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Article in *Journal of Wildlife Management* · January 2024

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RESEARCH ARTICLE

Bigger is better: age class-specific survival rates in long-lived turtles increase with size

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Funding information

U.S. Fish and Wildlife Service,
Grant/Award Number: F17AC00677

Abstract

Vital rates for small, non-breeding individuals are important components of population dynamics for many species, but often individuals of these sizes are difficult to locate, capture, and track. As such, biologists frequently lack reliable estimates of juvenile survival because sample sizes and recapture rates for this life stage are low. Long-lived animals often take many years to reach sexual maturity and spend much of this time in the smaller size classes, making them sensitive to changes in survival rates. We estimated the survival rates of all size classes for the northern map turtle (*Graptemys geographica*) using a mark-recapture dataset with >3,500 captures from 2019–2021 and 210 nests from 2018–2021. As turtle size increased, annual survival probability increased regardless of sex. Estimated annual survival probability for turtles >18 cm long (i.e., adult females >15 years) was about 0.95, over 4 times higher than turtles that were 3 cm long (i.e., hatchlings <1 year; 0.22 annual survival probability). Although we did not observe a difference in survival probability between sexes of any size class, adult females are nearly twice the size of adult males, leading to an increased annual survival probability for females of 0.95, compared to 0.80 for males. Changes in adult survival had the greatest influence on population estimates over time, with temporary decreases, such as those due to poaching or an environmental disaster, potentially leading to unrecoverable decreases in the overall population size. Our study provides detailed survival rates for all size classes in a long-lived turtle, which are necessary to assess population stability and can be used to determine the most effective conservation or management practices.

KEYWORDS

anthropogenic effects, freshwater, *Graptemys*, hatchling, juvenile survival, life table, map turtle

Increases in anthropogenic changes to natural habitat have caused declines in many once common species (Murphy and Romanuk 2014, Diaz et al. 2019). With such declines occurring, population monitoring and effective management decisions are necessary to keep common species from declining (Jachowski et al. 2015, Watson and Watson 2015). This can be complicated because decisions often focus on ease of implementing actions and may overlook specific size classes that are difficult to study (Gibbs et al. 1999, Rose et al. 2021). Moreover, understanding and identifying variation in vital rates between sex- and life-stage attributes is necessary to determine population growth rates or extinction probability (Caswell 2001, Otero et al. 2011). Determining sex-specific capture and detection probabilities of different size classes are important for accurately and precisely estimating a species' population growth under given environmental conditions (Brook et al. 2000, Eberhart-Phillips et al. 2017). The cryptic nature of many species, difficulty in capturing specific size classes, or overall low population size (particularly for threatened or endangered species) can limit the ability to collect sufficient age-specific data to accurately estimate important ecological parameters (Brook et al. 2000, Lamy et al. 2013).

Survival rates are often the most sensitive parameters determining animal population sizes and can be used to determine trends in population growth and viability (Murray and Patterson 2006, Pike et al. 2008). Survival analysis quantifies the influence of genetic, demographic, ecological, and environmental factors on the mortality risks to species, sexes, or specific size (or age) classes (Ricklefs 1991, Charlesworth 1994). Size-specific survival rates may guide land managers seeking to use limited resources to the greatest effect by targeting resources towards the most vulnerable life stage. For example, removal of mesopredators, such as raccoons (*Procyon lotor*), can increase nest success in turtles and increase the number of small (i.e., hatchling) turtles in a population (Munscher et al. 2012, Urbanek et al. 2016). Empirical determination of size-specific survival rates is often difficult, as the necessary intensive field surveys can be expensive and time-consuming, often taking decades to attain sufficient sample size and data (Larson et al. 2004, Martin et al. 2017). Field surveys also rely on the investigator's ability to capture, mark, and, most importantly, recapture free-living animals (Pike et al. 2008, Silvy 2012). In species where capture of the smallest size classes (i.e., earliest life stages or juveniles) is logistically difficult or detection probabilities are low, little to no information on these age classes may exist (Congdon et al. 1993, Morafka 1994, Morafka et al. 2000). These challenges lead to truncated survival data (Young 1963, Gilbert et al. 2014), estimations based only on adult variables (Pike et al. 2008, Rodriguez-Caro et al. 2019), or a modeled survival probability (Gilbert et al. 2014, Plard et al. 2019) that follows an assumed ontogenetic decline where mortality risk declines with age (Levitis 2011). Theory and practice demonstrate the importance of understanding how survival differs for a range of sizes and sexes, but unbiased estimates and empirical data on these rates are still rare for many vertebrate taxa (Gaillard et al. 2000, Smith and Green 2006, Honeycutt et al. 2019).

Many turtle species spend years in smaller, sexually immature size classes, which can lead to slow growth and relatively low recruitment in populations (McCann and Shuter 1997, Manlik 2019). Despite the ecological importance and conservation concern of smaller size classes, the body of knowledge on specific vital rates and population dynamics in turtles is biased toward a limited number of species (e.g., painted turtles [*Chrysemys picta*], bog turtle [*Glyptemys muhlenbergii*], northern red-bellied turtle [*Pseudemys rubriventris*], and red-eared slider [*Trachemys scripta scripta*]; Bodie and Semlitsch 2000, Schlaepfer et al. 2005, Lovich et al. 2018). Declines in adult survival rates in turtles via increased road mortality (Gibbs and Shriver 2002, Steen and Gibbs 2004, Steen et al. 2006), habitat alteration (Bowne et al. 2018), and poaching events have been documented (Portelinha et al. 2014, Gong et al. 2017, Senko et al. 2022), but little is known regarding

the population-level effects of decreased survival in other life stages (e.g., hatchling, juvenile, subadults). Sensitivity and elasticity analyses have been widely used to assess the effect of vital rate changes on population size, growth rates, or other indicators of population viability (Benton and Gant 1999, Mills and Linberg 2002, Wang et al. 2017). Such efforts are important in guiding wildlife management efforts by identifying life stage-specific vital rates with the strongest influence on population dynamics (Manlik et al. 2018). In turtles, this has occurred through evaluations of alternative management strategies, including head-starting hatchlings (Carstairs et al. 2019, Thompson et al. 2020), habitat protection (Browne and Hecnar 2007), predator control (Engeman et al. 2005, Robley et al. 2016), and nest protection (Schindler et al. 2017, Campbell et al. 2020).

Northern map turtles (*Graptemys geographica*) are primarily aquatic and inhabit rivers and large lakes throughout their geographic range, which extends from Vermont to Oklahoma, USA, north into Quebec, Canada, and south to Louisiana, USA. During the active season (~Apr to Oct), turtles leave the water to bask daily on woody debris, rocks, or banks. Sex can typically be identified between 1–2 years of age using secondary sexual characteristics (e.g., longer and thicker tail, and cloacal placement relative to shell margins; Lindeman 2013). Age can be estimated by counting growth rings (i.e., annuli) on epithelial tissues of the carapace, typically 1 growth ring will represent 1 year of life (Congdon et al. 2001); although, accurate growth ring counts can be difficult in adult turtles, including northern map turtles, because discernable wearing of rings is evident and continues throughout a turtle's life (Nagle and Congdon 2016). Adult map turtles exhibit pronounced sexual dimorphism, with females growing to nearly twice the length of males (18.0–27.3 cm straight carapace length [SCL] vs. 9.0–15.9 cm SCL, respectively; Gibbons and Lovich 1990). Males reach sexual maturity at 3–5 years of age (Iverson 1988) and females are mature after about 10 years (Lindeman 2013, Nagle and Congdon 2016), with divergence in growth rates occurring at about 3 years of age (Iverson 1988). In Michigan, USA, non-breeding male map turtles are typically 2.7–8.4 cm SCL and females are 2.7–17.5 cm SCL (Otten 2022). Males reach sexual maturity at about 4 years of age (calculated from carapace scute growth rings; Iverson 1979), corresponding to a >7.0-cm plastron length (PL) and 8.5-cm SCL. The smallest gravid female observed nesting was estimated to be 14 years of age (calculated from abdominal scute growth rings), with a 14.8-cm PL and 17.6-cm SCL (Otten 2022). Individuals of both sexes within this population can live to be >40 years of age based on original growth ring counts, sizes, and recapture data.

We estimated annual survival rates of all size, sex, and age classes in the northern map turtle. We hypothesized that as the size of turtles increased, the annual survival rates would also increase, and that decreasing adult mortality would have the greatest influence on the overall population size.

STUDY AREA

We conducted this study along 20.2 km of the Kalamazoo River from Talmadge Creek to East Dickman Road in Calhoun County, Michigan, USA (Figure 1). The Kalamazoo River within the study site ranges from 9.0–40.0 m wide and 0.2–3.5 m deep, with abundant basking structures in the form of woody debris and exposed banks. The elevation is between 250 m and 260 m. Riparian areas dominated by upland and floodplain woodlands buffer most of the river, with limited human development occurring in the farthest downstream 2.5-km stretch of the study site (Figure 1). A more detailed description of topography, land use, weather, rainfall, and dominant flora and fauna within the Kalamazoo River watershed can be found in Fongers (2008) and Wesley (2005). The study site has a humid continental climate, characterized by hot summers (\bar{x} = 20.2–22.4°C from Jun to Aug) and cold winters (–4.6 to –1.3°C from Dec to Feb) with moderate amounts of rainfall throughout the year (81–115 mm from Apr to Oct; National Oceanic Atmospheric Administration Kalamazoo Battle Creek Airport station [KAZO]).

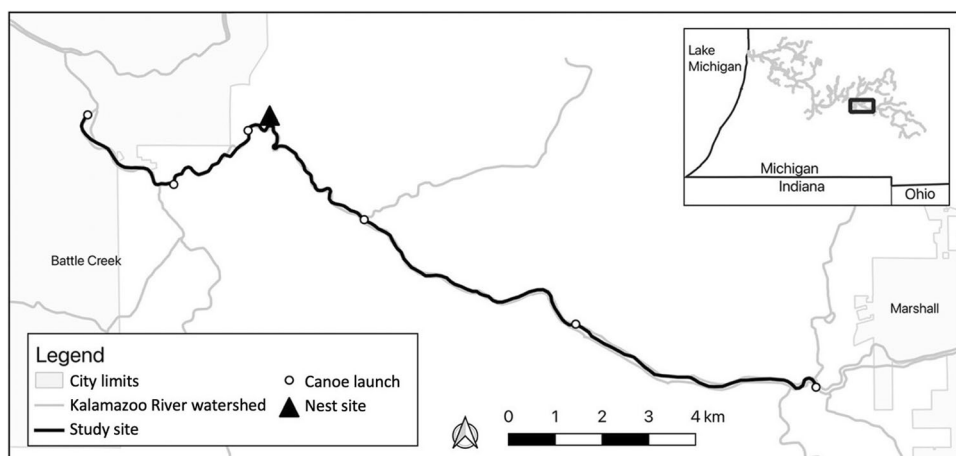


FIGURE 1 Location of northern map turtle mark-recapture surveys, which we conducted along a 20.2-km stretch (in bold) of the Kalamazoo River in Calhoun County, Michigan, USA, in 2019–2021. We conducted nest surveys in 2018–2021 at a single location (nest site).

METHODS

Mark-recapture data collection

We captured northern map turtles from 2 April 2019–24 August 2021, using long handled dipnets with 3-cm mesh from a boat or kayak (Lagler 1943), which allowed the capture of the smallest turtles in the population (~3 cm SCL). We supplemented dipnet captures with sporadic snorkeling surveys (Marchand 1945), and hand captures made during female nesting forays, typically late May through June. We captured turtles throughout the entire study site along both banks during each day of survey. We identified previously marked individual turtles by their unique pattern of shell notches; for individuals that had not previously been captured, we individually marked them by filing unique shell notches along marginal scutes (Cagle 1939). We recorded capture location of each turtle using a handheld global positioning system unit (Garmin International, Olathe, KS, USA; <3-m accuracy), identified sex when possible, measured SCL and PL along the midline to the nearest millimeter, recorded mass to the nearest gram, and counted growth rings when possible. At each capture, we took photos of the turtle's carapace and plastron to aid in identification of individuals, and released all turtles at the point of capture within 24 hours. If we captured an individual multiple times, we used only the first SCL measurement and identification of sex for total capture analysis (i.e., if we first captured an individual of unknown sex in May 2019 at 3.5-cm SCL and recaptured it in May 2021 at 7.2-cm SCL and identified it as male, we used only the results from the first capture). We compared the overall sex ratio of captured, sexed individuals from 2019–2021 to a 1:1 sex ratio.

Survival and recapture analysis

We used northern map turtle mark and recapture data collected from 2019–2021 to calculate annual survival and recapture probabilities. To determine the effect of body size (i.e., SCL) on annual survival, we used the Cormack-Jolly-Seber (CJS) method (Cormack 1964, Jolly 1965, Seber 1965) in Program MARK using the RMark interface in R version 4.2.1 (White and Burnham 1999, Laake 2013, R Core Team 2018). This approach estimates survival and recapture probabilities over time, while testing for effects of sex, body size, level of effort, and time between

surveys from individual encounter histories via maximum likelihood estimate methods (Lebreton et al. 1992, Williams et al. 2002). Because northern map turtles are sexually dimorphic and typically cannot be identified to sex until 1–2 years, we did not include sex as an individual survival covariate because only the smallest turtles were of unknown sex, and the largest were females.

We constructed the capture history of each individual according to its capture or non-capture during a sampling event. Sampling events were based on calendar month, with 7 events occurring in 2019 (Apr–Oct), 8 in 2020 (Mar–Oct), and 4 in 2021 (Apr, May, Jun, and Aug). We included only the first capture of an individual during each sampling event for survival analysis. We converted monthly survival probabilities to annual survival probabilities based on the number of months surveyed each year (Krebs 2014). We used only the sex identified at an individual's first capture for analysis, as juveniles of unknown sex that were captured in subsequent years of survey were then identifiable to sex. For body size, we binned individuals by SCL measurement at the time of first capture (e.g., 2.0–2.9 cm = 2 cm, 3.0–3.9 cm = 3 cm, 4.0–4.9 cm = 4 cm). We calculated time as the number of months between survey events, and we calculated the level of effort as the number of days surveyed during each sampling event.

We constructed and fit 20 models that included all combinations of time, SCL, and SCL \times sex, and a null model for survival probability and sex, time, SCL, level of effort, and null for recapture probability. We conducted a goodness-of-fit test prior to model selection to assess whether our data met the assumption of the general model (Arnason-Schwarz model; Pradel et al. 2003). We performed the goodness-of-fit test using the R2ucare package in R (Choquet et al. 2009; Gimenez et al. 2018a, b) to examine the heterogeneity of capture and apparent survival probabilities, and to test for overdispersion in the data, as indicated by the variance inflation factor (\hat{c}). A \hat{c} estimate near 1 indicates the model has reasonable fit to the data, whereas \hat{c} estimates >3 indicate structural deficiencies in the global model (Gonzalez-Tokman et al. 2012). An initial overall \hat{c} of 3.56 for the fully parameterized model indicated a poor fit of our data, so we used a Quasi Akaike's Information Criterion (QAIC_c) corrected for bias and overdispersion to compare the 20 models (Anderson et al. 1994, Gonzalez-Tokman et al. 2012). The models with the smallest QAIC_c values were considered the best supported. If the difference in QAIC_c was <2 , we assumed there was no difference between alternative models (Gonzalez-Tokman et al. 2012).

Nest surveys and reproductive rate data collection

We collected northern map turtle nest data from 2018–2021 to determine annual fertility, mean clutch size, nest predation rates, and hatching success. We conducted nest surveys at a 1.5-ha upland sandy area (Figure 1; nest site) where we observed 75–115 adult females annually making ≥ 1 nesting forays (i.e., overland movements >10 m from the river). Otten (2022) provides a detailed description of the nest site and methods used for locating nests. The location of the nest site (i.e., open sandy area, 10–250 m from the river edge, and 5–25 m above the water line) was such that all northern map turtles captured here were in the process of completing a nesting foray. We captured females immediately after nesting, or when a female was returning to the water after attempting to nest. We measured and marked all females captured at the nesting site as described above.

We used annual fertility rates from the literature. In 2 separate studies, in an urban canal in central Indiana ($n = 10$; Rush 2008) and a 3-year study in Pennsylvania, USA ($n = 43$; Ryan and Lindeman 2007), 100% of radiographed northern map turtles contained calcified eggs. Therefore, we assumed each female within the study site nested at least once annually. We observed multiple females nesting at the nest site twice in 1 year, or double-clutching, with 9 days being the fewest number of days observed between successful nesting events. We were often unable to locate the first or second nest of a double-clutching female because of the number of researchers, cryptic nature of some nesting turtles (i.e., nesting at base of grass or edge of forest), and the number of turtles nesting at one time at the nest site. We assumed that all females captured at the nest site were nesting; therefore, to determine double-clutching rates, we recorded an individual as double-clutching if 2 confirmed nests were

located in 1 year, or if an individual had 1 confirmed nest but was captured at least twice at the nest site with a minimum of 10 days between captures.

We numbered each nest, recorded the individual female that constructed it, and excavated and counted the number of eggs. If a female double-clutched in 1 year and both nests were located, we considered each nest independent of one another and used each individual nest in determining mean clutch size. From 2018–2020, we reburied and protected nests with predator-proof cages to calculate hatching success, and we left 19 uncaged to determine predation rates. In 2021, we caged all nests. We monitored all nests daily for predation until the first week of July. We used only uncaged nests to calculate predation rates and recorded a nest as depredated if it had been excavated and eggshells from recently consumed eggs were present in or around the nest cavity, or not depredated if there were no signs of predation. We calculated nest predation rates by dividing the number of uncaged nests that were not depredated by the number of uncaged nests.

We resumed monitoring nests in the first week of August 2018–2021 at 2-day intervals to determine hatching success of nests that were not depredated. Monitoring for hatchling emergence continued through September and resumed the following April when temperatures permitted. In late August and early September 2021, we excavated any remaining nests from which hatchlings had not yet emerged. When we observed a hatchling in a caged nest on the soil surface, we excavated the entire nest, counted, and measured hatchlings (e.g., length, width, mass), notched marginal scutes with nail clippers, and released all hatchlings at the river's edge. We considered an egg to have successfully hatched if there was a fully developed hatchling with it, whether on the surface in the nest cage, in the soil fully developed alive or dead out of the egg, in the egg with a portion of the egg split open, or if no hatchling was located but the egg was split enough for a hatchling to emerge and the shell was still underground. We considered an egg unsuccessful if the egg did not fully develop, or the hatchling was found dead inside the egg before the egg had been opened by the hatchling. At the end of the incubation period, we calculated hatching success of each caged nest as the number of hatched eggs divided by the clutch size.

Elasticity and sensitivity analysis

We used the calculated probability of survival, combined with an estimated population size based on empirical data, to conduct sensitivity and elasticity analysis to understand how the study population may respond to events such as widespread adult mortality, a head-start program to increase juvenile recruitment, or nest protection to increase neonate survival. For elasticity and sensitivity analysis, we built a 5-stage age class Lefkovitch matrix model (Figure 2; Caswell 2001) using fecundity (i.e., mean annual female production) and survival probability calculated from the nest and mark-recapture datasets, and the estimated abundances of each age class from Otten (2022). We created our Lefkovitch matrix model under the following assumptions: only females were included, our estimates of fecundity and survival would not change over time, and fecundity and survival depend only on the age class an individual is in. For the model we used 5 age classes, rather than age-specific data, for each year. We used the following 5 age classes: 1) eggs, 2) hatchlings (i.e., turtles within their first year or <4.0 cm SCL), 3) juveniles (i.e., unsexable turtles 4.0–6.0 cm SCL, typically 1–3 years old), 4) subadults (i.e., non-breeding females typically 6.1–17.5 cm SCL or 3–14 years old), and 5) adults (i.e., breeding females >17.5 cm SCL or ≥14 years of age). For each of the 5 age classes, we calculated fecundity, probability of surviving and remaining in the current age class in the next time interval, and probability of surviving and moving up to the next age class in the next time interval. Each time interval was a single year.

For fecundity, we assumed that only adults reproduce and that annual cohorts exhibit a 1:1 sex ratio. We calculated fecundity as the mean number of female eggs produced by each female turtle each year, accounting for double-clutching:

$$\text{Fecundity} = \frac{\text{mean clutch size}}{2} (\text{for } 1 : 1 \text{ sex ratio}) \times (\% \text{ breeding} + \text{rate of double clutching}). \quad (1)$$

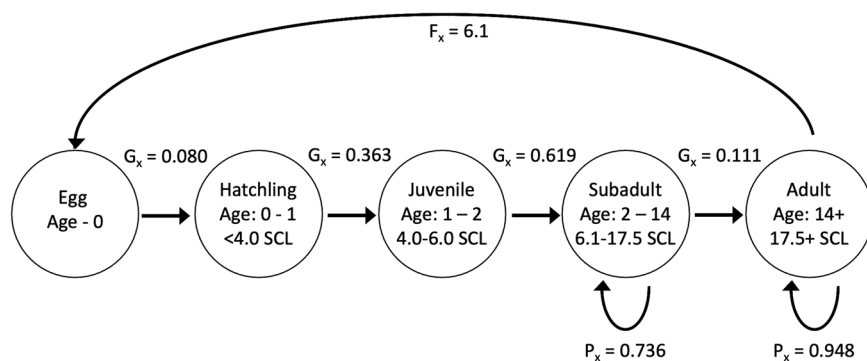


FIGURE 2 A 5-stage Lefkovitch model calculated from northern map turtle surveys conducted on the Kalamazoo River in Michigan, USA, 2019–2021. We considered only females for each age class. We calculated fecundity (F_x) for adult females captured during nest surveys conducted from 2018–2021. We calculated the probability of surviving and staying in the same age class (P_x), and of surviving to the next age class (G_x), using Cormack Jolly Seber mark-recapture methods in the RMark package.

To determine the probability of eggs surviving and moving up to the hatchling age class, we used nest predation rates (calculated from uncaged nests) and hatching success of caged nests:

$$\text{Egg survival to hatchling stage} = \% \text{not predated} \times \text{hatching success.} \quad (2)$$

We calculated survival probability of the other 4 age classes as described above using the CJS method in program RMark (R Software; White and Burnham 1999, Laake 2013, R Core Team 2018). We included age class and sex for survival probability covariates and the null recapture probability covariate. This model estimates the probability of surviving and moving up to the next age class for hatchlings and juveniles, as these age classes contained individuals for only 1 year, and the probability of surviving and remaining in the current age class for subadults and adults. To determine the probability of subadults surviving to the adult stage, we assumed that 9 1-year time intervals occurred for the subadult age class. We also assumed the proportion of subadults in the starting population was divided equally amongst annual cohorts of the subadult age class, with only the oldest subadults reaching sexually maturity the following year.

We used a proportional sensitivity and elasticity analysis to assess the effects of each age class's vital rates on population growth in this population of relatively abundant northern map turtles. Sensitivity and elasticity analyses are frequently used as a population ecology tool to guide wildlife management of a variety of species. Sensitivity analysis is used to assess the effect of an additive change to vital rates, whereas elasticity analyses assess the effect of a proportional change to vital rates (Enneson and Litzgus 2008; Manlik et al. 2018, 2022). We first determined the time-specific growth rate after 30 years, and whether the resultant population was stable, decreasing, or increasing with the calculated fecundity and survival rates. Under current conditions, we found the population to be decreasing, so we then evaluated each age class's survival rate independently, increasing in increments of 0.5%, to determine the rate that would create a stable or increasing population over 30 years. Also, because factors such as habitat fragmentation, road construction, and boat strikes can increase adult mortality in turtle populations (Aresco 2003, Bennett and Litzgus 2014, Hamer et al. 2018, Howell and Seigel 2019), we compared the change in population size over 30 years by decreasing adult survival by 1%, 5%, and 10%.

To evaluate the effect of common, temporary management techniques such as nest protection, predator removal, and head-starting programs on population size, we increased survival rates of either the hatchling or juvenile age class for the first 4 years of a 30-year period, before returning to the previously calculated survival rate. We increased survival rates in each of the 4 years at the same rate until the estimated population size after 30 years

was stable or increasing. We also evaluated the effect of an event that temporarily increased adult mortality (e.g., poaching, winterkill, catastrophic environmental event) in the population after 30 years by decreasing adult survival rates for the first 2 years in our model by 1%, 10%, and 25%. We selected these mortality rates and this timeframe because estimates of map turtle mortality due to poaching are limited but winterkills of northern map turtles can kill nearly 10% of known nesting females in a single season (Catrysse et al. 2015) and catastrophic oil spill events can decrease the number of females in a single population by nearly 25% in the first few years following the spill (Otten et al. 2022). Thus, rare and isolated events can have substantial influences on population trends for decades following the event itself.

RESULTS

During 172 days of survey, we made 3,536 captures of 1,726 individual northern map turtles (Figure 3; Table 1), nearly half of which we recaptured at least once ($n = 804$). Individuals were recaptured 1–11 times for 1,810 recaptures. The overall catch per unit effort for the study was 20.6 turtles/day, ranging from 19.1 in 2021 to 23.0 in 2020. The estimated sex ratio of turtles identifiable to sex during the study differed from 1:1, with 0.64 males captured for every 1 female captured (Table 1; $Z = 6.8$, $P < 0.01$). Individuals too small to positively identify to sex made up 42.3% of all individuals captured, followed by females (38.1%; Figure 3).

Survival and recapture analysis

Of the 20 candidate models for survival and recapture probability, the best-supported model retained size of turtle when first captured (SCL) affecting survival, and time affecting recapture probability. This model accounted for >99% of annual variation in survival probability of northern map turtles (Table A1). Generally, as the size of turtles increased, annual survival probability also increased (Figure 4; Table A2); however, the lowest annual survival

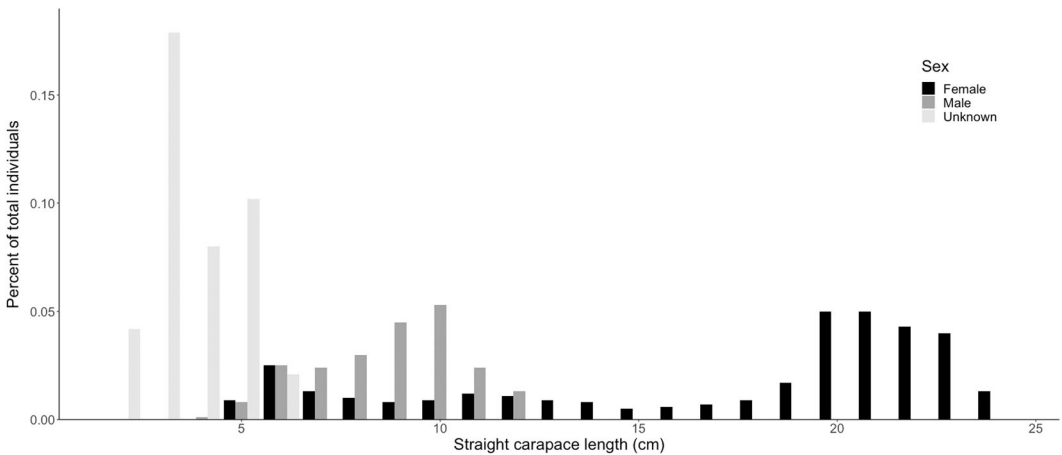


FIGURE 3 Percent of captured individual northern map turtles of each sex within each size category (straight carapace length [SCL] in cm). We captured turtles during surveys on the Kalamazoo River in Calhoun County, Michigan, USA, 2019–2021. For individuals captured multiple times during surveys, we included only the first capture with an associated SCL measurement, and only the sex identified upon an individual's first capture (i.e., an individual of unknown sex that was first captured in May 2019 and was subsequently identified as a male when recaptured in May 2021, was included in analyses as unknown sex).

TABLE 1 Overall effort and capture results of northern map turtles from the Kalamazoo River in Michigan, USA, 2019–2021. Days surveyed was the number of days in which active turtle trapping occurred within the study site. The number of captures (captures) and individuals captured (ind) for males, females, and unknown sex are included for each year of survey.

	Days surveyed	Females		Males		Unknowns		Combined	
		Captures	Ind	Captures	Ind	Captures	Ind	Total captures	Total ind
2019	98	665	358	413	253	833	507	1,911	1,118
2020	54	575	366	356	225	312	240	1,243	831
2021	20	264	220	93	90	25	25	382	335
Total	172	1,504	658	862	418	1,170	730	3,536	1,726 ^a

^aThe number of combined individuals differs because some individuals were captured in multiple years.

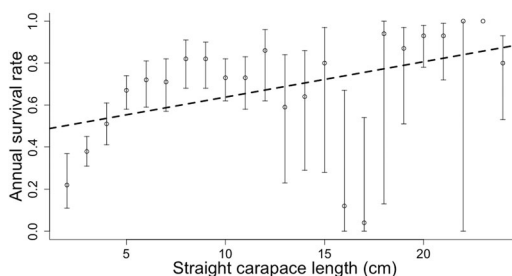


FIGURE 4 Annual survival probability and 95% confidence intervals of northern map turtles from the Kalamazoo River, Calhoun County, Michigan, USA, based on size (straight carapace length in cm) at first capture. We calculated and modeled survival probability in RMark from 3 years (2019–2021) of mark-recapture data. Size was the only covariate included in the best-supported model, but turtles of unknown sex made up nearly all captures <5 cm, and females made up all captures >13 cm. Line of best fit added as dashed line.

probabilities (0.04 to 0.12, 95% CI = 0.00–0.67) occurred in turtles 16.0–17.9 cm SCL, which corresponded to turtles that were female and approximately 13–15 years of age based on counts of growth rings. Turtles of unknown sex, which are generally <2 years of age (based on counts of growth rings) and <5.0 cm SCL, had the next lowest annual survival probability, ranging from 0.22 (95% CI = 0.11–0.37) to 0.51 (95% CI = 0.41–0.61). Adult female northern map turtles, or individuals with an SCL > 18.0 cm and ≥ 15 years of age, had the highest annual survival probability, ranging between 0.80 (95% CI = 0.53–0.93) and 0.99 (95% CI = 0.99–0.99). The recapture probability was best modeled as a function of time (Table A1), with the probability of recapture differing between survey events, ranging from 0.01 (95% CI = 0.01–0.02) to 0.25 (95% CI = 0.16–0.36).

Nest surveys and reproduction rates

From 2018–2021, we captured 201 individual female northern map turtles 572 times during nesting forays, which represented nearly half of all sexually mature females marked at the study site ($n = 428$). We located 210 northern map turtle nests, which had a mean clutch size of 10.0 eggs \pm 2.7 [SD]; Table 2). Double-clutching occurred 55 times, representing 27.4% of known nesting individuals. We successfully located both nests an individual laid in the same year 19 times, with mean clutch size being identical in the first (10.4 \pm 1.9) and second nest (10.4 \pm 2.1).

TABLE 2 Northern map turtle nest results from a single nesting location along the Kalamazoo River in Michigan, USA, during surveys conducted from 2018–2021. Total nests represent the number of nests located each year. A portion of nests were protected from predators with caging each year to determine hatching success rates. Depredated nests were those where we located fresh dug up and empty eggshells. We used only uncaged nests to calculate predation rates (depredated uncaged). Total eggs were the number of eggs counted from nests laid each year. Mean clutch size was the mean number of eggs laid per nest each year. Depredated eggs were the number that we found dug up and eaten, and unhatched are the number of eggs that we dug up that had either not developed, were unfertile, or had been destroyed by roots. For each nest, we calculated hatching success as number of hatchlings that hatched out of eggs divided by total clutch size.

	Nests				Eggs				Hatching success
	Total	Uncaged	Depredated, uncaged (%)	Depredated, caged	Total	Mean clutch	Depredated	Un-hatched	
2018	52	4	4 (100)	4	467	9.0	75	105	73.2%
2019	80	10	9 (90)	17	838	10.5	329	140	72.5%
2020	36	5	4 (80)	0	377	10.5	30	51	85.3%
2021	42	0	NA	9	412	9.8	80	94	71.7%
Total	210	19	17 (89.4)	30	2,094	10.0	514	390	75.3%

TABLE 3 Northern map turtle female survival and fecundity rates used in the 5-stage Lefkovich model. The Lefkovich model included survey data from 2019–2021 on the Kalamazoo River in Michigan, USA. The total number of starting individuals (n) in each age class was estimated from Otten (2022). We calculated fecundity (F_x) for adult females captured during nest surveys conducted from 2018–2021. We calculated the probability of surviving and staying in the same age class (P_x), and of surviving to the next age class (G_x), using Cormack Jolly Seber mark-recapture methods in the RMark package in R.

Age class	Estimated age (yr)	SCL ^a (cm)	n	F_x	P_x	G_x
Eggs	0		2,800	0	0	0.080
Hatchling	0–1	<4.0	250	0	0	0.363
Juvenile	1–2	4.0–6.0	100	0	0	0.619
Subadult	2–14	6.1–17.5	200	0	0.736	0.111
Adult	>14	>17.5	500	6.1	0.948	0

^astraight carapace length.

Seventeen of 19 uncaged nests were depredated (89.5%). Additionally, 30 of 191 nests that were protected with caging were also depredated (15.7%). During 4 years of nest surveys, 1,190 of 1,580 eggs hatched, for an overall hatching success rate of 75.3% (Table 2). Most eggs that failed to hatch appeared to be non-viable (i.e., we cut failed eggs open to look for any sign of development and did not find any) or were damaged by plant roots during incubation.

Elasticity and sensitivity analysis

We determined survival rates of the 5 age classes. Overall, annual survival probability increased with age class (Figure 4; Table 3). The egg stage had the lowest survival, with 8.0% of eggs laid each year estimated to survive to

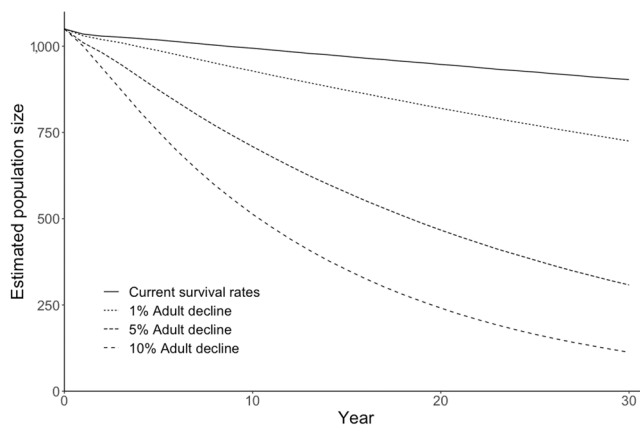


FIGURE 5 Estimated population size of female northern map turtles from the Kalamazoo River in Calhoun County, Michigan, USA, under varying adult survival rates. The starting population of each age class was estimated from Otten (2022), and the current population estimates are based on Lefkovitch 5-stage matrix models, which included 5 age classes, from mark-recapture data from 2019–2021, with survival probability calculated in RMark. Population estimates include only females and assume that survival and recapture rates remain constant over time. Under current survival rates estimated with empirical data, the northern map turtle population at the study site is declining by nearly 0.5% annually. We also estimated the total population size after 30 years under varying increased annual adult mortality rates of 1%, 5%, and 10%, rates typically seen because of habitat fragmentation, road construction, and boat propellor strikes.

the hatchling stage. Hatchling survival to the juvenile stage was 36.3%, and the annual rate of juveniles surviving to the subadult stage was nearly double that, at 61.9%. Subadults had an 11.1% probability of surviving to the breeding adult stage (Figure 4; Table 3). Subadults staying in the same age class and adults had high annual survival at 73.6% and 94.8%, respectively. The fecundity of adult females was 6.1 female eggs per year.

An estimated starting population of 1,050 individual females made up of 250 hatchlings, 100 juveniles, 200 subadults, and 500 adults, and 2,800 eggs, demonstrated an annual growth rate of 0.995, equating to a 14% decrease in the population after 30 years. For the population to remain stable after 30 years, one of the following stage-specific survival rates would need to increase: eggs by 1%, hatchlings by 4.5%, juveniles by 8%, subadults by 3%, or adults by 0.5%. Increasing the annual adult survival rate by only 1% would increase the population by nearly 75 individuals (7.1%) after 30 years; however, decreasing annual adult survival by 1% would decrease the population size by an estimated 31%. A 5% decrease in annual adult survival would decrease the population size by 70.7%, and 10% lower adult survival would decrease the estimated population size by nearly 90% after 30 years (Figure 5).

Doubling the number of eggs that hatch during the first 4 years of a 30-year period, before returning to the originally calculated 8% hatching success rate in each of the next 26 years, would keep the population size stable. Similarly, head-starting 50 hatchlings until they reached subadult size (>6.0 cm SCL) in each of the first 4 years of a 30-year period would produce a stable population after 30 years. Decreasing adult survival by 1%, 10%, and 25% for the first 2 years of a 30-year period, which might occur because of poaching, winterkill, or a contaminant spill event, would decrease the population size by 15%, 26%, and 43%, respectively (Figure 6).

DISCUSSION

Size- and age class-specific survival rates are key parameters for conservation and management decisions, especially in long-lived, late-maturing species. Survival estimates for the youngest life stages are still lacking for most species, especially turtles. We used empirical data collected from mark-recapture surveys on northern map

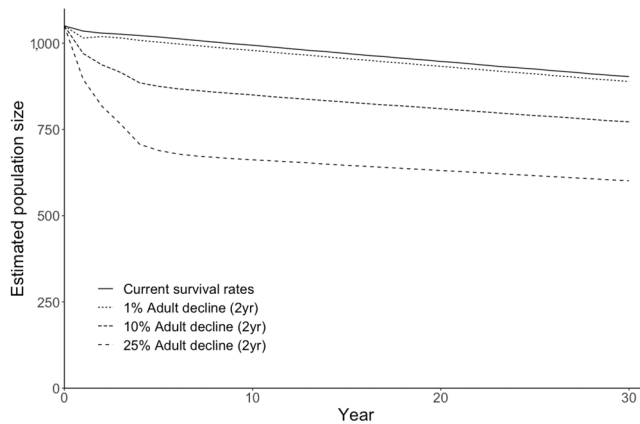


FIGURE 6 Estimated population size of female northern map turtles from the Kalamazoo River in Calhoun County, Michigan, USA, based on elasticity analysis. The starting population of each age class was estimated from Otten (2022), and the current population estimates are based on Lefkovich 5-stage class matrix models, which included 5 age classes, from mark-recapture data from 2019 to 2021, with survival probability calculated in RMark. Population estimates include only females and assume that survival and recapture rates remain constant over time. The current survival rates show the population is declining by nearly 0.5% annually. We also estimated the total population size after 30 years under increased varying adult mortality rates of 1%, 10%, and 25% during only the first 2 years of the 30 years to simulate a potential poaching or catastrophic environmental event.

turtles to estimate size- and age class-specific survival probability in a wild population of riverine turtles across the entire size range of the species. These estimates may provide life stage- and size-specific metrics that may be used to evaluate extinction risk and population viability, and help with management decisions for other relevant turtle species for which those vital rates are lacking.

Our results support a pattern of ontogenescence in northern map turtles, where age class-specific survival rates increased with age (Levitis 2011, Hoekstra et al. 2020, Reinke et al. 2020), followed by senescence when survival decreased in the oldest, largest individuals (Warner et al. 2016). As turtles increased in size each year, annual survival probability increased concomitantly, such that the larger individuals in the population (i.e., adult females) had nearly 95% annual survival probability, whereas slightly smaller individuals (i.e., large males and subadult females 8–13 cm SCL) had annual survival probabilities of about 80%. Our estimates of annual survival probability were similar to the only other analysis of survival rates in northern map turtles. In that study, a Canadian population of northern map turtles had annual survival probability slightly higher in females (87–94%) compared to males (81–83%; Bulté and Blouin-Demers 2009, Bulté et al. 2009). A decrease in annual survival probability of the largest (i.e., oldest) females (>24 cm SCL) and males (>13 cm SCL) in the population suggests that wild northern map turtles, like painted turtles, exhibit senescence (Warner et al. 2016).

Larger individuals had the highest annual survival probability, which suggests that size, rather than age, is the most important determinant of individual survival; adult males >40 years old have an identical probability of annual survival as females of the same size that are 30 years younger. Although size may enhance an individual's ability to navigate difficult terrain or travel long distances, individuals of both sexes and all age classes in this population move long distances, travel against strong currents, and circumvent anthropogenic structures (Otten et al. 2023). Thus, the positive correlation between annual survival and body size we demonstrate here may instead be related to a decrease in predation as turtle size increases; however, adult females travel overland annually to reach nest sites, often 50–125 m from the river, increasing potential for predation or injury due to anthropogenic disturbance (Otten 2022). Although accurate age determination can be difficult because growth rates slow in large adult females, we did not observe a difference in annual survival between size classes ≥ 18 cm SCL (~15 years of age).

Survival rates of hatchling and juvenile turtles are difficult to determine because of the cryptic nature of these life stages, and the difficulty of capturing them with traps designed primarily for adults (i.e., hoop traps). Using dipnets with smaller mesh size yielded similar capture rates between small and large turtles, resulting in a mark-recapture dataset in which nearly a third of all individuals captured ($n = 519$) over 3 years of study were turtles <2 years of age (i.e., <5.0 cm SCL). Moreover, our top model predicting recapture probability included time, but not size or sex, further suggesting capture and recapture rates were similar across the sizes of individuals. Our overall estimate of 35% annual survival for first-year (<4.0 cm SCL) northern map turtles in the Kalamazoo River falls within the range reported for other aquatic turtle species (0.11–0.42; Congdon et al. 1993, Heppell 1998, Paterson et al. 2012, Dragon 2015, Knoerr et al. 2022).

The lowest annual survival in turtles was individuals 16–17.9 cm SCL, which represents the approximate size at which subadult females in the population become gravid for the first time. The decrease in survival of newly reproductive females may be due to their vulnerability to novel risks associated with nesting forays (Horne et al. 2003, Steen et al. 2006, Carstairs et al. 2019). This includes traveling long distances to nesting sites for the first time, an increased risk of predation during overland movements, increased anthropogenic threats such as road mortality, or time-consuming efforts to find suitable nest sites (Freedberg et al. 2005, Mitrus 2006, Lohman et al. 2008, Nagle and Russel 2020).

For turtles with high adult survival rates, such as our study population, often very few management options exist to further increase already high adult survival. Indeed, in the Kalamazoo River, there are few predators of adult map turtles, and we observed no adult deaths due to road mortality or other anthropogenic impacts. In turtle populations with high rates of adult mortality due to roads (Gibbs and Shriver 2002, Steen et al. 2006, Piczak et al. 2019) or predation (Lanszki et al. 2006, Karson et al. 2018), specific management activities could mitigate these declines (Heaven et al. 2019, Boyle et al. 2021). Our life stage-based survival model allowed us to predict how management activities would affect numbers of turtles in each age class, and population size and growth rates overall. If adult survival rates remain constant, even the large map turtle population at our study site would require a slight increase in either annual adult survival or egg success to avoid a continued decline after 30 years. There was no evidence that the population would recover after the loss of even a few additional adult females, a result similar to that for another common species, the common snapping turtle (*Chelydra serpentina*; Keevil et al. 2018).

Recent studies of freshwater turtles have concluded that caging nests to protect against predation, or head-starting hatchlings to augment recruitment, may be valuable conservation tools for declining turtle populations (Schindler et al. 2017, Spencer et al. 2017, Carstairs et al. 2019, Campbell et al. 2020, Thompson et al. 2020). Models for some species suggest that head-starting to increase hatchling survival could be successful at increasing population size; however, unless survival rates of other life-stages are also increased, the population would decline immediately after head-starting initiatives cease (Spencer et al. 2017, Bougie et al. 2022). Head-starting can be labor-intensive, expensive, and may produce similarly low or even lower survival rates compared to juveniles produced naturally (Tetzlaff et al. 2019, Golba et al. 2022). Our population models support the idea that although head-starting hatchlings would increase population size during the years in which head-starting occurred, in each subsequent year without head-starting the population size would decline by 0.5% if all other survival rates remained constant. In populations with high nest predation, protecting a small number of nests with predator-proof cages annually would increase hatching success. Our elasticity analysis indicated that doubling hatching success (i.e., from 8% to 16% of all eggs laid) for 4 years would maintain a stable population after 30 years, suggesting that devoting a small amount of energy to caging about 25 nests each year would be sufficient to keep the estimated population at approximately 1,050 individuals.

For declining turtle species, multiple threats at different life stages should be addressed concurrently to maximize the likelihood of successful conservation efforts (Crawford et al. 2014). The same is true for a species not currently of conservation concern; to maintain a stable population in even a common, abundant species, survival rates must be increased for ≥ 2 different life stages, which could be achieved through a variety of management options. Our estimates of age class-specific survival rates in a model turtle species could be useful in population models for species where low sample sizes and limited resources may make species-specific survival estimates difficult.

MANAGEMENT IMPLICATIONS

Our results suggest that freshwater turtles exhibit ontogenescence, and that slight fluctuations in age class-specific survival rates will have long-term effects on population sizes and trends. Understanding how changes in survival rates across life stages affect overall population trends, which size or age classes are most sensitive to slight perturbations in survival rates, and which management actions will be most effective at increasing population growth are important for maximizing the efficiency of limited conservation resources. Precise estimates of survival rates in early life stages are very rare for turtles in general, despite the importance of early life stages in contributing to population growth through recruitment into the breeding population. Our study provides age class-specific survival estimates for a model turtle species based on mark-recapture data that could be used as placeholders in population models for similar species for which sufficient data to calculate species-specific parameters are lacking, leading to biologically based management decisions. For example, in imperiled species of turtles where management funds may be limited, focus on increasing survival in age classes with the lowest annual survival rates but highest number of individuals may increase the population size quickly. This could be done through management of mesopredators that prey upon small turtles. Our results indicate that even an apparently common, abundant species is undergoing population decline, and will continue to do so if survival rates of ≥ 1 life stages are not increased via management intervention.

ACKNOWLEDGMENTS

The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the United States Fish and Wildlife Service or others, collectively or as individual entities. This research was funded by the United States Fish and Wildlife Service, Nottawaseppi Huron Band of the Potawatomi Tribe, Match-E-Be-Nash-She-Wish Band of the Pottawatomi Indians, National Oceanic and Atmospheric Administration, Michigan Department of Natural Resources, Michigan Department of Environment, Great Lakes, and Energy, and Michigan Department of the Attorney General. We thank L. L. Williams and C. McCready for logistical support and I. T. Clifton, M. K. Haywood, N. Torres, E. J. Barfuss, E. McDonald, N. Huffman, N. Runyan, and P. Madden for field assistance. Thanks to W. T. Clan, K. O. Tubby, T. A. Maytals, and A. T. Grind for technical support.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All research was conducted in accordance with Michigan Department of Natural Resources scientific collection permits issued to J. M. Refsnider (2018, 2019, 2020, and 2021) and University of Toledo's Institutional Animal Care and Use Committee (protocols 108797 and 400109).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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Associate Editor: Richard Inman.

How to cite this article: Otten, J. G., and J. M. Refsnider. 2024. Bigger is better: age class-specific survival rates in long-lived turtles increase with size. *Journal of Wildlife Management* e22544.
<https://doi.org/10.1002/jwmg.22544>

APPENDIX A

TABLE A1 Top models describing survival (ϕ) and recapture (p) probability of northern map turtles in the Kalamazoo River in Michigan, USA, 2019–2021. For each candidate model we list model rank, variables included (model), number of parameters (K), difference in AIC_c value from top model (ΔAIC_c), Akaike weight (w_i), and $QAIC_c$ adjusted by a \hat{c} of 3.56. Variables included in survival probability included size of individual (i.e., straight carapace length [SCL]), SCL \times sex, time between surveys (time), and constant survival probability (.). Variables included in recapture probability included SCL, sex, time, level of effort (effort), and constant recapture probability (.). Only the top 5 models and the null model are included.

Rank	Model	K	ΔAIC_c	w_i	$QAIC_c$
1	ϕ (SCL) ρ (time)	41	0.00	0.99	2,386.68
2	ϕ (SCL \times sex) ρ (time)	56	16.55	0.00	2,412.90
3	ϕ (.) ρ (time)	19	217.32	0.00	2,416.08
4	ϕ (SCL) ρ (effort)	25	232.18	0.00	2,428.89
5	ϕ (time) ρ (time)	36	223.70	0.00	2,442.33
17	ϕ (.) ρ (.)	2	710.37	0.00	2,530.13

TABLE A2 Estimated annual survival rate and 95% confidence intervals calculated from the top model for northern map turtles from the Kalamazoo River in Michigan, USA, using mark-recapture data collected in 2019–2021. The total number of individuals (n) used for survival rates calculations in the RMark package in R were based on only the first straight carapace length (SCL; cm) measured for each individual. Approximate age was based on SCL data derived from this population (Otten 2022) and a population in Indiana (Iverson 1988). Turtles >14 cm SCL included only females. Age for individuals >18.0 cm was difficult to accurately determine because of slower growth rates, difficulty in counting annual growth rings, and length of time of survey.

SCL (cm)	n	Approximate age	Survival rate	Lower 95% CI	Upper 95% CI
<3	72	0–1	0.22	0.11	0.37
3–3.9	308	0–1	0.38	0.31	0.45
4–4.9	139	1–2	0.51	0.41	0.61
5–5.9	204	2–3	0.67	0.58	0.74
6–6.9	122	3–4	0.72	0.59	0.81
7–7.9	65	4–5	0.71	0.57	0.82
8–8.9	70	5–6 (5–7 male)	0.82	0.68	0.91
9–9.9	92	6–7 (7–9 male)	0.82	0.68	0.90
10–10.9	107	7–8 (>9 male)	0.73	0.62	0.82
11–11.9	63	8–9 (>9 male)	0.73	0.58	0.83
12–12.9	42	9–10 (>10 male)	0.86	0.62	0.96
13–13.9	15	10–11 (>10 male)	0.59	0.23	0.84
14–14.9	13	11–12	0.64	0.29	0.86
15–15.9	9	12–13	0.80	0.28	0.97
16–16.9	10	13–14	0.12	0.00	0.67
17–17.9	12	14–15 ^a	0.04	0.00	0.54
18–18.9	15	>15	0.94	0.13	1.00
19–19.9	29	>15	0.87	0.51	0.97
20–20.9	86	>15	0.93	0.78	0.98
21–21.9	86	>15	0.93	0.72	0.99
22–22.9	74	>15	1.00	0.00	1.00
23–23.9	68	>15	1.00	1.00	1.00
>24	22	>15	0.80	0.53	0.93

^aApproximate age and size in which females first become sexually mature.