The Status of Snapping Turtles in the Coastal Plain of Virginia: commercial harvest, conservation, demography, and regulatory recommendations

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1. Background

The Snapping Turtle

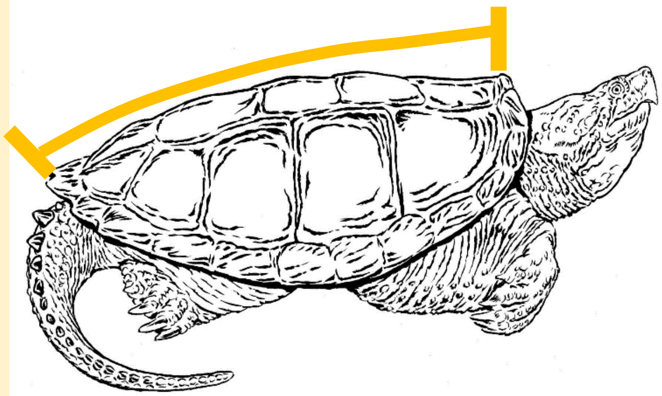
The snapping turtle, *Chelydra serpentina*, is the second largest freshwater turtle in the United States (US) [1]. The geographic range of the snapping turtle is extensive, covering 37 of the 50 US states, including all states east of the Rocky Mountains, extending from lower Florida and Texas northward into Canada, from southeastern Alberta to Nova Scotia [1,2]. Snapping turtles are long-lived with an estimated maximum life span in the wild exceeding 50 years, with males growing larger than females, and maximum weights exceeding 22.7 kg [3–5]. Snapping turtles sexually mature at approximately age 7 years in eastern Virginia, but require as long as 18 years to reach sexual maturity at high latitudes and lay a single clutch of 26 – 55 eggs annually on average, which experience egg to hatchling survival rates as low as 6% [2]. Snapping turtles continue to lay eggs throughout adulthood, and lay larger clutches as they grow in size, which underscores the importance of older breeding individuals to population viability [6].

Commercial Harvest of Turtles

Many iconic and once-plentiful turtle species such as the Central American river turtle, *Dermatemys mawii* [7], the pig-nosed turtle, *Carettochelys insculpta* [8] and the alligator snapping turtle, *Macrochelys temminckii* [9,10] have experienced steep population declines due to overharvesting and are now at historically low levels across much of their ranges. Turtles are commercially harvested for their meat, which feeds both local and international markets [11–13]. China is the world's leading consumer of turtle meat, and Chinese consumption is considered a primary threat to the world's turtle populations [13–15]. The collapse of Asian turtle populations over the last few decades, largely due to overharvesting, has resulted in a shift from domestic harvest of wild turtles to aquaculture and international import, thus increasing harvest pressures on turtle species around the world [16,17].

Snapping turtles have come under increased pressure over the last 15 years from commercial harvesters to meet the demands of the international food market. Increases in the US export of live snapping turtles raise concerns for the viability of the species. Export records are maintained at the federal level, only account for live individuals, and do not differentiate between males and females. Females are generally exported live to support aquaculture, but the bulk of males harvested in the US are butchered, canned, and exported. Gravid females fetch the highest prices from turtle exporters as the presence of eggs increases their value to farming operations (Millington Seafood, Spots Seafood, pers. comm.). Exported turtles are classified as either wild caught or farmed. Although turtles from farming operations make up the bulk of exports annually, the distinction between wild caught and farmed turtles may be tenuous as we know of no documentation on how much farms supplement their stock with wild caught individuals, nor the rate at which the wild caught turtles are then exported as “farmed” individuals.

In 2013 alone over 125,000 pounds of common snapping turtles were reported as commercially harvested from Virginia waterways. This is likely an underestimation of the total harvest as there is an indication that not all watermen are fully reporting their harvests, and private harvest is not required to be reported. Based on annual state reports, the 2013 harvest nearly doubled the harvest from 2012, and represents a nearly 13-fold increase over recorded harvest since 2002. Turtle harvest laws in neighboring states have been tightened, which has resulted in increased pressure on Virginia’s snapping turtle populations. North Carolina first imposed a moratorium on commercial fishing of snapping turtles until the sustainability of harvest could be studied, and followed up that moratorium by instituting bag limits on commercial harvest [18]. Increased restrictions in Maryland included increasing the minimum size limit from 9.5 inches curved carapace length (CCL) to 11 inches CCL, and limiting harvesting to tidal waters only [19]. High turtle prices, combined with a relatively weak U.S. economy likely contributed to an increase in the number of Virginia commercial harvest permits sold to out-of-state watermen, from 1 to 26 over the last 15 years. The influx of harvesters and the 13-fold increase in snapping turtle harvest raises questions about the sustainability of Virginia's snapping turtle populations under the current harvesting regime.



How curved carapace length (CCL) is measured

2. Objectives

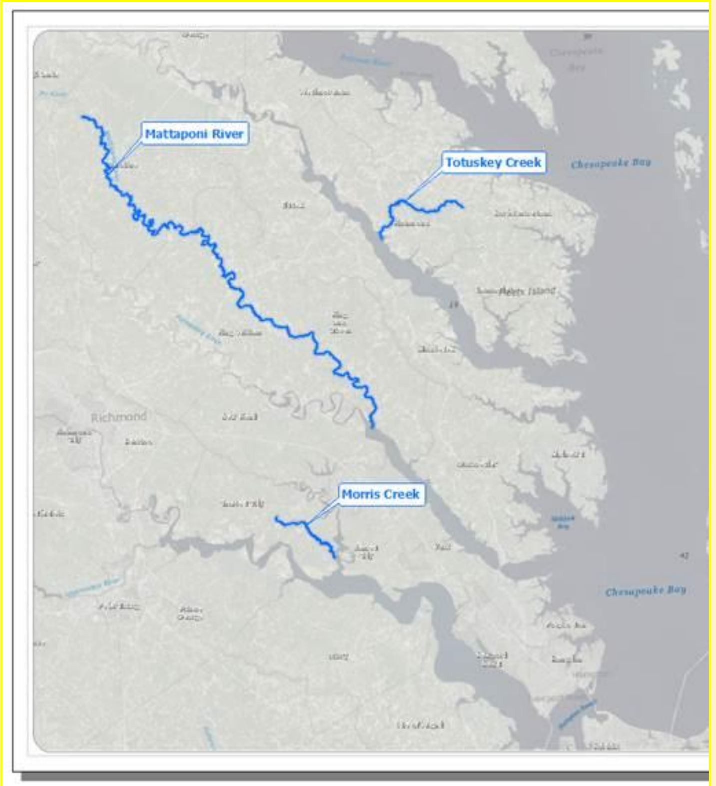
- Review levels of historic commercial harvest of snapping turtles in Virginia for the years 2002-2015 by reviewing harvest reports submitted by waterman annually.
- Characterize the demography of populations on three Virginia rivers, each representing a range of commercial harvest pressure, using mark-recapture techniques and analysis.
- Establish the first home range estimates, both overall and seasonally, for snapping turtles in an open-river environment using radio-tracking and telemetry methods, geographic information system (GIS) software, and kernel density estimation.
- Assess the viability of Virginia snapping turtle populations under various levels of commercial harvest pressure, using the population estimates derived from the mark recapture portion of this study, as well as demographic rates from the literature.
- Use sensitivity analyses to identify the size class(es) most critical to overall population persistence.
- Make recommendations based on the above objectives as to the direction of commercial harvest regulations governing snapping turtles in the Commonwealth of Virginia.

3. Methods

3.1 Historic Commercial Harvest in Virginia

The levels of reported harvest presented here were aggregated from commercial harvest reports submitted by waterman annually. Watermen were required to file a detailed report of their harvesting activities (rivers harvested, poundage and number of individuals harvested, method, and where their harvest was sold); otherwise, they would not receive a harvest permit in the subsequent year. The harvest report also requires landmark locations to accurately identify which sections of larger waterways are being harvested. The harvest report was required to be filed by the end of October of the harvest season in some years, or by the start of the following harvest season on June 1st in other years. The requirement was changed to the October deadline in 2013 to allow Virginia Department of Game and Inland Fisheries (DGIF) a longer period in which to review annual harvest activity. For reports that reported either pounds or number of turtles harvested, but not both, the missing metric was estimated based on the average turtle size harvested in that year. Each year a certain number of harvest reports are returned with a designation of “No Activity”, meaning a harvester purchased a permit for a given year but did not harvest turtles. We have eliminated the “no activity” reports from our dataset because we are concerned with the number of active harvesters removing turtles over time, and not the number of permits sold.

3.2 Mark-Recapture



We conducted a mark-recapture study of snapping turtle populations in three tributaries of eastern Virginia rivers: Morris Creek, a tributary of the Chickahominy River, the Walkerton area of the Mattaponi River, and Totuskey Creek, a tributary of the Rappahannock River. These three waterways were selected to represent a range of historic turtle harvest intensities gleaned from Commonwealth of Virginia annual landing reports, which commercial snapping turtle harvesters are required to file. Morris Creek, 37º 17’59.95”N - 76º 53’57.20”W, a site with no historic harvest and which was closed to harvest by VDGIF as part of this study, is approximately 12 – 21 meters wide and is banked by marsh grasses and cypress that transitions into mixed hardwood forest. The Walkerton area of the Mattaponi River, 37º 43’23.74”N - 77º 01’28.63”W, is characterized by patches of marsh vegetation, a small island, and is up to 304 meters in width. This site is considered to have a moderate level of historic commercial harvest relative to all Virginia rivers reported as commercially harvested from 2000 to 2011 (annual landing reports, DGIF). Totuskey Creek, 37°52'24.49"N - 76°44'52.85"W, is approximately 91 meters wide and is adjacent to grassy marsh with interspersed cypress and mixed hardwoods. This site is a high harvest site when compared to all commercially harvested rivers in Virginia (annual landing reports, VDGIF). The estimated sampling areas of each site are 48.53 ha (Morris Creek), 69.71 ha (Walkerton), and 73.43 ha (Totuskey Creek). The predominant plant species present among the sites are broad arrowhead (*Sagittaria latifolia*), water hyacinth (*Eichhornia crassipes*), and bladderwort (*Utricularia ssp.*).

Turtles were trapped from July to October in 2012, and from May to October in 2013, 2014, and 2015. The project design consisted of two trapping sessions per year at each site. Each trapping session consisted of setting up traps on eight days, Monday-Thursday, over a two-week period; thus, each trapping cycle across all sites spanned 6 weeks. Sampling was conducted using 20 hoop nets (Memphis Net and Twine Company), baited with punctured sardine cans to attract snapping turtles. Nets were three feet in diameter, six feet long, and had 2.54 cm (1 in) mesh. Each site had 48 potential trap locations that were selected based on a combination of biotic and abiotic factors that would predict the presence of snapping turtles (i.e., presence of plant cover, mud banks, and proximity to rivulets and main stem of the waterway). Distance between traps locations was similar at each site. Each sampling day, 20 of the 48 locations were selected using a random number generator. Between 9 a.m. and 3 p.m. traps were placed in the 20 selected locations for sampling. The next day, over the same time period, all turtles were removed from traps, weighed, sexed, and measured for curved carapace length (CCL) and carapace width [20]. Capture location, water temperature, and ambient temperature were also recorded. Each snapping turtle collected was fit with a unique numbered tag, National Band #7331, by drilling a small hole in a posterior marginal scute and attaching the tag with a stainless-steel bolt and screw. Turtles were then released back into the water at the capture location. Traps were then re-baited and placed in 20 randomly selected locations (except on Friday) for the next day’s sampling. When turtles were later recaptured they were re-weighed and re-measured, with their recapture location information logged.

3.3 Telemetry and Home Range Analysis

Between July 2012 and October 2014, 23 snapping turtles from the no-harvest site (Morris Creek) were outfitted with radio transmitters (Holohil systems, model AI-2F) with individuals selected to represent both sexes and a broad range of sizes. Transmitters were bolted to marginal carapacial scutes, and each unit had an expected battery life of three years. As part of the larger mark/recapture project, turtles were captured through the use of baited hoop nets. In order to more evenly balance the sex ratio that was dominated by males in 2012, an additional two female turtles were tagged in 2013, and six female turtles in 2014, for 23 turtles in total (14 males, 9 females). Physical measurements were taken for each turtle including curved carapace length, carapace and plastron length and width, and shell height and weight. Sex was determined using the methods of Mossiman and Bider, 1960 [20]. Tracking was conducted periodically in 2012 (14 tracking days) & 2013 (five tracking days) for the turtles that had been tagged to that point, and more intensely (30 tracking days) in 2014 (once all transmitters had been deployed) to establish overall and seasonal home ranges. Telemetry points were taken for the following days in 2013: February (27), May (15), September (9). Telemetry points were taken in the following seasons and days in 2014: spring (May 19-23 & 26-30), summer (August 18-22 & 25-29), and autumn (September 29-October 3 & October 6-10). Tracking was performed using a radio receiver (TRX-48S, Wildlife Materials) and a three element directional antenna (Yagi, Wildlife Materials). All positions were logged using a handheld GPS unit (Juno 3B, Trimble Inc.). Differential corrections for all data points were performed using local correction stations with pathfinder office version 5.30 which is native to Trimble devices.

4 Data Analysis

4.1 Mark-Recapture Analysis

A capture history was established for each turtle and these histories were analyzed using Program MARK to estimate survival probability, capture and recapture probability, immigration/emigration, and population size for each site. Parameter estimates created within Program MARK are obtained using maximum likelihood estimation. Among the model configurations within Program MARK, we selected the robust design using the Huggins c & p data type, which assumes a population to be closed (no migration nor mortality) during a sampling period and open between sampling periods. We tested an array of candidate models with various time, harvest, and research-specific dependencies. The top model was selected based on the Akaike information criterion weight (AIC_w) which is calculated relative to all models under consideration [21,22].

Estimates of survival (*s*), emigration (γ'), and immigration (γ'') were estimated for the period between sessions where the population is considered to be open. Estimates of capture (*p*) and re-capture (*c*) were for the within session period where the population is considered to be closed. The estimate of population size (*N*) was generated for each session using the capture histories of each individual site, with the mean population estimate ($\widehat{N}$) being the average of the population size estimates for all sessions at each site.

We approached survival in our candidate model array in three ways; models with constant survival among sites, models with site specific constant survival, and models where survival was separated into two measures: those years and sites with recorded commercial harvest (s_h) and those without commercial harvest (s_n), based on our knowledge of the harvest history at each of the sites. Within that framework we ran model permutations that tested for time dependence and differences in capture (*p*) and recapture probability (*c*), which assume the individual is in the study area at the time of sampling. We also tested for differences in temporary emigration (γ’) and immigration (γ’’) probabilities.

Each day we sampled a subset of a given site by randomly selecting 20 trap locations out of a possible 48. In the model with temporary emigration and immigration, the population estimate considers only those individuals in the sampled area at the time of sampling (Gary White, *pers. comm.*). We interpret the temporary emigration estimate to represent those individuals that are still within the area of our study site, but outside of our daily randomized sampling area, as none of the turtles we fitted with transmitters were ever tracked outside of the study site area. Because turtles were not observed moving out of the sampling area (see Telemetry Results), we interpret the temporary emigration and immigration to represent turtles not sampled due to incomplete sampling. However, as the best fit model has y’ = y”, this has the unsatisfying result of 50% of turtles being in the sampling area for any non-zero migration value. Instead, we interpreted the ‘temporary migration’ to represent the incomplete sampling design. As such, we needed to adjust the mean population estimate ($\widehat{N}$) to account for the portion of the population that remained within our study site but that were not exposed to trapping within the daily randomized sampling area. Thus, an adjusted population estimate was calculated using equation (1) where the adjusted mean population estimate($\widehat{N}_{adj}$) is equal to the mean population estimate ($\widehat{N}$) divided by the proportion of trap sites sampled (*p* =0.42).

$$\widehat{N}_{adj} = \frac{\widehat{N}}{p} \qquad (1)$$

4.2 Matrix modeling (Population Viability Analysis (PVA))

Parameter Estimation

Harvest

Harvest levels were estimated by averaging the annual number of individuals harvested over the four years for each study site. Number of turtles harvested in each waterway were taken directly from state landing reports filed by harvesters each year (Table 1). The mean annual harvest reported on each site was divided by the mean adjusted population estimate (equation 1), which was calculated from mark-recapture data in Program MARK and averaged over the four years of the study. This calculation is shown in equation (2) where P is the proportional harvest of a given site and is equal to the mean estimated harvest ($\widehat{H}$) divided by the adjusted mean population estimate ($\widehat{N}_{adj}$) of that site (Table 1).

$$P = \frac{\widehat{H}}{\widehat{N}_{adj}} \qquad (2)$$

Survival

Survival rates for all immature stages were taken from the literature (Table 2). Nest survival rates ranged from 0.056 to 0.245 with a mean estimate of 0.18 ± 0.077 (SD) [6,23,24]. Hatchling survival rate was estimated based on two separate studies, which contained three total estimates [6,25]. Two of the estimates were from field collected data, while the third was based on computer simulation. The average hatchling survival probability among the three estimates was 0.24 ± 0.16. As nest survival and subsequent hatchling survival occurs within a one-year period, nest and hatchling survival rates were combined into one metric (Y) by multiplying the two (0.04). The juvenile survival rate (*J*) of 0.77 ± 0.06 was calculated by taking the arithmetic mean survival rate of all juvenile classes (n = 11) provided by Congdon et al. (1994). The adult survival estimate (*S*) is the mean survival estimated from six populations ranging from West Virginia, USA to Ontario, Canada, including this study [6,26–29] (Table 2).

Fecundity

Annual fecundity rates for all adult stages were taken from the literature. We incorporated size class specific fecundity values (Table 2) because clutch size is positively correlated with female size [2,30,31]. The following equation (3), which is adapted from the fecundity equation found in Zimmer-Shaffer et al. (2014), was used to calculate fecundity for each of the nine adult size classes ($F_1 - F_9$) and the values for each parameter and their source(s) are given in Table 2. Fecundity is equal to the clutch size (*C*) of a given size class (*i*) multiplied by breeding frequency (*B*), adult survival (*S*), and sex ratio (*R*).

$$F_i = C_i \times B \times S \times R \qquad (3)$$

Growth Rates

We estimated size-specific growth rates by fitting data from the mark-recapture portion of our study for the adult stages using a non-linear model. Annual growth rates were calculated from 14 recaptured adult turtles (Table 3). In reviewing growth data, both from the literature and from data collected in this study, we found that growth in mature turtles begins to slow and ultimately settles at a constant rate for the remainder of the life [32]. To accommodate this pattern, we fit the data representing the adult size classes (20.32 cm to 32.99 cm) with an exponential decay curve that transitions into a constant growth rate at and above 33 cm. To calculate growth rate as a function of size we used equation (4) where *G* represents the growth rate in cm/yr, I is the initial size (cm) of a turtle in a given size class, α is the y-intercept (hypothetical growth rate at turtle length = 0 cm), and b determines the rate of exponential decline. The growth rate was adjusted to $G_{adj} = G + 0.1$ because zero growth rates are undefined in the exponential equation. The equation was fit using the function nlsLM in the R package minpack [33].

$$G_{adj} \sim \alpha * e^{-b*I} \qquad (4)$$

To calculate the average duration a turtle spent in each size class we calculated the average growth rate across the size interval of each size class. For size classes with exponentially declining growth rates, from 20.32 to 32.99 cm, this was accomplished by integrating between the upper and lower bounds of each adult size class (equation 5). For size classes at and above 33 cm, the growth rate was a constant 0.48 cm/yr.

$$\phi = \int_{lower}^{upper} \alpha * e^{-b*I} \qquad (5)$$

The integral (ϕ) was then used to calculate the mean duration of time in years (d) spent by a turtle in each adult size class using equation (6), where duration is equal to size interval (2.54 cm) divided by the integral ϕ (cm/yr) across a given size class.

$$d = \frac{2.54\ cm}{\phi\ cm/yr} \qquad (6)$$

Population Viability Analysis

Population matrices were constructed to analyze the effect of commercial harvest on snapping turtle population viability. Transition values in the population matrices were estimated using the survival, growth, and fecundity estimates. The matrices were constructed using R statistical software (R Development Core Team 2012). Analyses were run using R and the package 'primer' [34].

We created a hybrid age/size class matrix to characterize snapping turtle demography and to allow for the evaluation of various regulatory approaches in managing snapping turtle harvest. Immature stages, from the nest/hatchling stage (Y) through the 6 juvenile stages (J_1 – J_6) were modelled as age-based, with each representing one year. Virginia snapping turtles reach maturity after 7 years, which corresponds to a carapace length of approximately 20.32 cm, based on historic estimates [35]. After the seventh year, any surviving turtles move into the first adult size class (A_1) (20.32 – 22.86 cm), and from there proceed to size classes A_2 through A_9 conditional on growth and survival. Each adult size class has a parameter value that represents surviving and remaining in the current size class (P) and a value for surviving and moving to the next size class (G), with the sum of both equaling adult survival. Adult survival is defined as the survival rate of the adult size classes following commercial harvest and other mortality factors. Further, adult stages have a corresponding fecundity value (F_i), which represents the reproductive rate of a given size class. Each adult size class spans 2.54 cm (1 in) to facilitate evaluation of current, past, and potential harvest regulations. The resulting 16 x 16 matrix (M) (equation 7) accommodates all current regulatory approaches and allowed for evaluating the efficacy of alternative regulations at achieving sustainable snapping turtle harvest.

$$M = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & F_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 & F_8 & F_9 \\ Y & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & J_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & J_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & J_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & J_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & J_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & J_6 & P_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_1 & P_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_2 & P_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_3 & P_4 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_4 & P_5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_5 & P_6 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_6 & P_7 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_7 & P_8 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_8 & P_9 \end{bmatrix} \qquad (7)$$

Adult Size Class Transitions

Each adult turtle in year t has one of three fates in year t + 1: death, remain in same size class, or transition to the next size class. Adults in the largest size class (> 40.64 cm CCL) cannot transition to a larger size class, thus, either survive and remain in the same size class or die. To calculate transition probabilities of adult turtles, we used equation 8 [36]. The probability of a turtle remaining in size class i (P_i) is a function of the product of the proportion of surviving individuals (p_i) and the average duration an individual will spend in that size class (d_i).

$$P_i = \left(\frac{1 - p_i^{d_i - 1}}{1 - p_i^{d_i}}\right) p_i \qquad (8)$$

Conversely, G_i is the proportion of individuals in size class i that transition to the next size class over a single time step.

$$G_i = \left(\frac{p_i^{d_i}\,(1 - p_i)}{1 - p_i^{d_i}}\right) \qquad (9)$$

Population Matrix Modeling

Harvest was incorporated into the model by reducing all *P* and *G* values within a harvestable size range by the percent harvested, i.e., in a population with $h = 0.22$ proportion of turtles harvested, the value of $P_{harvest} = P*(1-h)$. By varying the levels of harvest to match historic harvest in our three study sites and adjusting which adult size classes are open to commercial harvest, we estimated the population growth rate (λ) of many regulatory scenarios from the dominant eigenvector of the matrix. In total, we assessed the viability of turtle populations under no harvest, and 16 unique harvest regulation scenarios under each of two harvest levels (16% and 44%) using the matrix as outlined above. Further, we increased the harvest level within our matrix from 1% to 100%, in increments of 1%, to identify the point where the resultant population growth rate switched from being in decline to stable/sustainable.

Sensitivity Analysis

We conducted sensitivity and elasticity analyses to identify which stages were most critical to maintaining population persistence for each of the three harvest levels. Sensitivity analyses were conducted according to the methods presented and executed within R using the package 'primer' [34]. Sensitivities (*s*) were calculated using equation (10), where $v_i w_j$ is the product of each pairwise combination of elements from the dominant left (stage specific reproductive value) and right eigenvector (proportion of individuals in a given stage at stable stage distribution), represented by v_i and w_j respectively. The sum of the products for each vector is represented by $v \cdot w$ [34].

$$s_{ij} = \frac{v_{ij} w_{ij}}{v \cdot w} \qquad (10)$$

Elasticities are the sensitivities, as calculated above, weighted by transition probabilities. Elasticities (e) are used to examine how proportional changes in each transition probability (a_{ij}) affects the growth rate of the overall population (λ), equation (11) [34].

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\delta\lambda}{\delta a_{ij}} \qquad (11)$$

Results from sensitivity analyses highlight how changes in vital rates, such as mortality due to harvest, affect the population growth rate. In short, sensitivity and elasticity analyses reveal how sensitive the population growth rate is to perturbations in vital rates for a given adult size class when all other elements in the matrix are held constant. This allows identification of the adult size classes that contribute the most to the overall population growth rate at each harvest level [37].

4.3 Telemetry Analysis

We tracked the movements of 23 snapping turtles over three seasons to understand habitat use in the open water systems. For each turtle, we generated home range estimates using kernel density estimation [38]. Kernel density estimation (KDE) incorporates utilization distributions (UD), the probability of an animal being at a location over a specific time period. Kernel density estimation is considered to be robust to differences in sample size, but requires a priori setting a bandwidth unless an adaptive kernel is applied [39,40]. The estimated UD of each location is calculated using equation (12) with n representing the number of locations collected. The bandwidth is represented by h, X contains the coordinate information, and x is the point from which the kernel estimate is calculated. Finally, K is the symmetric bivariate kernel function [39].

$$UD = \frac{1}{nh^2}\sum_{i=1}^{n} K\left[\frac{x-X_i}{h}\right] \qquad (12)$$

The bandwidth (h) determines the width of individual kernels, which directly influences the amount of smoothing applied to the data [39]. Using too small a bandwidth would break each location into its own kernel whereas using too large a bandwidth would create a single surface; hence, bandwidth choice can be critical when applying KDE's. For this study, all kernel density estimates used a reference bandwidth and utilization distributions were projected on a raster with 5 m resolution. The reference bandwidth calculates the optimum smoothing parameter (h using equations (13) and (14) where n is the number of points collected and $\hat{\sigma}$ is the mean standard deviation for the two dimensions ($x(1)$ and $x(2)$), which represent the x and y coordinates [40].

$$h = \hat{\sigma} n^{-1/6} \quad (13)$$

$$\hat{\sigma} = \{\frac{1}{2}\left[\hat{\sigma}^2{}_{x^{(1)}} + \hat{\sigma}^2{}_{x^{(2)}}\right]\}^{\frac{1}{2}} \quad (14)$$

5. Results

5.1 Historic Commercial Harvest in Virginia

Between 2002 and 2015 an estimated 721,000 pounds of snapping turtles were harvested from Virginia waterways (Figure 1) according to reports from VDGIF. The harvest ranged from a low of 11,522 pounds in 2002 to a high of 125,565 pounds in 2013 with a mean annual harvest of 51,506 pounds (±32,662). An average of 3,100 individuals were harvested annually with a peak of nearly 8,000 turtles harvested in 2013. The number of active watermen reporting commercial harvest rose from one to a peak of 26 over this same period.

5.2 Population Estimates

Over the duration of this study, 175 snapping turtles were captured, marked, measured, and released. Of these 175 turtles captured, 22 were recaptured once and 2 were recaptured twice. A total of 13.7% of turtles were recaptured at least once. Of the 175 unique turtles captured 54 were female and 121 were male. Of the 24 unique recaptures 18 were male and six were female. The average weight per turtle, across sexes, was 7.4 ± 3.6 (SD) kg with an average curved carapace length (CCL) of 37.6 ± 16.8 cm. Seventy-six turtles were captured at Morris Creek, 55 at Walkerton, and 44 at Totuskey Creek. Figure 2 shows the adult size distribution of unique captures by site. The no-harvest site shows a more even distribution of turtles captured among the adult size classes than the two sites under harvest pressure.

Of the models analyzed within program MARK, the top six based on AIC weight (AIC_w) are shown in Table 4. We show only these three as they are the only models with AIC_w greater than 5%. In the top model, and three out of the top four, the parameters for survival vary based on whether a site was harvested or unharvested in a given year. Equal capture/recapture probabilities were supported, over site specific probabilities, by the top two models analyzed. The parameter estimates based on the top model are shown in Table 5. Annual survival probability was dependent on whether a river was harvested (s_h = 0.74) or unharvested (s_n = 0.91) in that year. The difference between these two estimates suggests that the effect of harvest is a reduction in adult survival of 0.17. Capture and recapture probabilities were equal and constant over time at $p = 0.009$ per sampling day and will be referred to as capture probability from here forward. The estimate of capture probability (0.009) results in a per session (8 trap days) capture probability of 7% ($1-(0.991)^8 = 0.07$). Estimates of immigration and emigration were also equal and constant over time at $\gamma = 0.44$; thus, will be referred to as migration from here forward. We interpret the immigration/emigration value to reflect area of the study site is that is not being effectively sampled because none of the ratio-tagged turtles emigrated from the study area.

The highest adjusted population estimate was at the no-harvest site, Morris Creek, with 373.19 ± 243.7 (SD) adult turtles, followed by Walkerton, (16% harvest) at 281.48 ± 288.59 adult turtles, and the lowest estimate was at Totuskey (44% harvest) at 216.37 ± 186.84 adult turtles (Table 6). Population estimates and number of captures/re-captures, by sampling period and site, are given in Table 7. The estimated densities (turtles/ha) were 7.69 at Morris Creek, 4.04 at Walkerton, and 2.94 at Totuskey.

5.2 Harvest

According to state records, Walkerton was harvested in 2013 and 2014, while Totuskey Creek was harvested in all four years covered by this study (2012-2015). The average number of turtles annually harvested (±SD) from Walkerton and Totuskey Creek were 44.75 (±49.08) and 94.5 (±23.2), respectively (Table 1). The estimated mean proportion of the population harvested at Walkerton and Totuskey Creek sites were 16% and 44%, respectively, based on mean adjusted population size estimates and landing reports on file with the Virginia Department of Game and Inland Fisheries.

5.4 Population Viability Analysis

Our fully parameterized model (M_p) under a no-harvest scenario is presented below in equation (12). The growth rates, stage durations, and transition values for each of the nine adult stages in this matrix are presented in Table 8.

$$M_p = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 9.43 & 9.43 & 9.43 & 19 & 19 & 19 & 19 & 19 & 27 \\ 0.04 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.77 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.77 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.77 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.77 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.77 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.77 & 0.174 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.760 & 0.373 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.561 & 0.527 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.408 & 0.64 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.295 & 0.717 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.218 & 0.788 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.147 & 0.828 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.107 & 0.863 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.072 & 0.935 \end{bmatrix} \quad (12)$$

The matrix predicts an annual population growth rate of approximately 4% ($\lambda = 1.039$), under a no-harvest scenario. Using 16% and 44% harvest scenarios, under current Virginia regulations, the model predicts approximate annual population declines of 0.4% ($\lambda = 0.996$) and 3.8% ($\lambda = 0.962$), respectively. When we reduce the minimum size limit from the current Virginia regulation of 27.94 cm (11 in) curved carapace length (CCL) to the previous minimum size limit of 22.87 cm (9 in), the estimated population growth rates under the 16% and 44% harvest scenarios result in population declines of 3.6% ($\lambda = 0.964$) and 12% ($\lambda = 0.88$), respectively (Figure 3). In total, we ran 33 model permutations to explore how a range of potential harvest regulations, including slot limits, may affect the population growth rates of snapping turtles in Virginia open water systems (Table 9). Of these 33 scenarios, thirteen resulted in positive growth rates and of those, four had an estimated growth rate within 1% of the estimate at our no harvest site ($\lambda = 1.039$). When we remove the no-harvest scenario, nine out of the twelve (75%) remaining positive growth scenarios were minimum size limit regulations and three were slot-limit regulations (25%). Further, we found that our matrix could sustain a harvest level of 13% under current regulations with a marginally positive growth rate ($\lambda = 1.002$) (Figure 4). Under the high harvest levels observed at Totuskey Creek, we estimate that harvest would only become marginally sustainable ($\lambda = 1.013$) with minimum-size limits of at least 33 cm (13in).

Sensitivity and elasticity analysis indicate that the survival of adult size classes four through six (27.95 cm – 35.59cm) are the most critical to population persistence under a no harvest scenario (Figure 5). At the 16% harvest rate, analyses indicate that adult size classes one, three, and four (20.32 cm – 22.86 cm, 25.40 cm – 30.49 cm) are most critical. At the 44% harvest rate, adult size classes one and three (20.32 cm – 22.86 cm, 25.40 cm – 27.94 cm) are most critical. The full table of elasticity values for each harvest level are provided in Table 10.

5.5 Telemetry

The average number of location data points (± SD) collected for each turtle between July 2012 and October 2014 was 25.7 (± 3.4) (range: 20-33), with 591 total locations collected. The number of locations collected were similar across seasons, among spring 6.3 (± 0.9), summer 7.3 (± 1.3), and autumn 6.5 (± 1.1). The estimated mean home range size across sexes was 2.6-6.2 times larger for summer than for spring and autumn using kernel density estimation (KDE) and a 95% contour (Table 11). All home range estimates are given in Table 12. We found no statistical difference in home range size between males and females ($t = 0.337$, $df = 19.157$, $p = 0.74$).

Turtle mass was positively correlated with estimated mean home range size across sexes and seasons (p = 0.042, r^2 = 0.14). Among seasonal estimated home range sizes, the summer (p = 0.018, r^2 = 0.2), and autumn (p = 0.02, r^2 = 0.2) were significantly related to turtle mass, explaining 17-20% of the variation in home range size. There was no relationship between turtle mass and home range size in spring (p = 0.46, r^2 = -0.02). We found effects of season on home range size with home ranges in spring smaller than in summer (p = 0.002).

6. Discussion

Conclusions/**Recommendations**

The sustainability of wild turtle harvest under increasing market pressures is in question based on the demonstrated susceptibility of turtle populations to harvest-induced collapse [6,8,41,42]. For snapping turtles, it has been suggested that even modest levels of prolonged harvest are unsustainable and can result in severe population declines [6,26,43]. Between 2002 and 2015 state landing reports indicate that on average 3,100 snapping turtles were removed from Virginia waterways annually. Our population estimates based on mark-recapture data collected from three waterways in the Commonwealth of Virginia suggest that prolonged harvest has negatively impacted population densities. When compared to our no-harvest site, which we assume is representative of pre-harvest conditions, commercial harvest has reduced population densities at our moderate harvest site (~16% annual harvest) and our high harvest site (~44% annual harvest) by 47% and 62%, respectively, although the estimates had overlapping confidence intervals (Table 6). Further, the two harvested sites sampled as part of this study had estimated annual harvest rates that exceed levels of sustainability predicted by our model under mean demographic parameters. **In order to support the recovery of populations under prolonged commercial harvest pressure we recommend that a moratorium on commercial**

snapping turtle harvest be put in place for a period of no less than one generational cycle (7 years) for rivers that have demonstrated prolonged commercial harvest according to historic landing reports. Further, Morris Creek (off of the Chickahominy River) should remain closed to commercial harvest permanently. Its value as a control system makes it invaluable and irreplaceable to future research, conservation, and monitoring efforts.

Our results indicate that the commercial harvest of snapping turtles in river systems in the Commonwealth of Virginia is not sustainable under current state regulations. Further, sensitivity analyses indicate that the size classes most in need of protection are the very ones targeted for removal by current regulations (Figure 5). Our results suggest that prolonged harvest has disrupted size class distributions and can potentially lead to population structures skewed toward smaller less fecund individuals. This finding is consistent with studies of other turtle species [8,44]. Our study indicates that in the management of snapping turtles, as opposed to fish, minimum-size limits are likely more effective than slot-limits (Table 9). Our results suggest that to avoid the potential of harvest induced collapse, at a minimum, commercial harvest should be restricted to those individuals exceeding 35.6 cm (14 in) curved carapace length. **We recommend that if harvest remains open, or is re-opened following the recommended moratorium, that the minimum size limit be increased to 35.6 cm, which would allow for an estimated 3.5% annual growth rate under high harvest conditions (44%). An increase to the minimum size limit would protect a greater portion of reproductive adults and potentially reduce population restructuring. Ongoing monitoring is also recommended to ensure that any management decisions remain effective and that snapping turtle populations are adequately protected.**

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Table 1. Estimated annual harvest rates for the two sites under historic commercial harvest presented in this manuscript. Population size was estimated using Program MARK as outlined in the methods section while data on number of turtles harvested was taken directly from state landing reports on file with the Virginia Department of Game and Inland Fisheries. Adjusted mean population estimates are the mean population estimates divided by the proportion of trap sites sampled (Methods, equation 1). Annual harvest percentages were rounded up to the next whole number.

Walkerton

Year	**Turtles Harvested**	**Population Estimate**
2012	0	83.55
2013	118	249.24
2014	61	119.09
2015	0	21
Mean Harvested		44.75
Mean Population Estimate		118.22
Adjusted Mean Population Estimate		281.48
Estimated Annual Harvest		16%

Totuskey Creek

Year	**Turtles Harvested**	**Population Estimate**
2012	125	76.8
2013	60	153.6
2014	93	98.05
2015	100	35.02
Mean Harvested		94.5
Mean Population Estimate		90.86
Adjusted Mean Population Estimate		216.35
Estimated Annual Harvest		44%

Table 2. Snapping turtle (*Chelydra serpentina*) demographic rates used in the creation of mixed age/stage population matrices. Parameter values shown were taken either from the literature, with reference cited, or from the mark-recapture portion of this study where noted. Mean demographic values were used in matrix construction when a parameter has more than one referenced value.

Parameter	Value	Study Location	Source
Nest survival	0.23	Michigan, United States	Congdon et al. 1994
	0.157	Quebec, Canada	Robinson and Bider 1988
	0.22	Michigan, United States	Congdon et al. 1987
	0.056	New York, United States	Petokas and Alexander 1980
	0.245	South Dakota, United States	Hammer 1969
Hatchling survival	0.17	Michigan, United States	Congdon et al. 1994
	0.47	Michigan, United States	Congdon et al. 1995
	0.09	Michigan, United States	Congdon et al. 1999
Juvenile survival	0.77	Michigan, United States	Congdon et al. 1994
Adult survival	0.97	West Virginia, United States	Flaherty et al. 2008
	0.966	Ontario, Canada	Galbraith and Brooks 1987
	0.963	Wisconsin, United States	Paisley et al. 2009
	0.939	Minnesota, United States	Paisley et al. 2010
	0.93	Michigan, United States	Congdon et al. 1994
	0.929	Ontario, Canada	Galbraith and Brooks 1987
	0.91	Virginia, United States	Colteaux and Johnson 2017 (current study)
	0.88	Michigan, United States	Congdon et al. 1994
Clutch size (20.32-27.94 cm)	23.6	North Carolina, United States	Congdon and Gibbons 1985
Clutch size (27.95-40.64 cm)	55	Virginia, United States	Mitchell and Pague 1991
	40	Illinois, United States	Steyermark 2008
Clutch size (>40.65 cm)	83	Quebec, Canada	Bleakney 1957
	52	Connecticut, United States	Finneran 1947
Breeding frequency	0.85	Michigan, United States	Congdon et al. 1994
Sex ratio	0.5		Ernst and Lovich 2009
Size at emergence	2.85 cm	West Virginia, United States	Janzen 1993
Virginia size at maturity	est 20.32 cm (CCL)	Virginia, United States	Mitchell 1994

Adult duration	1.21 years	Virginia, United States	Colteaux and Johnson 2017 (Current Study)
Harvestable adult duration	3.74 years	Virginia, United States	Colteaux and Johnson 2017 (Current Study)
Virginia harvestable adult duration	23.15 years	Virginia, United States	Colteaux and Johnson 2017 (Current Study)
Mean harvest rate (2012-2015)	0	Morris Creek, Virginia, United States	Colteaux and Johnson 2017 (Current Study)
	0.16	Walkerton, Virginia, United States	Colteaux and Johnson 2017 (Current Study)
	0.44	Totuskey Creek, Virginia, United States	Colteaux and Johnson 2017 (Current Study)

Morris Creek (Charles City County, Virginia)

Table 3. Snapping turtle (*Chelydra serpentina*) growth rates used in the creation of the population matrix presented in this manuscript. Growth rates shown were determined following recapture of turtles previously caught and marked. All growth rates were adjusted by a nominal 0.1 cm to allow for the inclusion of turtles who were recaptured but which showed zero growth between captures.

Turtle Number	Initial Size	Growth Rate	Sex
1	40.64	0	Female
2	40.64	0	Male
3	31.11	0.65	Male
4	33.65	0.66	Male
5	39.37	0	Male
6	25.40	1.60	Female
7	22.86	1.79	Male
8	35.56	0	Male
9	40.00	0.81	Male
10	40.64	0	Male
11	32.38	0.38	Female
12	30.48	0	Female
13	36.83	0.81	Male
14	36.83	1.43	Male

Table 4. Model output from Program MARK utilizing the robust design (Huggins c & p). Models are listed in descending order by model fit based on the parameters shown given the mark-recapture data. Only those models with an AIC weight (AIC_w) greater than 5% are shown. AIC weight is calculated relative to all models under consideration. The notation key is as follows: survival (*s*), immigration (γ'), emigration (γ''), capture probability (*p*), and recapture probability (*c*). The symbol (*t*) indicates time dependence in a parameter and constant over time is indicated by (.). Fixed denotes where a given parameter was fixed to a specific value with that value shown within parentheses. Site is denoted by subscripts, $_M$ for Morris Creek, $_W$ for Walkerton, and $_T$ for Totuskey Creek. The numbers following a notation of time dependence in relation to site indicates the years included in that dependence, with multiple years contained within the same parentheses.

Model	AIC	AIC_W	Likelihood	Parameters	Deviance
$s(t_{M2012\text{-}2015}, t_{W2012\ \&\ 2015})$, $s(t_{W2013\text{-}2014}, t_{T2012\text{-}2015})$, γ'& γ''(.), *p* & *c*(.)	1024.98	0.36	1.0	4	476.65
$s(t_{M2012\text{-}2015}, t_{W2012\ \&\ 2015})$, $s(t_{W2013\text{-}2014}, t_{T2012\text{-}2015})$, γ'(.), γ''(.), *p* & *c*(.)	1026.42	0.18	0.49	5	475.98
s(.), γ'(.), γ''(fixed(0)), $p(._M)(._W)(._T)$, $c(._M)(._W)(._T)$	1026.76	0.15	0.41	4	478.43
$s(t_{M2012\text{-}2015}, t_{W2012\ \&\ 2015})$, $s(t_{W2013\text{-}2014}, t_{T2012\text{-}2015})$, γ'(.), γ''(.), *p* (.), *c*(.)	1026.78	0.193	0.41	6	474.22
s(.), γ'& γ''(.), $p(._M)(._W)(._T)$, $c(._M)(._W)(._T)$	1027.86	0.09	0.24	5	477.67
$s(._M)(._W)(._T)$, γ'& γ''(.), *p* & *c*(.)	1028.1	0.08	0.21	5	477.67

Table 5. Parameter estimates for the top model selected (see Table 4) within Program Mark. Lower and upper represent the bounds of the 95% confidence interval for each parameter. Site is denoted by subscripts, $_M$ for Morris Creek, $_W$ for Walkerton, and $_T$ for Totuskey Creek. Survival was split between years with and without recorded harvest. The numbers following a notation of time dependence (*t*) in relation to site indicates the years included in that dependence. The notation key is as follows: survival (*s*), immigration (γ'), emigration (γ''), capture probability (*p*), and recapture probability (*c*).

Parameter	Estimate	Std. Error	95% Lower	95% Upper
$s(t_{M2012\text{-}2015})(t_{W2012\ \&\ 2015})$	0.91	0.14	0.26	0.99
$s(t_{W2013\text{-}2014}, t_{T2012\text{-}2015})$	0.74	0.15	0.37	0.93
γ' & γ''	0.44	0.33	0.05	0.91
p & *c*	0.009	0.004	0.004	0.02

Table 6. Mean population estimates, by site, for three snapping turtle (*Chelydra serpentina*) populations within Virginia. Each site experienced a different level of historic commercial harvest (in parentheses) based on annual harvester landing reports on file with the Virginia Department of Game and Inland Fisheries. Individual population estimates by sampling period are presented in Appendix Table 2 and were created within Program Mark using mark-recapture data from this study. Mean population estimates (μ) were divided by the proportion of trap sites sampled (Methods, equation 1) to calculate the adjusted mean population estimates (μ_{adj}) for each site. The estimated size of each study site (Est.Size) was used to establish per hectare density estimates (Density).

Site	Population Est. (μ)	Population Est. (μ_{adj})	Std. Dev.	Est. Size	Density
Morris Creek (0%)	156.73	373.19	243.66	48.53 ha	7.69 turtles/ha
Walkerton (16%)	118.22	281.48	288.59	69.71 ha	4.04 turtles/ha
Totuskey Creek (44%)	90.87	216.37	186.84	73.43 ha	2.94 turtles/ha

Table 7. Population estimates for each site and sampling period. There were two sampling periods at each site annually, one early in the year and one later in the year. Population estimates, standard errors (Std. Error), and confidence intervals were generated from the top model from program MARK (Table 5). Population estimates are equal to zero when no captures or recaptures occurred over a given sampling period. The same population estimate for two different sampling periods occurs when those periods have a duplicate number of captures. The raw estimates are provided here, for the adjusted mean population estimates see Table 6. The number of captures and re-captures for each sampling period are given in the last two columns respectively.

Site	Sampling Period	Population Estimate	Std. Error	95% Lower	95% Upper	Captures	Re-Captures
Morris	1 (2012)	135.9	80.51	48.13	402.32	5	0
Morris	2 (2012)	252.2	114.94	112.2	600.17	19	2
Morris	3 (2013)	207.21	99.32	88.5	512.55	11	2
Morris	4 (2013)	56.04	34.92	19.75	175.9	3	1
Morris	5 (2014)	364.28	159.57	166.52	840.35	23	3
Morris	6 (2014)	70.05	40.96	25.96	206.92	5	0
Morris	7 (2015)	98.07	52.7	38.76	268.16	5	2
Morris	8 (2015)	70.05	40.96	25.96	206.92	5	0
Walkerton	1 (2012)	55.02	44.16	14.78	221.95	2	0
Walkerton	2 (2012)	112.09	58.48	45.28	298.58	8	0
Walkerton	3 (2013)	414.42	182.4	187.93	957.72	23	5
Walkerton	4 (2013)	84.06	46.87	32.31	237.62	3	3
Walkerton	5 (2014)	168.13	81.25	71.8	419.57	12	1
Walkerton	6 (2014)	70.05	40.96	25.96	206.92	5	0
Walkerton	7 (2015)	42.03	28.68	13.77	144.5	2	1
Walkerton	8 (2015)	0	-	-	-	0	0
Totuskey	1 (2012)	27.5	29.19	5.62	153.05	1	0
Totuskey	2 (2012)	126.1	64.21	51.86	328.9	9	0
Totuskey	3 (2013)	223.15	105.76	96.09	546.88	13	2

Totuskey	4 (2013)	84.06	46.87	32.31	237.62	4	2
Totuskey	5 (2014)	196.15	92.52	85.22	479.85	13	0
Totuskey	6 (2014)	0	-	-	-	0	0
Totuskey	7 (2015)	56.04	34.92	19.75	175.94	3	2
Totuskey	8 (2015)	14.01	14.59	3.22	77.3	1	0

Table 8. Stage specific demographic values used in the creation of population matrix presented in this manuscript. Each adult stage (A_1- A_9) is given along with the corresponding size range of each stage. Duration represents the average amount of time, in years, that a turtle spends in a given stage. P_i indicates the probability of a turtle remaining in a given stage from one year to the next, and G_i indicated the probability of a turtle to move to the next available stage in the following year. The A_9 stage has no values for duration, P_i, or G_i as once a turtle enters this stage it either survives or dies as there is no larger class to graduate to.

Stage	Growth Rate (cm/yr)	Duration	P_i	G_i
A_1 (20.32 cm – 22.86 cm)	2.09	1.22	0.174	0.76
A_2 (22.87 cm – 25.39 cm)	1.56	1.63	0.373	0.561
A_3 (25.40 cm – 27.94 cm)	1.16	2.2	0.527	0.408
A_4 (27.95 cm – 30.49 cm)	0.75	2.94	0.64	0.295
A_5 (30.50 cm – 32.99 cm)	0.64	3.95	0.717	0.218
A_6 (33.00 cm – 35.59 cm)	0.48	5.32	0.788	0.147
A_7 (35.60 cm – 38.09 cm)	0.48	7.14	0.828	0.107
A_8 (38.10 cm – 40.63 cm)	0.48	9.6	0.863	0.072
A_9 (> 40.64 cm)	0.48	--	--	--

Table 9. Resulting population growth rates (λ) for the 35 harvest regulation scenarios run in this study. The symbol • indicates harvest level and which adult size classes ($A_1 - A_9$) are open to commercial harvest under a given scenario. Also provided is whether the regulation is minimum size or slot limits. Adult sizes are given in curved carapace length (cm). * indicates current Virginia commercial harvest minimum size regulation (since 2012), and ** indicates the previous minimum size regulation for Virginia.

Harvest Level			Adult Size Class									λ	Category
0%	16%	44%	20.32-22.86	22.87-25.39	25.40 - 27.94	27.95 - 30.49	30.50 - 32.99	33.00 - 35.59	35.60 - 38.09	38.10 - 40.63	40.64		
•												1.039	No harvest
	•		•	•	•	•	•	•	•	•	•	0.951	Minimum size limit
		•	•	•	•	•	•	•	•	•	•	0.838	Minimum size limit
	•			•	•	•	•	•	•	•	•	0.964	Minimum size limit**
		•		•	•	•	•	•	•	•	•	0.88	Minimum size limit**
	•				•	•	•	•	•	•	•	0.979	Minimum size limit
		•			•	•	•	•	•	•	•	0.92	Minimum size limit
	•					•	•	•	•	•	•	0.996	Minimum size limit*
		•				•	•	•	•	•	•	0.962	Minimum size limit*
	•						•	•	•	•	•	1.011	Minimum size limit
		•					•	•	•	•	•	0.994	Minimum size limit
	•							•	•	•	•	1.022	Minimum size limit
		•						•	•	•	•	1.013	Minimum size limit
	•								•	•	•	1.03	Minimum size limit
		•							•	•	•	1.026	Minimum size limit
	•									•	•	1.035	Minimum size limit
		•								•	•	1.033	Minimum size limit
	•										•	1.038	Minimum size limit
		•									•	1.037	Minimum size limit

Harvest Level			Adult Size Class									λ	Category
0%	16%	44%	20.32-22.86	22.87-25.39	25.40 - 27.94	27.95 - 30.49	30.50 - 32.99	33.00 - 35.59	35.60 - 38.09	38.10 - 40.63	40.64		
	●		●								●	1.027	Slot Limit
		●	●								●	1.002	Slot Limit
	●		●	●							●	1.014	Slot Limit
		●	●	●							●	0.966	Slot Limit
	●		●	●	●						●	0.999	Slot Limit
		●	●	●	●						●	0.931	Slot Limit
	●		●	●	●	●					●	0.984	Slot Limit
		●	●	●	●	●					●	0.898	Slot Limit
	●		●	●	●	●	●				●	0.970	Slot Limit
		●	●	●	●	●	●				●	0.874	Slot Limit
	●		●	●	●	●	●	●			●	0.958	Slot Limit
		●	●	●	●	●	●	●			●	0.863	Slot Limit
	●		●	●	●	●	●	●	●		●	0.953	Slot Limit
		●	●	●	●	●	●	●	●		●	0.863	Slot Limit

Table 10. Elasticity analyses, by harvest level, under mean demographic rates using current Virginia commercial harvest regulations. Key: *H* (Nest/Hatchling), *J1-6* (Juvenile age classes), *A1-9* (Adult size classes).

Harvest Level = 0%

H	J_1	J_2	J_3	J_4	J_5	J_6	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9
0	0	0	0	0	0	0	0.004	0.004	0.005	0.01	0.009	0.008	0.005	0.003	0.003
0.052	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.052	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0.052	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0.052	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0.052	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0.052	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.052	0.01	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.048	0.027	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0.044	0.045	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.039	0.062	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0.029	0.064	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0.02	0.062	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0.012	0.047	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0.006	0.032	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	0.029

Harvest Level = 16%

H	J_1	J_2	J_3	J_4	J_5	J_6	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9
0	0	0	0	0	0	0	0.007	0.009	0.011	0.022	0.013	0.006	0.002	3.8e-04	6e-05
0.071	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.071	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0.071	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0.071	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0.071	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0.071	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.071	0.015	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.063	0.038	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0.054	0.06	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.043	0.06	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0.021	0.039	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0.008	0.02	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0.002	0.006	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0.0004	1.4e-03	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	6e-05	2.2e-04

Harvest Level = 44%

H	J_1	J_2	J_3	J_4	J_5	J_6	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8	A_9
0	0	0	0	0	0	0	0.012	0.015	0.019	0.03	0.005	4.9e-04	1.6e-05	1.8e-7	5.6e-10
0.083	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.083	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0.083	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0.083	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0.083	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0.083	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.083	0.018	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.071	0.045	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0.056	0.067	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.036	0.03	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0.006	0.006	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0.0005	5.6e-04	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	1.6e-05	1.9e-05	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	1.8e-07	2.2e-07	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	5.6e-10	6.7e-10

Table 11. Average home range estimates for turtles in this study, overall and by season. Kernel density estimation (KDE) was used to create all estimates shown. Values shown are in hectares with standard deviations (SD), with number of estimated home ranges used (N) for each variable.

Sex	N	Annual	SD	Spring	SD	Summer	SD	Autumn	SD
All	23	10.77	12.38	1.90	1.71	9.66	15.01	3.68	4.34
Male	14	11.45	13.35	2.30	1.88	12.38	18.83	4.28	4.28
Female	9	9.68	11.40	1.46	1.49	6.62	8.24	2.98	4.68

Minimum Convex Polygon (Morris Creek) **Kernel Density Estimation (Morris Creek)**

Table 12. Home range estimates for each turtle in this study. Turtle ID corresponds to transmitter number used. Home range estimates shown are for annual home range (inclusive of all years and seasons), spring, summer, autumn using kernel density estimation (KDE), with sex of turtle given as either male (m) or female (f). All values shown are in hectares, with number of locations collected (N) given for each variable.

				Annual		**Spring**		**Summer**		**Autumn**
Turtle ID	Sex	Weight(kg)	N	KDE	N	KDE	N	KDE	N	KDE
174021	m	6.27	26	5	6	2.48	7	4.12	6	1.47
174022	m	17.27	33	27.28	7	1.52	8	39.71	7	14.4
174023	m	10	22	5.66	5	0.36	5	1.59	6	0.65
174024	m	13.36	23	43.52	5	3.78	8	41.12	4	7.68
174025	m	9.82	22	32.83	4	5.75	6	52.73	5	7.2
174026	m	13.05	23	3.38	6	0.78	5	0.71	5	2.04
174027	m	6.32	26	6.29	6	2.3	5	1.58	7	5.06
174028	m	11.68	29	15.66	6	4.42	9	10.69	6	10.6
174029	m	7.64	28	5.54	6	5.4	7	0.60	7	3.58
174031	f	7.55	33	0.58	9	0.4	8	0.11	9	0.44
174032	f	3.64	31	1.4	7	0.37	8	0.43	8	1.14
174033	m	4.64	23	3.28	6	0.58	5	2.18	6	3.18
174034	m	7.18	29	2.39	7	1.77	8	1.08	5	0.35
174035	f	5.91	24	5.21	7	1.81	6	7.72	6	1.08
174036	m	7.64	29	1.03	7	0.35	8	1.10	7	0.05
174037	m	9.18	23	4.3	7	2.42	7	5.83	6	2.18
174038	m	15.18	24	4.17	8	0.29	7	1.62	5	1.07
174039	f	2.59	20	5.01	6	0.53	7	3.02	6	1.33
174040	f	7.86	24	32.97	6	2.38	8	25.89	6	15.2
174041	f	5.91	24	15.57	6	4.87	9	7.21	6	3.58
174042	f	5.36	23	22.18	6	1.73	8	9.75	7	1.95
174043	f	3.77	25	1.42	6	0.36	9	1.90	8	0.27
174044	f	5.41	27	2.94	7	0.66	8	1.61	7	1.89

Figure 1. Historic commercial harvest of snapping turtles in Virginia. Data shown were taken directly from annual reports filed with the Virginia Department of Game and Inland Fisheries by watermen as required by their permit.

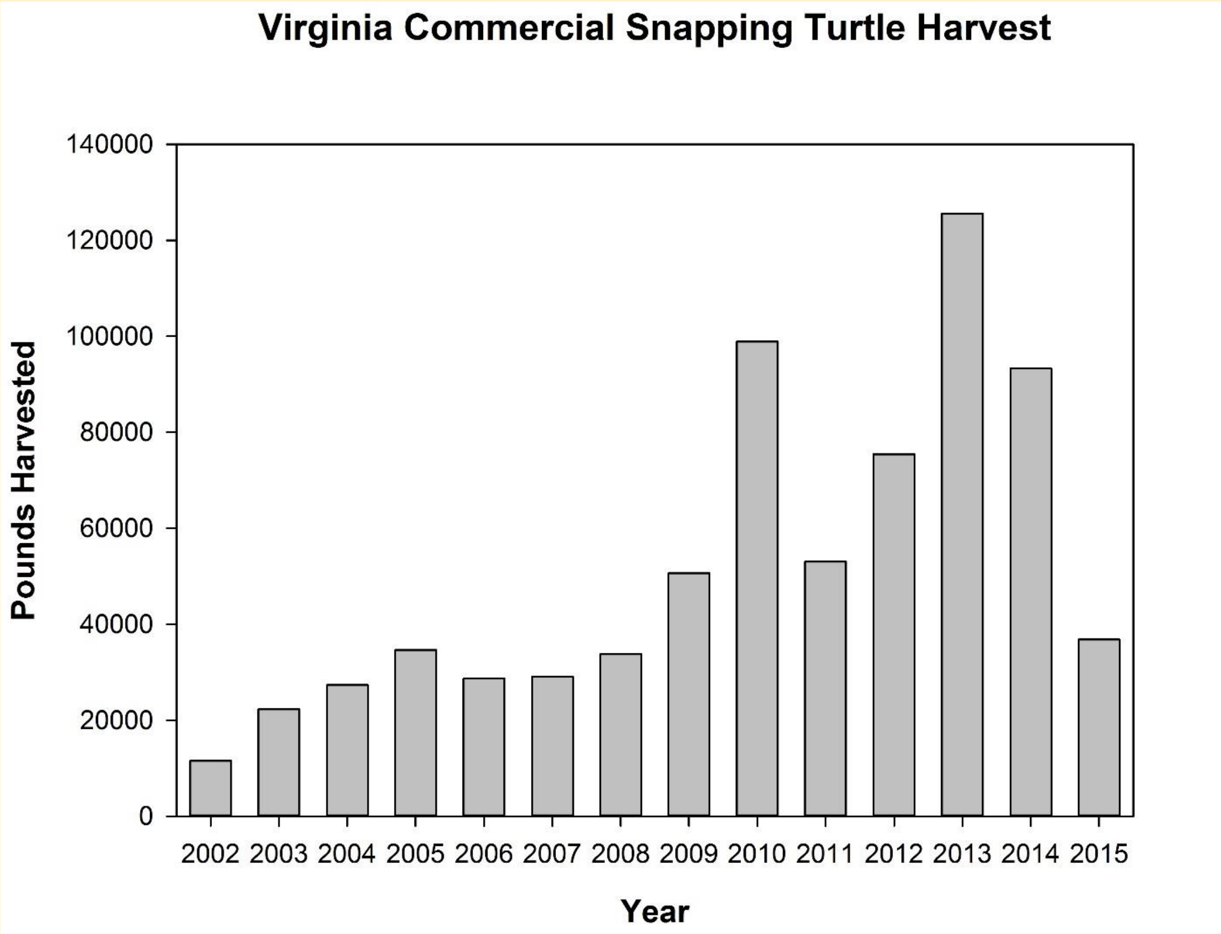


Figure 2. Distribution of unique turtles captured by size class for each site covered in this manuscript. Total unique captures at each site are: Morris Creek (76), Walkerton (55), Totuskey Creek (44). Specific measurements for each adult size class (*A_1* through *A_9*) are listed in Table 3. Turtles falling below the first adult size class (*A_1*) are grouped together in the less than *A_1* category (<20.32 cm curved carapace length)

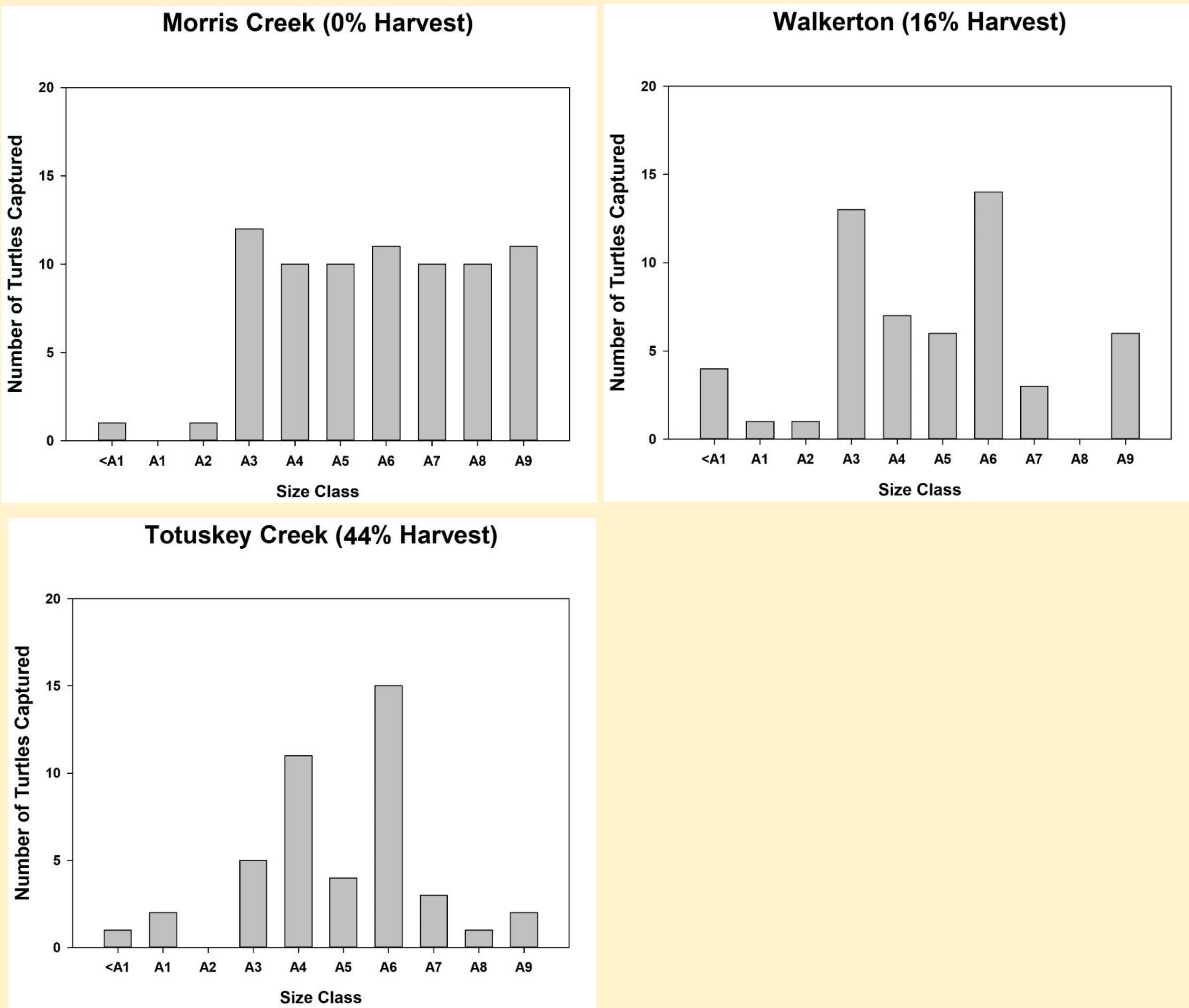


Figure 3. Results from population viability analyses at three commercial harvest levels (0%, 16%, 44%). The black vertical line represents the current Virginia minimum size limit regulation of 27.95 cm curved carapace length.

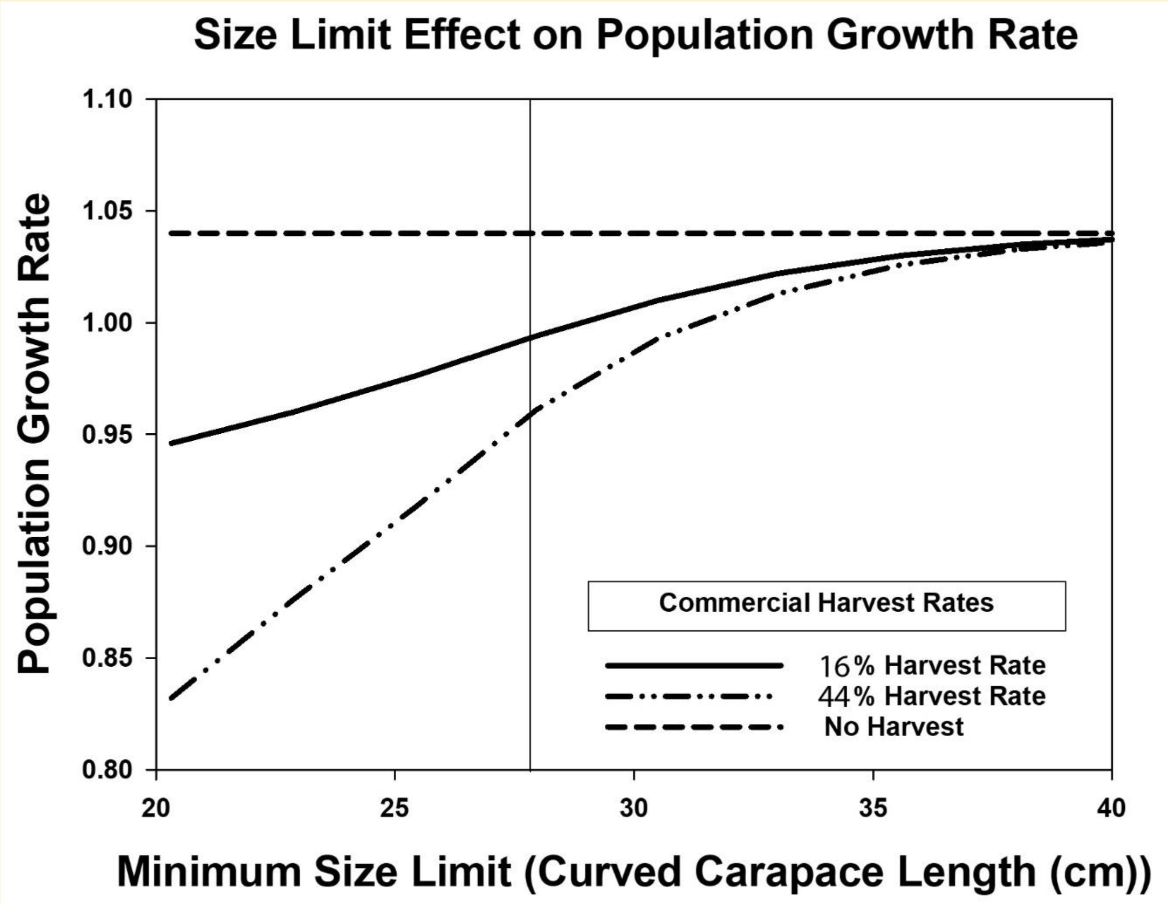


Figure 4. The effect of increasing levels of harvest on population growth rate. We increased the harvest level within our matrix from 1% to 100%, in increments of 1%, to identify the point where the resultant population growth rate switched from being in decline to stable. We present a portion of the range to better visually isolate this point. Results presented are under the current Virginia minimum-size limit of 27.94 cm curved carapace length. Dashed line indicates the level of harvest where population stability is reached ($\lambda = 1$).

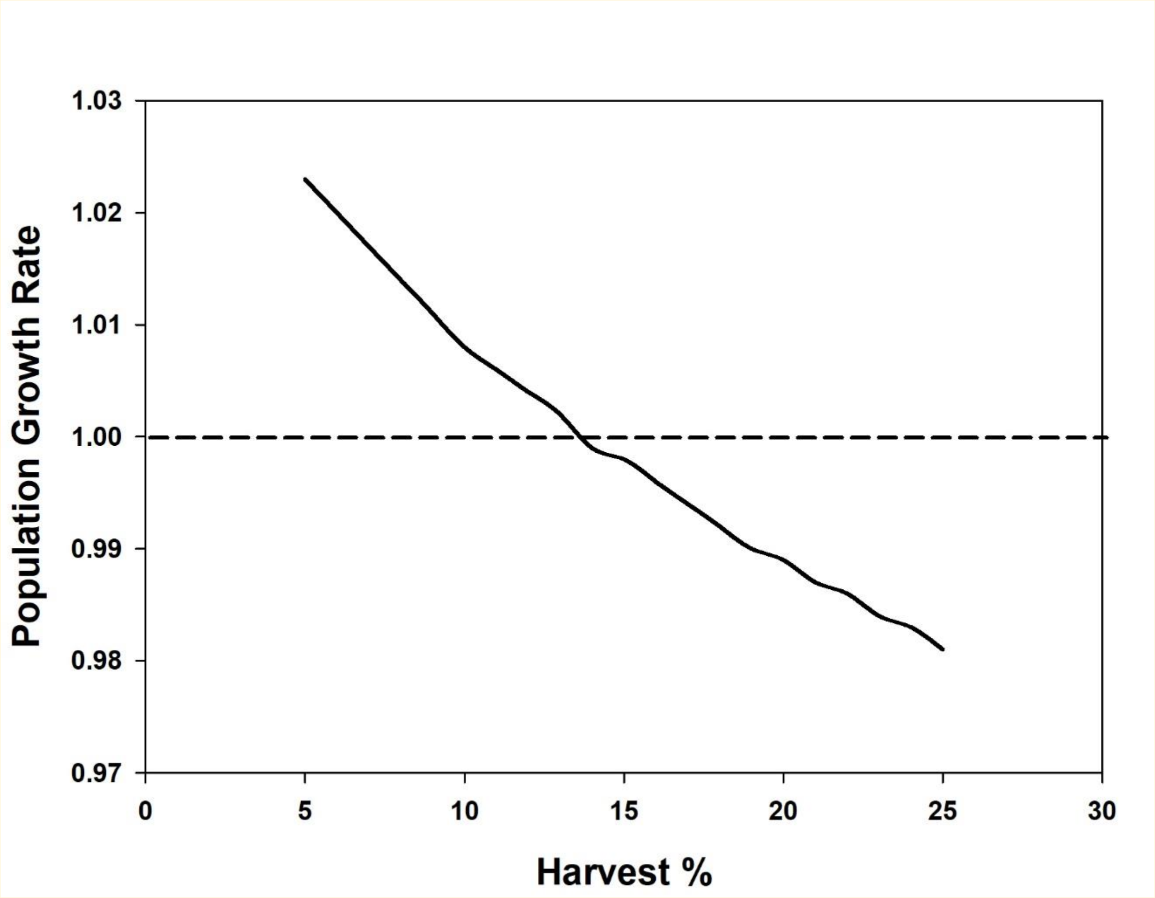
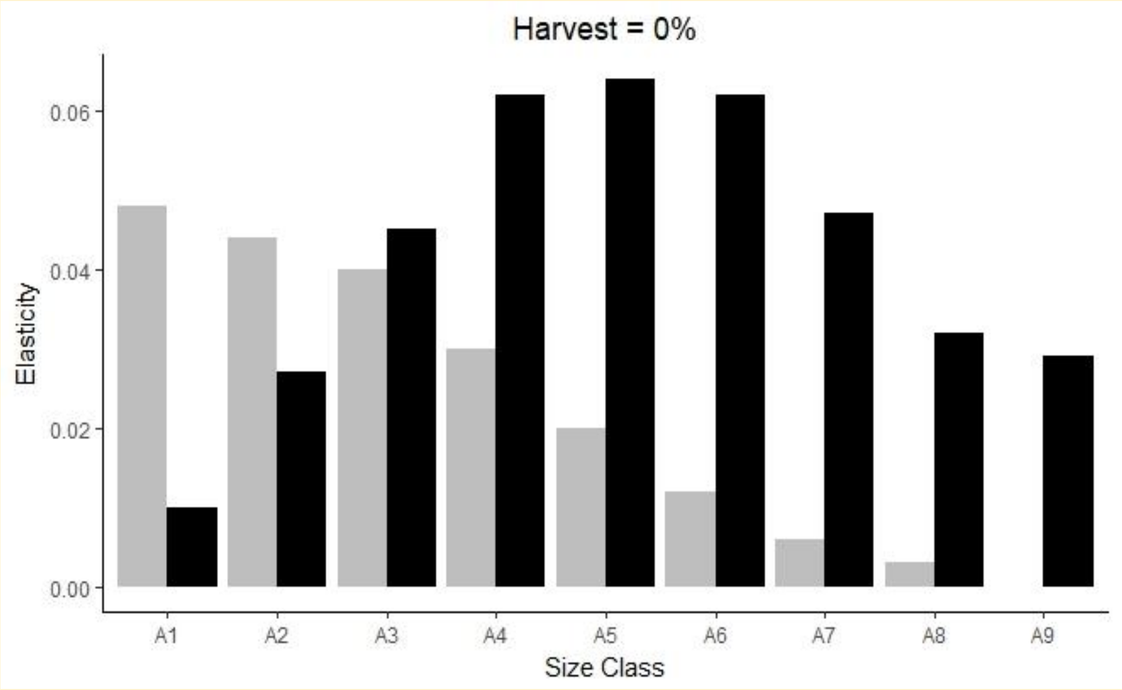
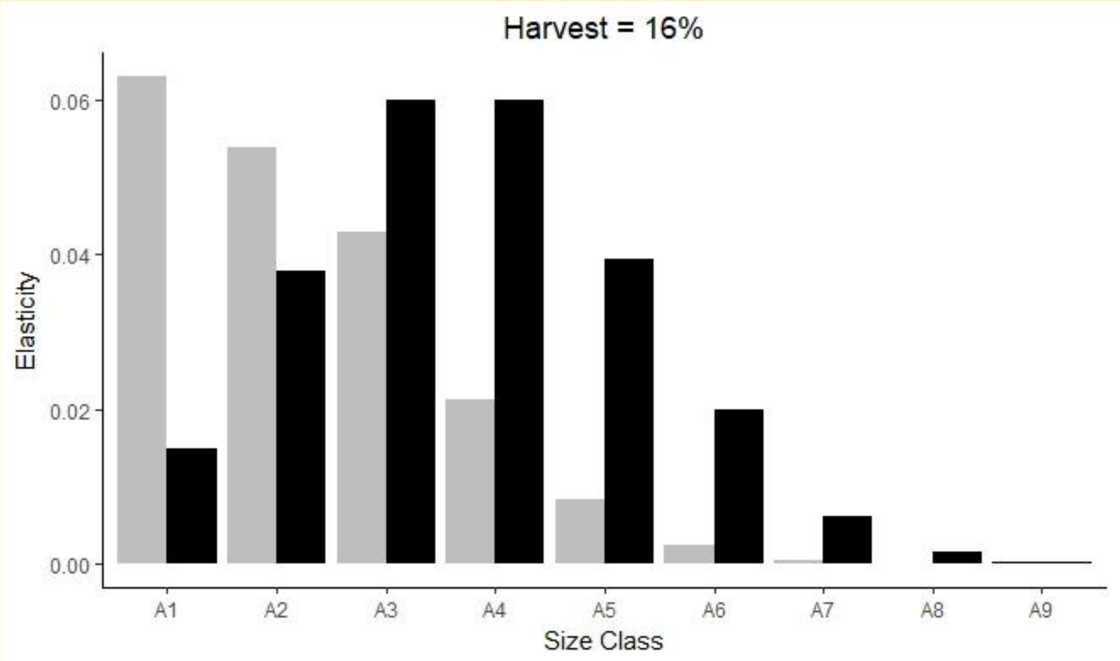
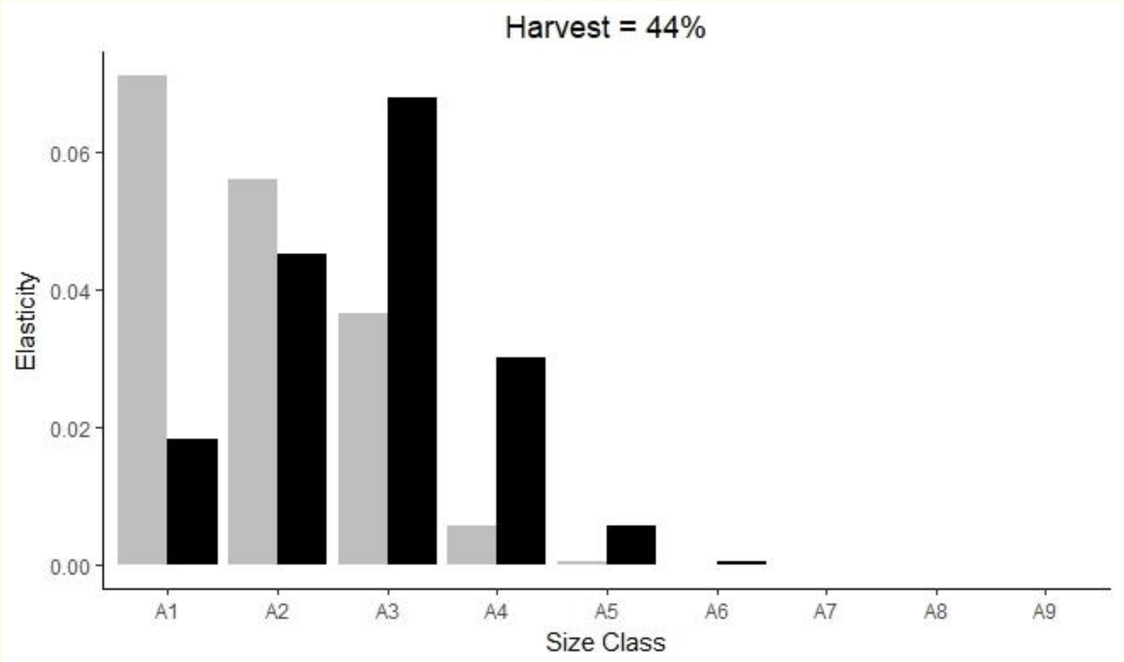


Figure 5. Stable-state elasticity values under mean demographic rates for each of the nine adult stages (*A1* – *A9*) outlined in our matrix. Graphs are presented for each of the three harvest levels (0%, 16%, 44%) used in this study under current Virginia minimum-size harvest regulations. Bars represent the proportion of the population of a given stage that either transitions to the next stage (gray bar) or remains in stage (black bar). The largest adult stage (*A9*) has no transition value as turtles either remain in stage or perish.







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