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Determining abundance and survival of sea turtles at foraging areas: a logistically feasible field approach using multiple analytical methods

Allen M. Foley[1,*], Blair E. Witherington[2], Trent L. McDonald[3], Shigetomo Hirama[4], Robert F. Hardy[5,7], Barbara A. Schroeder[6,8]

[1]Florida Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Jacksonville, Florida 32218, USA

[2]Inwater Research Group, Inc., Jensen Beach, Florida 34957, USA

[3]McDonald Data Sciences, Laramie, Wyoming 82070, USA

[4]Gainesville Field Laboratory, Florida Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Gainesville, Florida 32601, USA

[5]Florida Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, Florida 33701, USA

[6]Office of Protected Resources, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, United States Department of Commerce, Silver Spring, Maryland 20910, USA

[7]*Present address:* Office of Protected Resources, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, United States Department of Commerce, Silver Spring, Maryland 20910, USA

[8]*Present address:* Florida Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Jacksonville, Florida 32218, USA

ABSTRACT: The importance of monitoring long-term trends in abundance and survival of sea turtles at foraging areas has been asserted for decades, but few studies have accomplished this. We report on 19 yr (2000–2018) of monitoring these trends in Florida Bay (Florida, USA) and present the corroborative results of 3 analytical methods as an example of a successful, cost-effective, and logistically feasible approach for monitoring sea turtle abundance and survival in coastal foraging habitats. We conducted transect surveys for loggerheads *Caretta caretta* and green turtles *Chelonia mydas* annually over 4–10 d periods, with a mean total transect length of 200 km yr^{-1}. Loggerheads were primarily large immatures and adults, whereas all green turtles were immatures. Distance sampling models estimated an annual mean of 537 loggerheads and 378 green turtles. Annual numbers of green turtles rose from <100 to >600 over the 19 yr period, while no trend was observed for loggerheads. Concurrently, we captured loggerheads 1320 times, representing 886 individuals. A closed mark–recapture (MR) model and spatially explicit open mark–recapture (SMR) models estimated annual means of 568 and 597 loggerheads, respectively. We observed no change in annual abundance estimates based on trend lines, even when adults and immatures were considered separately by sex. As determined by the SMR, the mean annual survival of adult and immature female loggerheads was ≥0.90, whereas annual survival of immature male loggerheads was 0.75. These survival estimates for Northwest Atlantic loggerheads are the first based on a foraging area study.

KEY WORDS: Loggerhead · *Caretta caretta* · Green turtle · *Chelonia mydas* · Abundance · Survival · Distance sampling · Spatially explicit mark–recapture · Schnabel method · Foraging area

1. INTRODUCTION

Conserving imperiled species requires information on population change (Campbell et al. 2002). Among the most telling metrics affecting population and species recovery are changes in abundance and in vital rates such as survival (Fox 1993). These changes foretell declines, monitor recovery

*Corresponding author: allen.foley@myfwc.com

progress, and inform conservation actions (Burgman et al. 1993).

Sea turtles are long lived, late-maturing marine animals with iteroparous reproduction and extensive breeding migrations. Their life history is characterized by migratory shifts among developmental foraging habitats; however, within habitat locations, sea turtles exhibit fidelity to home foraging areas (Musick 1999). Measuring demographic parameters is often challenging because most life stages occur in marine habitats that can be difficult to access and survey. In addition, sea turtle population changes become biologically significant only after temporal trends have spanned decades due to delayed maturation and long reproductive life spans (Crouse et al. 1987, Heppell et al. 1999, 2003, National Research Council 2010).

Sea turtles are most accessible for study when they come ashore to nest. As a consequence, nearly all long-term abundance and survival data come from nesting beach studies. Nest counts represent an index of the number of annual breeding females (Witherington et al. 2009, Ceriani et al. 2019), and mark–recapture (MR) of these females provides data for survival estimates (Heppell et al. 2003, Pfaller et al. 2018). Nest-count trends are the most common data in sea turtle species assessments (National Research Council 2010, Hays et al. 2024), extinction risk assessments (Ceriani & Meylan 2017), and recovery plans (NMFS & USFWS 2008). Studies conducted on sea turtle nesting beaches also provide estimates of hatchling production (Brost et al. 2015) and initial hatchling survival (Triessnig et al. 2012, Erb & Wyneken 2019).

Nesting beach studies are necessary and informative, but they do not account for all life stages. Data on immature sea turtles are especially valuable for population assessments because they can help predict population changes not yet reflected in adult assemblages (Bjorndal and Bolten 2000). Estimating abundance and survival of life stages on foraging grounds have been urged for decades (NOAA & DOI 2023). However, challenges associated with these studies are significant and include the ability to consistently and safely sight and capture turtles, complicated logistics, vessel availability and reliability, and generally high cost. Movements of sea turtles also complicate studies at foraging areas due to potential emigration and immigration, which are difficult to assess. Moreover, these studies seldom extend past a decade, which represents less than a quarter of a generation for sea turtles such as loggerheads *Caretta caretta* (NMFS & USFWS 2008).

We are aware of only 6 studies of sea turtles at a foraging area lasting longer than a decade that report on abundance and survival (Bjorndal et al. 2005, Casale et al. 2007, Patrício et al. 2011, Arendt et al. 2012a, Colman et al. 2015, Limpus & Coffee 2019), only one of which included loggerheads in the Northwest Atlantic (Arendt et al. 2012a). These studies all employed in-water sampling and persistent identification tags that allow MR analyses. MR analyses use data from capture events (identity and date) to estimate detection probability, abundance, and survival, under the assumption that capture probabilities have been modeled accurately (Kendall et al. 1997, McDonald & Amstrup 2001, Barker et al. 2004).

Herein, we report on a 19 yr study (2000–2018) of loggerheads at a foraging area in southern Florida (USA). These loggerheads are part of the Northwest Atlantic Distinct Population Segment (DPS), which is listed as Threatened under the US Endangered Species Act. The Northwest Atlantic is the largest of the 9 global DPSs (Ceriani et al. 2019). Nest counts on Florida beaches, which host 89% of nests in this DPS (Ceriani & Meylan 2017), showed no significant trend during our study period (Ceriani et al. 2019).

Our primary objectives were to estimate the abundance of foraging loggerheads and green turtles *Chelonia mydas* and to estimate survival rates of loggerheads. We collected encounter (sighting) data for both species and estimated annual abundances using line-transect distance sampling methods (Buckland et al. 2015). We did not capture green turtles, but we regularly captured loggerheads, and information from these capture events allowed us to estimate loggerhead abundance using 2 MR methods. We used intra-annual resights of temporary numerical marks to estimate a closed MR model (Schnabel method; Schnabel 1938, Chao & Huggins 2005). We used identities and location information from inter-annual loggerhead captures to estimate a spatially explicit open MR model (Borchers & Efford 2008, Borchers 2012). The latter method also estimated survival by sex and maturity status.

We present these field and analytical methods as an example program for monitoring sea turtle abundance and survival in coastal foraging habitats. Logistically feasible field methods rarely permit multiple abundance estimates. This feature makes our approach robust and desirable for several reasons. Investigators can compare and corroborate estimates from independent analytical methods. Estimates from at least 1 analytical method can be obtained even when the assumptions from other methods are questionable. Lastly, abundance estimates from 2 analytical methods (line-transect and closed MR) can be obtained after a single sampling session, while age-

and sex-specific abundance and survival estimates can be obtained by a third method (open MR) after at least 3 field-sampling sessions.

2. MATERIALS AND METHODS

2.1. Study area

Florida Bay is a shallow, subtropical estuary at the southern tip of the Florida peninsula and is located between the Everglades freshwater wetlands and the chain of islands known as the Florida Keys. The waters in Florida Bay are compartmentalized by partially submerged banks and islands, which cause damping of diurnal and semidiurnal tides and pronounced gradients in salinity and turbidity (Fourqurean & Robblee 1999).

Selection of our study area and survey and capture methodologies were informed by approximately 10 yr (beginning in 1990) of reconnaissance within the waters of Florida Bay and the nearby Florida Keys. This period included visual sea turtle searches from small vessels and both tangle-net and hand captures. Frequent observations of green turtles *Chelonia mydas* and loggerheads *Caretta caretta* and regular recaptures of individual loggerheads combined with logistically feasible accessibility supported our choice of a study area centered on the Lower Arsnicker Keys in southwestern Florida Bay, within the boundaries of Everglades National Park. This location also represents the center of sea turtle sightings by Witzell & McCoy (1995) during aerial surveys in 1984 and 1985. For the present work, our study area encompassed 21.86 km^2 of waters near the Arsnicker Keys, about 10 km north–northwest of Long Key (latitude range 24.885–24.934° N and longitude range 80.792–80.854° W, Monroe County; Fig. 1).

The study area is a basin largely bounded by carbonate mud banks. Depth ranges from 0.5 to 2.5 m.

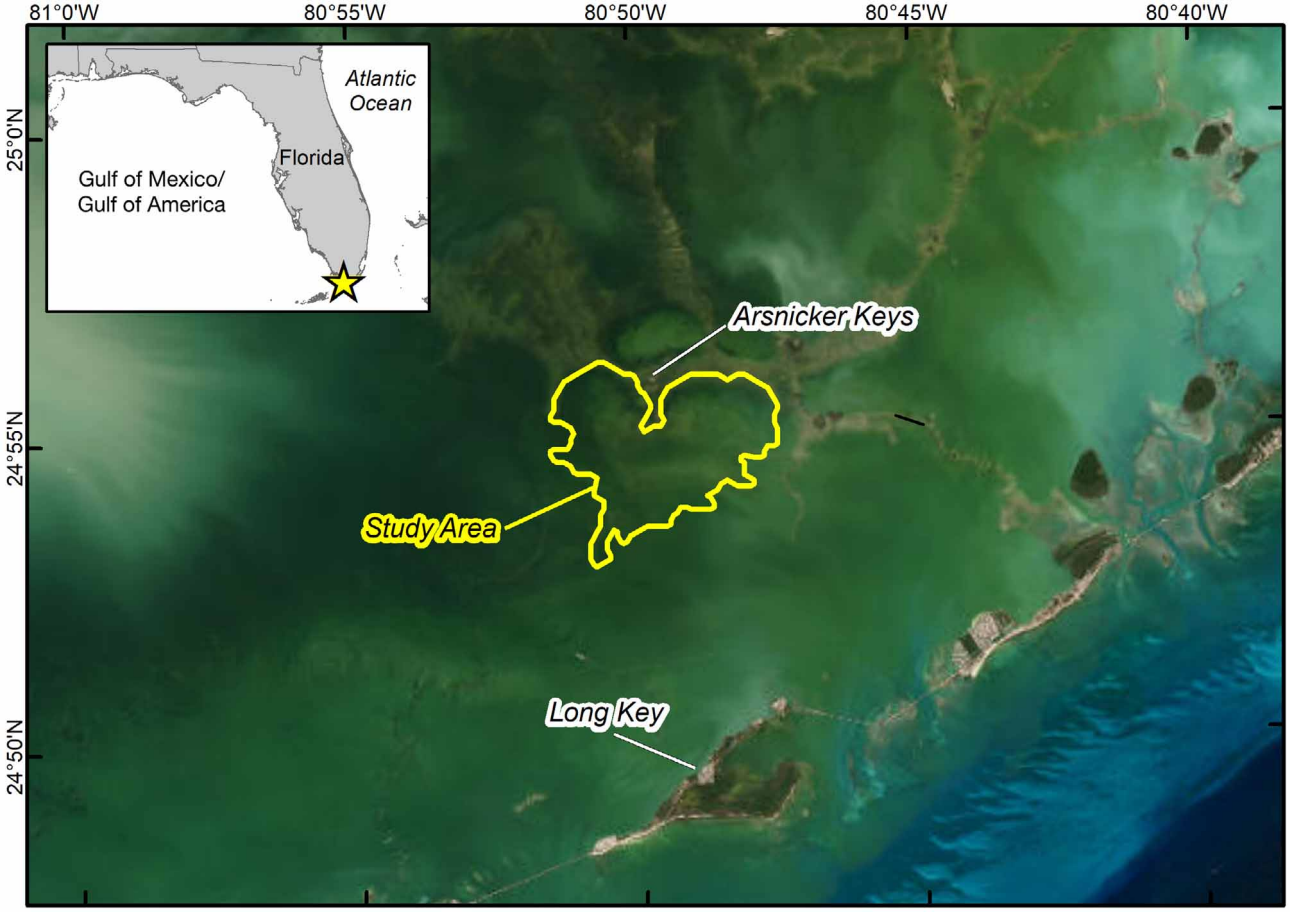

Fig. 1. Location and extent of the study area (yellow outline) in southwestern Florida Bay, Florida, USA. Republished from Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community under a CC BY license, with permission from Esri, original copyright 2022

During our early summer study period, salinities average 35–40 ppt and water temperatures average 28–31°C. The benthic habitat mostly consists of a hard-bottom community of sponges and soft corals, with mixed macroalgae and sparse seagrass (primarily *Thalassia testudinum*), although areas of continuous seagrass are also present. Water clarity was usually sufficient to clearly see the bottom, and work was usually not conducted in areas where the bottom was not visible. The climate is tropical with 2 predominant seasons (northern hemisphere summer and winter).

Habitat characteristics appeared unchanged for most of the study period. However, an extensive cyanobacterial bloom began in late 2013 and continued until early 2014. The algal bloom resulted in deep green, turbid water and a die-off of sponges and other invertebrates (Duermit-Moreau et al. 2022).

2.2. Transect surveys and sea turtle captures

During annual field sessions, we conducted haphazard unmarked nonlinear transect (HUNT) surveys (Bresette et al. 2010) for both loggerheads and green turtles with an aim toward maximizing captures of loggerheads. We used 2 flat-bottomed boats (6.5 m), each with 2 dedicated observers standing on top of a 2 m high platform. Each of these observers searched for turtles on opposite sides of the boat while the boat traveled slowly (generally <8 km h^{-1}). At least one other observer on the bow focused on the area directly ahead of the boat (on the transect line). We used a Global Positioning System (GPS) unit to determine the location coordinates at the beginning and end of each transect and at approximately 40 s intervals during searches. We defined on-transect search mode as a period when the observers were properly stationed and observing. When a turtle was sighted during on-transect search mode, the species, time, position of the boat, and distance of the turtle perpendicular to the transect line were recorded. If the sighted turtle was a loggerhead, we ended the on-transect search mode and focused on capturing the turtle. A snorkeler positioned on the bow dove near the turtle and attempted to capture it by hand. We also captured some loggerheads that were not sighted during on-transect search mode and defined these as off-transect captures.

We lifted captured turtles into the boat over a smooth, rounded dip in the boat's gunnel, placed the turtle on a padded mat, and kept it shaded and wet. After scrubbing the injection site with povidone-iodine and 70% alcohol, we collected a 5–6 ml blood sample from the dorsal cervical sinus using a 22-gauge, 3.8 cm vacutainer needle into a 6 ml heparinized vacutainer tube. The blood was centrifuged on board, and the plasma and red blood cells were placed into separate cryotubes and stored in an on-board liquid nitrogen tank for testosterone and genetic analyses. We measured straight-line carapace length (SCL) from the nuchal notch to the pygal tip and tail length from the caudal edge of the plastron to the tail tip. We weighed, externally examined, photographed, and checked all captured turtles for existing flipper tags and internal passive integrated transponders (PIT tags).

If a captured turtle had not been previously tagged, we applied 1 inconel metal tag to the proximal trailing edge of each front flipper. We injected a PIT tag into the dorsal surface of the front flipper in the flexor carpi ulnaris muscle using a sterile hypodermic needle. In both cases, prior to tagging, we scrubbed the tagging site once (metal flipper tags) or twice (PIT tags) with 10% povidone-iodine and 70% alcohol. Prior to release, we wrote a unique number on the turtle's carapace with a white nontoxic Markal Paintstik® livestock marker to enable identification of recently captured turtles from a distance to avoid capturing or counting an individual more than once within the sampling session. We minimized double-counting green turtles by excluding turtles recognized from previous recent sightings using unique physical characteristics. Loggerheads were released at the site of capture, usually within 30 min of capture.

2.3. Determination of sex and maturity status

We assigned sex based on one of the following: tail length, gonad examination, plasma testosterone concentration, a combination of tail length and SCL, or a documented nesting emergence. The tail length used to indicate a male was ≥30 cm (the longest tail length of a documented female loggerhead in our study was 25 cm). Individuals with an SCL ≥85.0 cm and a tail length ≤26 cm were identified as female if we could not determine sex by another method. This criterion was based on our finding that no male loggerhead from our study area had an SCL ≥85.0 cm and a tail length ≤26 cm.

We determined plasma testosterone concentrations using either a radioimmunoassay (RIA, 2000–2012; Owens et al. 1978, Braun-McNeill et al. 2007) or an enzyme-linked immunosorbent assay (ELISA, 2013–2018; Allen et al. 2015). A loggerhead was identified as female if plasma testosterone was ≤540 pg ml^{-1} (RIA) or ≤292 pg ml^{-1} (ELISA) and male if SCL <80 cm

and testosterone ≥794 pg ml^{-1} (RIA) or ≥555 pg ml^{-1} (ELISA). The size filter was intended to exclude adult or pubescent females with high testosterone. These ranges were based on the testosterone concentrations of 74 immature loggerheads of known sex from our study area (Table S1 in the Supplement at www.int-res.com/articles/suppl/esr01502_supp.pdf).

We categorized any male loggerhead with a tail length ≥36 cm as an adult because all males with mature gonads that we examined via laparoscopy had a tail at least this long. We categorized any male loggerhead with a tail length <36.0 cm as immature. We categorized a female as an adult if it was documented on a nesting beach or if gonadal examination indicated maturity. We categorized other females with an SCL ≥86.4 cm as adults because the mean SCL of known adult females from our study area was 86.4 cm (N = 43; range = 75.7–96.4 cm). We categorized all other loggerheads with SCL <86.4 cm, whether female or of unknown sex, as immature.

We recognized that maturity classification based on size is not exact because size at maturity is variable (Miller 1997). The open MR method we applied required us to assign sex and age to every capture event. Despite some inaccuracy, our classification scheme based on size represented the best method for balancing specificity and sensitivity.

2.4. Abundance estimates

2.4.1. Distance sampling

We collected line-transect distance sampling data during HUNT surveys that allowed us to develop detection functions for both loggerheads and green turtles. Observers estimated the turtle's initial sighting location perpendicular to the transect line (boat course) using the approximate length and width of the boat (7 and 3 m, respectively) as a reference (visual estimate, recorded to the nearest meter). Observers also used a digital inclinometer (Johnson Level & Tool, 40-6060) to estimate the angle (θ) from the observer's eye to the water's surface at the spot the turtle was sighted when that spot was perpendicular to the transect line. For these inclinometer estimates, we calculated the perpendicular distance of the turtle from the transect line by multiplying the tangent of θ by the distance from the water to the observer's eye (typically, 3–4 m). We collected perpendicular distances by both methods during 2011–2018. The median distances differed by less than 1 m (4.0 vs. 4.7 m, visual vs. inclinometer) and the dispersion of the distributions were similar (standard deviation, 20.9 vs. 32.0 m, visual vs. inclinometer). Mean distances (9.3 vs. 12.5 m, visual vs. inclinometer) differed by 3.2 m, largely because of a small number of outliers in the inclinometer records. We regressed the visual estimates onto inclinometer estimates and found a significant linear relationship ($r^2 = 0.6144$, $p < 0.001$). We used the visual estimates in subsequent calculations because they exhibited a lower standard deviation.

We pooled distance sampling data across 2011–2018 and estimated a single distance function for each species. We justified using a single distance function given the following: (1) pooling increased the precision of the estimates (n pooled distances = 609 for loggerheads and 430 for green turtles), (2) abundance estimates from annually estimated detection functions, when sample size allowed, were well within the confidence intervals (CI) of abundance estimates computed by combining distances over years, (3) search methods (e.g. boat speed, observer platforms, observer experience) remained constant during the entire study, (4) low numbers were detected during a few years, and (5) annual differences in sightability would likely be due to weather conditions that we accounted for in the combined distance function. We did not collect distance sampling data during 2000–2009; however, given the annual consistency of the survey methodology, we applied the detection function determined for 2011–2018 to observations for the earlier period.

We examined the effects of 2 weather covariates (wind speed and percent cloud cover, both averaged over half-day intervals) on sightability. Weather data were obtained from NOAA (NDBC 2022a,b). We classified wind speed into 4 increments: <17.5, 17.5–34.9, 35–49.9, and ≥50 km h^{-1} and cloud cover into 4 increments: <20, 20–44, 44.1–65.9, and ≥66%. We examined the fit of half-normal, negative exponential, and hazard rate distance functions (Buckland et al. 2015) with and without the single and combined weather covariates. We estimated all distance functions using the 'distEstim' function in the R package 'Rdistance' (McDonald et al. 2023). We excluded observations beyond the 95th quantile of estimated distances (42 m for loggerheads and 15 m for green turtles) because such long distances are known to cause instability in distance models (Buckland et al. 2015). Akaike's information criterion corrected for small sample size (AICc) ranked the fit of the hazard rate function above that of the half-normal and negative exponential functions. AICc also estimated the fit of models with and without weather conditions to be equivalent. Therefore, we used the hazard rate dis-

tance function without weather covariates for all subsequent calculations.

For each species and year, we computed the density of turtles (D) as:

$$D = n[2L(ESW)]^{-1} \quad (1)$$

where n is the number of observed turtles, L is the total length of transects, and ESW is the effective strip half-width derived as the area under the estimated detection function from 0 to the upper truncation distance (Williams et al. 2002; 42 m for loggerheads and 15 m for green turtles). We assumed perfect detection on the transect (i.e. $g(0) = 1$) because observer locations and clear water allowed observers to view the full water column ahead of the vessel. We estimated annual abundance (N) within the study area as:

$$N = D(a) \quad (2)$$

where D is turtle density and a is the size of the study area (21.858 km^2).

We computed CI for N and D by bootstrap resampling individual transects with replacement within year. Once resampled, we combined year to estimate a common bootstrap distance function. We used the common distance function to estimate annual density and abundance from the bootstrap data. After 500 bootstrap iterations, we computed 95% bootstrap CI using the bias-corrected and accelerated method (Manly 1997).

2.4.2. Closed MR estimates (Schnabel method)

We estimated annual loggerhead abundance using the Schnabel method (Schnabel 1938), which is an intra-annual closed population MR method. We assumed separate capture sessions for each day of sampling and assumed a closed population (i.e. no deaths, births, immigration, or emigration) during our annual sampling period (4–10 d).

As described previously, we marked the carapace of every captured loggerhead with a large, white number. These marks lasted only a few weeks; hence, marked individuals lost their identifying numbers before the next annual sampling session. When we sighted a carapace-marked loggerhead, we noted the date, location, and carapace number. If we sighted an unmarked loggerhead, we attempted to capture and mark the turtle. For this analysis, we only used the first resighting of an individual no sooner than the day following marking.

We estimated abundance (N) using the Schnabel estimator, modified slightly to reduce bias when marking <10% of the population. Our Schnabel estimator was:

$$N = \Sigma(C_d M_d)(\Sigma R_d + 1)^{-1} \quad (3)$$

where C_d is the total number of loggerheads encountered (captured or only sighted; unmarked or marked) on day d of the annual sampling effort, M_d is the cumulative number of loggerheads marked and released prior to day d, and R_d is the number of loggerheads marked on a previous day that were sighted on day d. This estimator assumed equal probability of encounter among individuals within a season, and no behavioral changes in response to capture. Both ($C_d M_d$) and R_d were summed over the day we conducted field sampling during that year. We estimated 95% CI for N using the lower and upper 95% quantiles from a Poisson frequency distribution, where mean ΣR_d is the number of observed loggerheads (Krebs 2014).

2.4.3. Spatially explicit MR model

We estimated loggerhead abundance and apparent survival rate by sex and maturity status using a spatially explicit open MR (SMR) model (Borchers & Efford 2008, Chandler & Royle 2013, Royle et al. 2014). SMR models use both capture locations and search locations to inform estimates of capture probability, which inform and improve estimates of abundance and survival.

We superimposed search effort over a grid of 100 m hexagons (measured side-to-side) in the study area. We considered hexagons to be virtual traps where turtles were captured, and we assigned each capture location to the hexagon where it occurred (Borchers 2012; traps; Fig. S1). For each year, we considered a hexagon to be active when it contained search effort and inactive when it did not. Active hexagons could contain captures of multiple individuals during a single year, but no individuals were captured more than once during any year. The set of active traps varied annually according to search effort locations.

We required a determination of sex for all individuals in the spatially explicit model. We were able to determine sex for the vast majority of individuals (828 of 886, 93.5%), but we could not determine sex for a subset of immature turtles. We randomly assigned sex to these immature individuals (N = 58) based on the sex ratio of the remaining immature individuals (N = 673).

For modeling, we classified the individual capture histories into 4 groups based on sex and maturity status (adult female, adult male, immature female, immature male; see Section 2.3). We estimated the year that immature turtles transitioned to maturity by building a logarithmic growth model for SCL between captures. We applied the growth model to estimate the year in which an immature turtle's SCL exceeded the sex-specific average SCL thresholds computed for confirmed adult turtles. Our logarithmic growth model regressed the differences in SCL among repeated captures of the same turtle onto the logarithm of time between captures and SCL at the previous capture (Fig. S2). The average SCL was 86.4 cm for adult female loggerheads and 88.4 cm for adult male loggerheads. We censored immature turtle capture histories (removed them from the immature population) in the year that their estimated SCL exceeded 86.4 cm if female or 88.4 cm if male. If we recaptured a censored immature after its censor year, we re-started its capture history as an adult in that year.

We developed separate SMR models for all 4 loggerhead sex and maturity status combinations to produce annual estimates of both abundance and survival. These models assumed every individual had a fixed activity center, which was estimated by the model using capture locations. The model assumed that the probability of capturing a turtle in a specific hexagon declined with increasing distance from the hexagon to the turtle's activity center.

We estimated the SMR models using the 'openCR' package in R (Efford 2022). Our models used the 'multi' type traps of 'openCR' and the 'PLBsecrf' parameterization that contains parameters for capture hazard magnitude (λ_0), capture hazard scale (σ), apparent survival (ϕ), and per capita recruitment rate (f). We modeled detection using the hazard half-normal function that determined the probability of capturing turtle i in hexagon j, i.e. $g(d)_{ij}$, as:

$$g(d)_{ij} = 1 - e^{-\lambda(d_{ij})} \quad (4)$$

where the capture hazard function, $\lambda(d)$, is:

$$\lambda(d) = \lambda_0 e^{-\frac{d^2}{2\sigma^2}} \quad (5)$$

and d_{ij} is the distance from turtle i's activity center to the center of hexagon j. We modeled the 2 capture probability parameters λ_0 and σ as constant through time because we did not have enough captures of the same individual to estimate temporal variations in capture. A key characteristic of these SMR models is that they include capture heterogeneity by considering both activity centers and search locations. We modeled temporal trends in the population dynamic parameters ϕ and f using various functions of year, as detailed in the next section. We used the log-link function for all parameters, except ϕ, for which we used the logistic link function.

We assumed that activity centers of some captured turtles were outside our study area but within appropriate habitat. We defined the latter as water with a depth ≥0.5 m (habitat; Fig. S2). Within this habitat, we constructed an activity-center mask of 100 m hexagons where activity centers could be located (mask; Fig. S1). We extended this activity-center mask outside the study area until the net probability of capturing a turtle with an activity center outside the mask was ≤1% (net capture probability; Fig. S1). Activity centers were not allowed to move among years because captures were not frequent enough to allow estimation of multiple activity centers per individual.

We estimated temporal trends in apparent survival (ϕ) and per capita recruitment (f) by fitting the 19 models listed in Table 1. In addition to linear trend (in the logit and log spaces) and annual parameter models (~T and ~t), we included models with smoothed trends (~spline3, ~spline4, and ~spline5) and models with constant parameters within predefined study periods (~period2, ~period3, and ~period4). The 3 smoothed trends used cubic b-spline basis functions with evenly spaced knots between the years 2000 and 2018. The predefined study periods divided the total study period into approximately equal periods, as follows: 2000−2008 and 2009−2018 (~period2); 2000−2005, 2006−2011, and 2012−2018 (~period3); and 2000−2004, 2005−2008, 2009−2013, and 2014−2018 (~period4).

Following parameter estimation, we derived estimates of annual density using:

$$D_t = \sum_{i=1}^{n} h_{it}(a_i)^{-1} \quad (6)$$

where h_{it} is the capture indicator for animal i during year t (i.e. $h_{it} = 1$ if animal i was caught during year t; otherwise, 0) and a_i is the estimated effective sampling area (Borchers & Efford 2008) for animal i, which was modeled as constant over time. We estimated the abundance during year t in the study area as the density in year t times area, i.e.

$$N_t = D_t(a) \quad (7)$$

Following density estimation, we ranked all models based on the AIC and performed model averaging of survival and derived abundance. We computed CI of these model-averaged estimates by bootstrap resam-

Table 1. Covariate models fitted to parameters of the spatially explicit mark–recapture (MR) model. The symbol '~1' denotes an intercept-only model; '~T' fits a linear trend to the parameter in its transformed space; '~t' fits 1 parameter for every interval between capture occasions; '~spline3', '~spline4', and '~spline5' fit nonparametric smoothing spline trends to the parameter with 3, 4, and 5 degrees of freedom, respectively. The symbols '~period2', '~period3', and '~period4' fit constant parameters within approximately evenly spaced 2, 3, or 4 study periods and variable parameters among the intervals. Study periods were 2000–2008 and 2009–2018 for 'period2'; 2000–2005, 2006–2011, and 2012–2018 for 'period3'; and 2000–2004, 2005–2008, 2009–2013, and 2014–2018 for 'period4'

Model Number	Spatially explicit MR parameter			
	Capture hazard magnitude (λ_0)	Capture hazard scale (σ)	Apparent annual survival (ϕ)	Per capita recruitment rate (f)
1	~1	~1	~1	~1
2	~1	~1	~T	~1
3	~1	~1	~1	~T
4	~1	~1	~T	~T
5	~1	~1	~t	~1
6	~1	~1	~1	~t
7	~1	~1	~t	~t
8	~1	~1	~spline3	~1
9	~1	~1	~spline3	~spline3
10	~1	~1	~spline4	~1
11	~1	~1	~spline4	~spline3
12	~1	~1	~spline5	~1
13	~1	~1	~spline5	~spline3
14	~1	~1	~period2	~1
15	~1	~1	~period2	~spline3
16	~1	~1	~period3	~1
17	~1	~1	~period3	~spline3
18	~1	~1	~period4	~1
19	~1	~1	~period4	~spline3

pling HUNT transects within year, refitting models with AIC weights >0.01, and re-computing the model averaged estimates of survival and abundance from the bootstrap dataset.

2.5. Other statistical analyses

We estimated mean abundance during the study using simple averages of each method's annual estimates. We estimated the variance and CI for these long-run means using a Monte Carlo bootstrap method. Our Monte Carlo bootstrap method simulated individual annual estimates using random deviates from a mixture of 2 half-normal random variables. One half-normal was defined on the interval between 0 and the actual abundance estimate, while the other was defined as the interval between the actual estimate and infinity. We used half-normal mixtures, with 50:50 mixing probability and different standard errors for each, to account for asymmetry in the true distribution of individual estimates. We simulated 10 000 values from the mixture distribution associated with each year in the analysis, yielding 10 000 simulated mean abundance values. We computed 95% CI from these 10 000 using the bias-corrected and accelerated method (Manly 1997).

All other statistical analyses were performed using SigmaPlot for Windows (v 14.0). This included the determination of trends in annual data points using the dynamic curve-fitting feature.

3. RESULTS

3.1. Transect surveys, demographics, and residency

We conducted HUNT surveys for sea turtles in our study area in June of every year from 2000–2018, except for 2003 and 2010 due to logistical constraints. We were usually able to work at least 8 d each year and conduct surveys along approximately 200 km of transects (Figs. S3–S5), sighting a mean of 79 loggerheads *Caretta caretta* and 34 green turtles *Chelonia mydas* annually (Table 2). We captured loggerheads 1156 times after sighting them during HUNT surveys and 164 times after opportunistic sightings while not on HUNT surveys. These captures represented 886 individuals. The size–frequency distribution of captured loggerheads revealed 2 peaks (at about 65–76 cm SCL and 83–89 cm SCL; Fig. 2). The mean SCL of loggerheads captured each year decreased during the first half of the study period and increased during the second half, although there was no change overall (Fig. 3).

Most loggerheads were captured only once, but 28.2% were captured 2–10 times during this study. The percentage of loggerheads each year that were captured previously steadily increased and surpassed 60% in the final year (Fig. 4). Four loggerheads that were captured in our study area during the first year were recaptured during the last year, indicating ≥18 yr of residency. One of these turtles and 5 other loggerheads captured during 2018 were first captured by us in our study area in 1997, before our current work on determining abundance and survival began, indicating ≥21 yr of residency.

Table 2. Results of haphazard unmarked nonlinear transect (HUNT) surveys for loggerheads and green turtles. HUNT surveys were conducted in the southwestern Florida Bay study area during June over a 19 yr period (2000–2018). No work was conducted in 2003 and 2010

Year	Number of days worked	Total length of transects (km)	Loggerheads sighted on transect (n)	Green turtles sighted on transect (n)
2000	9	155.7	69	4
2001	6	254.0	41	12
2002	10	271.0	98	8
2004	6	136.8	61	2
2005	8	100.5	73	8
2006	4	57.3	43	3
2007	8	133.6	79	19
2008	9	179.2	105	38
2009	8	202.4	94	27
2011	9	260.3	89	69
2012	7	222.9	76	23
2013	8	205.2	109	53
2014	4	136.6	13	32
2015	8	318.6	88	94
2016	8	224.6	99	73
2017	8	224.7	115	62
2018	8	312.8	90	49
Mean	8	199.8	79	34

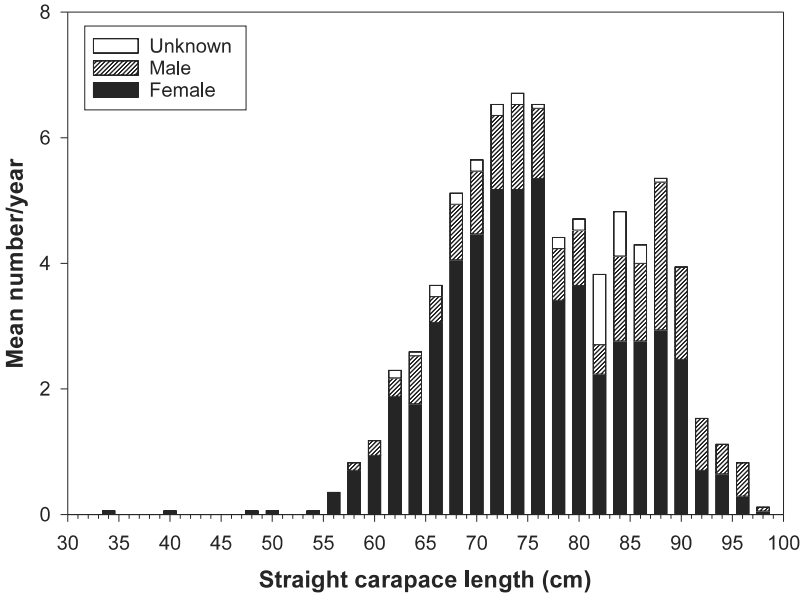

Fig. 2. Mean size frequency distribution by sex (if known) of 876 loggerheads captured in our southwestern Florida Bay study area during an 8 d period (mean) in June over a 19 yr period (2000–2018). No work was conducted during 2003 and 2010. Carapace length was measured from the nuchal notch to the pygal tip. No measurement of carapace length was made for 10 individuals because of carapace damage. See Table S2 for a description of how sex was determined. This distribution includes all carapace length measurements made each year (N = 1302), including those of re-captured individuals. No individuals were recaptured during the same year

All sighted green turtles appeared to have an SCL <70 cm. We captured 47 green turtles between 1991 and 2001 either in our study area before the current work began or in an adjacent basin (<10 km from our current study area); the mean SCL of these green turtles was 44.2 cm (SE = 1.57 cm, range = 25.5–66.1 cm).

Sex was determined for 828 (93.5%) of the 886 loggerheads; 638 (77.1%) were female and 190 (22.9%) were male (Table S2). Sex was unknown for individuals for which plasma testosterone concentration could not be determined (n = 55, 6.2%) or for which plasma testosterone concentration and SCL did not meet our criteria for assigning sex (n = 3). At first capture, we assigned immature status to 731 (82.5%) loggerheads and adult status to 155 (17.5%). Based on sex and maturity status at their first capture (excluding the 58 immature loggerheads for which sex was not determined), there were 557 (67.3%) immature females, 116 (14.0%) immature males, 81 (9.8%) adult females, and 74 (8.9%) adult males.

The interval between first and last capture (based on maturity status determined at first capture) indicated that residency periods in our study area were longer for adult loggerheads (3225 d, N = 53, SE = 259 d, range = 345–6564 d) than for immature loggerheads (1463 d, N = 197, SE = 117 d, range = 347–6564 d; $p \leq 0.001$, rank sum test). Nevertheless, some immature loggerheads may have become permanent residents of our study area. Fourteen loggerheads (9 males and 5 females) that were classified as immature at their first capture were classified as adult at a later capture.

During the current study, we also conducted other work in our study area that involved tracking adult and immature loggerheads via satellite telemetry. The adults were tracked to document movements associated with reproductive activity and the immatures were tracked to document habitat use. We were able to determine

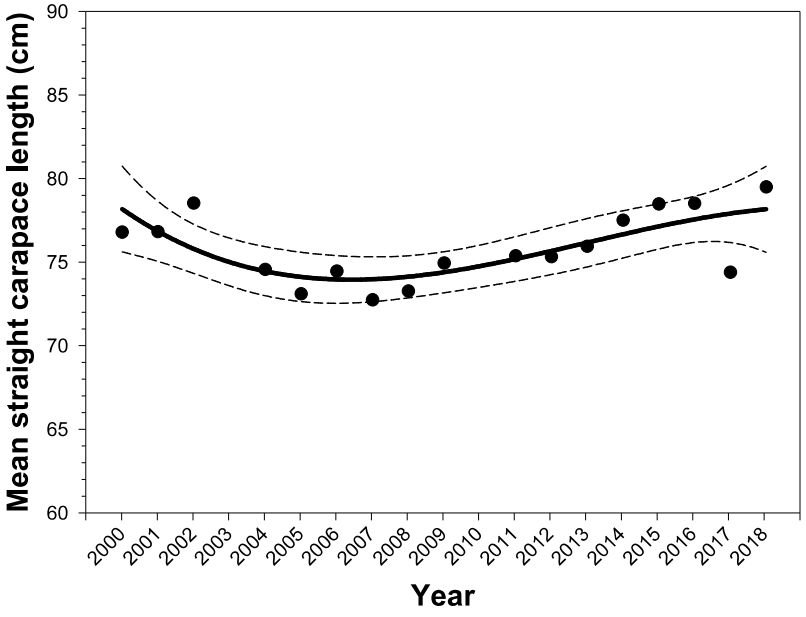

Fig. 3. Annual trend in mean straight carapace length of loggerheads captured each year in the southwestern Florida Bay study area during an 8 d period (mean) in June over a 19 yr period (2000–2018). No work was conducted during 2003 and 2010. We estimated the trend using cubic regression with 95% CI. Carapace length was measured from the nuchal notch to the pygal tip

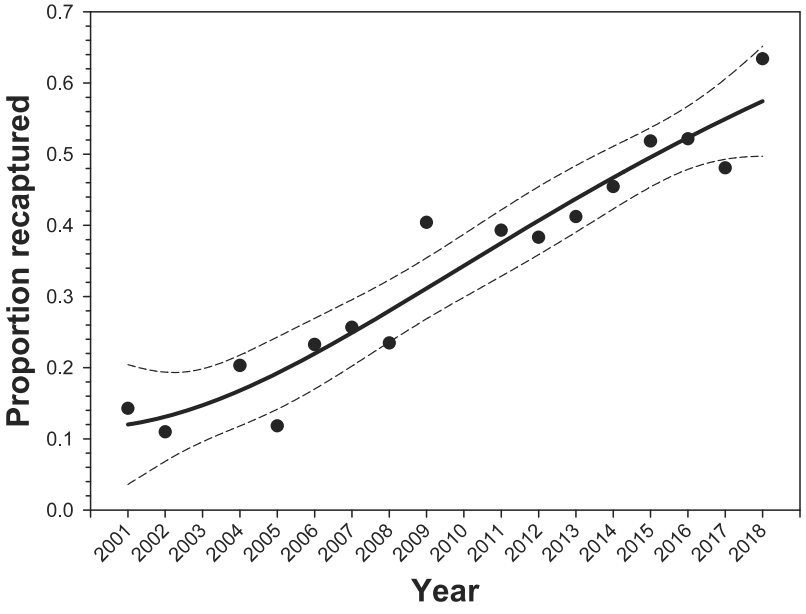

Fig. 4. Annual proportion of loggerheads captured in the southwestern Florida Bay study area during an 8 d period (mean) in June over a 19 yr period (2000–2018) that had been captured during a previous year (beginning in 2001). A total of 886 individuals were captured, with 250 (28.2%) being recaptured 2–10 times. No work was conducted during 2003 and 2010. We estimated the trend using logistic regression with 95% CI

the 50 and 90% utilization distributions (UDs) for 3 adult male loggerheads and 9 immature loggerheads (1 male and 8 females) during June–September of 2011 and 2012. These data revealed that our study area was comparable in size (21.86 km^2) to areas typically used by loggerheads there during the summer. Our study area was larger than the 50 and 90% UDs of all the adult males and larger than all but 1 of the 50% UDs and almost half of the 90% UDs of the immatures (Table S3). We also found that the UDs overlapped broadly but not completely with our study area (Table S3), showing that these loggerheads frequented areas both within and around our study site.

3.2. Abundance and survival estimates

3.2.1. Distance sampling abundance estimates

The effective transect half-width was 8.8 m for sighting loggerheads and 4.5 m for sighting green turtles. The mean annual abundance estimates, as determined by the distance sampling models, were 537 loggerheads (95% CI = 527–616) and 378 green turtles (95% CI = 361–456). The numbers of loggerheads in the study area were higher than the numbers of green turtles almost every year during the first half of the study period but were either equal to or less than the number of green turtles during the second half of the study period (Fig. 5A,C). The trend in the annual numbers of green turtles increased during much of the study period, but the trend in the annual numbers of loggerheads did not change (Fig. 5B,D).

3.2.2. Schnabel method abundance estimates

We temporarily marked a mean of 76 loggerheads and resighted a mean of 6 of these turtles annually. We were able to estimate the abundance of loggerheads in our study area each year (except 2003 and 2010, when no work was conducted) using the Schnabel method

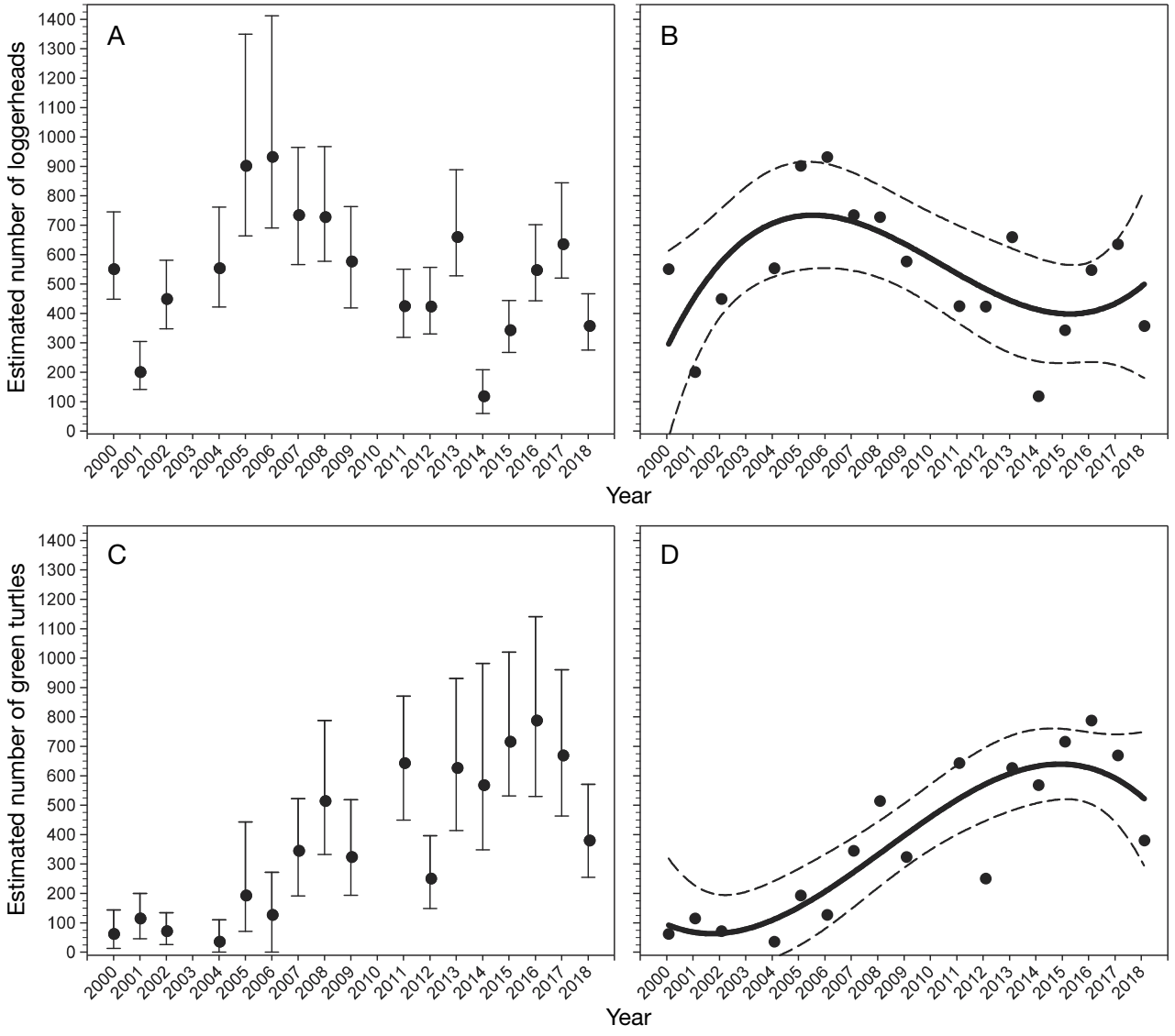

Fig. 5. (A,C) Annual estimated abundances (with 95% confidence intervals) of (A) loggerheads and (C) green turtles in the southwestern Florida Bay study area determined by distance sampling during an 8 d period (mean) in June over a 19 yr period (2000–2018). No work was conducted during 2003 and 2010. (B,D) Trends in the annual estimated abundances, as represented by cubic regression with 95% confidence intervals

(Table 3). When we excluded the 3 years (2004, 2006, and 2012) in which we did not resight any marked turtles, the mean abundance estimate was 568 (95% CI = 551–852).

3.2.3. SMR abundance and survival estimates

The annual SMR estimates of loggerhead abundance ranged from 64 to 858 individuals (mean = 597, 95% CI = 545–615). When we excluded the data for 2014 (when an extensive cyanobacterial bloom took place), the SMR estimates of loggerhead abundance ranged from 399 to 858 individuals (mean = 631, 95% CI = 575–651). The mean annual density of loggerheads in our study area according to SMR estimates was 27.3 km^{-2}. Mean annual abundances by sex and maturity status were 448 immature females (90.3% of immature turtles), 48 immature males (9.7% of immature turtles), 63 adult females (61.9% of adult turtles), and 39 adult males (38.1% of adult turtles). The CI of the SMR abundance estimates for most years overlapped (Fig. 6); however, the estimate for 2005 was higher than the estimates for 2001 and 2018, and the estimate for 2014 (during the cyanobacterial bloom) was lower than the estimates for all other years. There

Table 3. Loggerhead abundance estimated annually using the Schnabel method. Number of loggerheads marked and resighted each year in the southwestern Florida Bay study area and abundance estimates using the Schnabel method during an annual 8 d (mean) sampling session in June over a 19 yr period (2000–2018). No work was conducted during 2003 and 2010. NA: not applicable

Year	Number marked	Number resighted	Abundance estimate (95% CI)
2000	70	4	478 (226–1011)
2001	42	3	201 (88–443)
2002	90	4	893 (421–1887)
2004	51	0	1662 (377–NA)
2005	93	3	1066 (468–2344)
2006	43	0	766 (179–NA)
2007	108	3	1446 (635–3180)
2008	98	12	408 (249–691)
2009	93	13	331 (207–603)
2011	88	5	734 (362–1483)
2012	59	0	2154 (503–NA)
2013	95	10	472 (232–675)
2014	11	1	24 (8–46)
2015	81	4	656 (309–1385)
2016	91	9	466 (262–853)
2017	102	19	346 (231–569)
2018	82	7	431 (234–805)
Mean	76	6	738

was no trend in the annual estimated abundances for all turtles combined or for any of the maturity or sex subgroups (Fig. 7).

The mean annual survival rate estimates and 95% CI were 0.96 (0.88–0.99) for adult females, 0.91 (0.89–0.93) for adult males, 0.90 (0.86–0.98) for immature females, and 0.75 (0.63–0.84) for immature males (Fig. 8). The annual survival rate estimates tended to be lowest for immature males and tended to be highest for adult females. There was no change in the annual survival rate estimates for immature and adult males during the 19 yr study period (all CI overlapped); however, the survival rate estimates for adult females decreased from 2009 to 2013 and were highest for immature females from 2014 to 2017 (Fig. 8).

3.3. Comparisons of abundance estimates

The mean annual estimated number of loggerheads in our study area based on each of the analytical methods were as follows: 537 using distance sampling, 568 using the Schnabel method (excluding 2004, 2006, and 2012), and 597 using the SMR model. The trends in the annual loggerhead abundances estimated by each of these 3 techniques were similar, and none of the methods showed any change in abundance during our study period (Fig. 9).

4. DISCUSSION

4.1. Population characteristics

The size range of green turtles *Chelonia mydas* within our study area is typical of the immature green turtle assemblages in other neritic areas along the coasts of the southeastern USA (Coyne 1994, Shaver 2000, Ehrhart et al. 2007, Epperly et al. 2007, Foley et al. 2007, Kubis et al. 2009, Montello et al. 2022). No green turtles in our study area appeared to be greater than 70 cm SCL, indicating they were all immature (Musick & Limpus 1997).

The loggerhead *Caretta caretta* aggregation in our study area mostly comprises large immatures and adults. This type of mixed-stage loggerhead aggregation has been found throughout the eastern USA (Schmid 1995, 1998, Hopkins-Murphy et al. 2003, Witzell & Schmid 2004, Ehrhart et al. 2007, Epperly et al. 2007, Arendt et al. 2012a, Herren et al. 2018, Chabot et al. 2021). The proportion of adult loggerheads in our study area was 17.5%, among the highest reported in the USA. Nevertheless, this aggregation is dominated by immature females, which accounted for 67.3% of loggerheads captured. Immature males accounted for only 14% of turtles captured. A preponderance of immature females is typical, as aggregations of immature loggerheads in neritic areas of the USA have all been female biased (Wibbels et al. 1991, Limpus & Limpus 2001, Braun-McNeill et al. 2007, Arendt et al. 2012b, Braun McNeill et al. 2016, Shertzer et al. 2018).

4.2. Abundance and trends

We estimated the annual abundance of loggerheads and green turtles using distance sampling. We did not observe any annual trend in loggerhead abundance and found an increasing trend for green turtles. Loggerheads were more abundant than green turtles during the first half of our study period; however, the annual numbers of these species were similar during the second half of the study. These results correspond with other studies on the status of North Atlantic loggerhead and green turtle populations. The numbers of green turtle nests in Florida have been strongly increasing over recent decades (Chaloupka et al. 2008, Mazaris et al. 2017), and the abundance of

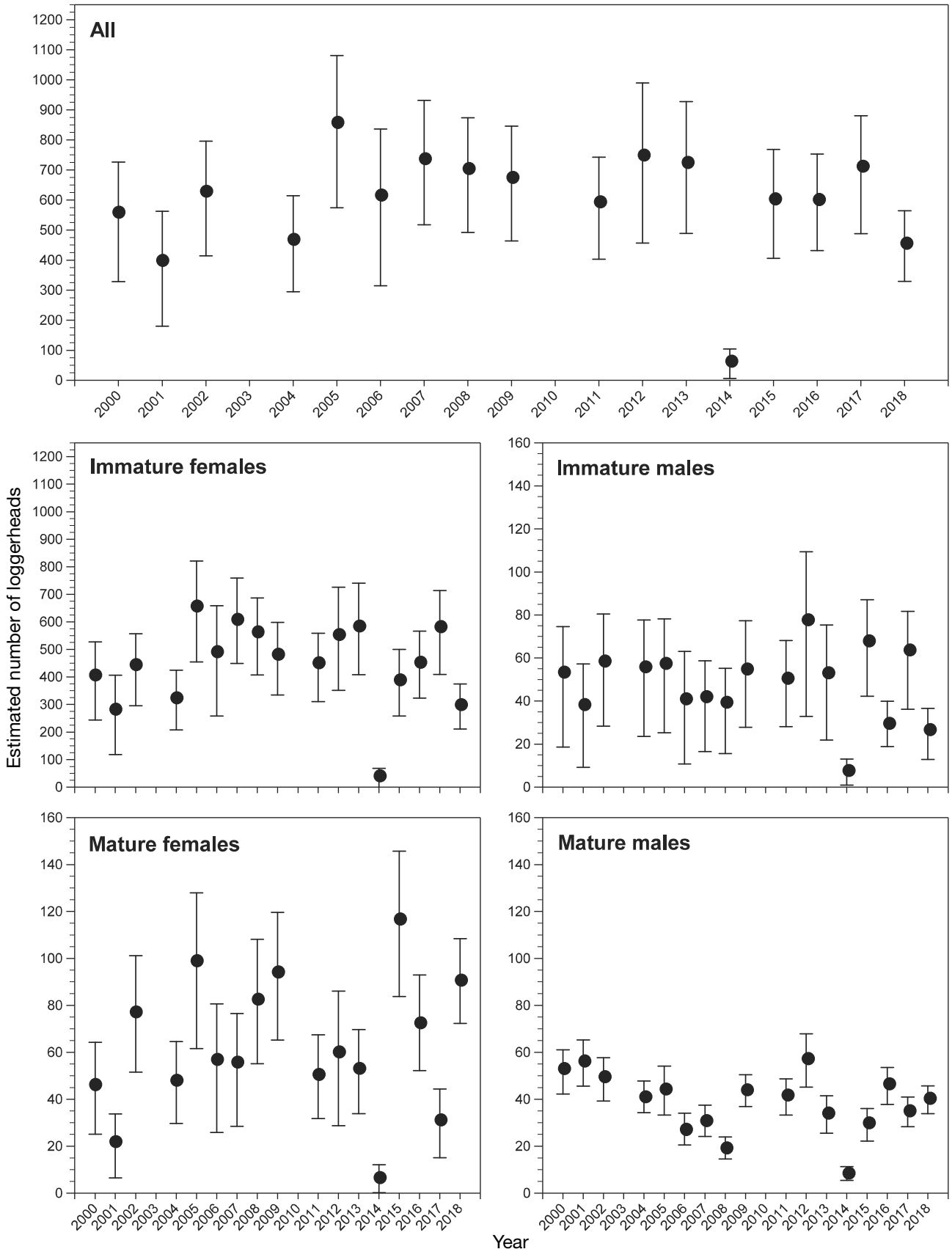

Fig. 6. Estimated annual loggerhead abundances (with 95% confidence intervals) for all loggerheads, and by sex and maturity status (immature females, immature males, adult females, and adult males), in the southwestern Florida Bay study area determined using spatially explicit mark–recapture models. Sampling occurred during an 8 d period (mean) in June over a 19 yr period (2000–2018). No work was conducted during 2003 and 2010. We estimated the year that immature turtles transitioned to maturity using a logarithmic growth model that estimated straight carapace length (SCL) between captures. We censored immature turtle capture histories (removed them from the immature population) in the year that their estimated SCL exceeded 86.4 cm if female, or 88.4 cm if male. Note the difference in scale of the *y*-axis is an order of magnitude greater for all turtles and for immature females

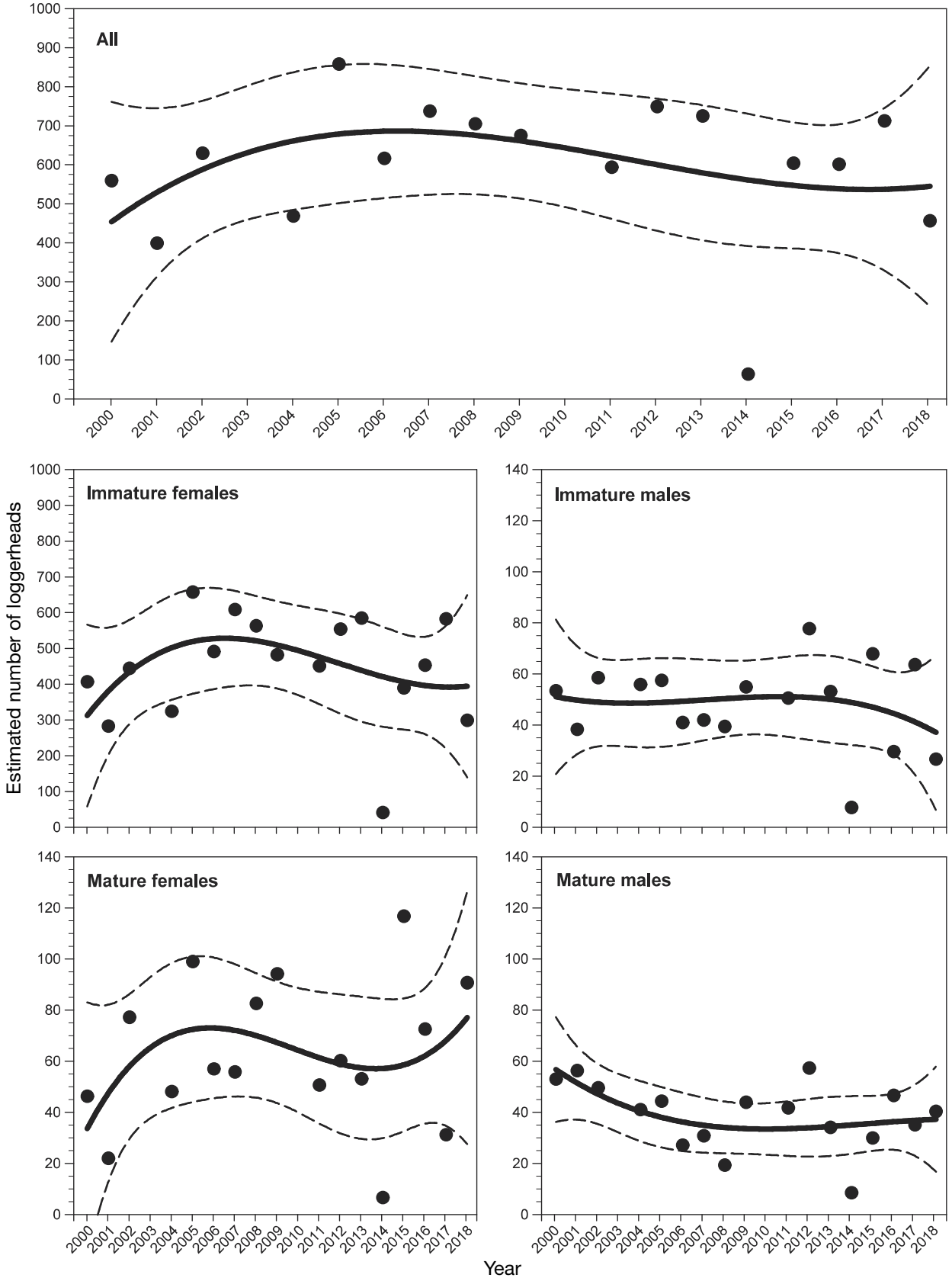

Fig. 7. Trends in the estimated annual loggerhead abundances for all loggerheads, and by sex and maturity status (immature females, immature males, adult females, and adult males), in the southwestern Florida Bay study area determined using spatially explicit mark–recapture models. The trends are represented by cubic regressions with 95% CI. Sampling occurred during an 8 d period (mean) in June over a 19 yr period (2000–2018). No work was conducted during 2003 and 2010. We estimated the year that immature turtles transitioned to maturity using a logarithmic growth model that estimated straight carapace length (SCL) between captures. We censored immature turtle capture histories (removed them from the immature population) in the year that their estimated SCL exceeded 86.4 cm if female, or 88.4 cm if male. Note the difference in scale of the *y*-axis for all turtles and for immature females

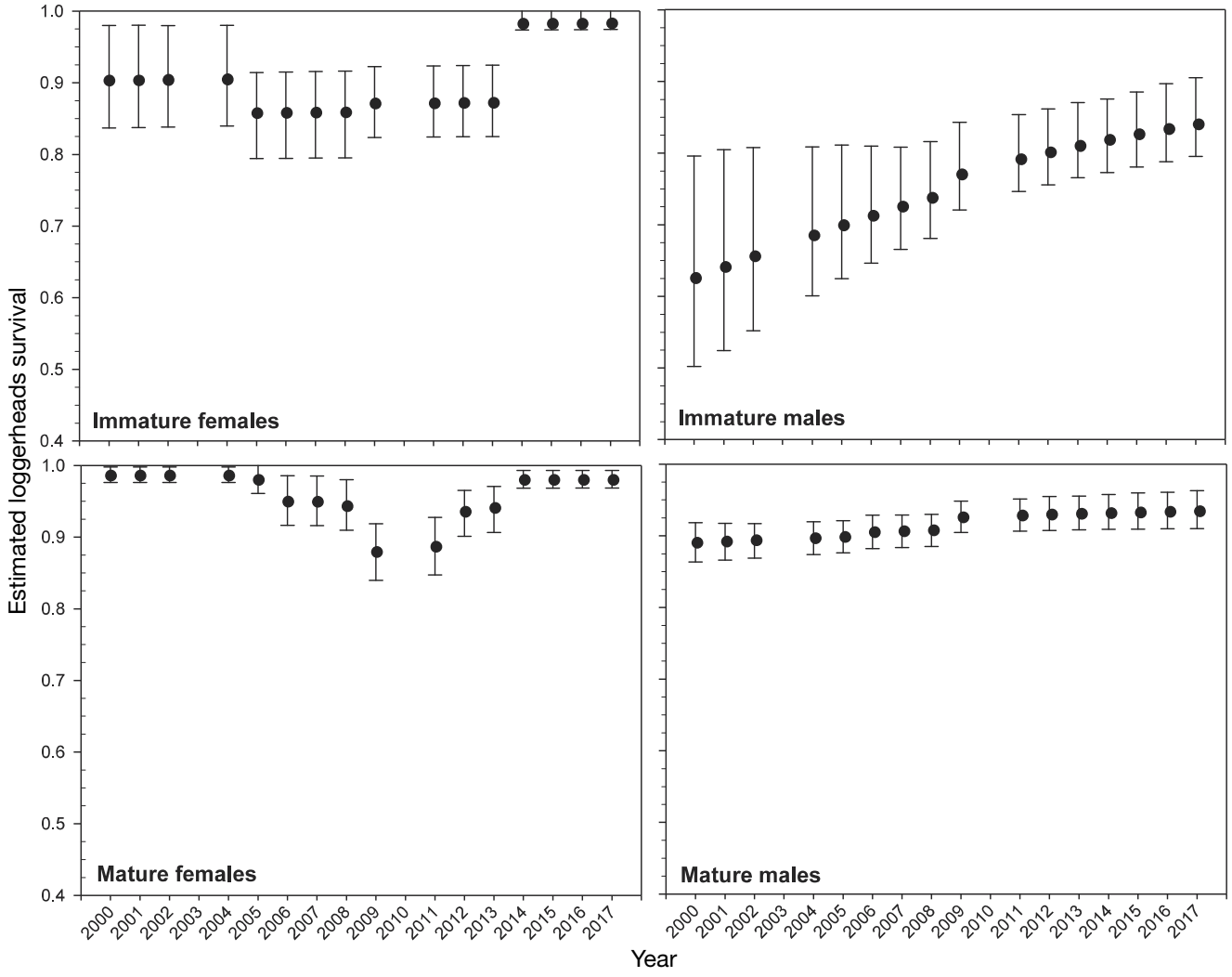

Fig. 8. Estimated annual loggerhead apparent survival and 95% confidence intervals by sex and maturity status (immature females, immature males, adult females, and adult males) in the southwestern Florida Bay study area determined by spatially explicit mark–recapture models. Sampling occurred during an 8 d period (mean) in June over a 19 yr period (2000–2018). No work was conducted during 2003 and 2010

immature green turtles has been increasing both in Florida (Witherington et al. 2006, Ehrhart et al. 2007) and in other parts of the USA (Braun McNeill et al. 2018). Overall, the North Atlantic green turtle population is showing signs of recovery (Valdivia et al. 2019). In contrast, signs of recovery for the North Atlantic loggerhead population have been more elusive (NMFS & USFWS 2008). The numbers of nests in Florida (the largest rookery) have exhibited periods of increase and decrease, but there is no clear evidence of change in the number of adult loggerhead females (Ceriani et al. 2019). The trends in abundance of loggerheads at foraging areas have been reported to be decreasing (Mansfield 2006), increasing (Turtle Expert Working Group 2009), and not changing (Turtle Expert Working Group 2009, Arendt et al. 2012a).

We also estimated the annual abundance of loggerheads using a relatively simple closed MR model (Schnabel method) and a much more sophisticated open SMR model. As with distance sampling, the MR models did not show any annual trend in loggerhead abundance during the study period. Additionally, the distance sampling and both MR models all generated similar mean annual abundances (500–600 loggerheads). To our knowledge, this is the first time that these 3 different methods for determining abundance have been applied contemporaneously. The general agreement between the estimates likely indicates that each technique produced relatively accurate results.

The SMR method required extensive spatial processing, programming, and estimation time while the Schnabel method was based on simple counts and

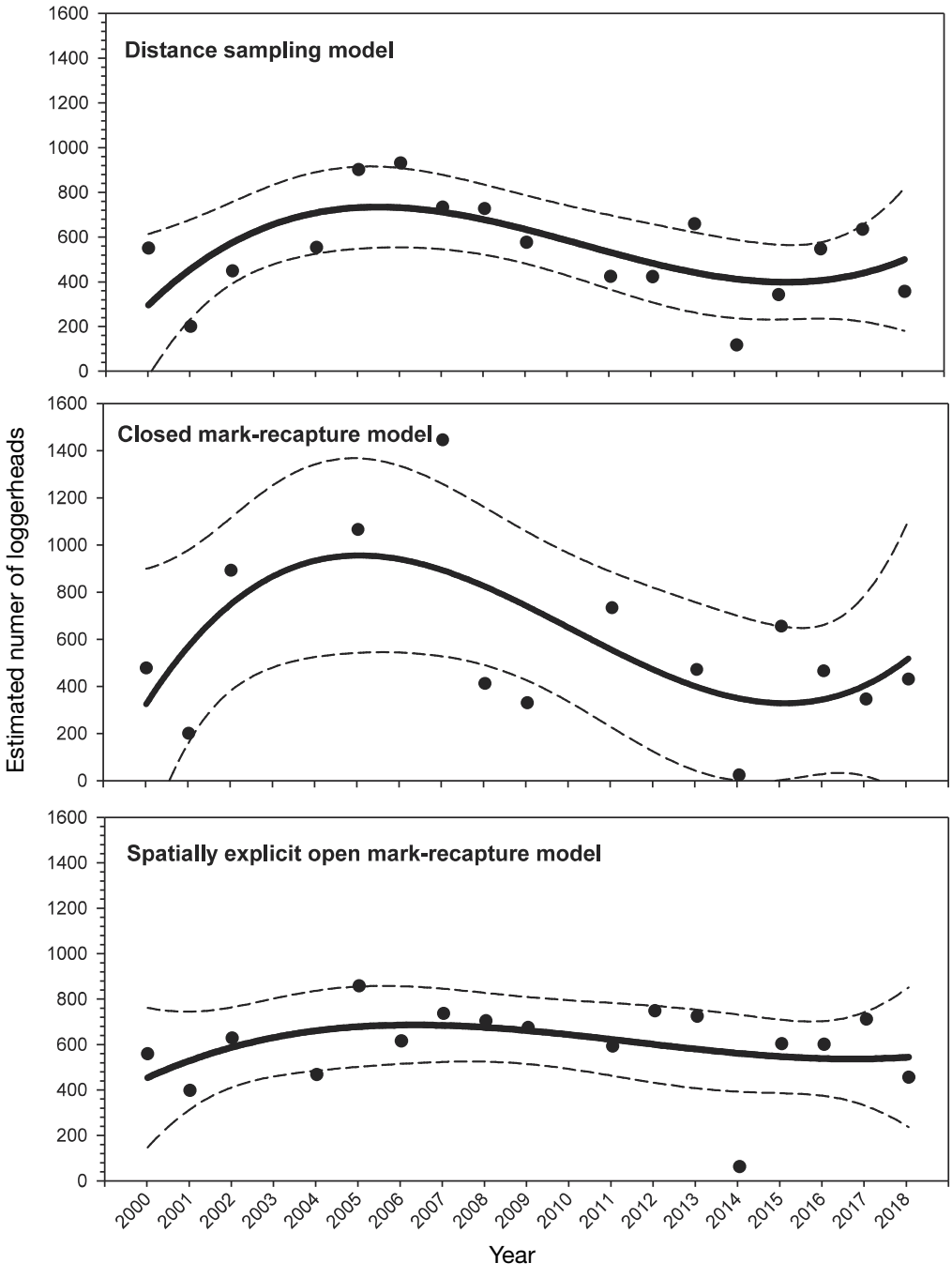

Fig. 9. Trends in estimated annual loggerhead abundance determined by the distance sampling model, closed mark–recapture model (Schnabel method), and spatially explicit mark–recapture model in the 21.86 km^2 southwestern Florida Bay study area. The annual abundance estimates for the 3 yr when no loggerheads were resighted for the Schnabel method (2004, 2006, and 2012) are excluded for that technique. We estimated the trends using cubic regression with 95% confidence intervals. Sampling occurred during an 8 d period (mean) in June over a 19 yr period (2000–2018). No work was conducted during 2003 and 2010

was computed using a basic spreadsheet. We consider the SMR method to be the current state-of-the-art approach for estimating both the abundance and survival rates of sea turtles. This method incorporates substantial capture heterogeneity because it accounts for differences in mean location, both inside and near the principal capture area. Reducing uncertainty in abundance estimates is essential in management decisions for which the precautionary principle is a guide, especially decisions to modify conservation

measures. Closed MR abundance estimates such as the Schnabel method are known to be biased low (i.e. underestimate true abundance) when the method fails to account for heterogeneity in capture probability, either spatial or otherwise (Cubaynes et al. 2010, King & McCrea 2019). Given agreement among the Schnabel, SMR, and distance methods in this study, we conclude that heterogeneity in individual sighting probability was not large enough to cause significant bias. Nevertheless, we recommend caution when using MR estimates for sea turtle foraging assemblages and recommend inclusion of spatial and temporal sighting covariates to help assess potential bias.

The 95% CI were smallest for the abundance estimates associated with the SMR modeling. Nevertheless, the CI were still relatively large. For example, we were generally unable to detect a difference between 2 abundance estimates until they approximately doubled or halved. This limits our ability to detect subtle to modest trends over short periods, but this is not unlike the case of using nest-count data to detect changes in the abundance of adult females. Fluctuations in nest counts, although an index of adult female abundance, are influenced by breeding periodicity and clutch frequency, which complicates the interpretation of trends in abundance (Broderick et al. 2001, Chaloupka 2001, 2002, Solow et al. 2002, Richards et al. 2011, Ceriani et al. 2019).

We observed changes to foraging habitat following the 2013−2014 cyanobacterial bloom that likely temporarily influenced local loggerhead abundance. Our study area is in a region where these blooms have been documented since 1991 (Butler et al. 1995). They are associated with mortality of sponges (Butler et al. 1995) and seagrass (Hall et al. 1999) and have altered the benthic community structure (Duermit-Moreau et al. 2022). The bloom in our study area in late 2013 through early 2014 (Duermit-Moreau et al. 2022) occurred after our 2013 sampling period and prior to our 2014 sampling period. When we conducted our work in 2014, the sighting conditions were excellent, but we found few loggerheads and our abundance estimate for that year was the lowest of any year (for all 3 models). We recaptured 5 loggerheads in that year, all of which had lost weight (mean weight loss of 8.2 kg, range = 2.4−14.9 kg). An immature female loggerhead with a satellite transmitter remained within our study area until early 2014, when she left Florida Bay. She had still not returned when her location transmissions stopped late in the summer of 2014. We believe that this behavior was representative of that of other loggerheads that left the study area because of inadequate food resources. The numbers of loggerheads in our study area rebounded during the following year, presumably as their food resources recovered. These habitat changes likely explain the lowered abundance estimates in our study area in 2014. Overall, the available evidence suggests this reduction in abundance did not reflect a broader population change.

4.3. Survival

Our SMR models generated estimates of apparent survival because they cannot distinguish between mortality and permanent emigration. To better characterize actual survival, the frequency of permanent emigration of the adult and immature loggerheads needs to be considered. Adult loggerheads typically exhibit strong site fidelity and potentially low rates of permanent emigration. Females consistently return to the same foraging area after nesting (Limpus & Limpus 2001, Broderick et al. 2007, Marcovaldi et al. 2010, Foley et al. 2014, Hart et al. 2014, Tucker et al. 2014), and adult male loggerheads exhibit similar foraging-area fidelity (Schofield et al. 2010, Pajuelo et al. 2012, Thomson et al. 2012, Casale et al. 2013, Varo-Cruz et al. 2013, Pajuelo et al. 2016, Shimada et al. 2020). It may not be unusual for a loggerhead to spend its entire adult life in one area (Musick & Limpus 1997). The intervals between first capture and last capture in our study may indicate that the adult loggerheads tended to be longer-term residents in our study area than the immature loggerheads were. This interval was almost 9 yr for those classified as adults at first capture but only about 4 yr for those classified as immature when first captured. In a separate study of reproductive behavior, we were also able to track the movements of 23 adult loggerheads captured in our study area during 2000−2013 over a mean individual tracking period of 362 d (SE = 53 d, range = 54−990 d, Table S4). All of these individuals were in the vicinity of our study area (typically within 10 km) when their tracking period ended.

Immature loggerheads also show strong foraging-area fidelity and may remain in the same area into adulthood (Musick & Limpus 1997). This was the case for some of the immature loggerheads in our study area. Fourteen loggerheads that we originally captured as immatures, we later captured as adults. However, in conceptual models of ontogenetic habitat stages in sea turtles, it is recognized that immature individuals may emigrate from a juvenile developmental habitat to an adult foraging habitat when nearing maturity (Musick & Limpus 1997). These

types of movements for large, immature loggerheads have been suggested to occur in the eastern USA (Hopkins-Murphy et al. 2003). In another separate study on habitat use during 2011–2013, we were able to track the movements of 13 immature loggerheads captured in our study area over a mean individual tracking period of 228 d (SE = 59 d, range = 27–738 d, Table S4). In contrast to the adults, 4 (31%) of the immature loggerheads were not in Florida Bay when their tracking period ended, and these turtles were never recaptured during subsequent sampling sessions, indicating they may have permanently emigrated. The possibility that the immature loggerheads have a higher frequency of emigration than the adult loggerheads needs to be taken into account when comparing their survival estimates.

The annual survival estimates for most of the loggerheads in our study are higher than other estimates for Northwest Atlantic DPS loggerheads (Pfaller et al. 2018). Our estimates for adult females, adult males, and immature females are among the highest reported for loggerheads (Pfaller et al. 2018). In contrast, the estimated mean annual survival of immature male loggerheads in our study area is among the lowest reported (Pfaller et al. 2018). We did not detect a difference in survival between adult males and females, unlike the findings of a study of adult loggerhead survival in Greece that reported adult males had lower survival (Schofield et al. 2020).

We have provided the first known survival estimates for loggerheads in the Northwest Atlantic DPS based on a foraging area study rather than a study of nesting females. In a meta-analytic evaluation of studies that determined survival estimates for adult sea turtles, Pfaller et al. (2018) concluded that the most robust estimates would be those associated with long-term MR studies at foraging areas that incorporate PIT tagging and use statistical modeling that accounts for biases, including imperfect detection and temporary emigration. Our study is the first to our knowledge that incorporates all of these methodologies in estimations of survival.

In a population model for loggerheads in the Northwestern Atlantic, Crouse et al. (1987) indicated that the annual survival rates of adult females and large immatures must be >0.85 and >0.80, respectively, to allow for population increase. Thus, the high annual survival (>0.90) of immature female and adult loggerheads in southwestern Florida Bay is an encouraging finding. In contrast, we obtained lower survival estimates for immature males (mean = 0.75), which could further exacerbate increasingly female-skewed sex ratios (Hays et al. 2023). However, our SMR model associated high uncertainty (approximately ±30%) with the immature male survival estimates early in the study period (2000–2008). Later in the study period (2009–2017), the uncertainty surrounding these estimates was similar to the uncertainty associated with the estimates for immature females (approximately ±10%). MR models, including our SMR model, cannot differentiate permanent emigration from death and hence estimate apparent survival (1 minus actual death minus permanent emigration). The estimates of our SMR model for immature males could have been lowered by a higher rate of permanent emigration for this group. We cannot draw conclusions about the emigration of immature males because we tracked only 2 immature males in the habitat-use study mentioned above and both stayed near our study area. Additional studies that incorporate satellite tracking of immature males would provide more insight into the movements of these individuals and assist with interpretation of future survival estimates. Alternatively, the lower SMR model estimates for immature males may have resulted from capturing few immature males during the early part of the study period, before we were able to observe an adequate number of full 'immature lifetimes' (recall that we censored immatures when they aged out of the category). Later in the study, our SMR model incorporated more and longer observations of immature males. In contrast, this was not likely the case for immature females because their sample sizes were always higher compared to immature males. Therefore, we conclude the estimates of immature male survival during the latter portion of the study (i.e. 0.77 to 0.84) are more likely to be representative of survival during the entire study period.

Given that our study area is within the Everglades National Park (ENP) and large portions of nearby areas are within the Florida Keys National Marine Sanctuary (FKNMS), the loggerheads we studied may be afforded unusually high levels of protection from anthropogenic mortality factors. However, our ancillary tracking efforts revealed that these turtles have home ranges that include relatively large areas outside the ENP and FKNMS. Outside the ENP, the primary commercial fishery threat to these loggerheads is entanglement in the buoy lines of pot fisheries for spiny lobster and stone crabs (Adimey et al. 2014), a fishery that is concentrated in the waters surrounding our study area (Monroe County; Garlock et al. 2024). These turtles are also vulnerable to entanglement in lost or discarded recreational fishing gear (Adimey et al. 2014), but the greatest threat is likely from being struck by a motorized vessel (Foley et al. 2019). Adult

female loggerheads, which periodically migrate to nesting beaches, are especially vulnerable to this mortality factor (Foley et al. 2019, Welsh & Witherington 2023). About 10% of the loggerheads captured in our study had a vessel-strike injury (see Foley et al. 2019 for descriptions of vessel-strike injuries).

4.4. Considerations when monitoring foraging areas

We estimated loggerhead abundance within our study area using 3 methods. Each used turtle observations or captures from search vessels. We recognize the tradeoffs of this simultaneous data collection approach, one being that our HUNT transects focused on achieving captures for MR methods and were not randomly assigned. However, a benefit of gathering distance data to inform a detection function in conjunction with captures is that multiple methods can be used to produce abundance estimates at the same time and in the same location. We regard the distance estimates and MR estimates as independent, because distance estimates depend on sightings and MR estimates depend on captures. We know of no methodological characteristic that would bias both of these methods in the same or opposite direction at the same time. Given general agreement of the 3 methods, future studies may explore integrating all 3 into a single estimation framework (Argent 2004) which may result in reduced variation relative to the individual models.

Because our HUNT transects were not randomly or systematically placed, we had *a priori* reason to suspect sampling bias in our abundance estimates obtained by distance modeling. We assessed this risk of bias by comparing the loggerhead abundance estimates obtained by the distance methods and the 2 MR methods. We found the range of these 3 estimates only spanned 27% of the highest estimate. The distance estimate was the lowest, differing by only 9% from the SMR model estimate, which does not indicate substantial sampling bias in our HUNT transects. We suggest that this bias was minimal because of the extensive sampling, both in terms of loggerheads observed and transect length surveyed, relative to the number of loggerheads in the study area and to the size of the area represented. The transect method also benefited from a negligible degree of double counting, because the vast majority of observed loggerheads were also captured and externally marked; this was an added benefit to capturing turtles in association with distance sampling. To reduce double-counting green turtles during transect surveys, we regularly considered unique physical characteristics of individuals sighted in close spatial and temporal proximity.

NOAA recommended that distance sampling be conducted separately from capture efforts (NOAA & DOI 2023). While this separation may be beneficial, it presents tradeoffs between effort and study design. Although efforts to count turtles on transects randomly assigned in space and time, separated from turtle captures for MR estimates, would be ideal, such separation would have doubled the effort and budget required for this project. The core of our work was an SMR study, which produced the most reliable estimates of abundance.

Determining the abundance and survival (and any associated trends) of loggerheads at a foraging area is a significant accomplishment. The need for these data has been continuously asserted for over 3 decades (Thompson 1989, National Research Council 1990, 2010, Bjorndal & Bolten 2000, NMFS & USFWS 2008, Schroeder et al. 2020). However, the usefulness of trends at a single foraging area is geographically limited unless the data can be used to help inform the status of a larger population. In the Northwest Atlantic Ocean, the loggerhead population is divided into 5 recovery units (NMFS & USFWS 2008). Most of our turtles are likely from the largest recovery unit but represent only a fraction of this unit due to its large size. Nevertheless, the trends in loggerhead abundance in our study area corresponded with trends observed on nesting beaches. Likewise, green turtle abundance in our study area mirrored green turtle trends reported for Florida nesting beaches and other foraging areas. These findings suggest that even a single foraging area can provide important trend information, and, especially when coupled with similar studies at other foraging areas and nesting beaches, contribute to increased understanding of population trends.

One of the demographic recovery criteria in the recovery plan for the North Atlantic loggerhead is that abundance at foraging areas is increasing for at least 1 generation (defined as 50 yr, NMFS & USFWS 2008). Determining abundance at a foraging area is a labor-intensive, expensive activity, and conducting this activity over at least a 50 yr period is a daunting task. Making this effort as effective and efficient as possible will increase the probability that this monitoring can be conducted over the long-term at multiple sites. Our study is an example of how a large amount of useful information, including estimates of abundance and survival, and a variety of other critical demographic data can be collected each year at a foraging area during relatively short (8 d) sampling periods. We could not exert greater effort without substantially

more sustained financial investment, staff, and logistical support. We believe our analytical methods would yield useful estimates (i.e. unbiased, with relatively high precision) in other studies if field efforts obtain >100 distance observations (Buckland et al. 2015) and if MR efforts produce annual capture probabilities >25%. However, the results obtained depend on other factors, such as animal movements, the length of study, and the consistency of search effort.

5. CONCLUSIONS

We observed an increase in the numbers of green turtles *Chelonia mydas* in our study area but no change in the numbers of loggerheads *Caretta caretta* based on distance sampling. However, our distance sampling methodology could have introduced sampling biases because our transects were not randomly or systematically placed. To address this, we presented two lines of evidence that indicated the abundance estimates based on our distance sampling efforts were credible. The first was the correspondence of our observed trends with recent assessments demonstrating that the North Atlantic green turtle population is making progress toward recovery (Valdiva et al. 2019) while the loggerhead is not (Ceriani et al. 2019). The second was the close agreement between our annual loggerhead abundance estimates as determined by our distance sampling to those determined by our SMR model.

Our estimates of abundance and survival for immature and adult male and female loggerheads *Caretta caretta* are the first for a Northwest Atlantic DPS foraging area. Studies generating such data for loggerhead foraging areas in the Northwest Atlantic are rare but are crucially needed to monitor population status. We strongly recommend the establishment of additional foraging area studies within the range of the Northwest Atlantic loggerhead DPS, so that abundance and survival data can be combined and compared across the range of the DPS. Creation of a mosaic of index foraging area studies for the DPS is vital to detect changes in abundance or survival and to collect other demographic data to monitor population status. Monitoring should include trends in demographic parameters, such as size-frequency distributions, sex ratios, genetic structure, and health status indicators.

The use of 3 contemporaneous modeling approaches yielded similar abundance estimates, which supports the reliability of our survey methodology. In addition, capturing sighted turtles enabled the collection of critical demographic data. The continuation of this work will allow longer-term trend monitoring and provide data to monitor progress toward recovery, as specified in the Northwest Atlantic Loggerhead Recovery Plan. Studies at foraging areas are complex and costly—logistics and funding strongly influence survey design and implementation. Our methodology was successfully implemented over a relatively long timeframe, is cost-effective and logistically feasible, yields comparable abundance data using different methodological approaches, generates survival estimates, collects a range of demographic data, and is highly likely to continue into the foreseeable future. We encourage additional integrated foraging area studies to assess abundance and survival, acknowledging that habitat conditions strongly influence methodological approaches.

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