










## ARTICLE

# Hidden in plain sight: Integrated population models to resolve partially observable latent population structure

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**Funding information**

South Carolina Department of Natural Resources, Grant/Award Numbers: 2009094, 20100899

**Handling Editor:** Robert R. Parmenter

**Abstract**

Population models often require detailed information on sex-, age-, or size-specific abundances, but population monitoring programs cannot always acquire data at the desired resolution. Thus, state uncertainty in monitoring data can potentially limit the demographic resolution of management decisions, which may be particularly problematic for stage- or size-structured species subject to consumptive use. American alligators (*Alligator mississippiensis*; hereafter alligator) have a complex life history characterized by delayed maturity and slow somatic growth, which makes the species particularly sensitive to overharvest. Though alligator populations are subject to recreational harvest throughout their range, the most widely used monitoring method (nightlight surveys) is often unable to obtain size class-specific counts, which limits the ability of managers to evaluate the effects of harvest policies. We constructed a Bayesian integrated population model (IPM) for alligators in Georgetown County, SC, USA, using records of mark-recapture-recovery, clutch size, harvest, and nightlight survey counts collected locally, and auxiliary information on fecundity, sex ratio, and somatic growth from other studies. We created a multistate mark-recapture-recovery model with six size classes to estimate survival probability, and we linked it to a state-space count model to derive estimates of size class-specific detection probability and abundance. Because we worked from a count dataset in which 60% of the original observations were of unknown size, we treated size class as a latent property of detections and developed a novel observation model to make use of information where size could be partly observed. Detection probability was positively associated with alligator size and water temperature, and negatively influenced by water level. Survival probability was lowest in the smallest size class but was relatively similar among the other five size classes (>0.90 for

† Deceased October 28, 2014.

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each). While the two nightlight survey count sites exhibited relatively stable population trends, we detected substantially different patterns in size class-specific abundance and trends between each site, including 30%–50% declines in the largest size classes at the site with greater harvest pressure. Here, we illustrate the use of IPMs to produce high-resolution output of latent population structure that is partially observed during the monitoring process.

#### KEYWORDS

*Alligator mississippiensis*, Bayesian, harvest, hierarchical model, integrated population model, population dynamics, population structure, South Carolina, state uncertainty

## INTRODUCTION

In wildlife populations, demographic variation in reproductive output, predation risk, or harvest pressure is frequently reflected in sex-, age-, or size-specific abundances and vital rates (Servanty et al., 2011; Tuljapurkar et al., 2009). Management decision-making often relies on monitoring data, which is thereby limited in its predictive power by the data's demographic resolution—the scale at which individuals can be assigned to a demographic group (Lyons et al., 2008; Sauer & Knutson, 2008). Demographic data with high resolution may contain sex, age, or size specificity, whereas low-resolution data collapse multiple demographic groups. While intensive forms of monitoring (e.g., mark-recapture studies) are likely to produce high-resolution demographic data in which the state of interest (e.g., sex, size) can be precisely observed, such options may be too costly or time-intensive to implement on broad spatiotemporal scales (Kendall et al., 2019; Saracco et al., 2008). Alternatively, survey-based monitoring methods (e.g., counts, occupancy) or opportunistic data collection offer the potential for lower expense and increased spatial coverage but may come at the cost of added uncertainty for some or all states of observed individuals (Fischer et al., 2021; Saracco et al., 2008; Tenan et al., 2017). A common manifestation of state uncertainty is partial observability, in which the demographic state (e.g., sex, age, reproductive status) cannot be determined to the desired level of resolution for all observed individuals (Conn & Cooch, 2009). Managers of monitoring programs with extensive partial observability may resort to reducing the data's demographic resolution to avoid extensive censoring or to reduce bias in population projections (Caswell, 2001), which may ultimately constrain the desired demographic resolution of management actions (e.g., size-structured vs. total individual harvest quotas) and increase uncertainty in their outcomes.

Leveraging data with a relatively low resolution to identify latent population structure within populations is an

emerging area of interest, as it has the potential to produce higher resolution results for a lower cost. For example, Link et al. (2003) developed a model to derive age-structured abundance and survival estimates from a 64-year census of endangered whooping cranes (*Grus americana*) using aggregated, low-resolution data that distinguished only two classes of birds: first-year individuals and adults. In an extension of the *N*-mixture model framework (Royle, 2004), Zipkin et al. (2014) incorporated a classification probability term into the detection process to account for state uncertainty when assigning individuals to one of two demographic groups (e.g., adult/juvenile, male/female) during sampling. Though each approach offers a different mechanism to enhance low-resolution data, both require relatively large sample sizes of low-resolution datasets (Link et al., 2003; Zipkin et al., 2014) that may not be feasible for many monitoring programs.

Integrated population models (IPMs) offer a flexible, efficient tool to jointly analyze multiple data streams, thus increasing the precision of parameter estimates and providing a standardized error structure to reduce uncertainty (Besbeas et al., 2002; Schaub & Abadi, 2011). Incorporating multiple data streams enables the IPM to account for all demographic processes that influence changes in population growth rate. A comprehensive demographic model allows the estimation of additional parameters, both ecological (e.g., immigration) and observational (e.g., classification rate), that would be inestimable for any of the individual model components in isolation (Arnold et al., 2018; Schaub & Abadi, 2011; Zipkin & Saunders, 2018). Therefore, IPMs present an opportunity to synthesize multiple datasets, often of dissimilar demographic resolutions, in a common framework to identify latent population structure.

The American alligator (*Alligator mississippiensis*) is a species of ecological and economic importance in the southeastern United States (Mazzotti & Brandt, 1994). Throughout their life span, alligators undergo an approximately 10-fold increase in body length paired with ontogenetic shifts in diet and habitat use (Nifong et al., 2015;

Subalusky et al., 2009; Wilkinson et al., 2016), allowing the species to fill different ecological roles (e.g., meso- vs. apex-predator) as they grow (Rootes & Chabreck, 1993a; Somaweera et al., 2013, 2020). Alligators require 11–16 years to reach sexual maturity and continue to reproduce throughout their life span, which likely exceeds 65 years (Wilkinson et al., 2016). However, substantial uncertainty exists regarding both the factors that influence asymptotic body size and the influence of body size on fecundity (Larriera et al., 2004; Thorbjarnarson, 1996; Wilkinson, 1983; Wilkinson et al., 2016; Zajdel et al., 2019).

Following two decades of protection by the Endangered Species Act triggered by overharvest, alligators are currently managed under consumptive use programs throughout most of their range (Rhodes, 2002). For size- or age-structured species, like alligators, harvest decisions may cause significant changes to population structure and ultimately, population growth (Hauser et al., 2006; Koons et al., 2006). In addition to detecting changes in population structure, high-resolution monitoring data may also be useful for developing more biologically realistic predictive models to evaluate the consequences of harvest decisions and inform finer resolution harvest policies (e.g., size class-specific quotas). Nightlight surveys (also known as spotlight surveys) are the most widely used method to monitor crocodilians (Bayliss, 1987; Strickland et al., 2018; this study). However, nightlight surveys often produce low-resolution count data in which the majority of detected individuals cannot be assigned to a specific age or size class (Balaguera-Reina et al., 2018; Gardner et al., 2016; Skupien & Andrews, 2017; Strickland et al., 2018). For alligators in particular, a lack of data regarding size class-specific population trends may leave alligator populations particularly vulnerable to harvest-induced population declines due to their complex life history, delayed maturity, and long life span (McIlhenny, 1935; Wilkinson et al., 2016).

We developed an IPM for an alligator population subject to spatially variable harvest pressure on the middle coast of South Carolina, USA (Figure 1), near the northern limit at which high densities of alligators occur. Specifically, we synthesized data from a long-term, mark-recapture study (1979–2017) and from low-resolution nightlight surveys (counts; 2011–2016) with prolific uncertainty about size class assignment of detected alligators, as well as clutch size and harvest data (2011–2016). Our goal was to reduce state uncertainty in count data through integration with a high-resolution dataset within an IPM framework to produce abundance estimates that were specific for size classes that spanned the entire size range. We also sought to obtain size class-specific survival estimates and evaluate environmental variables that influence detection probability in nightlight surveys.

## METHODS

### Alligator management

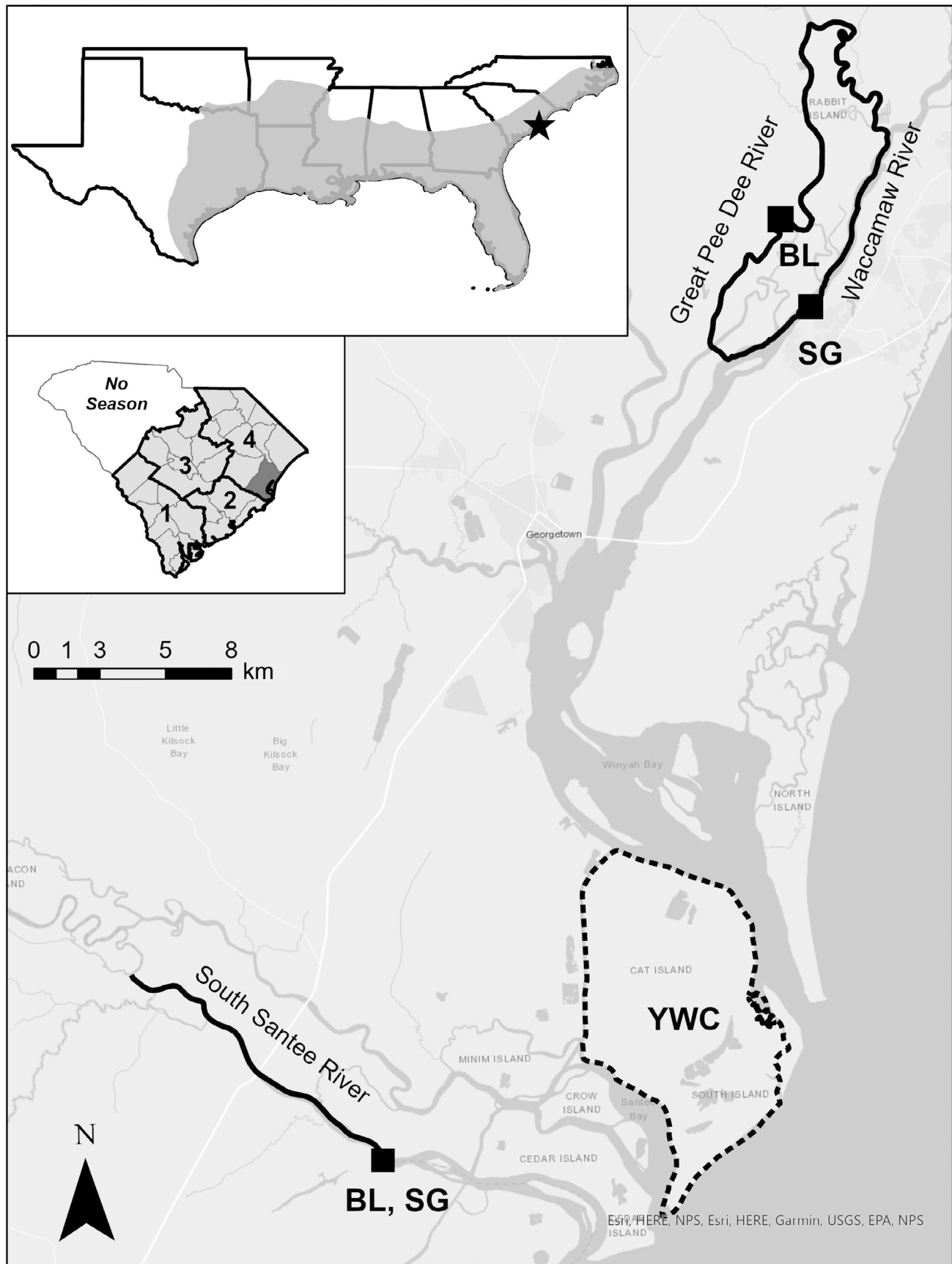
The South Carolina Department of Natural Resources (SCDNR) has administered alligator harvest (hunting) programs for private lands since 1995 and public waterways since 2008 (SCDNR, 2017). Boat- and truck-based nightlight surveys are the primary method used by SCDNR to monitor alligator populations within the state. We used SCDNR private and public harvest data from Georgetown County (GXN) and a portion of Charleston County (Figure 1) for 2011–2015 only, to overlap with the time range of nightlight survey data. The SCDNR also administers a nuisance removal (euthanasia) program that was established in 1988. However, the vast majority of nuisance take occurs near human population centers (SCDNR, unpublished data), meaning that the nuisance alligators were unlikely to be encountered on the nightlight counts or mark-recapture study. See Appendix S1 for detailed descriptions of the harvest programs, handling of harvest records in the IPM.

### Study area

We studied a coastal population of alligators in Georgetown County, SC, USA (Figure 1; 2681 km<sup>2</sup>). The city of Georgetown receives 78–184 cm of annual precipitation; the dry season occurs during October–March, and the wet season is during June–September. Mean temperatures during the alligator's active season (April–October) range between 17–27°C and 8–14°C during brumation (November–March) (Wilkinson et al., 2016). GXN is comprised of extensive and diverse alligator habitat that includes coastal marsh, wooded wetlands, and impounded (diked) wetlands on a mixture of private and public lands. For our analysis, we synthesized alligator private and public harvest data, nightlight survey counts from multiple coastal rivers, and mark-recapture-recovery and clutch size data from the Tom Yawkey Wildlife Center (YWC; 6033 ha; 33.217° N, 79.236° W), all within or bordering GXN.

### Tom Yawkey Wildlife Center

We captured alligators and surveyed for nests on South and Cat Islands within the state-operated YWC, which has been closed to alligator hunting since the early 1900s. YWC is part of the headland that separates two river deltas in GXN and is surrounded by marine (>35 salinity parts per thousand; ppt) and brackish water habitats (5–35 ppt) (Figure 1), where the mean tidal range is 116 cm



**FIGURE 1** Legend on next page.

(<https://www.saltwatertides.com/dynamic.dir/scarolina/sites.html>). Our sampling area included tidal marsh (2524 ha) and managed impounded wetlands (hereafter impoundments; 1012 ha) in which the salinity ranged from 0 to 35 ppt (Wilkinson et al., 2016). See Lawson et al. (2020) for a complete description.

## Coastal rivers

We conducted nightlight surveys (Bayliss, 1987) in cooperation with SCDNR along two routes: (1) a combination of the Great Pee Dee and Waccamaw Rivers and (2) the South Santee River (Figure 1). The Great Pee Dee and Waccamaw route (GPD; 38.4 km) began at the Samworth Wildlife Management Area boat ramp (33.475° N, 79.186° W) and formed a circuit, which included sections from each river, and two excavated connecting channels. The Great Pee Dee is a fairly narrow (30 m at the boat launch in Figure 1) “red water” river indicative of high nutrient loads, contrasted with the Waccamaw, which is much wider (300 m at the stream gauge in Figure 1) and classified as a “black water” river with fewer nutrient inputs. The GPD survey route is surrounded by a combination of suburban homes, flooded forests, and naturally tidal freshwater marsh in which salinities are <0.5 ppt (Bennett et al., 1989; Conrads & Roehl, 2007). The South Santee River route (SAN) started at the Santee Coastal Reserve Wildlife Management Area boat ramp (33.154° N, 79.354° W) and extended 12.8 km upstream. The South Santee River is surrounded by a series of fresh and brackish water impoundments like those contained on YWC. Within each survey route, salinity typically ranges from 0.0 to 26.7 for SAN and 0.0 to 4.9 for GPD from early May to mid-August (A. J. Lawson, unpublished data).

## Demographic data collection

### Mark–recapture and nesting studies

We captured alligators of all size classes to evaluate demographics as part of a long-term (1979–2017)

mark–recapture study on YWC (Appendix S1: Table S1a). Alligators were captured using a combination of modified baited trip-snares (Murphy & Fendley, 1973), walk-through snares placed on trails or nest sites (Wilkinson, 1994), camera traps placed at nest sites (for recaptures), snare poles, snatch hooks (Cherkiss et al., 2004), and hand captures (for small alligators only). Annual capture effort (CE) and techniques varied to accommodate different research foci over the 39-year time span, which targeted different demographic groups or individuals (description in Wilkinson et al., 2016). Except for incidental carcass discoveries or poaching of marked individuals, no data were collected during 1983–1992, 1994–2004, and 2008 (Appendix S1: Table S2).

Captured adults (>180-cm total length [TL]) were uniquely marked using the methods and materials described in Lawson et al. (2020). For individuals >120-cm TL, we determined the sex through cloacal examination (Chabreck, 1963) and recorded two standard body measurements ( $\pm 0.5$  cm): TL and snout-vent length (SVL). Hatchlings ( $\leq 30$ -cm TL) captured at nests were marked with individually identifiable web tags (1979–1982: Conservation Tags 1005-1) and a scute-notching (1979–1993) and toe-clipping (1979–1993) combination that reflected their hatch year (tail scute) and nest number (toe), whereas nonhatchling alligators were assigned individually identifiable scute-notching and toe-clipping patterns. Alligators <120-cm TL were measured for TL only and were released without determining sex (P. M. Wilkinson, personal communication). After marking and measurements, all alligators were released to their capture sites.

Concurrent with the mark–recapture study, we conducted aerial surveys using a helicopter (MD 500 and R44) to locate alligator nests (2011–2016). Helicopter surveys (2–3) were conducted approximately one week apart between 10 June and 30 June each year. Upon discovery from the air, personnel located each nest on foot within 3–72 h and opened the cavity to record the number of eggs (clutch size). Empty nest mounds were revisited daily until oviposition occurred or until the nest was determined to be false or abandoned (i.e., no visits by the female after 7–10 days).

**FIGURE 1** Map depicting the location of an American alligator capture–mark–recovery study (1979–2017) at the Tom Yawkey Wildlife Center (YWC; indicated by the dashed border), and two nightlight survey routes (thick black lines) on the Great Pee Dee and Waccamaw Rivers, and the South Santee River (2011–2016), which forms the border between Georgetown (GXN) and Charleston Counties (black star in inset) in South Carolina, USA. The black squares represent boat launches (BL) or stream gauges (SG) that recorded water levels (WLs) and water temperature (WT) for each survey route. The upper inset shows South Carolina in relation to the alligator’s distribution, whereas the lower inset shows the four alligator management units in South Carolina subject to a public harvest program: 1, Southern Coastal; 2, Middle Coast; 3, Midlands; and 4, Pee Dee (GXN shaded dark gray).

## Nightlight survey counts

We conducted nightlight surveys on the two routes from 2011 to 2016, excluding 2012, using flat-bottomed boats equipped with 44,700–85,700 W (60–115 horsepower) out-board motors. Surveys were initiated  $\geq 30$  min after sunset and completed  $\geq 90$  min before sunrise. We did not conduct surveys the night of a full moon or within  $\pm 1$  day, during extreme water-level (WL) events, or during heavy rain or wind ( $> 15$  km h<sup>-1</sup>). We generally restricted surveys to weekdays to avoid increased recreational boat traffic on weekends. Each year we conducted two to eight replicate surveys for each route from early May to mid-August, prior to the onset of alligator nest hatch. At the beginning and end of each survey, we recorded the date, time, personnel present and their designated roles, and environmental conditions. We recorded air temperature ( $\pm 0.1^\circ\text{C}$ ) and wind speed ( $\pm 0.1$  km h<sup>-1</sup>) using a Kestrel 4000 weather meter, and measured water temperature (WT) ( $\pm 0.1^\circ\text{C}$ ) at approximately 3.2-km intervals using YSI EcoSense 300A with a 1-m probe. While conducting each survey, we recorded waypoints for our start and end locations, water measurement sites, alligator locations, and route deviations using a GPS unit (Garmin GPSMap 62).

During each survey, the boat traveled 5–24 km h<sup>-1</sup> along the river centerline as two personnel (observers)

shined spotlights (Brinkman Q-Beam Max Million III Spotlight,  $3 \times 10^6$  candlepower) into the adjacent water to detect alligator eyeshine (Bayliss, 1987), which reflects a distinct red-orange color from the tapetum lucidum. Each survey used two or more trained observers to detect eyeshine (see Lawson, 2019 for additional details regarding observer roles and training). When safe and logistically feasible, we approached observed alligators ( $\geq 10$ -m distance) to estimate snout length and assign individuals into one of six size classes (Table 1) based on TL: (1) hatchling:  $\leq 30$  cm; (2) juvenile: 30–121 cm; (3) sub-adult: 122–182 cm; (4) small adult: 183–243 cm; (5) large adult: 244–304 cm; or (6) bull:  $\geq 305$  cm. Size classifications were assigned based on an allometric relationship between snout length and TL (Chabreck, 1966), where 2.54 cm (1 in.) snout length equates to 30 cm (1 ft) TL. When a size classification could not be confidently made, the individual was classified as either one of two general age classes that approximately distinguish reproductively mature from immature animals, that is, “unknown adult” ( $\geq 183$ -cm TL) or “unknown immature” ( $< 183$ -cm TL). Because of their correspondence with age, we refer to these groupings as age classes for ease of presentation. If the alligator could not be confidently placed into any size or age category, we classified the alligator as “unknown.”

**TABLE 1** Summary information for American alligators (*Alligator mississippiensis*) by size class and sex.

| Size class, <i>j</i> | Name         | TL<br>range (cm) | Female proportion,<br>FP <sub><i>j</i></sub> (mean ± SD) | Sex | SVL<br>range (cm) | Growth<br>prob., ψ <sub><i>j</i></sub> <sup>a</sup> |
|----------------------|--------------|------------------|--|-----|-------------------|---|
| Immature             |              |                  |  |     |                   |   |
| 1                    | Hatchlings   | ≤30              | 0.72 ± 0.02  | F   | ≤15.51            | 1.00  |
|                      |              |                  |  | M   | ≤15.60            | 1.00  |
| 2                    | Juveniles    | 31–121           | 0.37 ± 0.02  | F   | 15.51–63.03       | 0.16  |
|                      |              |                  |  | M   | 15.60–63.40       | 0.17  |
| 3                    | Subadults    | 122–182          | 0.47 ± 0.02  | F   | 63.03–94.55       | 0.19  |
|                      |              |                  |  | M   | 63.40–95.10       | 0.26  |
| Mature               |              |                  |  |     |                   |   |
| 4                    | Small adults | 183–243          | 0.47 ± 0.07  | F   | 94.55–126.06      | 0.09  |
|                      |              |                  |  | M   | 95.10–126.80      | 0.19  |
| 5                    | Large adults | 244–304          | 0.35 ± 0.10  | F   | 126.07–157.58     | 0.01  |
|                      |              |                  |  | M   | 126.80–158.50     | 0.12  |
| 6                    | Bulls        | ≥305             | 0.00   | F   | ≥157.58           | 0.00  |
|                      |              |                  |  | M   | ≥158.50           | 0.00  |

*Note:* Size classes were divisions of total length (TL), the distance from snout tip to tail tip. Ranges of TL were the basis of classifying detected alligators during nightlight surveys conducted in coastal South Carolina, USA (2011–2016). In a mark-recapture-recovery study at the Tom Yawkey Wildlife Center (Figure 1; 1979–2017), assignments into TL size classes were based on a measurement of snout-vent length (SVL), the distance from the snout tip to the vent posterior, expressed as TL through a sex-specific allometric relationship between SVL and TL (Wilkinson et al., 2016). Growth probability (prob.) reflects the sex-specific probability of an individual in size class *j* at time *t* transitioning to *j* + 1 at *t* + 1, conditioned on survival.

Abbreviations: F, female; M, male.

<sup>a</sup>Growth probabilities for *j* = 2, ..., 5 were estimated through Markov chain Monte Carlo simulation (Appendix S3), whereas all others were fixed values.

## Auxiliary data

We used breeding and nesting productivity data from multiple studies conducted in coastal South Carolina from 1980 to 1982 (Wilkinson, 1983), and sex ratio information derived from the YWC mark-recapture data and previous studies (Rhodes & Lang, 1996; Woodward, 1996) to parameterize our models. Appendix S2 contains an expanded methodological description and auxiliary data summary.

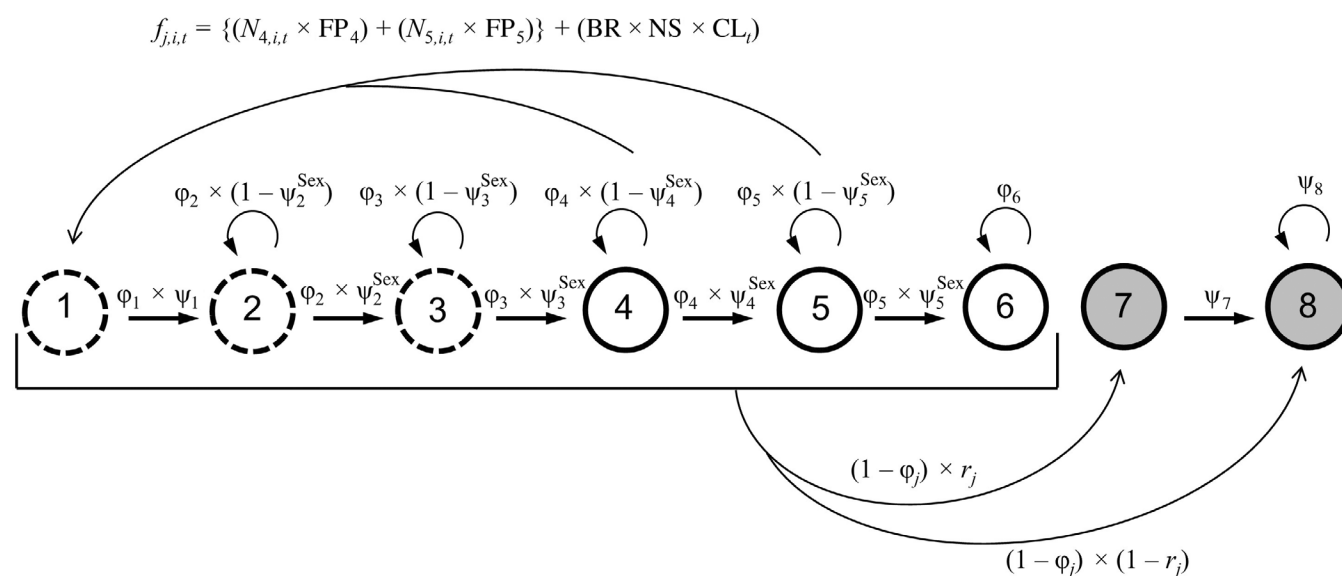
## Integrated population model

### Multistate mark-recapture-recovery model

We used a multistate mark-recapture-recovery model (Lebreton et al., 1999, 2009) to estimate size class-specific demographic parameters. Multistate models enable

state-specific estimation of apparent survival ( $\phi$ ), detection probability ( $p.m$ ), recovery probability ( $r$ ), and the probability of transitioning among states ( $\psi$ ) conditioned on survival. Our model included six live states (size classes) and two dead states (Figure 2), in which the parameters were estimated through a marginalized likelihood (Yackulic et al., 2020).

We constructed capture histories for all marked individuals from the YWC study population and assigned each individual to a size class used in the classification of nightlight survey counts. However, we inferred TL for size class assignment from measurements of SVL (Table 1), as alligators often lose portions of their tail as they age; classification by converting from SVL thus prevented the artifact of size shrinkage of animals in subsequent captures. Because the allometric relationship between SVL and TL (among individuals with intact tails) differed by sex in our study population (females:  $TL = SVL \div 0.517$ ; males:  $TL = SVL \div 0.520$ ; Wilkinson



**FIGURE 2** Life cycle diagram of the American alligator that served as the basis of the multistate mark-recapture-recovery estimation model and the abundance state process of the integrated population model. Each circle consists of a single state ( $j$ ). States 1–6 represent live states as defined by different size classes (Table 1), in which the dashed circles represent immature (nonbreeding) size classes (1, hatchlings; 2, juveniles; 3, subadults) and the solid circles reflect mature (breeding) size classes (4, small adults; 5, small adults; 6, bulls). The closed, solid gray circles reflect additional states recognized in the mark-recapture-recovery estimation model: A recently dead state ( $j = 7$ ) and an absorbing, terminal, dead state ( $j = 8$ ). The bolded  $\psi_j$  terms reflect growth or transition probabilities that were fixed to 1.0. Each year, surviving individuals ( $\phi_j$ ) could remain in the same size class ( $1 - \psi_j^{\text{Sex}}$ ; self-looping arrows) or graduate to the next sequential size class ( $\psi_j^{\text{Sex}}$ ; straight right-pointing arrows). Individuals that did not survive ( $1 - \phi_j$ ; lower arcs) could either enter the recently dead state if their carcass was recovered (e.g., incidental carcass discovery of a marked individual) with probability  $r$ , and then compulsorily transition to the absorbing state in the following year, or directly enter the absorbing state if their carcass was not encountered ( $1 - r$ ). Note that  $r$  was set to 0 for the hatchlings and juveniles because we did not observe any dead recoveries of these size classes. The upper arc arrows show the reproduction mechanism of the abundance state process as reproductive contributions of females in size classes 4 and 5. Fecundity ( $f_{j,i,t}$ ) is the product of size class and site-specific (survey route;  $i$ ) abundance at time  $t$  ( $N_{j,i,t}$ ); female proportion in the size class ( $FP_j$ ; Rhodes & Lang, 1996; Woodward, 1996); proportion of breeding females ( $BR$ ; Wilkinson, 1983); and nest survival ( $NS$ ) and the average annual clutch size ( $CL_t$ ) at the Tom Yawkey Wildlife Center (Wilkinson, 1983), summed for each reproductive size class. Alligators that emerge from the nest must survive 0.75 of the year to enter state 1 by the time of the subsequent nightlight survey.

et al., 2016), we created a series of SVL-based (in centimeters) size class thresholds for each sex (Table 1). For capture events in which SVL was not measured, we predicted SVL based on allometric relationships with other measurements taken or on estimated somatic growth from a previous capture, or we used TL directly if the tail was intact.

Captures of alligators at a size at which sex could not be determined through cloacal examination ( $TL < 120$  cm; Chabreck, 1963) were treated in one of three ways in the preparation of data for analysis. If the alligator was later captured or found dead at a size at which sex could be determined, the sex determined at that final encounter was assigned to all previous encounters. If the alligator was never reencountered at a size at which sex could be determined and if size class assignment at the time of capture was ambiguous without knowledge of the animal's sex (e.g., the size class assignment of an animal measuring 15.55-cm SVL is sex-dependent; Table 1), then the alligator was excluded from the analysis. However, if size class assignment at the time of capture was unambiguous, then sex was randomly assigned to all captures of the alligator by drawing a value from a Bernoulli distribution in which the success parameter represented the proportion of females for each size class from the literature (hatchlings: 0.72—Rhodes & Lang, 1996; juveniles 0.37—Woodward, 1996).

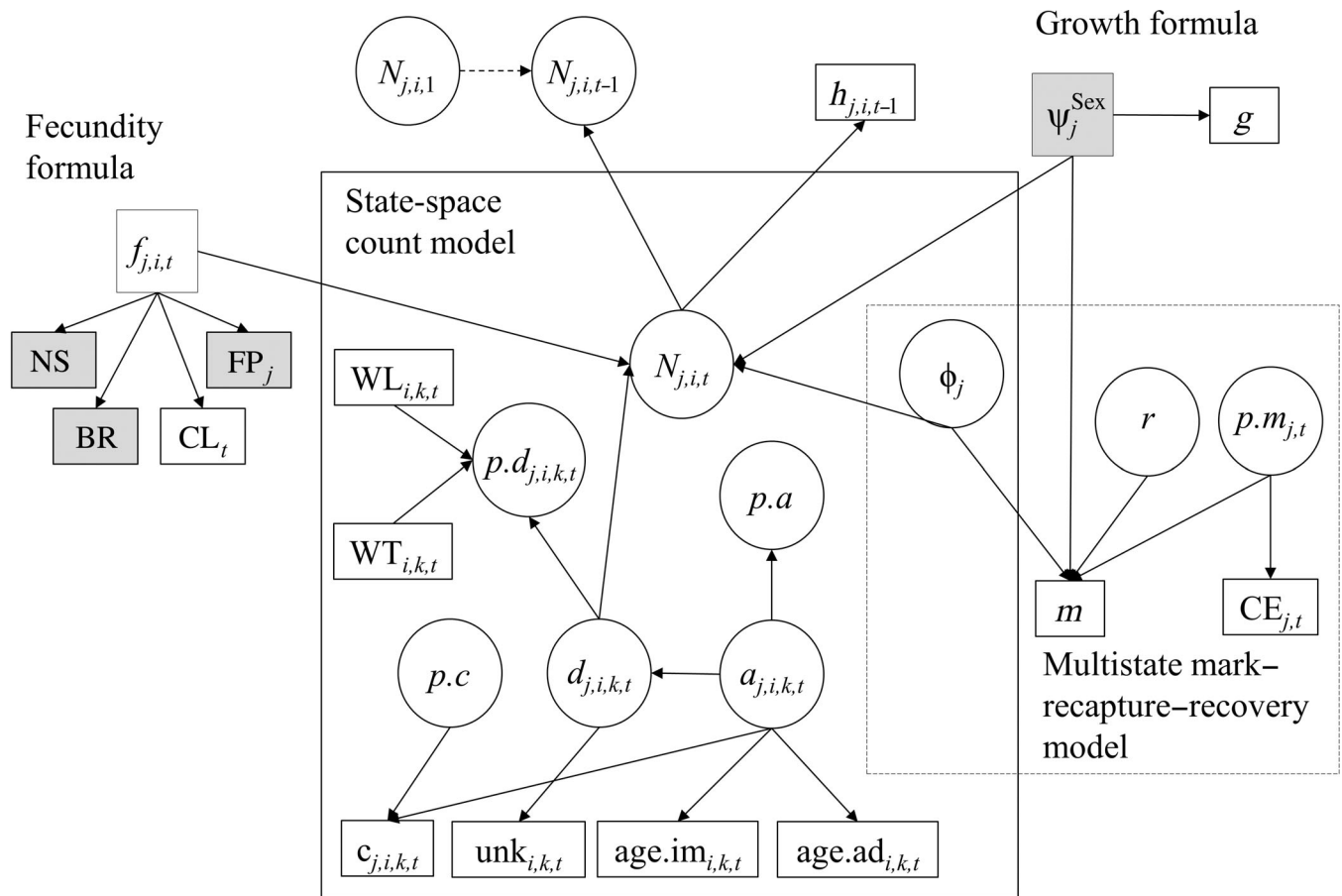
Mortality (recovery) observations were assigned to an observable, “recently dead” state in the year that they were detected, which allowed for correct accounting of the fact that the animal had lived up to that point. Animals either probabilistically (not observable) or deterministically (observed dead recoveries) transitioned to an absorbing “dead” state that persisted for all subsequent occasions in the animal's state history. Note that we only included mortality observations from incidental carcass encounters, adverse trapping events, or poaching in the multistate model, and we did not include public or private lands harvest records. Though YWC is closed to hunting, over the course of the study four individuals left the study area and were harvested in the private and public hunts, though these events were not reflected in the individual's capture history. As legal harvest was likely a negligible source of mortality of YWC alligators, we accounted for harvest in the IPM by incorporating the broadscale harvest data into the abundance model ( $h_{j,i,t-1}$  in Figure 3) rather than the multistate model. As a result, the multistate mark–recapture–recovery model estimates apparent survival, in which mortality and permanent emigration are confounded, that is reflective of a protected population, in which legal harvest exposure is greatly reduced, but not eliminated. Our model assumes that population vital rates were similar for YWC and our

two nightlight survey sites, with the exception of harvest outside YWC, which we modeled as additive to natural mortality (see *Abundance state process*).

Alligator somatic growth patterns differ between sexes (Wilkinson et al., 2016; Wilkinson & Rhodes, 1997); therefore, we parameterized transition (somatic growth) probabilities from each size class ( $j$ ) according to sex ( $\psi_j^{\text{Sex}}$ ). However, we captured relatively few hatchlings or juveniles for which we could eventually determine sex based on a later recapture (Appendix S1: Table S1b), leading us to assume that sex-specific transition probabilities for smaller size classes would be poorly estimated if derived solely within the multistate model. Therefore, in a separate analysis, we estimated sex-specific size class transition probabilities by fitting a somatic growth model to an expanded mark–recapture dataset and simulating growth of individual alligators (Appendix S3). Values from this simulation then served as fixed values of  $\psi_j^{\text{Sex}}$  in the multistate model (Table 1).

The state process component of our multistate framework represented a typical life cycle model in which individuals could initially be encountered in one of  $j = 1, \dots, 6$  size classes (Figure 2). From time  $t$  to  $t + 1$ , the state process allowed for four possibilities, in which an individual alive in size class  $j$  could survive with probability  $\phi_j$  and either (1) remain in the same size class with probability  $(1 - \psi_j^{\text{Sex}})$  or (2) transition to the  $j + 1$  size class with probability  $\psi_j^{\text{Sex}}$ . Alternatively, an individual could not survive ( $1 - \phi_j$ ) and either (3) transition into the recently dead state ( $j = 7$ ) in which they were recovered through a carcass discovery with probability  $r_j$ , or (4) transition to the absorbing dead state ( $j = 8$ ) in which they were not recovered ( $1 - r_j$ ). The probability of remaining within the bull size class ( $j = 6$ ), conditioned on survival, was fixed to 1.0, as were transitions from hatchling to juvenile size class (given survival), the recently dead state to the absorbing dead state, and the probability of remaining in the absorbing dead state. The structure of our model rendered some transitions impossible, including “skipping” a size class (i.e., nonconsecutive growth transitions), “shrinking” (i.e., moving from larger to smaller size classes), or “resurrection” (i.e., moving from a dead state to one of the live states). Lastly, we used an identity link to model time-invariant survival probability ( $\phi_j$ ) for each specific size class and for recovery probability ( $r$ ) for size classes 3–6, both of which used vague priors from a uniform distribution (0,1). The full transition matrix is provided in Appendix S4.

For the observation process component of the multistate model, an individual alive in size class  $j$  could either be detected with probability  $p.m_j$  or not detected with probability  $1 - p.m_j$ . We placed additional constraints on both the process and state components to improve



**FIGURE 3** Directed acyclic graph of an integrated population model (IPM) for American alligators in Georgetown County, SC, USA. Parameters for which we computed posterior distributions are represented by circles, whereas observed data and extrinsic variables (nonupdated; shaded gray) are rectangular, with indexing for size class ( $j$ ), site (survey route;  $i$ ), temporal survey replicate ( $k$ ), and year ( $t$ ). The growth formula represents an alligator growth dataset ( $g$ ; Wilkinson et al., 2016) that was used to derive transition probabilities for sex-specific growth ( $\psi_j^{Sex}$ ) outside of the IPM framework (Appendix S3). The large, dashed box represents the multistate mark-recapture-recovery model that used a mark-recapture dataset with dead recoveries ( $m$ ),  $\psi_j^{Sex}$ , and a capture effort covariate ( $CE_{j,t}$ ) to estimate probabilities of recovery ( $r$ ), detection ( $p.m_{j,t}$ ), and apparent survival ( $\phi_j$ )—a shared parameter within the integrated likelihood for the state-space abundance model. Input to the fecundity formula included the proportion of females in each size class ( $FP_j$ ; Rhodes & Lang, 1996; Woodward, 1996), the proportion of breeding females ( $BR$ ; Wilkinson, 1983), and nest success ( $NS$ ) and average annual clutch size ( $CL_t$ ) at the Tom Yawkey Wildlife Center (Wilkinson, 1983). The bottom row of boxes within the state-space model reflect different types of nightlight survey data: Sized ( $c_{j,i,k,t}$ ), Aged (immatures:  $age.im_{i,k,t}$ , adults:  $age.ad_{i,k,t}$ ), or Unknown age ( $unk_{i,k,t}$ ). These data were used to estimate two latent quantities specific to size class, the number of individuals encountered of known or unknown size (Detections;  $d_{j,i,k,t}$ ) and those encountered with size determined to at least immature/adult specificity (Aggregated;  $a_{j,i,k,t}$ ), with their associated detection probabilities ( $p.d_{j,i,k,t}$ ) and ( $p.a$ ). Detection probability  $p.c$  was conditioned on the size-classified counts. We modeled the effects of water level ( $WL_{i,k,t}$ ) and temperature ( $WT_{i,k,t}$ ) as survey replicate-level covariates on  $p.d_{j,i,k,t}$ . The true number of individuals in each size class ( $N_{j,i,t}$ ) was estimated in the process component of the state-space model by fecundity ( $f_{j,i,t}$ ),  $\psi_j^{Sex}$ , and  $\phi_j$ , as well as the previous year's true number of individuals ( $N_{j,i,t-1}$ ) and harvest ( $h_{j,i,t-1}$ ). We note that the true number of individuals in the first timestep ( $N_{j,i,1}$ ) is not part of the state-space model, so the dashed arrow between  $N_{j,i,1}$  and  $N_{j,i,t-1}$  reflects these collapsed dynamics.

parameter estimation and model convergence. We fixed  $r_1$ ,  $r_2$ ,  $p.m_1$ , and  $p.m_2$  to zero because the variation in CE for the smallest immature size classes ( $j \leq 2$ ) over our study precluded us from recapturing tagged alligators in the hatchling or juvenile state in subsequent occasions, and we did not observe any dead recoveries of these size classes. We encountered relatively few dead alligators in the larger size classes ( $j \geq 3$ ; Appendix S1: Table S1);

therefore, we constrained the  $r_j$  for those size classes to a single recovery parameter  $r$ . Due to the inconsistent CE over time (Appendix S1: Table S2), we did not consider temporal- or individual-level (beyond size class) variation in the survival parameters of the state process, though we did consider a covariate that allowed temporal as well as size class specificity of detection probability ( $p.m_j$ ).

## Count observation model

We developed a state-space model to estimate size class-specific abundance and detection probability, in which the observation component incorporated the count data from temporally replicated nightlight surveys. Nightlight survey data were comprised of three different observation types that represented increasing levels of demographic resolution: (1) “Unknown” includes individuals that were detected at site  $i$  during survey replicate  $k$  in year  $t$ , but could not be placed into any size or age class ( $\text{unk}_{i,k,t}$  in Figure 3); (2) “Aged” includes observations in which the individual was assigned to either the immature (size class  $j$  unknown but  $\leq 3$ ;  $\text{age.im}_{i,k,t}$  in Figure 3) or mature (size class  $j$  unknown but  $\geq 4$ ;  $\text{age.ad}_{i,k,t}$  in Figure 3; Table 1) age class; and (3) “Sized” includes observations in which the individual was assigned to one of the six size classes ( $c_{j,i,k,t}$  in Figure 3).

To estimate size class-specific abundance, we created three submodels in which numbers of alligators detected at increasingly finer demographic resolution were probabilistically linked to numbers (possibly latent) at coarser resolutions. The Detections level, the coarsest level of resolution, included all three observation types—*Unknown*, *Aged*, and *Sized*. We defined the latent quantity  $d_{j,i,k,t}$  as the number of alligators detected at site  $i$  during replicate  $k$  in year  $t$  that belonged to size class  $j$ . This quantity is generally unobservable because not all alligators detected that belong to size class  $j$  can be assigned to size class  $j$ . We modeled  $d_{j,i,k,t}$  as the outcome of a binomial process with success probability  $p.d_{j,i,k,t}$  and the number of trials  $N_{j,i,t}$ , that is, the abundance of alligators in size class  $j$  at site  $i$  at time  $t$ :

$$d_{j,i,k,t} \sim \text{binomial}(N_{j,i,t}, p.d_{j,i,k,t}). \quad (1)$$

Thus,  $p.d_{j,i,k,t}$  is the overall detection probability for individuals of size class  $j$ , regardless of whether an individual of that class can be assigned as such. The Aggregate level, the next finest level of demographic resolution, considers the *Aged* and *Sized* observation types. We defined the latent quantity  $a_{j,i,k,t}$  as the number of alligators assigned either to a size or age class that belonged to size class  $j$ . Again,  $a_{j,i,k,t}$  is generally unobservable because it includes alligators belonging to size class  $j$  that cannot be determined as such. We modeled  $a_{j,i,k,t}$  as the outcome of a binomial process with success probability  $p.a$  and index  $d_{j,i,k,t}$ :

$$a_{j,i,k,t} \sim \text{binomial}(d_{j,i,k,t}, p.a). \quad (2)$$

Parameter  $p.a$  is the probability that an individual, conditional on its detection, can be placed into either an aggregated age class ( $\text{age.im}_{i,k,t}$ ,  $\text{age.ad}_{i,k,t}$  in Figure 3) or a

specific size class. Lastly, the Classified level, the finest level of demographic resolution, includes only the *Sized* observations. Here, the count of individuals for a particular size class, site, and occasion,  $c_{j,i,k,t}$ , is a directly observable quantity. We modeled  $c_{j,i,k,t}$  as the outcome of a binomial process with success probability  $p.c$  and index  $a_{j,i,k,t}$ :

$$c_{j,i,k,t} \sim \text{binomial}(a_{j,i,k,t}, p.c). \quad (3)$$

Parameter  $p.c$  is the probability that an individual, conditional on having been identified to at least an age class, can be placed into a specific size class. Thus, through the parametric linkages among models, all three observation types ultimately inform size class-specific population abundance. We did not consider size, site, survey, or temporal variation for the detection probabilities for the Aggregate and Count levels; thus, these parameters lack the size ( $j$ ), site ( $i$ ), survey ( $k$ ), and time ( $t$ ) indexing.

We used a series of sum constraints within JAGS to link the raw observations to the quantities in Equations (1)–(3) above (Plummer, 2017):

$$\text{unk}_{i,k,t} = \sum_{j=1}^6 d_{j,i,k,t} - \sum_{j=1}^6 a_{j,i,k,t}, \quad (4)$$

$$\text{age.im}_{i,k,t} = \sum_{j=1}^3 a_{j,i,k,t} - \sum_{j=1}^3 c_{j,i,k,t}, \quad (5)$$

$$\text{age.ad}_{i,k,t} = \sum_{j=4}^6 a_{j,i,k,t} - \sum_{j=4}^6 c_{j,i,k,t}. \quad (6)$$

In Equation (4), the number of Unknown observations ( $\text{unk}_{i,k,t}$ ) must equal the difference between number of Detection observations, which includes all three data categories (Unknown, Aged, and Sized), and the number of Aggregate observations (Aged and Sized only). Equation (5) constrains the number of  $\text{age.im}_{i,k,t}$  observations, which must equal the number of Aggregate immatures ( $j \leq 3$ ) minus Classified immatures. Similarly, in Equation (6), the number of  $\text{age.ad}_{i,k,t}$  observations must equal the number of Aggregate adults ( $j \geq 4$ ) minus Classified adults.

Lastly, while our model accounts for imperfect detection, it assumes no errors in age- or size-class assignments, though we note that such errors are likely to influence estimates resulting in imprecision and/or bias (Kellner & Swihart, 2014). While we cannot verify the absence or composition of size classification (over- or underestimation) errors in our data, observers were not permitted to size alligators until sufficiently trained (see Lawson, 2019 for details regarding observer training).

## Abundance state process

For the state process component of our state-space model, we integrated the likelihoods for abundance ( $N_{j,i,t}$ ) from the observation component of the state-space model and apparent survival parameters ( $\phi_j$ ) from the multistate mark-recapture-recovery model (Figure 3). To complete the IPM specification, we parameterized a fecundity formula using mean annual clutch size data from YWC ( $CL_t$ ) and extrinsic reproductive variables (Appendix S2: Table S1) that were stochastically sampled from beta distributions in each iteration to incorporate parametric uncertainty (Appendix S2: Table S1). Within our life cycle model (Figure 2), only females in size classes 4 and 5 could contribute to population growth. Though females (F) were allowed to enter size class 6 (i.e.,  $\psi_5^F > 0$ ), we never documented a female with a measurement of SVL that would place it in size class 6 (Appendix S1: Table S2). As such, we defined annual fecundity ( $f_{i,t}$ ) for site  $i$  in year  $t$  as:

$$f_{i,t} = \{(N_{4,i,t} \times FP_4) + (N_{5,i,t} \times FP_5)\} \times (BR \times NS \times CL_t), \quad (7)$$

in which the number of individuals in each of size classes 4 and 5 is multiplied by the proportion of females for that respective size class ( $FP_j$ ; Woodward, 1996) to derive the number of females within the breeding size classes. The number of females is multiplied by the proportion of breeding females (BR), apparent nest survival (NS) rate, and average annual clutch size ( $CL_t$ ) for the YWC population. We used the same subcomponents of fecundity for females in size classes 4 and 5 because our auxiliary data did not reflect size-related differences (Appendix S2). Moreover, in a sensitivity analysis of American crocodile (*Crocodylus acutus*) life-history parameters, Briggs-Gonzalez et al. (2017) reported that age-specific variation in fecundity had minimal impact on the population growth rate.

We modeled the number of young-of-the-year hatchlings (YOY; individuals hatched in the current year) on occasion  $t$  at site  $i$  as a Poisson outcome, with fecundity from the current year as the mean and variance term:

$$YOY_{i,t} \sim \text{Poisson}(f_{i,t}).$$

Because we completed all nightlight surveys before hatching in the current nesting season, we never encountered YOY hatchlings. Therefore, all hatchlings ( $j = 1$ ) encountered during nightlight surveys in year  $t$  were hatched in year  $t - 1$  and survived for approximately six to nine months, and both  $f$  and YOY are

modeled as functions of conditions in year  $t - 1$ , not year  $t$ . The number of individuals in the hatchling size class ( $N_1$ ) observed during surveys in year  $t$  at site  $i$  is binomially distributed as a function of the nine-month hatchling survival rate and YOY in year  $t - 1$ :

$$N_{1,i,t} \sim \text{binomial}(YOY_{i,t-1}, \phi_1^{0.75}),$$

$$s_{1,i,t} \sim \text{binomial}(N_{1,i,t-1}, \phi_1).$$

We assume that the survival rate of hatchlings to the juvenile stage,  $\phi_1$ , also applies to YOY alligators prorated over a nine-month timescale.

To model transitions into all other size classes  $j \geq 2$ , we used a series of binomial distributions to implement the survival and somatic growth processes. First, we modeled the number of surviving individuals in year  $t$  ( $s_{j,i,t}$ ) as a stochastic outcome of a binomial draw based on the size class-specific survival probability ( $\phi_j$ ) and the total number of individuals to survive harvest in the previous year:

$$s_{j,i,t} \sim \text{binomial}(N_{j,i,t-1} - h_{j,i,t-1}, \phi_j), \quad (8)$$

in which  $N_{j,i,t-1}$  denotes the number of individuals alive prior to harvest in year  $t - 1$  and  $h_{j,i,t-1}$  is the number of individuals harvested in size class  $j$  at site  $i$  in  $t - 1$ . Size classes in our study population were exposed to different levels of harvest pressure, as public harvest regulations for alligators in South Carolina prohibit the take of individuals <120-cm TL. Therefore, we assumed  $h_{j,i,t} = 0$  for  $j \leq 3$  in Equation (8). We note that Equation (8) assumes an additive harvest mortality structure, as opposed to compensatory harvest mortality in which harvested individuals are assumed to represent a “surplus” of individuals that were likely to die over the same time period (Williams et al., 2002). We believe the additive structure used in the model is appropriate because when given the opportunity, alligator hunters generally select for relatively larger size classes that have the highest survival rates, based on the few existing crocodilian demographic studies (Briggs-Gonzalez et al., 2017). Moreover, multiple historical examples demonstrate that crocodilian populations are relatively sensitive to overharvest consistent with additive mortality, particularly with a fixed-quota harvest strategy as used in South Carolina (Bradshaw et al., 2006; Marioni et al., 2021; SCDNR, 2017; U.S. Fish and Wildlife Service, 1967; Webb et al., 1984).

Next, the number of individuals growing (transitioning) from size class  $j$  to  $j + 1$  was distributed binomially:

$$g_{j,i,t} \sim \text{binomial}\left(s_{j,i,t}, \left(\text{FP}_j \times \psi_j^F + (1 - \text{FP}_j) \times \psi_j^M\right)\right), j \geq 2,$$

in which the probability of growth was the sum of the size- and sex-specific growth probabilities ( $\psi_j^{\text{Sex}}$ ) multiplied by their respective sex proportion ( $\text{FP}_j$  for females and  $1 - \text{FP}_j$  for males) from the number of surviving individuals ( $s_{j,i,t}$ ). Because the transition into the juvenile stage by surviving hatchlings is compulsory, we model transition probability of hatchlings simply as follows:

$$g_{1,i,t} \sim \text{binomial}(N_{1,i,t-1}, \phi_1).$$

Finally, the total number of individuals for size class  $j$  is the sum of growing individuals from  $j - 1$  ( $g_{j-1,i,t}$ ) and the total of nongrowing (retained) individuals from size class  $j$ , determined by subtraction of growing individuals ( $g_{j,i,t}$ ) from the total that survived ( $s_{j,i,t}$ ):

$$N_{j,i,t} = g_{j-1,i,t} + (s_{j,i,t} - g_{j,i,t}). \quad (9)$$

Lastly, we were interested in describing general population trends within each site. Therefore, we obtained  $N_{i,t}^{\text{TOT}}$ , the sum of all size classes ( $j = 1, \dots, 6$ ) for site  $i$  at time  $t$ , as a derived parameter.

## Covariate structures and selection

Our model included the effects of three covariates. First, we created a covariate for the mark–recapture–recovery detection probability ( $p.m_{j,t}$ ) to account for temporal variation in CE, which varied in both duration (i.e., number of capture days) and intensity (i.e., number of capture methods used or personnel). Unfortunately, traditional metrics of CE or trap days were not consistently recorded. Experiences by the authors and other principal investigators on the YWC study indicated that at least one alligator was captured each field day (P. M. Wilkinson & T. R. Rainwater, personal communications). Therefore, for each day that an alligator was captured, we assigned a “1” if only one capture technique was used, or a “2” if two or more techniques were used. We summed the capture day scores within each year and z-standardized (mean: 0.0, SD: 1.0) the scores across years.

Both WL and WT are known to influence detection probability of alligators in nightlight surveys (Fujisaki et al., 2011; Waddle et al., 2015); therefore, we modeled these effects for the count-based detection probability ( $p.d_{j,i,k,t}$ ). We used the average river gauge height in feet ( $\pm 0.01$ ) during the survey as a measure of WL. Due to structural and hydrological differences between the two

survey sites, we z-standardized WL within each river for a more generalizable interpretation of results. We used the YSI measurements recorded during each survey to determine the average WT ( $\pm 0.1^\circ\text{C}$ ), and we z-standardized across both routes.

All four detection probabilities ( $p.m_{j,t}$ ,  $p.d_{j,i,k,t}$ ,  $p.a$ , and  $p.c$ ) were modeled with a logit link, though they differed in the number of covariates and other constraints:

$$\text{logit}(p.m_{j,t}) = \beta_j + \beta^{\text{CE}} \times \text{CE}_t,$$

$$\beta_j \sim \text{normal}(0, 0.37),$$

where  $\beta_j$  denotes the baseline mark–recapture detection probability for each size class, and  $\beta^{\text{CE}}$  is the effect of the CE, assumed common across size classes. We held the  $p.a$  and  $p.c$  terms constant across size classes, with no covariate effects:

$$\text{logit}(p.a) = \beta^a,$$

$$\text{logit}(p.c) = \beta^c,$$

$$\beta^a, \beta^c \sim \text{normal}(0, 0.37).$$

For the  $p.d$  term, we used a different formula for hatchlings compared with the other size classes. Alligator young are known to remain in groups with their mother over the first two years of life (McIllhenny, 1935). Hatchlings occurring in groups could violate the assumption of independent detections required of  $N$ -mixture models (Royle, 2004), which is known to bias parameter estimates (Martin et al., 2011). We therefore modeled hatchling detection ( $p.d_{1,i,k,t}$ ) as a beta-binomial process:

$$p.d_{i,k,t} \sim \text{beta}(\alpha_{i,k,t}, \beta_{i,k,t}),$$

$$\alpha_{i,k,t} = \theta \times p.d_{1,i,k,t},$$

$$\beta_{i,k,t} = \theta \times (1 - p.d_{1,i,k,t}),$$

in which  $\theta$  is the exponentiated form of a normally distributed variable with a mean of zero and 0.37 SD. We included a size class trend term for count detection that was not included in the covariate selection procedure:

$$\text{logit}(p.d_{j,i,k,t}) = \beta^d + \beta^{d.T} \times j + \beta^{\text{WL}} \times \text{WL}_{i,k,t} + \beta^{\text{WT}} \times \text{WT}_{i,k,t},$$

$$\beta^d, \beta^{d.T} \sim \text{normal}(0, 0.37),$$

where  $\beta^d$  reflects the baseline detection probability,  $\beta^{d,T}$  is the size class ( $j$ ) trend term, and  $\beta^{WL}$  and  $\beta^{WT}$  are the effects of WL and WT, respectively. All terms in the detection models were given a Jeffreys prior, which is weakly informative on the logit scale.

We used indicator variable selection with a “slab and spike prior” to evaluate the potential influence of the CE covariate on detection probability  $p.m_{j,t}$  and the WL and WT covariates on detection probability  $p.d_{j,i,k,t}$  (Hooten & Hobbs, 2015; Miller, 2002). Indicator variable selection is useful for assessing the degree of support for each set of candidate predictors (Hooten & Hobbs, 2015). Using this approach, the beta coefficient for covariate  $i$  ( $\beta_i$ ) is defined as the product of a binary indicator variable ( $w_i$ ) and a regression coefficient  $\gamma_i$ :

$$\beta_i = w_i \times \gamma_i,$$

$$w_i \sim \text{Bernoulli}(p.w_i),$$

$$p.w_i \sim \text{uniform}(0, 1),$$

$$\gamma_i \sim \text{normal}(0, \sigma_\gamma).$$

In each Markov chain Monte Carlo (MCMC) iteration, the  $i$ th covariate enters the model as a predictor when  $w_i = 1$  and is excluded from the model when  $w_i = 0$ . Thus, the posterior mean of  $w_i$  roughly reflects the probability of the covariate's inclusion in the model. As an additional metric of covariate support, we compared the relative “model weights,” in which the inclusion or exclusion of covariates in specific combinations induces eight unique models ( $2^3 = 8$  models;  $m_{1-8}$  in Appendix S4: Table S1) and the weights reflect the proportion of iterations in which the model (covariate combination) was selected. A complete list of model parameters, their definitions, and priors is given in Appendix S4: Table S2, whereas a summary of extrinsic variables and their stochastic distributions is provided in Appendix S2: Table S1.

## Model fitting

We used Bayesian inference to estimate all IPM parameters and derived quantities; to calculate their posterior distributions, we used MCMC in JAGS 4.3.0 (Plummer, 2017) run from the jagsUI package (Kellner, 2021) in program R (R Core Development Team, 2019). We ran three chains with a 50,000-iteration adaptive phase, followed by 600,000 iterations with the first 20,000 discarded as burn-in, and a thinning

rate of 40; this yielded a combined chain of 14,500 MCMC samples. We used noninformative wide priors for all parameters and checked for convergence by visually inspecting the trace plots and confirming that the Gelman–Rubin diagnostic statistic ( $\hat{R}$ ; Gelman & Rubin, 1992) satisfied our accepted convergence threshold ( $\hat{R} < 1.10$ ). Parameter estimates are presented as the median of the posterior distribution with their 95% credible intervals, unless otherwise noted.

## RESULTS

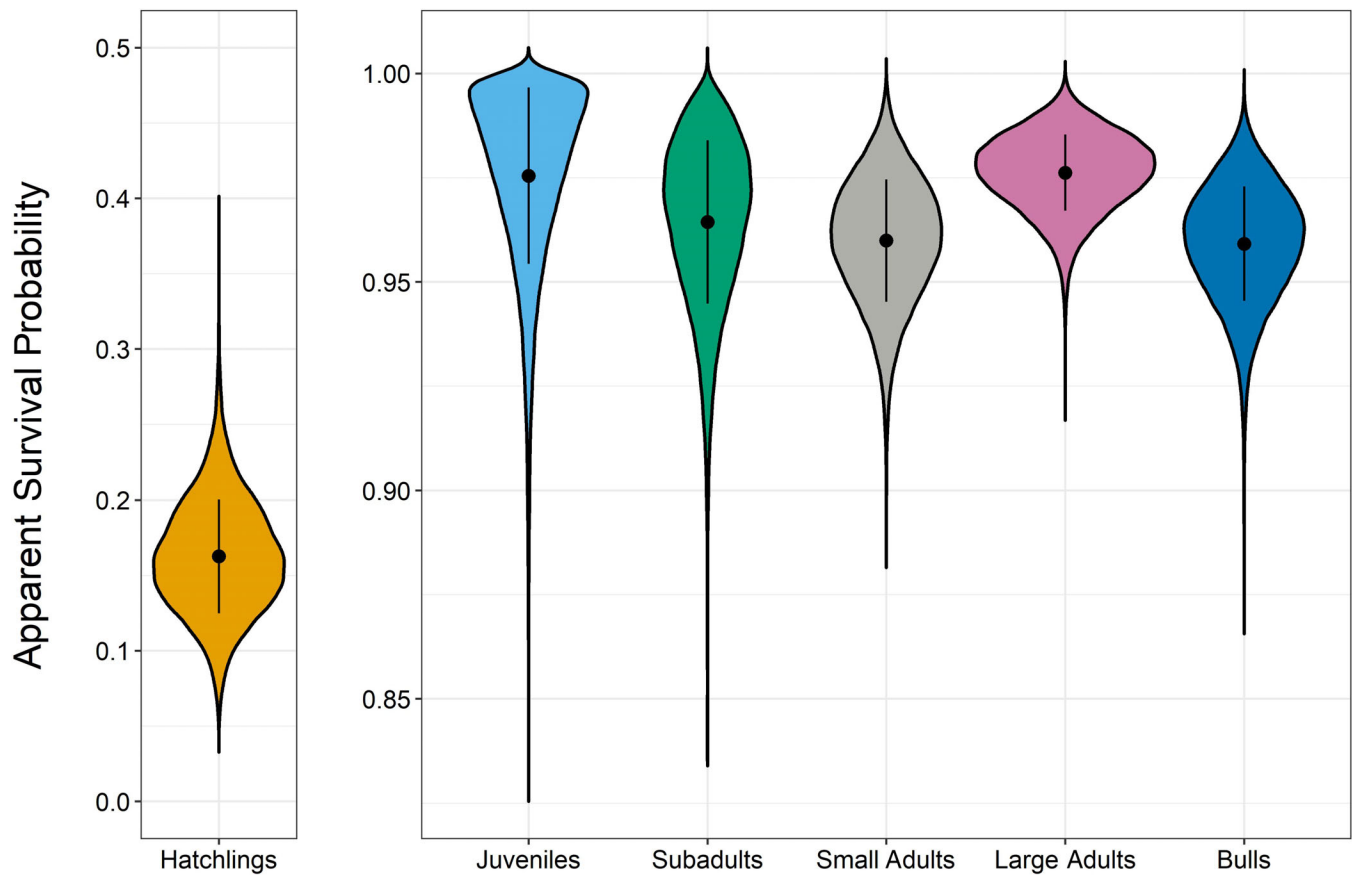
### Multistate mark–recapture–recovery

Our mark–recapture–recovery dataset was comprised of 557 individuals of known-sex (females: 275; males: 282; Appendix S1) and 282 unknown-sex individuals that were randomly assigned to a sex prior to data analysis. The majority of unknown-sex individuals were hatchlings captured prior to 1981 (Appendix S1: Tables S1 and S2). Apparent survival was lowest for the hatchling size class (0.160; 95% CI 0.093–0.242) and was relatively high and similar for all other size classes (Figure 4). Among the nonhatchling size classes, apparent survival was highest for juveniles (0.981; 0.921–0.999), followed by large adults (0.977; 0.956–0.992), subadults (0.967; 0.919–0.994), small adults (0.960; 0.929–0.986), and bulls (0.960; 0.930–0.983). Apparent survival estimates were more precise for size classes that had more capture observations (Figure 4; Appendix S1: Table S1).

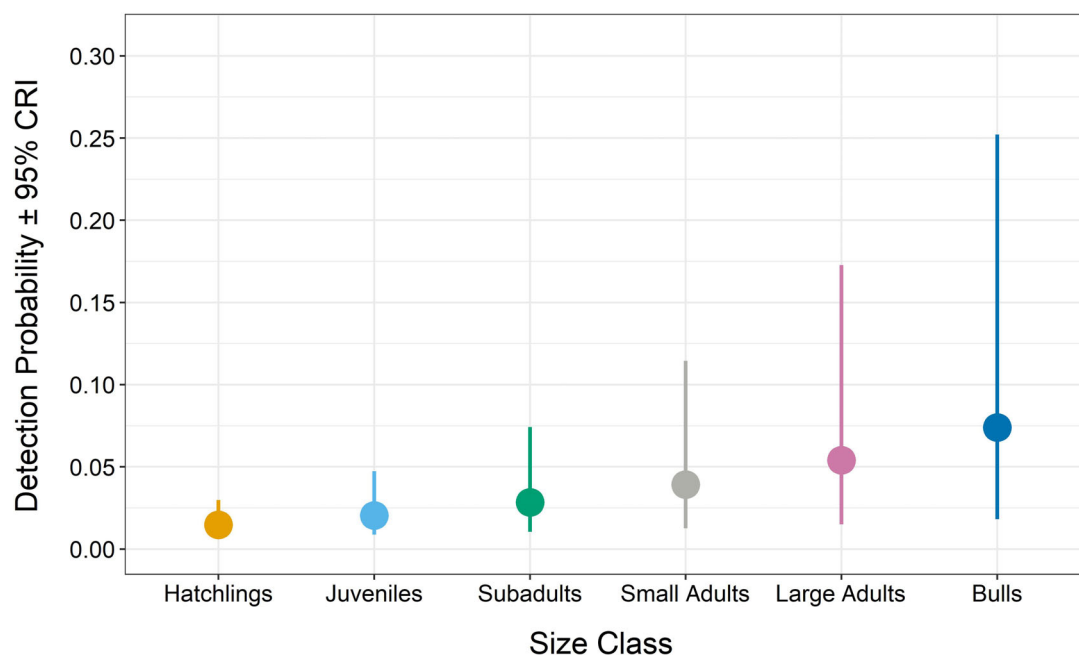
The size mark–recapture–recovery detection probabilities ( $p.m_{j,t}$ ) at mean CE were highest for large adults (0.080; 0.063–0.101), followed by small adults (0.074; 0.052–0.103), bulls (0.046; 0.030–0.069), and lowest for subadults (0.025; 0.008–0.061). The CE covariate had a high probability of inclusion ( $\omega_{CE} = 1.00$ ; Appendix S4: Table S1) and a positive effect on  $p.m_{j,t}$  ( $\beta^{CE} = 0.870$ ; 0.689–1.054), indicating a 2.39-fold increase in odds of detection per standard deviation increase in the covariate. Recovery probability for size classes  $j > 2$  was estimated to be 0.160 (0.092–0.260).

### Abundance state-space model

The two count detection covariates were WL ( $WL_{i,k,t}$  in Figure 3) and WT ( $WT_{i,k,t}$ ). We found a positive trend across size classes for  $p.d_{j,i,k,t}$  ( $\beta^T = 0.336$ ; 0.185–0.479; Figure 5) and strong support for the inclusion of both WL ( $\omega_{WL} = 0.81$ ; Appendix S4: Table S1) and WT ( $\omega_{WT} = 1.0$ ). WL had a negative effect ( $\beta^{WL} = -0.167$ ; -0.218 to -0.115) on  $p.d_{j,i,k,t}$ , whereas WT was positive



**FIGURE 4** Posterior distributions of American alligator apparent survival probabilities ( $\phi$ ) for six size classes within the protected Tom Yawkey Wildlife Center in coastal South Carolina, USA, 1979–2017. The solid black circles and error bars indicate the mean and standard deviation; note the different y-axis scales in each panel (left: hatchlings, right: nonhatchlings).



**FIGURE 5** Estimated size class-specific ( $j$ ) American alligator detection probabilities ( $p.d_j$ ) during nightlight surveys in coastal South Carolina from 2011 to 2017. CRI, credible interval.

( $\beta^{\text{WT}} = 0.211$ ; 0.152–0.271). Collectively, the model containing all covariate terms ( $m_8$ ; CE, WT, and WL) received the largest share of model weight ( $\omega$ : 0.81; Appendix S4: Table S1). The probability of size class determination given the ability to distinguish between immature and adult ( $p.c$ : 0.795; 0.762–0.825) was greater than the probability of being able to discern either age or size given detection ( $p.a$ : 0.379; 0.356–0.403).

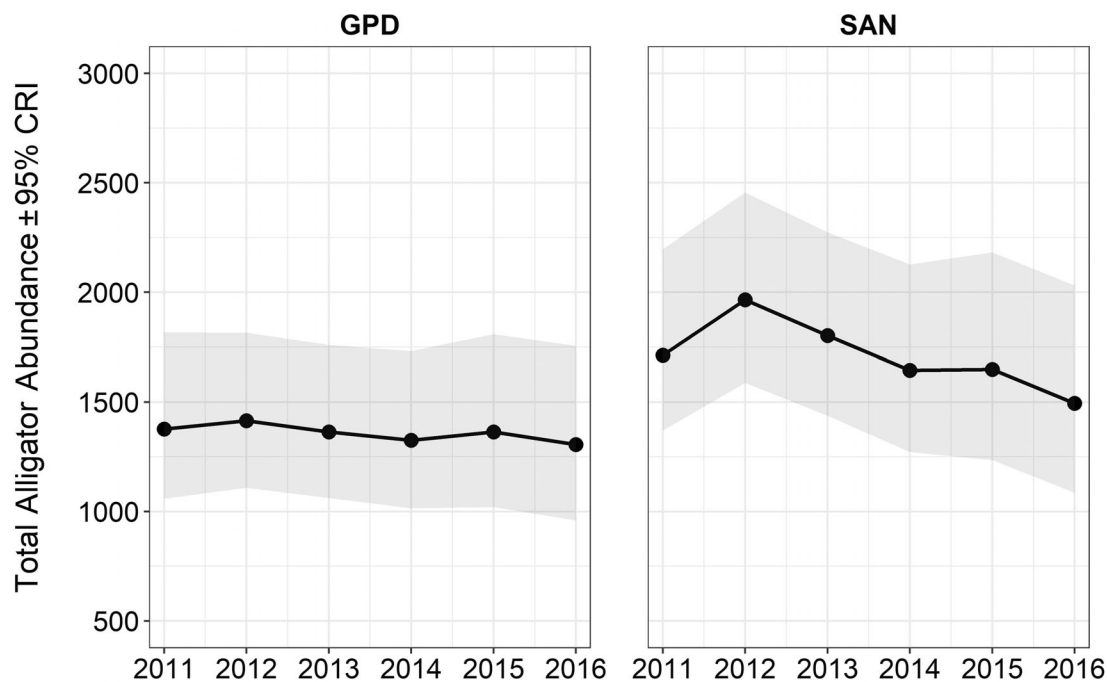
Total alligator abundance ( $N_{i,t}^{\text{TOT}}$ ) for each site showed subtle contrasting patterns (Figure 6). In GPD, total abundance remained relatively stable, varying between extremes of 1305 (959–1755; 2016) and 1414 (1108–1815; 2012) alligators, whereas SAN exhibited a clear peak in 2012 (1965; 1588–2456) followed by a consistent annual decline through 2016 (1493; 1086–2031). Both the average estimated density and total individuals (2011–2016) appeared higher across years for SAN (22.28 alligators  $\text{km}^{-1}$ ;  $\bar{N}_{i,t}^{\text{TOT}}$ : 1711; 1331–2211) compared with GPD (5.89 alligators  $\text{km}^{-1}$ ;  $\bar{N}_{i,t}^{\text{TOT}}$ : 1358; 1037–1781), despite the latter site containing more habitat (38.4 vs. 12.8 river km).

At the size class level, temporal patterns differed between the two sites (Figure 7). Hatchling abundance at both sites initially increased from 2011 to 2012 and then continued to increase at a slower rate (GPD; range of annual means: 167–331) or slowly decline (SAN; range: 158–515). Juveniles showed slightly contrasting, albeit highly uncertain, abundance patterns, reflected by a

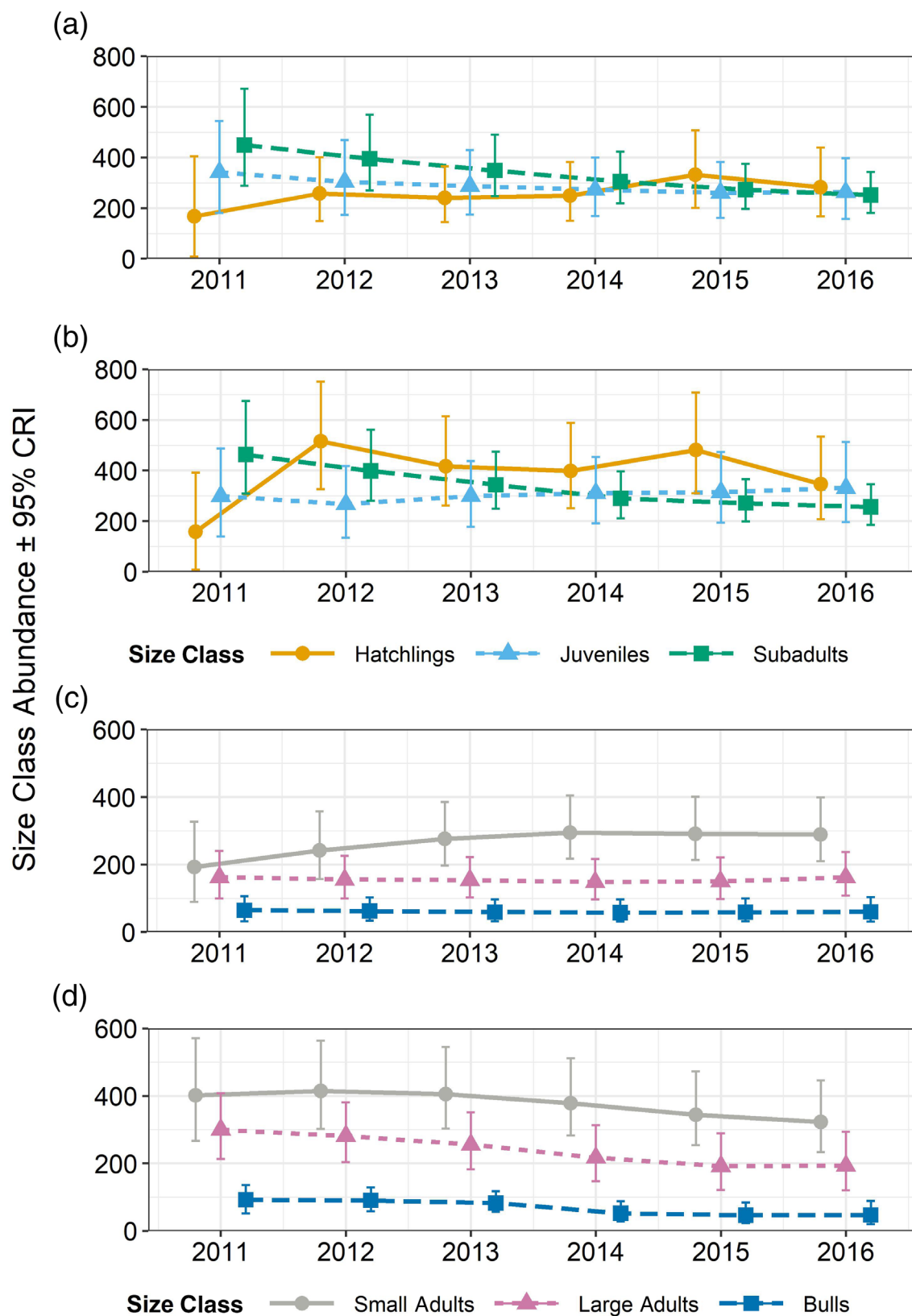
slight decline in GPD (range: 260–341) and a slight increase in SAN (range: 266–330), whereas subadults declined at both sites (GPD: 251–448, SAN: 255–462). All the adult size classes showed contrasting patterns among sites. On GPD, small adults increased from 2011 to 2014 and then remained stable (range: 192–294), whereas both large adult (range: 147–161) and bull abundance (range: 56–64) remained relatively flat the entire study period (Figure 7c). In contrast, all three adult size classes on SAN initially declined, but appeared to stabilize around 2014 or 2015, depending on the group (Figure 7d). Small adults ranged from 322 to 414 individuals, whereas large adults declined by 35% (range: 193–299) and bulls by 50% over the same period (range: 46–92).

## DISCUSSION

We constructed an IPM that synthesized multiple high-resolution datasets to resolve substantial state uncertainty in coarse-scale census data to estimate size class-specific abundance estimates for alligators. Linking the detection parameters in our observation model ( $p.d$ ,  $p.a$ , and  $p.c$ ) through a conditional structure was a novel development that allowed us to make efficient use of data collected at different resolutions of observer perception. The parameter estimates produced by the IPM provided important insights into alligator demography,



**FIGURE 6** Posterior distribution of American alligator total abundance (all size classes) on the Great Pee Dee and Waccamaw River (GPD; left panel) and South Santee River (SAN; right panel) in coastal South Carolina from 2011 to 2016. The dark gray shaded area represents the 95% Bayesian credible interval (CRI).



**FIGURE 7** Size class-specific American alligator abundance posterior means with 95% Bayesian credible intervals (CRIs) from nightlight survey counts on the Great Pee Dee and Waccamaw Rivers (left column) and the South Santee River (right column) from 2011 to 2016 in coastal South Carolina, USA. The top panels (a, b) show abundance estimates for immature size classes and the bottom panels (c, d) show adult size classes.

the detection process and nightlight survey design considerations, and drivers of site-level alligator abundance, which we discuss below, in turn.

The IPM we created is the first ever for crocodilians (to our knowledge) and the survival probability estimates derived from a multidecadal crocodilian mark–recapture study are among the most comprehensive for this species. The general pattern of low survival probability for the smallest sizes or ages and high survival among larger size classes has been observed in both American crocodiles in southern Florida (Briggs-Gonzalez et al., 2017) and Nile crocodiles (*C. niloticus*) in the Okavango Delta (Bourquin & Leslie, 2012). Our estimates of hatchling survival were markedly lower than those reported from a mark–recapture study of alligators at an inland freshwater lake in central Florida ( $0.41 \pm 0.06$  SE; Woodward et al., 1987), which could be attributed to salinity regimes in the two systems. Salinity, which is higher at YWC due to its coastal location, adversely affects the physiology of immature alligators and therefore may reduce survival in this age class (Faulkner et al., 2018; Laurén, 1985). While our study presents a large leap forward in understanding crocodilian vital rates, future studies are needed to identify potential environmental or anthropogenic drivers of variation in these rates, in both protected and harvested populations.

Our study further elucidates how environmental, demographic, and study design-related factors may influence alligator detectability during nightlight surveys, the primary method used for monitoring crocodilians (Bayliss, 1987; Fujisaki et al., 2011; Shirley et al., 2012). The negative relationship between WL and *p.d* (hereafter detection) we reported is well documented for nightlight monitoring of crocodilians (Fujisaki et al., 2011; Waddle et al., 2015; Woodward & Marion, 1978); as water levels rise, alligators have more water surface area and depth in which to submerge and evade detection. Similarly, alligator activity (i.e., visibility) is positively correlated with WT (Smith, 1975), which subsequently has a positive influence on detection, though the relationship may differ among size classes due to metabolic requirements (Lang, 1987). The positive trend we detected between alligator size class and detectability was also reported by Fujisaki et al. (2011) and is also likely driven by visibility, as the eyeshine of larger alligators is likely more obvious to observers than those of smaller individuals. Our detection estimates (range: 0.01–0.07) were similar to those reported from Florida by Waddle et al. (2015) for all size classes (0.11) and Fujisaki et al. (2011) for small (0.03) and large alligators (0.09). However, our detection probability estimates were substantially lower than Gardner et al.'s (2016) 0.5 estimate for all size classes in coastal North Carolina. Differences in detection

probability among studies could reflect differences in population structure as well as study design, specifically the temporal spacing between replicate surveys. Gardner et al. (2016) conducted three temporally replicated surveys within one week to meet the assumption of geographic closure. In contrast, the two temporal replicate surveys used by both Waddle et al. (2015) and Fujisaki et al. (2011) were spaced at least two weeks apart in Florida's Everglades, meaning that the assumption of geographic closure was likely violated and that their parameters were reflective of an open “superpopulation” in which abundance reflects all individuals that could potentially be encountered by the nightlight surveys (Royle, 2004). In this study, temporal spacing between replicate surveys was variable (24 h–14 days) within a highly connected area, during the alligator's peak movement period (Nifong & Silliman, 2017; Rosenblatt et al., 2013), meaning we likely sampled from a geographically open system. Thus, while both survey design approaches are valid, comparison and interpretation of parameters derived from different approaches require important context.

Despite the connected nature of our study area, we detected contrasting patterns in total alligator densities and immature size class-specific abundance temporal trends between the two sites. Though total abundance estimates were relatively similar between the two sites (Figure 6), SAN (approximately one third of the route length of GPD) appeared to have substantially higher alligator densities. We posit that the difference in density is likely a reflection of habitat, which, in turn, may drive differences in hunting pressure (i.e., hunters are attracted to high-density habitats). Multiple studies indicate that coastal alligators periodically forage in saline areas to take advantage of marine prey items (e.g., blue crabs *Callinectes sapidus*) (Nifong & Silliman, 2017; Rosenblatt & Heithaus, 2011). As such, alligators within the SAN route can take advantage of a freshwater–marine gradient with the South Santee River to balance osmoregulatory and foraging needs. In contrast, freshwater marshes such as those surrounding the GPD are typically nutrient-limited and host lower alligator densities. Site-specific differences in habitat are also reflected in the immature size class-specific abundance patterns. Suitable nesting habitat is relatively abundant on the Santee River Delta and scarce along the Great Pee Dee and Waccamaw Rivers within the GPD route (Wilkinson, 1983). As such, hatchlings were less abundant than both juveniles and subadults on GPD for most of the study (Figure 6a), whereas hatchlings were the most abundant size class on SAN for all years except 2011. We also note that the general deviation from the expected pattern for long-lived species in which abundance and size class are negatively correlated (Nichols

et al., 1976) (Figure 6a,b) is likely a reflection of habitat differences as well. Breeding females typically construct nests in highly vegetated habitat and remain close to the nesting site with their hatchlings and surviving young from the previous year following nest excavation (Chabreck, 1965; McIlhenny, 1935; Woodward et al., 1987), meaning that the nightlight surveys conducted in open-water habitats were less likely to encounter alligators in the smallest size classes. Adult females with young and other immature size classes are thought to avoid open-water habitats, such as large rivers where nightlight surveys take place, as a way to avoid predators like larger alligators that cannibalize young (Lawson et al., 2018; Rootes & Chabreck, 1993b; Somaweera et al., 2013).

In contrast, though the mature size classes followed the expected composition patterns and those of previous studies (Nichols et al., 1976), the size class-specific abundance trends differed markedly among sites (Figure 7c,d). On GPD, small adult abundance appeared to increase during the first half of the study and then stabilize, whereas the abundance of large adults and bulls remained relatively consistent over time (Figure 7c). In contrast, despite SAN containing better foraging habitat due to access to marine resources, all adult size classes declined during the study. The decline was largest for bulls (−50%), followed by large adults (−35%) and small adults (−18%) (Figure 7d). Given the low probability that an alligator lives long enough to reach 3.05-m TL (Wilkinson et al., 2016), the finding that bulls were least abundant of the size classes was somewhat expected. However, the contrasting patterns of decline between the two sites suggest other factors may be differentially affecting the population segments, namely, harvest. Over the course of the study, more than twice as many alligators were removed from SAN compared with GPD for both the public (500 vs. 196; Appendix S1: Table S3) and private harvests (93 vs. 46; Appendix S1: Table S3). This observation, coupled with the evidence of decline in all adult size classes in SAN and the lack of any such evidence for GPD, supports the proposition that the two population segments are experiencing different levels of harvest pressure and exhibiting different responses to harvest.

Compared with a conventional approach of synthesizing results from separate analyses of disparate datasets, the IPM framework we employed provided advantages for making inferences on quantities more efficiently (e.g., survival) and on quantities that were otherwise unattainable in any dataset individually (e.g., size class-specific abundances). Despite these advantages, our approach faced some limitations. However, all the limitations described below would have also impeded the use of a nonintegrated approach. First, each of our data sets—mark–recapture–recovery, nightlight survey counts,

clutch sizes, and harvest totals—were sparse and necessitated simplification within the constituent model components to facilitate estimation. For example, the assumption of constant survival over time is not realistic for some of the age classes, but it was a reasonable concession to the reality of the data in hand. Second, data provided to us had known deficiencies that could not be completely resolved and could have affected our inference. For example, the harvest data we incorporated into the model were based on self-reported alligator TL from hunters and did not account for missing tails. Thus, it is possible that our model inappropriately directed too much harvest into smaller size classes, resulting in positive bias in abundance of larger size classes. A strength of the IPM comes from the model of population dynamics that forms the foundation of the framework. Because functional processes link estimated quantities, the IPM is able to produce estimates abundance in years when no nightlight surveys were conducted. However, the ability to impute such quantities in the face of missing data depends on both the functional linkages in the model as well as prior distributions provided to uncertain quantities, such as abundance for the initial year of the study (2011). Together, these may create apparent statistical artifacts when data are missing in some years (and sparse elsewhere), such as the large one-year increase (2011–2012) in hatchlings in SAN.

Our IPM addresses a widespread, critical challenge in the conservation of species that are difficult to directly observe and exhibit complex life-history patterns, in which the preferred monitoring method produces data of lower demographic resolution than what is needed to make effective decisions and reduce uncertainty (i.e., “demographic resolution mismatch”; Hauser et al., 2006; Link et al., 2003). Hostetter et al. (2021) demonstrated the potential benefits of avoiding mismatch by examining the consequences of incorporating age structure into population models for polar bears (*Ursus maritimus*) in Canada. In a simulation study, they reported that age-structured Jolly Seber models produced higher precision estimates of survival, abundance, and recruitment compared with models that lacked age structure and increased the power to detect changes in abundance (Hostetter et al., 2021). In contrast, the use of low-resolution monitoring data may leave a population more vulnerable to perturbations in population structure (e.g., size-selective harvest) in long-lived species can have long-lasting impacts on population growth and abundance that may not be immediately detected (Hoy et al., 2020; Koons et al., 2006; Regehr et al., 2017). Worse, demographic resolution mismatch could also limit conservation actions or management interventions that could otherwise benefit the species. For example, managers may be forced to rely upon predictive models that make simplifying

assumptions about population structure (e.g., stable age or stage distribution) that are rarely met in practice and may lead to flawed inference from elasticity or sensitivity analyses (Koons et al., 2006, 2007). The method we describe here using IPMs to resolve latent population structure and thereby reduce demographic resolution mismatch could be extended to applications including uncertainty in age assignment for long-lived species with variable reproductive value (e.g., bears), species assignment for closely related species like mallard (*Anas platyrhynchos*) and black ducks (*A. rubripes*), or sex assignment for species that lack sexual dimorphism (e.g., raptors). Though some monitoring programs could be restructured to obtain the necessary level of resolution, or stopped entirely in favor of promising alternative methodologies (e.g., unmanned aerial vehicles), such options severely restrict the use of existing, long-term datasets.

Despite their potential low resolution, some long-term datasets may have inherent value for slow-growing or long-lived species in which the effects of management or conservation decisions may operate at a lagged timescale. The IPM described here provides a promising, flexible approach to merge high-resolution demographic data with low-resolution, but less costly, monitoring data to describe and quantify latent population structure and abundance trends. The flexible nature of IPMs offers the ability to synthesize multiple datastreams to produce more precise demographic parameter estimates that can be used in other contexts to guide not only conservation decisions but also improvements to the design of the monitoring program. Hence, IPMs are a valuable tool in conservation because they provide a means to both increase the resolution and precision of existing data, and potentially improve upon how monitoring data are collected for managed species.

## ACKNOWLEDGMENTS

We thank the many technicians and volunteers who assisted with nightlight surveys and alligator captures, and the Tom Yawkey Wildlife Center for logistical support. We specifically acknowledge Brad Taylor, Jamie Dozier, and Derrell Shipps who were instrumental in the completion of this study, as well as Allan Woodward, Erin Leone, and Mark Bara for use of the alligator growth data. We thank Beth Ross, Robert Baldwin, Anna Tucker, Dave Koons, and one anonymous reviewer for their helpful comments on earlier versions of this manuscript, and Nathan Hostetter for data and software review. This work was supported by the South Carolina Department of Natural Resources (grant numbers 2009094 and 20100899). We acquired all necessary alligator sample collection permits from the South Carolina Department of Natural Resources, and the study was approved by the

Institutional Animal Care and Use Committees at Clemson University (permit numbers 2015007, 2016059; 2015–2017) and the Medical University of South Carolina (permit number 3069; 2010–2017). This paper represents Technical Contribution Number 6731 of the Clemson University Experiment Station. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.


## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Model code (Lawson, Dunham, & Moore, 2022) is available from the US Geological Survey Office Source Code Archive at <https://doi.org/10.5066/P92I95YE>. Data (Lawson, Jodice, et al., 2022) are available in the US Geological Survey Science data catalog at <https://doi.org/10.5066/P9AEXW1Z>.

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## REFERENCES

- Arnold, T. W., R. G. Clark, D. N. Koons, and M. Schaub. 2018. "Integrated Population Models Facilitate Ecological Understanding and Improved Management Decisions." *Journal of Wildlife Management* 82: 266–74.
- Balaguera-Reina, S. A., M. D. Venegas-Anaya, B. Rivera-Rivera, D. A. Morales Ramírez, and L. D. Densmore. 2018. "How to Estimate Population Size in Crocodylians? Population ecology of American crocodiles in Coiba Island as study case." *Ecosphere* 9: e02474.
- Bayliss, P. 1987. "Survey Methods and Monitoring within Crocodile Management Programmes." In *Wildlife Management: Crocodiles and Alligators*, edited by G. J. W. Webb, C. Manolis, and P. J. Whitehead, 157–75. Sydney: Surrey Beatty & Sons.
- Bennett, C., T. Cooney, K. Jones, B. Church, and G. Murray. 1989. *Water Resources Data South Carolina 1990*. USGS Water-Data Report SC-89, Vol 1. Columbia, SC: US Geological Survey.
- Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. "Integrating Mark-Recapture-Recovery and Census Data to Estimate Animal Abundance and Demographic Parameters." *Biometrics* 58: 540–7.

- Bourquin, S. L., and A. J. Leslie. 2012. "Estimating Demographics of the Nile Crocodile (*Crocodylus niloticus* Laurenti) in the Panhandle Region of the Okavango Delta, Botswana." *African Journal of Ecology* 50: 1–8.
- Bradshaw, C. J. A., Y. Fukuda, M. Letnic, and B. W. Brook. 2006. "Incorporating Known Sources of Uncertainty to Determine Precautionary Harvests of Saltwater Crocodiles." *Ecological Applications* 16: 1436–48.
- Briggs-Gonzalez, V., C. Bonenfant, M. Basille, M. Cherkiss, J. Beauchamp, and F. Mazzotti. 2017. "Life Histories and Conservation of Long-Lived Reptiles, an Illustration with the American Crocodile (*Crocodylus acutus*)." *Journal of Animal Ecology* 86: 1102–13.
- Caswell, H. 2001. *Matrix Population Models*, 2nd ed. Sunderland, MA: Sinauer Associates.
- Chabreck, R. H. 1963. "Methods of Capturing, Marking, and Sexing Alligators." In *Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners* 17: 47–50. Columbia, South Carolina, USA.
- Chabreck, R. H. 1965. "The Movement of Alligators in Louisiana." *Journal of the Southeastern Association of Fish and Wildlife Agencies* 19: 102–10.
- Chabreck, R. H. 1966. "Methods of Determining the Size and Composition of Alligator in Louisiana." In *Proceedings of the Southeastern Association of Game and Fish Commissioners* 20: 105–12. Columbia, South Carolina, USA.
- Cherkiss, M. S., H. E. Fling, F. J. Mazzotti, and K. G. Rice. 2004. *Counting and Capturing Crocodilians*. Gainesville, FL: University of Florida.
- Conn, P. B., and E. G. Cooch. 2009. "Multistate Capture-Recapture Analysis under Imperfect State Observation: An Application to Disease Models." *Journal of Applied Ecology* 46: 486–92.
- Conrads, P. A., and E. A. Roehl. 2007. *Analysis of Salinity Intrusion in the Waccamaw River and Atlantic Intracoastal Waterway near Myrtle Beach, South Carolina, 1995–2002*. Scientific Investigations Report. Reston, VA: U.S. Geological Survey.
- Faulkner, P. C., M. L. Burleson, L. Simonitis, C. D. Marshall, D. Hala, and L. H. Petersen. 2018. "Effects of Chronic Exposure to 12‰ Saltwater on the Endocrine Physiology of Juvenile American Alligator (*Alligator mississippiensis*)." *The Journal of Experimental Biology* 221: jeb181172.
- Fischer, H. A., L. R. Gerber, and E. A. Wentz. 2021. "Evaluating the Fitness for Use of Citizen Science Data for Wildlife Monitoring." *Frontiers in Ecology and Evolution* 9: 1–14.
- Fujisaki, I., F. J. Mazzotti, R. M. Dorazio, K. G. Rice, M. Cherkiss, and B. Jeffery. 2011. "Estimating Trends in Alligator Populations from Nightlight Survey Data." *Wetlands* 31: 147–55.
- Gardner, B., L. A. Garner, D. T. Cobb, and C. E. Moorman. 2016. "Factors Affecting Occupancy and Abundance of American Alligators at the Northern Extent of Their Range." *Journal of Herpetology* 50: 541–7.
- Gelman, A., and D. B. Rubin. 1992. "Inference from Iterative Sampling Using Multiple Sequences." *Statistical Science* 7: 457–511.
- Hauser, C. E., E. G. Cooch, and J. D. Lebreton. 2006. "Control of Structured Populations by Harvest." *Ecological Modelling* 196: 462–70.
- Hooten, M. B., and N. T. Hobbs. 2015. "A Guide to Bayesian Model Selection for Ecologists." *Ecological Monographs* 85: 3–28.
- Hostetter, N. J., N. J. Lunn, E. S. Richardson, E. V. Regehr, and S. J. Converse. 2021. "Age-Structured Jolly-Seber Model Expands Inference and Improves Parameter Estimation from Capture-Recapture Data." *PLoS One* 16: 1–19.
- Hoy, S. R., D. R. MacNulty, D. W. Smith, D. R. Stahler, X. Lambin, R. O. Peterson, J. S. Ruprecht, and J. A. Vucetich. 2020. "Fluctuations in Age Structure and their Variable Influence on Population Growth." *Functional Ecology* 34: 203–16.
- Kellner, K. F. 2021. "jagsUI: A Wrapper Around 'rjags' to Streamline 'JAGS' Analyses." Version 1.5.2. <https://CRAN-R-project.org/package=jagsUI>.
- Kellner, K. F., and R. K. Swihart. 2014. "Accounting for Imperfect Detection in Ecology: A Quantitative Review." *PLoS One* 9: e111436.
- Kendall, W. L., S. Stapleton, G. C. White, J. I. Richardson, K. N. Pearson, and P. Mason. 2019. "A Multistate Open Robust Design: Population Dynamics, Reproductive Effort, and Phenology of Sea Turtles from Tagging Data." *Ecological Monographs* 89: e01329.
- Koons, D. N., R. R. Holmes, and J. B. Grand. 2007. "Population Inertia and its Sensitivity to Changes in Vital Rates and Population Structure." *Ecology* 88: 2857–67.
- Koons, D. N., R. F. Rockwell, and J. B. Grand. 2006. "Population Momentum: Implications for Wildlife Management." *Journal of Wildlife Management* 70: 19–26.
- Lang, J. 1987. "Crocodilian Thermal Selection." In *Wildlife Management: Crocodiles and Alligators*, edited by G. W. J. Webb, S. C. Manolis, and P. J. Whitehead, 301–17. Sydney: Surrey Beatty and Sons Pty Limited/Conservation Commission of the Northern Territory.
- Larriera, A., C. I. Piña, P. Siroski, and L. M. Verdade. 2004. "Allometry of Reproduction in Wild Broad-Snouted Caimans (*Caiman latirostris*)." *Journal of Herpetology* 38: 301–4.
- Laurén, D. J. 1985. "The Effect of Chronic Saline Exposure on the Electrolyte Balance, Nitrogen Metabolism, and Corticosterone Titer in the American Alligator, *Alligator mississippiensis*." *Comparative Biochemistry and Physiology-Part A: Physiology* 81: 217–23.
- Lawson, A. J. 2019. *Reducing Uncertainties in Conservation Decision-Making for American Alligators*. Clemson, SC: Clemson University.
- Lawson, A. J., K. D. Dunham, and C. T. Moore. 2022. "America Alligator Growth Simulation and Integrated Population Model for Georgetown County, South Carolina, USA: U.S. Geological Survey Software Release." <https://doi.org/10.5066/P92I95YE>.
- Lawson, A. J., P. G. R. Jodice, T. R. Rainwater, K. D. Dunham, M. Hart, J. W. Butfiloski, P. M. Wilkinson, and C. T. Moore. 2022. "American Alligator Demographic and Harvest Data from Georgetown County, South Carolina, 1979–2017: U.S. Geological Survey Data Release." <https://doi.org/10.5066/P9AEXW1Z>.
- Lawson, A. J., C. T. Moore, T. R. Rainwater, F. M. Nilsen, P. M. Wilkinson, R. H. Lowers, L. J. Guillette, K. W. McFadden, and P. G. R. Jodice. 2020. "Nonlinear Patterns in Mercury Bioaccumulation in American Alligators Are a Function of Predicted Age." *Science of the Total Environment* 707: 135103.
- Lawson, A. J., B. A. Strickland, and A. E. Rosenblatt. 2018. "Patterns, Drivers and Effects of Alligator Movement Behavior and Habitat Use." In *American Alligators: Habitats, Behaviors,*

- and Threats, edited by C. B. Eversole and S. E. Henke, 47–77. Hauppauge, NY: Nova Science Publishers.
- Lebreton, J. D., T. Almeras, and R. Pradel. 1999. “Competing Events, Mixtures of Information and Multistratum Recapture Models.” *Bird Study* 46: S39–46.
- Lebreton, J. D., J. D. Nichols, R. J. Barker, R. Pradel, and J. A. Spendel. 2009. “Modeling Individual Animal Histories with Multistate Capture-Recapture Models.” *Advances in Ecological Research* 41: 87–173.
- Link, W. A., J. A. Royle, and J. S. Hatfield. 2003. “Demographic Analysis from Summaries of an Age-Structured Population.” *Biometrics* 59: 778–85.
- Lyons, J. E., M. C. Runge, H. P. Laskowski, and W. L. Kendall. 2008. “Monitoring in the Context of Structured Decision-Making and Adaptive Management.” *Journal of Wildlife Management* 72: 1683–92.
- Marioni, B., J. A. L. Barão-Nóbrega, R. Botero-Arias, F. Muniz, Z. Campos, R. Da Silveira, W. E. Magnusson, and F. Villamarín. 2021. “Science and Conservation of Amazonian Crocodilians: A Historical Review.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 1056–67.
- Martin, J., J. A. Royle, D. I. Mackenzie, H. H. Edwards, M. Kéry, and B. Gardner. 2011. “Accounting for Non-Independent Detection when Estimating Abundance of Organisms with a Bayesian Approach.” *Methods in Ecology and Evolution* 2: 595–601.
- Mazzotti, F. J., and L. A. Brandt. 1994. In *Ecology of the American Alligator in a Seasonally Fluctuating Environment*, edited by S. Davis and J. C. Ogden, 485–505. Boca Raton, FL: Everglades: The Ecosystem and Its Restoration, CRC Press.
- McIlhenny, E. A. 1935. *The Alligator's Life History*. Boston, MA: The Christopher Publishing House.
- Miller, A. 2002. *Subset Selection in Regression*. Boca Raton, FL: Chapman & Hall/CRC.
- Murphy, T. M., and T. T. Fendley. 1973. “A New Technique for Live Trapping of Nuisance Alligators.” In *Proceedings of the Annual Conference of the Southeast Association of Game and Fish Commissioners* 308–11. Columbia, SC: Southeastern Association of Game and Fish Commissioners.
- Nichols, J. D., L. Viehman, R. H. Chabreck, and B. Fenderson. 1976. *Simulation of a Commercially Harvested Alligator Population in Louisiana*. LSU Agricultural Experiment Station Reports 470. Baton Rouge, LA: Louisiana University.
- Nifong, J. C., C. A. Layman, and B. R. Silliman. 2015. “Size, Sex and Individual-Level Behaviour Drive Intrapopulation Variation in Cross-Ecosystem Foraging of a Top-Predator.” *Journal of Animal Ecology* 84: 35–48.
- Nifong, J. C., and B. Silliman. 2017. “Abiotic Factors Influence the Dynamics of Marine Habitat Use by a Highly Mobile “Freshwater” Top Predator.” *Hydrobiologia* 802: 155–74.
- Plummer, M. 2017. JAGS: Just another Gibbs Sampler. Version 4.3.0 User Manual.
- R Core Development Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Regehr, E. V., R. R. Wilson, K. D. Rode, M. C. Runge, and H. L. Stern. 2017. “Harvesting Wildlife Affected by Climate Change: A Modelling and Management Approach for Polar Bears.” *Journal of Applied Ecology* 54: 1534–43.
- Rhodes, W. E. 2002. “Differential Harvest of American Alligators on Private Lands in Coastal South Carolina. Crocodiles.” In *Proceedings of the 16th Working Meeting of the Crocodile Specialist Group* 75–9. Gland and Cambridge: IUCN—The World Conservation Union.
- Rhodes, W. E., and J. W. Lang. 1996. “Alligator Nest Temperatures and Hatchling Sex Ratios in Coastal South Carolina.” *Journal of the Southeastern Association of Fish and Wildlife Agencies* 50: 520–31.
- Rootes, W. L., and R. H. Chabreck. 1993a. “Reproductive Status and Movement of Adult Female Alligators.” *Journal of Herpetology* 27: 121–6.
- Rootes, W. L., and R. H. Chabreck. 1993b. “Cannibalism in the American Alligator.” *Herpetologica* 49: 99–107.
- Rosenblatt, A. E., and M. R. Heithaus. 2011. “Does Variation in Movement Tactics and Trophic Interactions among American Alligators Create Habitat Linkages?” *Journal of Animal Ecology* 80: 786–98.
- Rosenblatt, A. E., M. R. Heithaus, F. J. Mazzotti, M. Cherkiss, and B. M. Jeffery. 2013. “Intra-Population Variation in Activity Ranges, Diel Patterns, Movement Rates, and Habitat Use of American Alligators in a Subtropical Estuary.” *Estuarine, Coastal and Shelf Science* 135: 182–90.
- Royle, J. A. 2004. “N-Mixture Models for Estimating Population Size from Spatially Replicated Counts.” *Biometrics* 60: 108–15.
- Saracco, J. F., D. F. Desante, and D. R. Kaschube. 2008. “Assessing Landbird Monitoring Programs and Demographic Causes of Population Trends.” *Journal of Wildlife Management* 72: 1665–73.
- Sauer, J. R., and M. G. Knutson. 2008. “Objectives and Metrics for Wildlife Monitoring.” *Journal of Wildlife Management* 72: 1663–4.
- Schaub, M., and F. Abadi. 2011. “Integrated Population Models: A Novel Analysis Framework for Deeper Insights into Population Dynamics.” *Journal of Ornithology* 152: S227–37.
- Servanty, S., J.-M. Gaillard, F. Ronchi, S. Focardi, É. Baubet, and O. Gimenez. 2011. “Influence of Harvesting Pressure on Demographic Tactics: Implications for Wildlife Management.” *Journal of Applied Ecology* 48: 835–43.
- Shirley, M. H., R. M. Dorazio, E. Abassery, A. A. Elhady, M. S. Mekki, and H. H. Asran. 2012. “A Sampling Design and Model for Estimating Abundance of Nile Crocodiles while Accounting for Heterogeneity of Detectability of Multiple Observers.” *The Journal of Wildlife Management* 76: 966–75.
- Skupien, G. M., and K. M. Andrews. 2017. “Factors Influencing the Abundance of American Alligators (*Alligator mississippiensis*) on Jekyll Island, Georgia, USA.” *Journal of Herpetology* 51: 89–94.
- Smith, E. N. 1975. “Thermoregulation of the American Alligator, *Alligator mississippiensis*.” *Physiological Zoology* 48: 177–94.
- Somaweera, R., M. Brien, and R. Shine. 2013. “The Role of Predation in Shaping Crocodilian Natural History.” *Herpetological Monographs* 27: 23–51.
- Somaweera, R., J. Nifong, A. Rosenblatt, M. L. Brien, X. Combrink, R. M. Elsey, G. Grigg, et al. 2020. “The Ecological Importance of Crocodylians: Towards Evidence-Based Justification for their Conservation.” *Biological Reviews* 95: 936–59.
- South Carolina Department of Natural Resources. 2017. *Alligator Hunting Season Report*. Columbia, SC: South Carolina Department of Natural Resources.

- Strickland, B. A., F. J. Vilella, and R. D. Flynt. 2018. "Long-Term Spotlight Surveys of American Alligators in Mississippi, USA." *Herpetological Conservation and Biology* 13: 331–40.
- Subalusky, A. L., L. A. Fitzgerald, and L. L. Smith. 2009. "Ontogenetic Niche Shifts in the American Alligator Establish Functional Connectivity between Aquatic Systems." *Biological Conservation* 142: 1507–14.
- Tenan, S., P. Pedrini, N. Bragalanti, C. Groff, and C. Sutherland. 2017. "Data Integration for Inference about Spatial Processes: A Model-Based Approach to Test and Account for Data Inconsistency." *PLoS One* 12: 1–18.
- Thorbjarnarson, J. B. 1996. "Reproductive Characteristics of the Order Crocodylia." *Herpetologica* 52: 8–24.
- Tuljapourkar, S., U. K. Steiner, and S. H. Orzack. 2009. "Dynamic Heterogeneity in Life Histories." *Ecology Letters* 12: 93–106.
- U.S. Fish and Wildlife Service. 1967. "Conservation of Endangered Species and Other Fish or Wildlife; United States List of Endangered Native Fish and Wildlife." *Federal Register* 32: 4001.
- Waddle, J. H., L. A. Brandt, B. M. Jeffery, and F. J. Mazzotti. 2015. "Dry Years Decrease Abundance of American Alligators in the Florida Everglades." *Wetlands* 35: 865–75.
- Webb, G. J. W., S. C. Manolis, P. J. Whitehead, and G. A. Letts. 1984. *A Proposal for the Transfer of the Australian Population of Crocodylus porosus Schneider (1801) from Appendix I to Appendix II of C.I.T.E.S.* Darwin: Conservation Commission of the Northern Territory Technical Report.
- Wilkinson, P. M. 1983. *Nesting Ecology of the American Alligator in Coastal South Carolina*. Columbia, SC: Study Completion Report.
- Wilkinson, P. M. 1994. "A Walk-through Snare Design for the Live Capture of Alligators." In *Proceedings of the 12th Working Meeting of the Crocodile Specialist Group, Volume 2*, 74–5. Gland, Switzerland: IUCN–The World Conservation Union.
- Wilkinson, P. M., T. R. Rainwater, A. R. Woodward, E. H. Leone, and C. Carter. 2016. "Determinate Growth and Reproductive Lifespan in the American Alligator (*Alligator mississippiensis*): Evidence from Long-Term Recaptures." *Copeia* 104: 843–52.
- Wilkinson, P. M., and W. E. Rhodes. 1997. "Growth Rates of American Alligators in Coastal South Carolina." *The Journal of Wildlife Management* 61: 397–402.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and Management of Animal Populations*. San Diego, CA: Academic Press.
- Woodward, A. R. 1996. *Determination of Appropriate Harvest Strategies for Alligator Management Units*. Final Report. Tallahassee, FL: Florida Game and Fresh Water Fish Commission.
- Woodward, A. R., T. C. Hines, C. L. Abercrombie, and J. D. Nichols. 1987. "Survival of Young American Alligators on a Florida Lake." *The Journal of Wildlife Management* 51: 931–7.
- Woodward, A. R., and W. R. Marion. 1978. "An Evaluation of Factors Affecting Night-Light Counts of Alligators." In *Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies* 291–302. Columbia, SC: Southeastern Association of Game and Fish Commissioners.
- Yackulic, C. B., M. Dohrill, M. Dzul, J. S. Sanderlin, and J. A. Reid. 2020. "A Need for Speed in Bayesian Population Models: A Practical Guide to Marginalizing and Recovering Discrete Latent States." *Ecological Applications* 30: e02112.
- Zajdel, J., S. L. Lance, T. R. Rainwater, P. M. Wilkinson, M. D. Hale, and B. B. Parrott. 2019. "Mating Dynamics and Multiple Paternity in a Long-Lived Vertebrate." *Ecology and Evolution* 9: 10109–21.
- Zipkin, E. F., and S. P. Saunders. 2018. "Synthesizing Multiple Data Types for Biological Conservation Using Integrated Population Models." *Biological Conservation* 217: 240–50.
- Zipkin, E. F., T. S. Sillett, E. H. C. Grant, R. B. Chandler, and J. A. Royle. 2014. "Inferences about Population Dynamics from Count Data Using Multistate Models: A Comparison to Capture-Recapture Approaches." *Ecology and Evolution* 4: 417–26.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Lawson, Abigail J., Patrick G. R. Jodice, Thomas R. Rainwater, Kylee D. Dunham, Morgan Hart, Joseph W. Butfiloski, Philip M. Wilkinson, K. W. McFadden, and Clinton T. Moore. 2022. "Hidden in Plain Sight: Integrated Population Models to Resolve Partially Observable Latent Population Structure." *Ecosphere* 13(12): e4321. <https://doi.org/10.1002/ecs2.4321>