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Elasticity analysis of green sturgeon life history

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Abstract I provide an analysis of a simplified life history model for green sturgeon, *Acipenser medirostris*, based on published and recent estimates of reproduction and growth rates and survival rates from life history theory. The deterministic life cycle models serve as a tool for qualitative analysis of the impacts of perturbations on green sturgeon, including harvest regulations based on minimum and maximum size limits ("slot limits"). Elasticity analysis of models with two alternative age–length relationships give similar results, with a high sensitivity of population growth rate to changes in the survival rate of subadult and adult fish. A dramatic increase in the survival of young of the year sturgeon or annual egg production is required to compensate for relatively low levels of fishing mortality. Peak reproductive values occur from ages 25 to 40. An increase or decrease in the maximum and minimum size limits can have a profound effect on the elasticity of population growth to changes in the annual survival rate of age classes specified by the slot, due to changes in the number of age classes of subadults and adults that are available for harvest. This analysis provides managers with a simple tool to assess the relative impacts of alternative harvest regulations. In general, green sturgeon follow life history patterns similar to other sturgeon, but species-specific demographic information is needed to produce more complex assessment and viability analysis models.

Keywords *Acipenser medirostris* · Elasticity analysis · Demography · Life history · Harvest

Introduction

For many threatened or endangered species, quantitative viability analysis is impossible due to a lack of basic demographic information (Heppell et al. 2000a, b; Morris and Doak 2002). Most vital rates of green sturgeon, *Acipenser medirostris*, are poorly known, but the species shares life history characteristics with other sturgeon species and with long lived fishes in general, which makes it possible to generally assess the potential impacts of perturbations on population growth rate through matrix sensitivity analysis (Heppell et al. 1999, 2000a; Gross et al. 2002). Such analyses, although unable to provide precise predictions of population size, do provide patterns of population response that can be used as indices to guide management, while remaining robust to many parameter uncertainties (de Kroon et al. 2000; Heppell et al. 2000b).

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A sensitivity analysis is a quantitative comparison of the relative impact of model parameters on a population response, which can be used to compare management alternatives qualitatively. The analysis calculates the change in the outcome of a model (e.g., the population growth rate or stage distribution) when a parameter in the model is altered. In linear models (i.e., those without density dependence) and models that do not include stochasticity, the sensitivity of the asymptotic population growth rate given by a transition matrix can be used as an index to make predictions such as, ''increasing large juvenile [loggerhead sea turtle] survival will have a relatively greater effect on population growth than saving eggs and hatchlings'' (Crouse et al. 1987). Applied to sturgeon, this simple analysis can suggest modifications to harvest rates applied to minimum and maximum size classes (''slot limits'') that reduce potential negative impacts on population growth rate, or to identify the relative increase in juvenile survival that would be needed to compensate for harvest of subadult or adult fish (Heppell et al. 1999).

There have been a limited number of population models produced for sturgeon (Van Winkle et al. 2002). Boreman (1997) used life tables to derive an ''eggs per recruit'' (EPR) calculation to show the reduction in per capita productivity under various fishing mortality rates. Because their natural mortality rate is so low, even small increases in the annual mortality rate of adults greatly decreases mean lifespan and, under density-independent conditions, lifetime egg production. A population viability model of the white sturgeon, *Acipenser transmontanus*, suggests that fragmentation by Snake River dams has adverse consequences when dams are close enough together to eliminate free-flowing river habitat (Jager 2001; Jager et al. 2001). Population viability analysis for sturgeon generally comes to a common conclusion: slow growth and intermittent spawning results in low intrinsic population growth rates, slow recovery from exploitation, and high sensitivity to harvest (Pine et al. 2001; Root 2002). Gross et al. (2002) developed a series of matrix models to evaluate sturgeon life history and the role of hatchery production and other mitigation efforts on sturgeon population recovery. The elasticity results from these models showed that proportional changes in adult and subadult sturgeon survival rates had relatively large effects on population growth rates, similar to other long-lived vertebrates (Heppell et al. 1999). However, the results also indicated that hatcheries could be effective if a large proportion of a stock was of hatchery origin, owing to the dramatic increase in egg and larval survival that can be attained in captive conditions. This points out the importance of including the relative change in vital rates that can be expected from a management action in the analysis; elasticity analysis alone is a derivative and only provides the relative change in population growth expected from the same proportional change in two vital rates (de Kroon et al. 2000).

As a heuristic exercise to explore the sensitivity of green sturgeon deterministic population growth to changes in age-specific survival rates, I calculated the elasticities of different life stages using two age-structured models. Because the number of age classes in these models was highly sensitive to the relationship between age and length, I further explored the models' elasticity patterns by incorporating two von Bertalanffy age–length curves. The purpose of this exercise was to identify which life stages may have the largest influence on population growth and to see how changes in the minimum and maximum length requirements for harvest might affect that rate. The results, although preliminary until demographic data are acquired, can be used in management planning and in the development of more sophisticated assessment models.

Methods

Model description

There were two life cycle models used in this analysis (Fig. 1). Both represent conceptual simplifications of age-structured transition matrices, with multiple age classes grouped into ''stages'' represented by the circles in each diagram. Model I is the most simplified case, where maturation

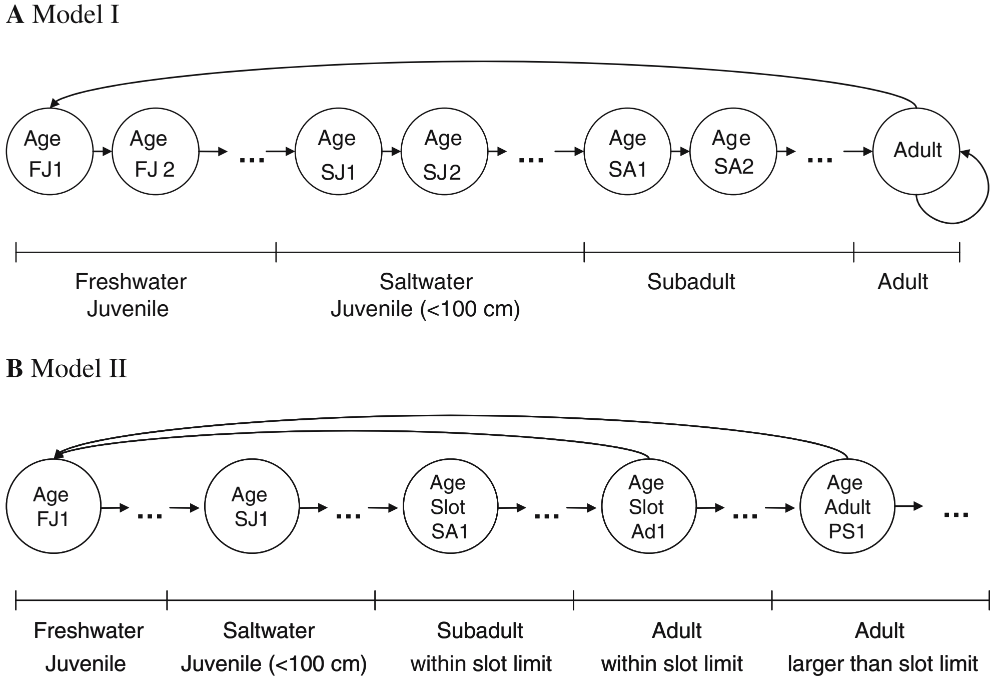

Fig. 1 Alternative model structures for a simple age-structured life history model of green sturgeon. Circles represent age classes, which are grouped into life stages that share survival rates (Table 1). The number of years in a life stage depends on the age–length relationship described by one of two growth curves (Table 1, Fig. 2). Arrows represent annual survival rates or age-specific fertility rates within a life stage. Fertility rates (arrows from adult age classes to Age 1) are based on the average number of one-year-old female offspring produced per female per year. (**A**) Model I, where adults are grouped into a single stage; (**B**) Model II, where adults are separated into age-classes with age-specific maturation and fertility rates. FJ = freshwater juvenile; SJ = saltwater juvenile; SA = subadult (107–174 cm TL), Ad = adult; PS = post-slot, or age classes of fish larger than the maximum size for harvest

occurs in the same year for all female sturgeon and all adults have the same mean fertility rate. This model structure allows for estimation of matrix elasticities (proportional sensitivity of population growth rate, λ, to changes in stage-specific survival) without estimates of juvenile survival rates or recruitment (Heppell et al. 2000b). Model II is a full age-structured model that requires juvenile survival rates (currently unknown) to calculate elasticities, but allows us to compare the proportional sensitivity of population growth to changes in the annual survival rate of subadults and adults within the legal slot limit for green sturgeon.

The number of years in each life stage must be determined with a growth curve, as most data for green sturgeon are given in lengths rather than age and the slot limit is based on total length. I used two von Bertalanffy equations to construct alternative models: one based on total lengths (TL, in cm) of fish caught in the Klamath River and estuary [$L_x = 238.35 \times (1 - \exp(-0.05322 \times (x + 1.9943)))$] (“USFWS”, USFWS 1993), and a more recent curve from the Oregon Department of Fish and Wildlife (“ODFW”, Farr et al. 2002) based on fork lengths (FL, in cm) of female fish sampled from various locations in Oregon [$L_x = 182.2 \times (1 - \exp(-0.0884 \times (x + 2.3771)))$] (Fig. 2). Fork lengths for this second growth curve were converted to total lengths using a relationship given by Rien et al. (2001): TL = 1.09 × FL. One problem with the ODFW curve is that the best-fit model gives an asymptotic length (L_∞) of 182 cm FL (198 cm TL), which is smaller than many spawning female green sturgeon in the Klamath River. The effect of this lower estimate of asymptotic length is a prediction of extremely slow growth (=longer stages) for large adult fish (Table 1).

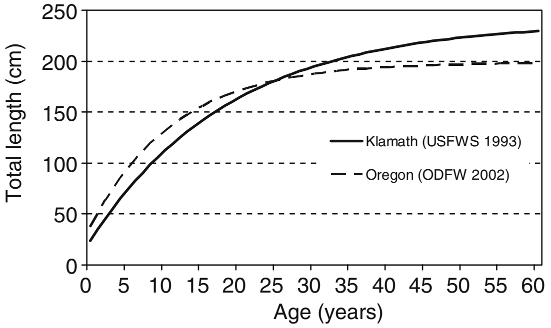

Fig. 2 Growth curves used in the demographic models. USFWS von Bertalanffy equation: $L_t = 238.35[1 - \exp(-0.0532(t + 1.9943))]$. ODFW von Bertalanffy equation: $L_t = 182.2[1 - \exp(-0.0884(t + 2.377))] \times 1.09$ to translate fork length (FL) to total length (TL; Rien et al. 2001)

Table 1 Stage information used in the models, based on growth curves shown in Fig. 2

Stage	Length (cm TL)	Age classes: USFWS growth curve	Age classes: ODFW growth curve
FW juvenile	10–65	0–3	0–2
SW juvenile	65–107	4–8	3–5
Subadult (includes <50% mature)	107–174	9–22	6–21
Earliest maturity	142	15	12
50% mature	174	23	22
Fully mature	196	31	47

TL = total length; FW = freshwater; SW = saltwater

Matrix elasticity analysis

For simple matrix projection models, the first step in a sensitivity analysis is to calculate the stable stage distribution (w) and the stage-specific reproductive values (v) of the projection matrix A. These are the right and left eigenvectors associated with the dominant eigenvalue λ, which are usually scaled such that $\Sigma(w_i) = 1$ and the reproductive value of individuals in the first stage (v_1) = 1. Caswell (1978) used these eigenvectors to calculate the sensitivity of λ to changes in any matrix entry (A_{ij}):

$$\frac{\partial\lambda}{\partial A_{ij}} = \frac{v_i w_j}{\langle w, v\rangle} \tag{1}$$

where $\langle w, v\rangle$ is the inner product of the two vectors, $\{v_1 \times w_1 + v_2 \times w_2\ ...\}$. The sensitivity index is a derivative that tells us how λ will change if a model parameter is increased or decreased by a small amount. Elasticity (=proportional sensitivity; de Kroon et al. 1986) calculates proportional changes in λ when matrix entries are changed by a small percent. The elasticity of λ to a change in a matrix parameter is:

$$\frac{A_{ij}}{\lambda}\frac{\partial\lambda}{\partial A_{ij}} = \frac{\partial\log\lambda}{\partial\log A_{ij}} = \frac{A_{ij}}{\lambda}\frac{v_i w_j}{\langle w, v\rangle} \tag{2}$$

Proportional changes can be more relevant than absolute changes when comparing the effects of changes in parameters that are not on the same scale, such as fecundity and annual growth rates (Caswell 2001). For example, elasticities are used to compare the impact of a 10% increase in annual fecundity versus a 10% increase in the probability of surviving each year. Because the effect of a management proposal is often estimated as a proportional change in a vital rate, rather than an absolute change, elasticity analysis can be a highly useful comparative measure. The elements of the elasticity matrix sum to 1.0 (Caswell et al. 1984; de Kroon et al. 1986), so elasticity analysis can be interpreted as a measure of the relative contribution of each parameter to the population growth rate λ. These proportional contributions can be added when a perturbation (such as harvest) will affect more than one age class.

Although simpler than many population models, deterministic matrix models still require age- or stage-based estimates of growth and survival. These are difficult to obtain for most species, and survival rates have generally not been estimated for green sturgeon due to aging error and small sample sizes. The stage-specific elasticities of an age-structured matrix with adults grouped into a single stage can be estimated without a complete life table using the following set of equations (Heppell et al. 2000b):

$$E(\text{fertility}) = \frac{P_{\text{ad}} - \lambda}{(\text{ASM} - 1) \cdot P_{\text{ad}} - (\text{ASM} \cdot \lambda)} \tag{3}$$

$$E(\text{juvenile}) = E(\text{fertility}) \cdot (\text{ASM} - 1) \tag{4}$$

$$E(\text{adult}) = 1 - [E(\text{fertility}) + E(\text{juvenile})] \tag{5}$$

where P_{ad} is mean adult survival rate (annual), λ is the asymptotic population growth rate given by the dominant eigenvector of a transition matrix (assumed to 1.0 for my analysis, reflecting a stable population), and ASM is age at sexual maturity. Heppell et al. (2000b) showed that these equations, which replace the need for a transition matrix, provide the exact elasticity values that would be obtained from a matrix for Model I (Fig. 1a), and are good approximations for the elasticities calculated for a full Leslie-type model, where adult age classes are considered individually. For the green sturgeon models, I split the juvenile stage into juvenile and subadult ‘‘stages’’ with the number of years in each stage dependent on the age–length relationship. Because elasticities are proportions and are additive, the stage elasticities for juvenile and subadult are given by *E*(fertility) multiplied by the number of years defined by the stage (Table 1).

Model parameterization

Model I, representing the most simplified representation of green sturgeon life history, provides a simple way to assess the sensitivity of population growth rate to changes in annual survival rate. Model I was not constructed as a complete matrix model, which would require age-specific survival rates. Instead, I parameterized Eqs. (3), (4) and (5) with a range of adult survival rates ($P_{\mathrm{ad}} = 0.84$–0.98), λ fixed at 1.0 and age at maturity set as the age at which 50% of females are capable of spawning, 174 cm TL. The two growth curves provided approximate ages of 50% mature of 23 and 22 years (USFWS and ODFW, respectively, Table 1). For all models, I designated the ‘‘subadult’’ stage as age classes within the size range 109–174 cm TL. The lower end of this size interval represents the size of recruitment to the fishery, based on a minimum size limit of 42 inches TL in Oregon and Washington (2006 regulations).

For Model II, in which the adult age classes are explicit, I needed the proportion mature by age and the number of eggs produced per female by age. Proportion mature by size was derived from ODFW data (Rien et al. 2001) and reflects the proportion of females that are capable of spawning, rather than the proportion that actually spawn in a given year (Table 2). Fecundity-at-size data were based on a relationship between egg number and fork length from fish in the Klamath River (Van Eenennaam et al. 2006): ovulated eggs = $4.875 \times 10^{-5}\,\mathrm{FL}^{4.188}$. For consistency, I used the growth curves to translate length to age. I set maximum age at 60 years and assumed that 33% of mature females spawned each year (Erickson and Webb 2006). Because the models are female-only, I also had to divide egg production by 2, assuming a 50:50 sex ratio. Thus, annual egg production by females in each age class (b_x) was equal to:

Table 2 Size class and fecundity of green sturgeon

FL (cm)	TL (cm)	Proportion mature	Ovulated eggs
130	141.7	0.05	35,000
140	152.6	0.05	47,000
150	163.5	0.1	63,000
160	174.4	0.5	83,000
170	185.3	0.7	107,000
180	196.2	1	136,000

Proportion mature estimated from Rien et al. (2001) for Columbia River females. Fecundity (ovulated eggs = $4.875 \times 10^{-5}\,\mathrm{FL}^{4.188}$) based on a sample of 60 fish from the Klamath River (Van Eenennaam et al. 2006). FL = fork length. Total length (TL) = 1.09FL (Rien et al. 2001)

$$b_x = (4.875 \times 10^{-5}\,\mathrm{FL}^{4.188}) \times \mathrm{mat}_x \times 0.33 \times 0.5 \tag{6}$$

where mat_x is the proportion mature in age class x.

I also had to make assumptions about survival rates in Model II. I assumed that natural mortality would be uniformly low for green sturgeon older than one year, and that most mortality occurs in the first year of life (age 0, whose survival rate to age 1 is included in the fertility term for these pre-breeding census matrix models). I arbitrarily assigned a proportional survival rate of 0.75 for age 1 juveniles. I assigned a natural mortality rate of $M = 0.08$ (annual survival $P_{\mathrm{ad}} = 0.9235$) for all age classes starting at age 2, representing a high annual survival rate that permits a reasonably high maximum age. For the two growth curves, an annual egg survival rate of 0.0003 and 0.0004 (USFWS and ODFW growth curves, respectively) resulted in an asymptotic population growth rate (λ) of around 1.00 with no fishing mortality. These assumptions are not grounded with field data, and serve as a baseline to compare model output and as a starting point for future analyses.

To analyze the two Model II matrices for a range of harvest scenarios affecting different size classes (slot limits), I calculated the reproductive value, stable age distribution and age-specific elasticities. The models developed for this assessment are deterministic and do not span the range of uncertainty that we have regarding green sturgeon vital rates. As such, while the analysis is generally robust, these results should be compared qualitatively.

Results

The elasticity estimates for Model I using Eqs. (3), (4) and (5) are nearly identical for the two growth curves, although the USFWS curve showed a larger contribution of freshwater juvenile survival due to the longer amount of time spent in that stage (4 years instead of 2 given by the ODFW growth curve) (Fig. 3). Because adult annual survival (based on natural mortality) is unknown for green sturgeon, I plotted elasticities for a range of values. The proportional contribution of subadult and adult survival to population growth is high, due to the large proportion of the population that is in this stage (year classes given in Table 1). Proportional changes in the survival rate of stages with high elasticities translate into relatively large proportional changes in population growth. To illustrate, I used elasticity ratios to calculate the proportional increase in fertility or young of the year (YOY) survival required to offset a reduction in adult or subadult survival due to fishing mortality (Fig. 4; Heppell et al. 1999). For high fishing mortality rates on subadult and adult green sturgeon, the increase in YOY

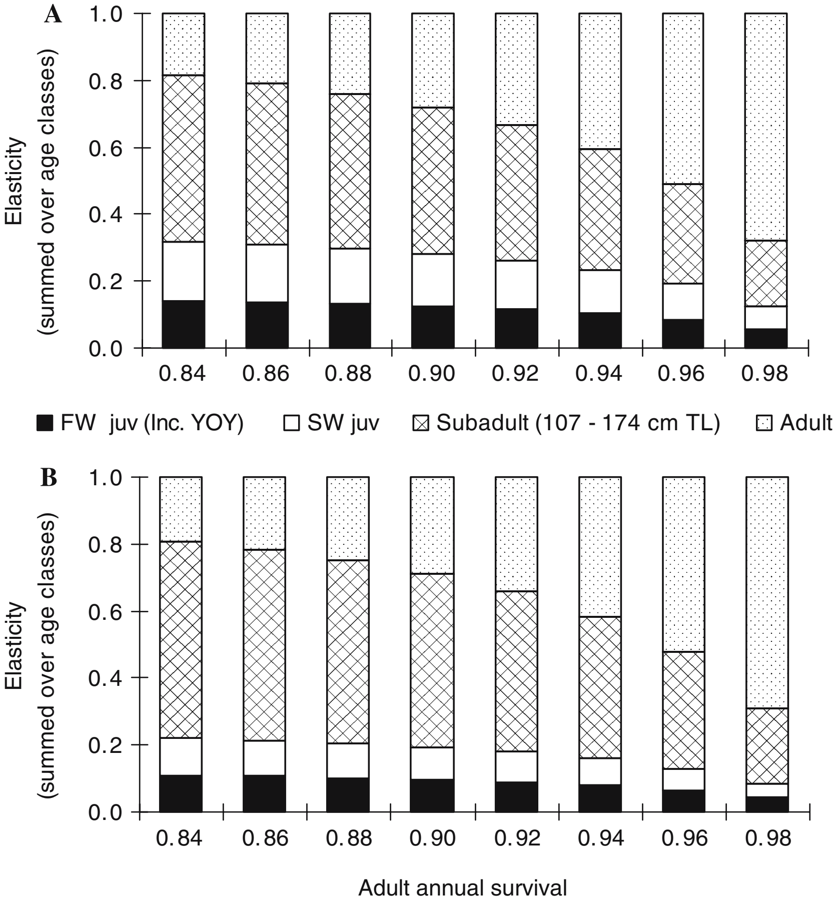

Fig. 3 Elasticity analysis for a hypothetical green sturgeon life history (Model I), based on an age-structured model elasticity estimation derived by Heppell et al. (2000b). The models group all adult age classes into a single stage. (**A**) Stage lengths based on USFWS growth curve. (**B**) Stage lengths based on ODFW growth curve. λ is assumed to be 1.0 for all models. FW juv = freshwater juvenile; SW juv = saltwater juvenile; YOY = young-of-the-year (age 0); TL = total length

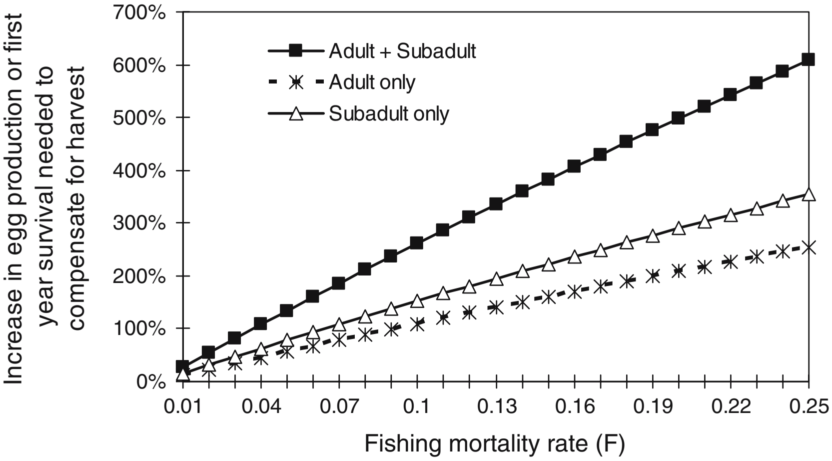

Fig. 4 Increase in first year survival or productivity needed to compensate (i.e., return population growth rate to pre-harvest level) for various levels of fishing mortality on subadults and adults, according to elasticity values given by Model I. Example shown is for the ODFW growth curve and an adult instantaneous natural mortality rate of 0.08 (annual survival = 0.9235) and pre-harvest $\lambda = 1.0$. The USFWS growth curve provided similar results

survival needed to compensate for the proportional loss of adults or juveniles is very high.

Reproductive values could be calculated for all age classes for Model II, a full age-structured model with YOY survival set at 0.00003 or 0.00004 to achieve λ close to 1.0. The egg production curve combines information on proportion mature and fecundity for each age class as defined by the length-at-age relationship (Fig. 5a). Although productivity of younger age classes overlaps for the two growth curve models, the USFWS growth curve shows much greater annual egg production for older fish. The reproductive value of each age class increases to around age 40 this model, at which point the increased egg production of older age classes is offset by the very low probability of a female reaching old age, and the maximum age (60 years; Fig. 5b). The model defined by the ODFW growth curve showed a lower and flatter reproductive value curve. This is due to the smaller maximum size and more rapid early growth rate predicted by the curve (Fig. 2). The reproductive value of an age class is one measure of the “value” of an individual in that age class, relative to individuals in other age classes. According to these simple models, green sturgeon shows the greatest reproduction contributions coming from fish aged 25–40.

For an unfished, but non-increasing population, the elasticity of λ to changes in the survival rate of each life stage is similar to the patterns predicted by the Model I approximation method (Fig. 6). The two growth curve models gave similar elasticity patterns, suggesting that our uncertainty about growth rates and stage length is not an important factor for elasticity comparisons. These elasticities represent the proportional contribution of the survival rate for each stage (which contains multiple age classes) to population growth, rather than per capita contributions.

I used Model II to determine how sensitive the population growth rate is to changes in survival rates for different slot limits (Fig. 7, Table 3) assuming a natural mortality rate of 0.08. This analysis shows how changes in the minimum and maximum size limits for harvest, in cm TL, affect the elasticity of λ to a change in the survival rate of age classes within the slot. For example, a slot limit of 100–160 cm TL results in an elasticity for the slot of about 0.38 for both the ODFW and USFWS growth curves. This elasticity value means that the survival rate of fish in that size range contributes about 40% to a change in λ, relative to other survival rates. Reducing the maximum size in the slot reduces the number of adult age classes in the catch, and greatly reduces the effect of survival rate changes in the slot (the

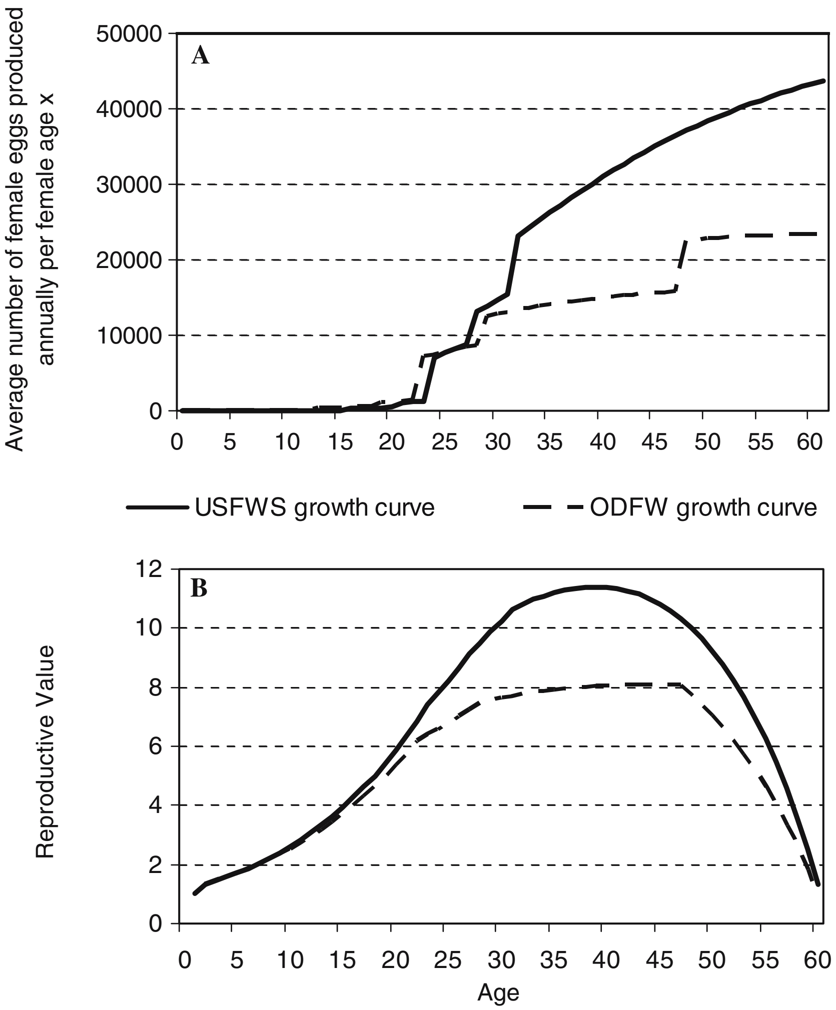

Fig. 5 (**A**) Fecundity-at-age (female eggs produced per female per year, b_x) and (**B**) reproductive values for the USFWS and ODFW growth rate models according to proportion mature and fecundity-at-size information in Table 2

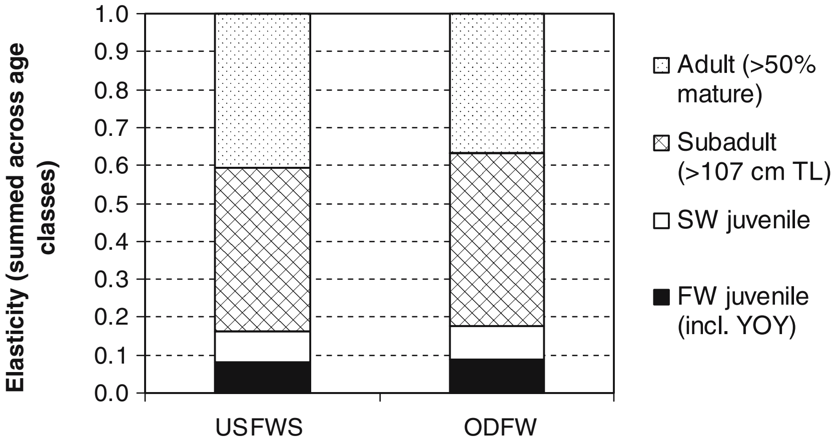

Fig. 6 Summed age-specific elasticities from Model II matrices using the USFWS and ODFW growth curves. The model assumes 3–5 years in freshwater and a subadult stage of age classes occurring between 107 cm TL (total length) and 174 cm TL (size at 50% mature)

"slot elasticity"). For a 107–152 cm TL (42–60 inch) slot limit, required by Oregon and Washington recreational fishing regulations in 2006, an instantaneous fishing mortality rate (F) of 0.1 results in a 2.3%–2.5% reduction in the population growth rate, depending on which

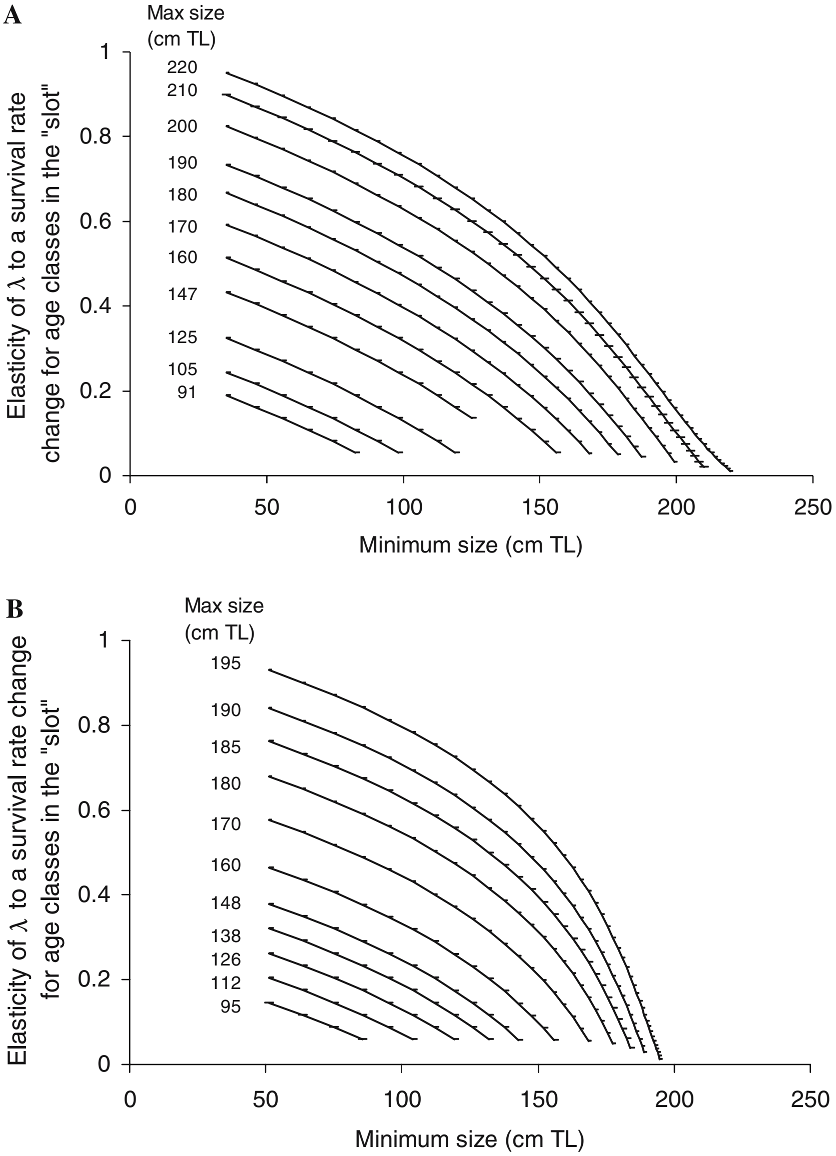

Fig. 7 Elasticity values for a "slot" of age classes defined by a range of minimum and maximum size limits for Model II. Each line represents the upper end of the slot, or the maximum harvest size, in cm TL (total length), while the minimum size is given by the *x*-axis. **A**: USFWS growth curve. **B**: ODFW growth curve

growth curve is applied (Table 3). When $F = 0.2$, population growth is reduced by 4.4%–4.7%. Given the low intrinsic rate of increase expected for sturgeon (Gross et al. 2002), this level of reduction could lead to population decline unless density-dependent changes in vital rates occurred to compensate.

Discussion

Population models and life history analysis can tell us much about how populations may respond to perturbation, including the potential benefits of management alternatives when a population is clearly declining (Heppell et al. 2000a, Gross et al. 2002). The preliminary analyses shown here illustrate that the sensitivity of λ to changes in subadult and adult mortality is high for green sturgeon, like other sturgeon and other long-lived, late-maturing species. This supports the contention that green sturgeon may be extremely susceptible to overharvest (Musick et al. 2000).

The elasticity analysis shown here can be used to compare potential effects of a change in harvest strategies. Slot limits vary by state, by

Table 3 Elasticities of two Model II-type matrices for the combined age classes within a "slot" defined by minimum and maximum total length (TL)

Min TL (cm/inch)	Max TL (cm/inch)	Years (approx.)	Elasticity of λ to a proportional change in annual survival of age classes within slot	Change in λ with $F = 0.1$	Change in λ with $F = 0.2$
USFWS growth curve					
107/42	183/72	9–25	0.449	–4.1%	–7.8%
107/42	168/66	9–21	0.348	–3.2%	–6.2%
122/48	168/66	11–21	0.294	–2.8%	–5.3%
107/42	152/60[a]	9–17	0.242	–2.3%	–4.4%
122/48	152/60[a]	11–17	0.188	–1.8%	–3.5%
ODFW growth curve					
107/42	183/72	6–26	0.577	–5.3%	–9.7%
107/42	168/66	6–18	0.375	–3.5%	–6.5%
122/48	168/66	8–18	0.317	–3.0%	–5.6%
107/42	152/60[a]	6–14	0.262	–2.5%	–4.7%
122/48	152/60[a]	8–14	0.203	–2.0%	–3.8%

Lengths are given in inches as well as cm because regulations are based on total length of fish in inches. F = instantaneous fishing mortality rate

[a] This maximum length nearly eliminates harvest on reproductive fish (females only)

location within states, and by year, and harvest regulations have been more conservative in recent years; a maximum length of 152 cm TL (60 inches TL) nearly restricts the recreational harvest to pre-reproductive fish for females (Table 2). Reducing the slot limit reduces the number of age classes harvested and, thus, the effect of harvest on the average population growth rate and population productivity. While this may seem an obvious conclusion, the models show that the relative magnitude of those changes may be substantial. For instance, a small change in the maximum size limit for a fishery has a large effect on the elasticity of λ to the survival rate of harvested fish (Fig. 7). The general patterns are determined by the life history of green sturgeon, and should be qualitatively robust despite our uncertainties about growth and natural mortality rates.

The primary goal of slot limits is to promote sustainable fisheries by eliminating the intentional harvest of large, mature, and highly fecund individuals. This strategy can be beneficial only as long as the fishing mortality rate (F) is low enough over a short enough time period to assure adequate survival of fish passing through the slot. The slot limits examined in this study follow current or proposed regulations in western states, and target primarily subadult and early maturing green sturgeon. In the absence of density-dependent growth or survival, fishing mortality on these life stages results in a decrease in the proportion of fish surviving to older age classes. Nevertheless, releasing older fish does provide a buffer for the population, relative to a minimum size limit alone, so long as F is not too high. For example, a fishing mortality rate of 0.08 applied to all age classes greater than 107 cm TL gives the same deterministic growth rate reduction (–3.5%) as an F of 0.2 applied to a slot limit of 107–168 cm TL (42–66 inches TL, ODFW curve model). This benefit of a slot limit can be realized, in part, because of the low rate of natural mortality that likely exists for this long-lived species.

Elasticity analysis can help managers decide which life stages are in most need of protection and which model parameters need additional research (Schemske et al. 1994; Heppell et al. 2000a), but there are a number of caveats to the interpretation and use of elasticity analysis in population assessment (de Kroon et al. 2000; Heppell et al. 2000b,). First, it is important to remember that elasticities are derivatives that represent relative contributions to population growth; they are not suitable for predicting the effect of large changes in vital rate parameters, and the elasticities themselves will change when lambda increases or decreases. Second, the analysis calculates changes in λ and hence assumes that the starting population is at a stable age or stage distribution and that parameters will not change dramatically in response to density. This is unlikely if the population experiences large recruitment variance or if habitat is limiting. Sturgeons are known to experience fluctuations in year class strength (Jager 2001; Gross et al. 2002), and are unlikely to ever reach a true stable age distribution. Shifts in age structure may alter the relative impact of harvest or other perturbations on year-to-year population growth (Morris and Doak 2002). However, because adults are long-lived, single year classes are a relatively small proportion of the overall adult population (Heppell et al. 1999), so the general patterns of sensitivity are likely to hold. Finally, when elasticity analysis is used to prioritize management actions, it must be coupled with an estimate of the effect of each action on the survival, growth or fertility rates of the population; elasticities alone only compare the effect of the same proportional change on two or more parameters (Heppell 1998; Gross et al. 2002). Additional considerations include the feasibility of particular management proposals, and the potential magnitude of their effect on a particular life stage. Although adult survival rates may have the highest elasticities in many long-lived organisms, the natural survival rate of adults might already be so high that no management alternative is likely to improve it (Green and Hirons 1991; Gross et al. 2002). Alternatively, some sensitive life stages may be inaccessible to managers, such as the saltwater juvenile life stage of green sturgeon. It is important to recognize that simply comparing the elasticities of a mean matrix does not reveal the causes of population decline, nor is it sufficient to warrant exclusion of research or management efforts directed at less sensitive life stages (Groom and Pascual 1998; Morris and Doak 2002). However, elasticity analysis is a valuable tool for initial management recommendations for poorly known species and as a first step in population viability analysis (Ferriere et al. 1996; Heppell et al. 2000a, b; Reed et al. 2002).

As we amass new information on green sturgeon life history and vital rates, assessment and viability models can be improved. The qualitative results shown here are likely to be generally robust to our uncertainty about survival rates (Heppell et al. 2000b), but further modeling with a range of vital rates should be attempted. Every effort should be made to estimate fishing and natural mortality rates for each stock and spawning river, either through cohort analysis of fishery-dependent and fishery-independent data or mark-recapture analysis. These studies should be focused on green sturgeon specifically (rather than on bycatch samples from studies of other species) and target all life stages, if possible. It is likely that green sturgeon have evolved a life history to not only cope with late maturity and low survivorship to maturity, but to relatively rare good recruitment years as well. Although fecundity increased with age and size in my models, I did not attempt to include an increase in egg quality, fertility, or frequency of reproduction with age. Age-specific maternal effects on offspring survival may further emphasize the importance of maintaining large, old females in the population (Boreman 1997; Berkeley et al. 2004). Future modeling efforts should account for uncertainty and include analyses with stochastic recruitment.

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