sea turtle data), when analyzed with the appropriate statistical technique (Maunder and Punt, 2004), are valuable for assessments of temporal trends. This approach implies, of course, that the trend attributes can be adequately explained and that high zero catches do not reflect poor survey design.

Despite consistency in model terms affiliated with model deviance, very little model deviance was actually explained. The modest amount of model deviance explained likely stemmed from random sampling conducted in an open marine system where juvenile loggerhead sea turtles may not be randomly distributed. Specifically, nonrandom distribution is suggested by site fidelity documented by telemetry studies in estuarine (Byles, 1988; Morreale, 1999; Avens et al., 2003; Mansfield et al., 2009) and coastal (Renaud and Carpenter, 1994; Arendt et al., 2012b) habitats. Habitat preferences would seem a likely explanation for nonrandom distributions, particularly given the suggestion by Hopkins-Murphy et al. (2003) that loggerhead sea turtles associate with dense, live-bottom habitats. Unfortunately, dense, live-bottom habitats are not conducive to trawling operations and, as such, these habitats were avoided where possible in this study. Furthermore, use of large-mesh trawl webbing and mud rollers on the trawl foot rope was included to minimize the collection of sponges and gorgonians whose collection is needed to distinguish probably hard and hard habitats from not hard habitats. Nevertheless, nearly half of sampling events occurred where habitats were characterized as probably hard or hard, and, in contrast to the suggestion by Hopkins-Murphy et al. (2003), catch rates from these sampling events were significantly more reduced than rates from not hard habitats. Seafloor type was either excluded or retained as a nonsignificant term in half of the final models. However, in the absence of data on gear efficiency and performance in these different habitats, it is not possible to rule out the importance of habitat features on spatial distribution patterns at this time.

Four model parameters (geographic subregion, distance from shore, seafloor type, and year) consistently accounted for at least two-thirds (and upwards to 97%) of explained model deviance, and different contributions were associated with each parameter among the various size classes examined. In pelagic habitats, environmental parameters, such as temperature, Chl-*a*, and mesoscale eddies, influence the spatial distribution of loggerhead sea turtles (Mansfield et al., 2009; Kobayashi et al., 2011). However, SST and Chl-*a* each were retained only as a nonsignificant term in just one final model in this study. This observation is in line with localized distribution patterns reported by Arendt et al. (2012b), an outcome that would have been expected to be more variable if spatial distributions fluctuated in response to fine-scale hydrographic changes. Hydrographic conditions can create density gradients that are known to greatly influence loggerhead sea turtle distributions in the winter (Epperly et al., 1995b) but are less likely to occur during the 2 months surrounding the summer solstice, as well as where this study was conducted. As noted by Atkinson et al. (1983), "The large heat capacity of water insures a highly damped response to daily air temperature cycles, but cycles at seasonal and inter-annual time scales have a large effect. Similar arguments apply to the inner shelf salinity field, which is controlled by seasonal and inter-annual cycles of river discharge." Accordingly, when coupled with prevalent southwesterly winds, excessive freshwater runoff in spring 2003 set up a coastwide cold-water upwelling event (see discussion in Maier et al.[4]). Concurrent with altered circulation patterns, the greatest number of captures (and recaptures) of loggerhead sea turtles occurred in 2003.

Conclusions

This study is the first to report on coastal loggerhead sea turtle catch rates in a large and central portion of one of the most important foraging grounds for this species in the NW Atlantic basin (Bowen et al., 2004). Our inability to detect a significant trend among annual catch likely was the result of the short duration of our study relative to the life history of this species, and simultaneous increases in variance concurrent with increased catch rates. Stable to increasing catch for loggerhead sea turtles that corresponds with maturing or mature individuals is encouraging for continued recovery of this threatened species in the NW Atlantic, a population that fares better than most populations of this globally distributed species (Wallace et al., 2010b). Regionally, the data presented herein begin to address one of 3 demographic recovery criteria that stipulate that increases in the in-water abundance of juvenile sea turtles must occur throughout a network of monitoring sites for at least one generation (NMFS and USFWS, 2008).

Analysis of trawl data previously has received mixed reviews (Bjorndal and Bolten, 2000), primarily because of nuances specific to data sets (e.g., a single fishery-dependent data set collected at a single location after perceived historic stock decimation). The randomized sampling design employed in this study minimized temporal and spatial bias and maximized temporal and spatial coverage. Randomized sampling design increased the probability that observed catch was proportional to actual abundance, rather than hyperstable, which could have resulted from intensely sampling areas of high abundance (Hilborn and Walters, 1992). Given that a wide range of sea turtle sizes were captured, we also do not suspect that data reported herein represent a hyperdepleted scenario, where only a portion of the population is vulnerable to capture (Hilborn and Walters, 1992). As such, the data presented herein support the use of trawl survey data to assess abundance trends for sea turtles, at least in habitats where potential damage to the seafloor or to the sampling gear itself does not preclude the use of such surveys. In areas where dense, live bottom occurs, alternative sampling methods would be required; within the geographic region associated with this study, such alternative methods could include visually sampled transects, given increased distribution of live-bottom habitats farther from shore (Van Dolah et al.[3]) where underwater visibility is improved.

Provided that sea turtle capture rates are expressed relative to a standardized and robust effort term (such as linear kilometer used in this study), comparisons among habitats and sampling methods should still be valid. Furthermore, given the large size distribution of loggerhead sea turtles captured in this study, where dense live bottom was not routinely sampled, evaluation of size-based habitat preferences is a salient management need. We, therefore, recommend that the data collection and analytical techniques presented herein be expanded to foraging grounds conducive to trawling across geographically diverse areas. This action would allow the most complete data on in-water catch to be considered with nest trend data, and in turn would promote comprehensive decision-making regarding the management of protected sea turtle species in neritic habitats.

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