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Commercial harvest and export of snapping turtles (*Chelydra serpentina*) in the United States: trends and the efficacy of size limits at reducing harvest

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ABSTRACT

As Asian turtle populations have crashed, China has increasingly turned to international import to meet domestic demand, which has increased pressure on global turtle populations. Snapping turtles (*Chelydra serpentina*) are being harvested in unprecedented numbers in the United States (US) to meet the needs of this international market. Here we report US snapping turtle live export from 1999 to 2013, and for the first time test the effectiveness of size limits in reducing commercial harvest numbers. Over three million live snapping turtles from farm and wild caught stock were exported from the US to Asia in 2012–14 alone. Increases in the export of wild caught snapping turtles to over 200,000 individuals in 2012 and 2014, compared to under 50,000 in other years, may indicate that farms are becoming unable to keep up with increasing demand. Annual harvest pressure at the state level increased linearly from 1998 to 2013, mirroring trends in federal export over the same time period. Our model estimates that size-limits were effective at reducing harvest by 30–87% in years with high harvest pressure. However, the majority of size limit regulations result in the removal of larger breeding adults, which has been shown to be detrimental to long term population viability. Regulatory approaches dedicated to the long term management of this iconic species will need to balance the short term gains, in the form of reduced harvest rates, with long term population viability.

1. Introduction

Many iconic and once-plentiful turtle species such as the Central American river turtle, *Dermatemys mawii* (Rainwater et al., 2012), the pig-nosed turtle, *Carettochelys insculpta* (Eisemberg, Rose, Yaru, & Georges, 2011), and the alligator snapping turtle, *Macrochelys temminckii* (Jensen & Birkhead, 2003; Riedle, Ligon, & Graves, 2008) 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 (Ceballos & Fitzgerald, 2004; Klemens & Thorbjarnarson, 1995; Mali, Vandewege, Davis, & Forstner, 2014). China is the world's leading consumer of turtle meat, and Chinese consumption is considered a primary threat to the world's turtle populations (Brown et al., 2011; Compton, 2000; Mali et al., 2014; van Dijk, 2000). 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 (Haitao, Parham, Lau, & Tien-Hsi, 2007; Haitao, Parham, Zhiyong, Meiling, & Feng, 2008).

Recent population collapses suggest that turtles may be particularly vulnerable to overharvest (Sung, Karraker, & Hau, 2013). Turtles are known to employ an iteroparous reproductive strategy, meaning an individual has multiple reproductive opportunities over its lifetime. Iteroparity offsets low survival rates for hatchling and/or juvenile age classes, coupled with late maturation, by taking advantage of an extended life span and high adult survivorship (Congdon, Dunham, & van Loben Sels, 1994; Ernst & Lovich, 2009; Lewison, Freeman, & Crowder, 2004). Sexual maturity and clutch frequency can vary with latitude within or among turtle species, with populations in higher latitudes maturing later, growing larger prior to maturity, and producing clutches less frequently (Shine & Iverson, 1995; Tinkle, 1961). Iteroparous species with delayed reproduction can be highly sensitive to the effects of prolonged

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harvest as reproductive opportunities are limited by the removal of larger mature juveniles and breeding adults (Congdon et al., 1994).

The snapping turtle, *Chelydra serpentina*, is a large-bodied North American species that has been targeted to supply international markets, the demand of which likely dwarfs that of domestic food and pet trades. 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 (Ernst & Lovich, 2009; Steyermark et al., 2008). 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 (Berry & Shine, 1980; Congdon & Gibbons, 1989; Galbraith & Brooks, 1989). Snapping turtles take 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% (Steyermark et al., 2008). Snapping turtles continue to lay eggs throughout adulthood, which underscores the importance of older breeding individuals to population viability (Congdon et al., 1994).

Increases in the US export of live snapping turtles over the last decade 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 the majority of US states, turtles are considered non-game species, thus harvest management is the responsibility of state departments governing fisheries (Brown et al., 2011). While commercial snapping turtle harvest has been closed in many states amid concerns of overharvesting, it remains open in others. In each state open to commercial harvest, the harvester is required to report catch size (in weight, individuals or both) and it is these data that agencies use to assess harvest rates. One tool commonly used to curb harvest rates is size regulations, which are designed to protect a particular size class for the benefit of the population as a whole. Size limits generally require an individual be above a certain metric (minimum size limits) or between two metrics (slot limits). Size limits have been shown to be effective at increasing abundance in some species like the common whelk, *Buccinum undatum* (McIntyre, Lawler, & Masefield, 2015; Power & Power, 1996; Wilde, 1997), but ineffective in others including the red king crab, *Paralithodes camtschaticus* (Halliday & Pinhorn, 2002; Kruse, Byrne, Funk, Matulich, & Zheng, 2000; Nieland et al., 2007). Further, size limits can result in the targeting of one size/age class critical to the viability of a species, such as older reproductive adults. Limiting harvest to large fecund individuals, which would tend to skew population structure to smaller less-fecund individuals, has been shown to have negative effects on some turtle species, but has not been studied in snapping turtles (Eisemberg et al., 2011; Sung et al., 2013). To our knowledge, the effectiveness of size limits at reducing harvest catch has never been tested in a turtle species.

The goals of this study are to evaluate the efficacy of size limits in reducing the commercial harvest of snapping turtles while also identifying trends in both federal export and commercial harvest among states. We examine international export, state regulations, and commercial harvest of snapping turtles at the state level within the natural range of this species in the US. We use Bayesian inference to analyze the effect of minimum size limit regulations across a range of commercial harvest pressures. Finally, we assess the performance of our model and discuss the implications of our findings to the management of turtle harvest.

2. Methods

2.1. Data

To evaluate snapping turtle harvest and export in the US, we assembled two datasets: federal export data for live snapping turtles, and state-specific commercial harvest records. Neither of these data sets distinguish between males and females. Hereafter we use the term ‘harvest’ to mean the collection of snapping turtles from wild populations, in contrast to collection of turtles in farm environments. Federal export data for live snapping turtles for the years 1999 (the year first available) to 2014 were accessed through the Law Enforcement Management Information System, which is maintained by the United States Fish & Wildlife Service. The federal data source is the only one that exists for tracking the export of live snapping turtles from the US and that provides information on how many of the snapping turtles are sourced from wild populations. The state of origin of exported turtles is not available, therefore the federal export level is the highest resolution available.

We contacted regulatory agencies in the 37 states that comprise the natural US range of the snapping turtle by phone or email between January 1, 2014 and August 15, 2014. From each agency we obtained information on whether commercial harvest of snapping turtles is open (legal) or closed (illegal) in the state. Further, we gathered information on what harvest regulations were in place for the states open to commercial harvest. Finally, we requested annual records of commercial snapping turtle harvest from each state if available.

Eleven of the states provided data sets, which ranged from 3 to 16 years in duration (see S1 Table). All state protocols related to harvester confidentiality were followed. The states that provided harvest data were as follows: Arkansas, Delaware, Iowa, Maryland, Massachusetts, Michigan, Minnesota, New Jersey, North Carolina, Pennsylvania and Virginia. All data provided were compiled from commercial harvester landing reports. For this study, we only used report data that included harvest year and biomass and/or number of individuals harvested.

Five of the 11 states that provided harvest data had minimum size limit regulations in place over the study period (Table 1). To standardize the harvest data to a single metric, we converted harvest data from two states (Massachusetts and Pennsylvania) from biomass harvested to number of individuals harvested by dividing total biomass by the mean weight of snapping turtles harvested. Mean weight was calculated from pooled harvest records from states that reported both biomass and individuals (Delaware, Maryland, and Virginia).

2.2. Bayesian harvest model

Robust testing of management strategies often requires the analysis of data sets aggregated from multiple agencies. Coordinating information from multiple agencies presents challenges as aggregated data sets often contain missing values and can vary in effort, methods, and reporting (Harwood & Stokes, 2003; Recknagel, 2011; Regan et al., 2005). When project goals involve making informed conservation and management decisions, recognizing and dealing with the challenges of aggregated data becomes crucial (Akçakaya et al., 2000; Harwood & Stokes, 2003). We employed a Bayesian framework to test the effects of size limit

Table 1
Commercial harvest status and size regulations of snapping turtles in public waters by state. Size limit (mm) is either in straight-line carapace length (CL), or curved carapace length (CCL), where a flexible tape measure follows the curvature of the top shell. All regulations were verified and effective as of the 2015 harvest season. States that are closed to commercial harvest have no size limits as denoted by "–".

State	Commercial Harvest	Size Limit
Alabama	Closed	–
Arkansas[b]	Open[a]	None
Connecticut	Open[a]	> 330 CL
Delaware[b]	Open	> 279 CL
Florida	Closed	–
Georgia	Open[a]	None
Illinois	Closed	–
Indiana	Closed	–
Iowa[b]	Open[a]	None
Kansas	Closed	–
Kentucky	Closed	–
Louisiana	Open	None
Maine	Closed	–
Maryland[b]	Open	> 279 CL
Massachusetts[b]	Closed	–
Michigan[b]	Closed	–
Minnesota[b]	Open	> 305 CL
Mississippi	Closed	–
Missouri	Open[a]	None
Nebraska	Closed	–
New Hampshire	Closed	–
New Jersey[b]	Open	None
New York	Closed	–
North Carolina[b]	Open[a]	None
North Dakota	Closed	–
Ohio	Open	> 330 CL
Oklahoma	Open[a]	< 406 CL
Pennsylvania[b]	Open[a]	None
Rhode Island	Open	> 305 CL
South Carolina	Open[a]	None
South Dakota	Closed	–
Tennessee	Open[a]	> 305 CL
Texas	Closed	–
Vermont	Closed	–
Virginia[b]	Open	> 279 CCL
West Virginia	Closed	–
Wisconsin	Open	> 305 & < 406 CL

[a] Additional regulations not related to size limit in place.
[b] States providing data for use in the harvest model. Michigan had a size limit >305 mm CL prior to closing commercial harvest in 2007. Massachusetts had no size limit prior to closing commercial harvest in 2015.

regulations as it is well suited to datasets with high levels of uncertainty (Ellison, 2004). Through the use of prior probability distributions and posterior predictive tests, Bayesian inference allows one to measure probability not as relative frequency but as a level of credibility in the likelihood of an event given the available data (Ellison, 2004).

While many studies aim to assess the sustainability of harvest or population recovery under certain conditions (Chaloupka & Balazs, 2007; Heppell & Crowder, 1996; Rogers et al., 2010), the goal of this study was focused specifically on the effectiveness of size limit regulations at reducing turtle catch by commercial operations. We adopted a phenomenological approach that extends a linear harvest model to accommodate nonlinear effects and fit it in a Bayesian inference framework. Although specific minimum size limits range from 279 to 330 mm (11–13 in.) carapace length, the limited availability of commercial harvest data did not allow us to differentiate between effects among specific size limits. Instead, we treated all size limits as equal effects.

We began with a harvest model that assumes the number of individuals harvested ($H_{i,t}$) in state i at time t is a function of a state effect (S_i), a year effect (Y_t), and linear and nonlinear effects of size limit regulations (β and a, respectively),

$$H_{i,t} = S_i * \beta^{\rho(i,t)} * Y_t^{(1+a\rho(i,t))} * \exp\left(e_{i,t}\right). \quad (1)$$

The regulatory policy of a state in a given year is indicated by $\rho_{i,t}$, which equals zero if there is no size limit regulation and one if there is a size limit regulation. The year effect can be viewed as a measure of harvest pressure at the national level in a given year, which could fluctuate for myriad reasons (Lagueux, Campbell, & Strindberg, 2014; Lan, Lee, Wang, & Chen, 2014). Unexplained variation in annual harvest pressures (e.g., as affected by state-specific temporal variation in turtle densities and harvester effort), process error, and observation error are incorporated into the uncertainty term $e_{i,t}$. The parameter β represents the proportional reduction in harvest due to size limit regulations. The nonlinear effect of size limit regulations is manifested through a power function (a) of annual harvest pressure (Y_t). When $a < 0$ the proportional reduction in harvest numbers is greatest in years of high harvest pressure, an effect that may benefit management when regulation is most needed. This nonlinear response to size limits may result from changes in harvester behavior. Specifically, size limits may discourage harvest effort by maintaining the number of harvestable turtles below profitable levels. In addition, if prices for turtles exceed a threshold that makes it profitable for a harvester to travel to a state without size limit regulations, it would result in concurrent decreases in harvest in regulated states and increases in unregulated states. Annual harvest pressures (Y_t) were estimated independently because model permutations that included lag effects (i.e., $Y_t = f[Y_{t-1}]$) failed to converge. Including a lag effect is also not consistent with observed and reported harvester behavior as harvesters will remove turtles from one location in a year and then move to a new unharvested area in the next year (J.D. Kleopfer, Rick Morin, pers. comm.).

The model is linearized by transforming to a log scale, where $h = \log(H)$, $s = \log(S)$, and $y = \log(Y)$, such that

$$h_{i,t} = s_i + \log\left(\beta\right)\rho_i + (1 + a\rho_i)y_t + e_{i,t}. \quad (2)$$

The temporal component (t) of ρ was removed to match the snapping turtle harvest data, i.e., a given state either had a size limit regulation, or it did not; there was no change in this condition in any of the states that provided data for the years analyzed. Estimating β in this model is problematic because we cannot separate this effect from s_i without reliable prior information for standardizing harvest within each state. Many factors likely determine the number of snapping turtles harvested in a state, including area of water habitat, snapping turtle density, public access to water bodies, and efforts of harvesters. Using available data, we attempted to standardize harvest by the area of water habitat in each state, but models using standardized harvest metrics fit the data poorly. Therefore, we focused on estimating the nonlinear effect of size limits (a), and combined state effects and linear effects of size limits into one parameter, such that

$$b_i = s_i + \log\left(\beta\right)\rho_i \quad (3)$$

We substituted b_i into Eq. (2) giving the process model,

$$h_{i,t} = b_i + (1 + a\rho_i)y_t + e_{i,t} \quad (4)$$

Note that b_i is independently estimated for each state; thus, standardizing the data by state *a priori* is unnecessary. Nonlinear effects of size limit regulations can be estimated separately from state-specific effects because of its interaction with fluctuating harvest pressure (y_t). Under the reasonable assumption that the linear effect of size limit regulations is either none or a reduction in harvest ($\beta < 1$) we deduce that Eq. (4) presents a conservative estimate of the effect of size limits on the number of snapping turtles harvested.

The full conditional probability model is given in Eq. (5):

$$\left[\underline{h}, \underline{b}, \underline{y}, \sigma \mid \underline{d}\right] \quad \alpha \quad [\underline{d} \mid \underline{h}, \sigma] \left[\underline{h}|, a, \underline{b}, \underline{y}\right] [a] [\underline{b}] \left[\underline{y}\right] [\sigma], \quad (5)$$

where the probability of the model parameters given the empirical harvest data ($\underline{d}$) is proportional to the probability of the empirical harvest data given the expected number of turtles harvested ($\underline{h}$) and model parameters. In the prior distributions below, we report precision τ, which is the reciprocal of the uncertainty term squared, $\tau = 1/\sigma^2$. Observed harvest numbers ($d_{i,t}$) are sampled from the latent number harvested with precision τ_h, as shown in Eq. (6).

$$d_{i,t} \sim norm\left(h_{i,t}, \tau_h\right). \tag{6}$$

The data do not afford separate estimates of process and observation error, so both were incorporated into the one uncertainty term. The precision term τ_h was sampled from a prior uniform distribution (Eq. 7).

$$\tau_h \sim unif\,(0, 5) \tag{7}$$

Latent harvest numbers were estimated using the process model (Eq. 4). The parameters for state effect (b_i), year effect (y_t), and nonlinear size limit effect (a) were sampled from normal distributions.

$$\begin{aligned} &b_i \sim \mathrm{norm}\,(7, 0.01) \\ &y_t \sim norm\,(x, l_t) \\ &\mathrm{a} \sim \mathrm{norm}\,(0, 0.01) \end{aligned} \tag{8}$$

The prior distributions for state effects (b_i) were sampled from vague priors with all means = 7, the approximate log average number of individuals harvested per state per year. Year effects (y_t) were sampled from priors with means proportional to the estimated annual number of exported wild-caught live snapping turtles (as reported by the Law Enforcement Management Information System) rescaled and logged so the prior for the reference year 1998 is 0. As export data were first available in 1999, the prior of wild-caught individuals in 1998 was based on 1999 data. The precisions (l_t) for year effects (y_t) were set to one for all years except 1998 where it was set to ten to function as a reference year. The first year was selected as the reference year because we are chiefly interested in how the effect of size limits changed as harvest increased over time. Size limit effect (a) was sampled from a vague prior normal distribution with mean of zero. Percent change (P) in harvest levels from 1998 to 2013 was estimated using Eq. (9) where H_{1998} is estimated harvest in 1998, and H_{2013} is estimated harvest in 2013.

$$P = \frac{H_{2013} - H_{1998}}{H_{1998}} * 100 \tag{9}$$

Posterior parameter distributions were estimated through an iterative process using a Markov Chain Monte Carlo algorithm. Three parallel estimation chains were run with different sets of initial parameter values to test for convergence (Gamerman & Hedibert, 2006). Each algorithm was run for 50,000 iterations following a burn-in period of 10,000 iterations. Convergence was tested visually using trace plots, density plots, and more formally using Gelman-Rubin diagnostics. Year effects for 1998–1999 and year effects for 2001–2002 were each combined to facilitate convergence in parameter estimates. Further, we tested for stationarity using the Heidelberg-Welch hypothesis test to ensure that the burn-in period and estimation period were sufficiently long. Model fit was determined using the Bayesian p-value (Gelman, Carlin, Stern, & Rubin, 2004) and by plotting estimated harvest values against observed values. Statistical analyses were conducted in R (R Core Team, 2012) and JAGS (Plummer, 2003). was run through the R environment using the package 'rjags' (Plummer, 2014).

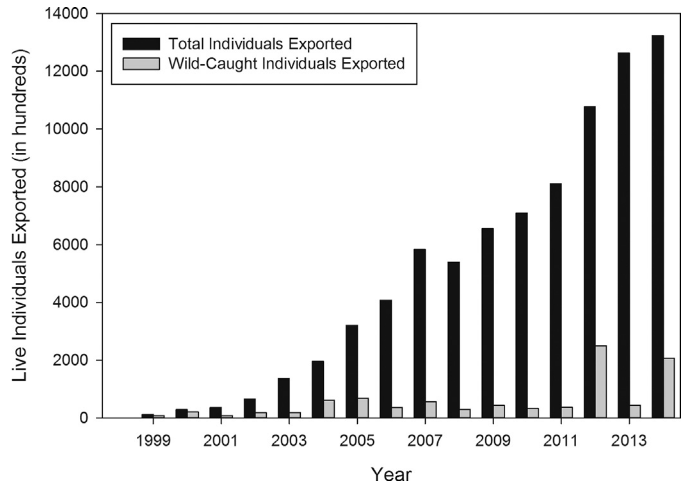

Fig. 1. Total number of live snapping turtles exported from the US per year from 1999 through 2014 (black bars). Number of live wild caught individuals exported, as part of total export, from the US per year from 1999 through 2014 (gray bars). Federal export data of live snapping turtles were obtained from the Law Enforcement Management Information System database via the United States Fish and Wildlife Service, Office of Law Enforcement.

3. Results

3.1. US export

The number of live snapping turtles exported from the US increased approximately linearly from 7279 individuals in 1999 to 1,324,089 individuals in 2014 (Fig. 1). The increase in exports was observed in both wild harvested and farmed turtles. The number of exported turtles from wild harvest fluctuated between ca. 18,000 and 68,000 individuals in most years, but export in 2012 and 2014 was up to an order of magnitude higher, at 249,609 and 207,383 harvested individuals, respectively. As export numbers increased, the percentage from wild harvest generally decreased, e.g., from 24% in 2002–2005 to 8% in 2006–2009, with the exception of the 2012 and 2014 anomalies, which were 23% and 16% of total export, respectively.

3.2. Commercial harvest

As of the 2015 commercial harvest season, 19 of the 37 states that make up the native range of the snapping turtle in the US were open to commercial harvest (Table 1). Massachusetts closed commercial harvest in 2015. Ten of the states open to commercial harvest have size limits in place. Eight states have minimum size limits that range from 279 mm to 330 mm carapace length, Oklahoma has a maximum size limit of 406 mm carapace length and Wisconsin employs slot limits where turtles can be harvested between 305 mm and 406 mm carapace length. The remaining states open to harvest either have no regulation in place or alternate regulations such as restricted areas or bag limits, the latter of which is defined as the maximum number of turtles that can legally be harvested by one person over a given time period. Bag limits are in place in five states (Connecticut, Georgia, North Carolina, Pennsylvania, and South Carolina).

For the sixteen years between 1998 and 2013, an estimated 348,529 snapping turtles were reported as commercially harvested among the 11 states that provided harvest data. The total annual harvest across reporting states was positively correlated with the number of wild caught live individuals exported ($r = 0.67$, df = 14, $p < 0.01$). The average annual harvest (±SD) in states with and without size limit regulations had similar distributions, 1.83 (±1.82) and

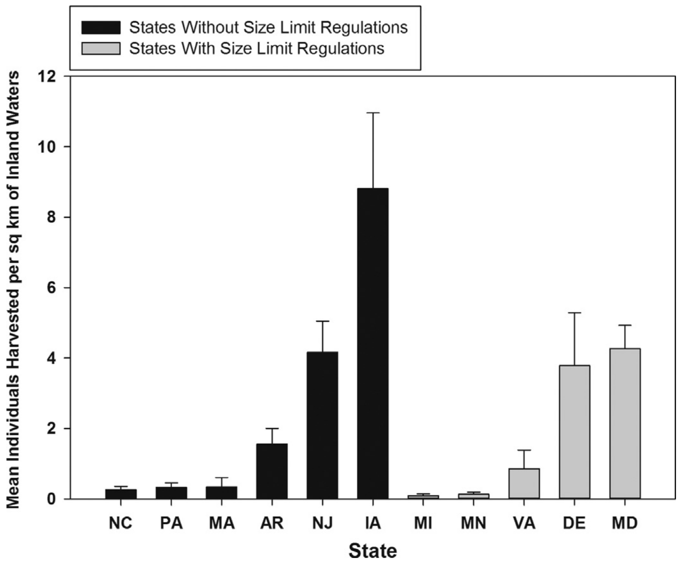

Fig. 2. Annual estimated mean number of individual snapping turtles commercially harvested per state (standardized by square kilometers of inland water). Black bars indicate states without size limit regulations; gray bars indicate states with size limit regulations. Error bars indicate one standard deviation from the mean. State abbreviations: North Carolina (NC), Pennsylvania (PA), Massachusetts (MA), Arkansas (AR), New Jersey (NJ), Iowa (IA), Michigan (MI), Minnesota (MN), Virginia (VA), Delaware (DE), and Maryland (MD).

2.57 (±3.10) individuals/km^2 of inland water, respectively (Fig. 2). Among the states without size limits, Iowa had the highest and Massachusetts the lowest estimated harvest with mean annual rates of 8.81 (±2.15), and 0.34 (±0.27) individuals/km^2, respectively. Among the states with size limits, Maryland had the highest and Michigan the lowest estimated harvest with mean annual rates of 4.27 (±0.66), and 0.09 (±0.06) individuals/km^2, respectively.

3.3. Harvest model analysis

The harvest model parameter estimates converged and provided a satisfactory fit to the data, as evidenced by four indicators. The Gelman-Rubin diagnostic indicated convergence in the Markov Chain Monte Carlo algorithm chains. The Heidelberg-Welch diagnostic test for stationarity and half-width mean passed for all parameters, indicating that the model distributions are stationary and additional iterations were not necessary. The estimated harvest values plotted against the observed harvest values show a generally good model fit, but with potential bias at very low harvest levels (S1 Figure). The Bayesian p-value was 0.50, indicating satisfactory model fit and permitting us to draw inferences regarding the effects of size limit regulations on snapping turtle harvest. Posterior estimates of parameters b_i (state effect), y_t (year effect), a (size limit effect), and σ (uncertainty) are presented in Fig. 3. The estimates of state effect correlate with the empirical mean annual harvest in the corresponding states (r = 0.87). Year effects on harvest (y) had high uncertainty, but there is an increasing trend in harvest from 1998 to 2013 (slope = 0.053/yr, adjusted $r^2 = 0.5698$, $p < 0.001$). Percent increase in harvest from 1998 to 2013 was an estimated 209%.

Estimates of the size-limit parameter a in the three estimation chains converged at a mean of −0.62 (95% CI = −1.03, −0.18), indicating that size limits reduced snapping turtle harvest, particularly in years when harvest pressure (y_t) is high. In the year of highest harvest pressure, 2012, harvest numbers in regulated states were reduced by approximately 71% (95% CI = 30%, 87%). Posterior means and standard deviations for all model parameters are given in Table S2.

4. Discussion

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 (Eisemberg et al., 2011; Fordham, Georges, & Brook, 2007; Congdon et al., 1994; Heppell, 1998). One such species is the snapping turtle, for which US harvest has increased 209% since 1998. The increase in harvest is congruent with changes in the wild-caught export rates over the same period, highlighting the potential link between domestic harvest and the international market (Cheung & Dudgeon, 2006; Haitao et al., 2007). The recent anomalous spikes in export of wild caught snapping turtles in 2012 and 2014 may hint that farms' abilities to provide the product are already taxed, although the increased harvester activity may be linked to other factors such as increased harvester effort in response to annual increases in the price of turtles.

Size limit regulations have been implemented in a vast array of aquatic species (McIntyre et al., 2015; Martell, Jensen, Walters, & Kitchell, 2008; van Poorten, Cox, & Cooper, 2013) and, with the exception of harvest closure, are the most widely used conservation tools for management of snapping turtle populations in the US (Table 1). Yet the effectiveness of size limits at reducing harvest of a turtle species has received little scientific examination prior to this study (Cain, 2010; Zimmer, 2013). Our results indicate that size limit regulations have been effective at reducing the total number of snapping turtles harvested in the US. Moreover, the reductive effects of size limits were enhanced in years with greater harvest pressure, as in 2012 where harvest was reduced by an estimated 71%, when the populations were in the most need of protecting.

The federal export data likely underestimates the number of wild harvested snapping turtles in the US for two main reasons. First, an unknown biomass of snapping turtle meat is processed and canned domestically before export, none of which is required to be recorded by the United States Fish and Wildlife Service. Second, the distinction between wild and farm stock in export records may be tenuous because we know of no regulations prohibiting wild-caught turtles from being exported as farm stock after being transferred to farm ponds. Thus, it is not known whether snapping turtle farms are truly sustainable, or whether they rely on restocking with wild caught turtles. If the latter is the case, the harvest of wild populations could be greater than export reports suggest, and aquaculture may not always reduce harvest pressure on wild turtles. Such is the case in frog farming in Asia, which is made economically viable by significant inputs of wild-caught individuals (Chan, Shoemaker, & Karraker, 2014). Restocking in this manner may provide a mechanism to launder wild-caught individuals with farm stock (Lyons & Natusch, 2011; Nijman & Shepherd, 2009). Concerns related to both the recording of processed turtle products and the classification of farm stock will need to be addressed before we can accurately assess the extent of annual snapping turtle harvest.

The harvest data set used in our analysis, while the most comprehensive to date on the subject, has limitations. The harvest data were collected from multiple agencies and the reporting was uncoordinated and fragmented. While taking a Bayesian approach can mitigate some of these issues by explicitly incorporating uncertainties, it cannot solve all problems and as such we were forced to make certain accommodations. First, data limitations prevented us from identifying the effects of specific size limits, e.g., 279 mm compared to 305 mm carapace length, however it has been shown that larger size limits generally protect a larger portion of the reproductive population from harvest (Cain, 2010). Further, we were unable to incorporate other harvest restrictions (i.e., bag limits, slot limits, restricted areas, shortened harvest seasons) into our final model because these alternative methods have not been implemented in enough states or over a long enough period for critical analysis.

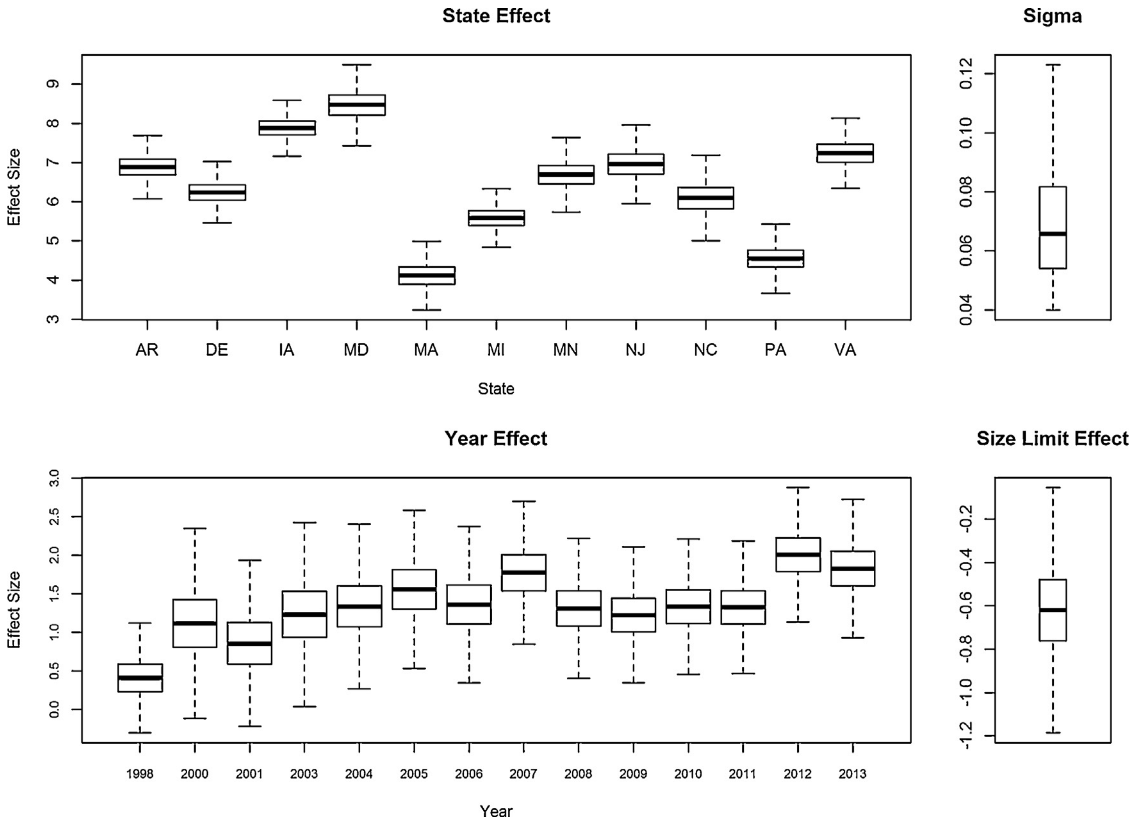

Fig. 3. Mean effects of state (b), year (y), and size limit (a) on harvest, and uncertainty parameter (σ). State effects represent the log number of turtles harvested beginning in 1998 for each state. Year effect represents a relative measure of harvest pressure across years, with the first year being selected as the reference. Size limit effect (a) is the estimated nonlinear effect of a size limit regulation on harvest number as annual harvest pressure (y) changes. State abbreviations are Arkansas (AR), Delaware (DE), Iowa (IA), Maryland (MD), Massachusetts (MA), Maryland (MD), Michigan (MI), New Jersey (NJ), North Carolina (NC), Pennsylvania (PA), and Virginia (VA).

This study does not examine the potentially negative demographic consequences of size limit regulations on population viability. The majority of state regulations governing commercial snapping turtle harvest are minimum size limits, which selectively remove large individuals from a population. The removal of larger breeding individuals can shift population structures to smaller, younger, less fecund individuals (Eisemberg et al., 2011; Sung et al., 2013; Thorbjarnarson, Lagueux, Bolze, Klemens, & Meylan, 2000; Tomillo, Saba, Piedra, Paladino, & Spotila, 2008; Zimmer-Shaffer, Briggler, & Millspaugh, 2014). The restructuring of populations towards younger age classes has been shown in the endangered big head turtle (*Platysternon megacephalum*), which is harvested for human consumption and traditional medicine (Sung et al., 2013). Given life histories of snapping turtles and most turtle species, i.e. low survivorship in early life stages, delayed maturation, and iteroparous reproductive strategy, protecting larger adults that have higher reproductive value is likely the more effective conservation strategy (Steyermark et al., 2008; Zimmer-Shaffer et al., 2014).

Effective management of snapping turtles and other turtle species under commercial harvest pressure needs to balance short-term gains, in the form of reduced harvest rates, with long-term population viability. Even at the maximum levels predicted by our model, reductions in the total number of snapping turtles harvested may fall short of the levels required to insure long-term viability of this species (Fordham, Georges, & Brook, 2008; Zimmer-Shaffer et al., 2014). Additionally, the long term demographic consequences of minimum size limits likely reduce population viability. Closure of commercial harvest of snapping turtles is the most effective way to support population persistence, as has been done in 18 states. However, for states that do not close harvest, an alternative strategy may be to add a maximum size limit threshold to existing minimum size regulations, thus creating a slot-limit, to ensure that both large adult breeding individuals and juveniles are protected. In the face of increasing commercial harvest pressure, better understanding of turtle demography is needed to determine whether size limit regulations, be they minimum, maximum, or slot are a potentially effective component in the long term management of this iconic species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jnc.2016.11.003. The complete model presented here is publicly archived through Dryad: http://dx.doi.org/10.5061/dryad.j5v05

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