American Fisheries Society Symposium 00:000–000, 2002

Sturgeon Conservation: Insights From Elasticity Analysis

MART R. GROSS
Department of Zoology, University of Toronto,
25 Harbord Street, Toronto, Ontario, Canada M5S 3G5

JOE REPKA
Department of Mathematics, University of Toronto,
Toronto, Ontario, Canada M5S 3G3

CORY T. ROBERTSON
Department of Zoology, University of Toronto,
25 Harbord Street, Toronto, Ontario, Canada M5S 3G5

DAVID H. SECOR
Chesapeake Biological Laboratory,
University of Maryland Center for Environmental Science,
Post Office Box 38, Solomons, Maryland 20688, USA

WEBB VAN WINKLE
5163 N. Backwater Avenue, Boise, Idaho 83703, USA

Abstract.—We use elasticity analyses for three sturgeon species, the shortnose sturgeon *Acipenser brevirostrum*, Atlantic sturgeon *A. oxyrinchus*, and white sturgeon *A. transmontanus*, to calculate the potential to increase population growth rate, λ, by improving survival and fecundity. Elasticity analysis is a means of assessing changes to λ resulting from conservation initiatives. The elasticity of λ to survival has a characteristic profile that includes a plateau of high elasticity values across the young of the year and the juvenile ages. However, survival elasticity falls at maturity and declines rapidly with increasing adult age. Changes to fecundity have relatively little impact; the total of the fecundity elasticities over all ages is equal to the single young-of-the-year survival elasticity. Even though the young-of-the-year survival elasticity is equal to that of any other juvenile age, the overall opportunity for affecting λ is strongest in the young-of-the-year age-class because of its exceptional potential for increase to survival. The juvenile and adult stages have roughly equal total survival elasticities. These findings are particularly relevant in understanding the contributions of hatcheries, harvest regulations and habitat restoration as strategies for sturgeon conservation. Hatcheries are focused on the young of the year, the demographically most sensitive component of sturgeon life histories, and thus have the potential to make significant increases to λ if the genetic, evolutionary and ecological impacts of hatcheries can be controlled. Harvest, even at low levels, can have a significant negative impact on λ when it affects multiple age classes. Managers can use elasticity analysis to calculate the total impact of harvest and to mathematically evaluate the trade-off in exploiting young versus older individuals. Habitat restoration strategies, usually assessed in terms of survivals of the age classes impacted, would also benefit from using elasticity analysis to interpret their contributions to λ. If restoration efforts target the survival of age classes with high elasticities, significant population growth may be achieved.

Sturgeon are a critical conservation concern (e.g., Birstein 1993; Boreman 1997; Secor et al. 2000a). Once widely distributed and highly abundant, sturgeon species today exist as fragmented populations occupying limited geographic areas and containing relatively few individuals (Beamesderfer and Farr 1997; Bemis and Kynard 1997). Many species require immediate conservation action to increase their population size (de Meulenaer and Raymakers 2000), but an incomplete understanding of their biology and population demography is hindering progress in the development of conservation strategies.

Sensitivity analyses of life history and demographic parameters have proven useful in evaluating conservation strategies for long-lived species (e.g., Dixon et al. 1997; Caswell 2000; de Kroon et al. 2000) but have not previously been applied to sturgeon. All sturgeon are long-lived, become sexually mature at a relatively old age, and have a multiyear interval between successive spawnings (Doroshov 1985; Boreman 1997). At the same time, there are notable differences in life history and demographic parameters among sturgeon species. We therefore provide elasticity analyses for three different sturgeon species to evaluate their response to improvements in survival and fecundity, and we discuss the management alternatives of augmentation by hatchery stocking, harvest regulations, and habitat restoration.

Sensitivity analyses allow us to evaluate how population growth rate, λ, responds to changes in vital demographic rates (e.g., survival and fecundity) and to identify the parameters on which λ is most functionally dependent (Caswell 2001). Sensitivity analyses should be understood as approximations in the sense of derivatives. They can be used to estimate the effect of small changes to parameter values; however, the estimates become less reliable for large changes. Large changes perturb the age structure within a population, so estimates based on the original structure may no longer be valid. Sensitivity analyses are nevertheless powerful tools in conservation, assisting management programs in maximizing their influence on population growth rate by identifying vital rates with high sensitivity (Heppell et al. 2000a).

A widely applied type of sensitivity analysis in conservation assessment is the 'elasticity' analysis, which allows estimation and comparison of the percentage changes in λ resulting from percentage changes in the vital rates of particular classes of individuals (Heppell et al. 2000b). Elasticity analyses involve matrix projection models that divide populations into classes of individuals that share similar demographic parameters (such as annual age-classes or the grouping of age-classes into the juvenile and adult stages), and show the proportional contribution made to λ by parameter changes at each of these classes (de Kroon et al. 2000). Perturbing matrix projection models and calculating the effect on λ through elasticity analyses reveals how prospective changes in the demographic parameters of any life history class will influence overall population growth rate. In sturgeon, elasticity analyses can predict how λ will change with small changes to the survival or fecundity of each age-class, allowing managers to evaluate the influence of any particular change on population growth rate. Alternatively, the models can predict how λ will change with small changes to the survival or fecundity of broader life history stages, such as juveniles or adults, allowing managers to address groups of individuals that may require similar conservation initiatives. For small changes, the resulting increases in λ will affect the abundance of each life history class by (approximately) the same percentage. For example, changes to adult survival will affect the size of the entire population, including both juveniles and adults; the size of this change can be estimated through λ. Such analyses provide a guide that can direct management strategies to the classes and parameters that will offer the greatest return (see Heppell and Crowder 1998, Caswell 2001, and reviews by Caswell 2000; de Kroon et al. 2000; Heppell et al. 2000b).

Our models address three sturgeon species with different life history schedules: the shortnose sturgeon *Acipenser brevirostrum*, Atlantic sturgeon *A. oxyrinchus*, and white sturgeon *A. transmontanus*. Individually, these models can provide specific insight into the elasticities of survival and fecundity at various stages of a sturgeon's life history. Together they provide a synthetic picture of how sturgeon populations may grow. We use the results of the models to discuss the capacity of "the three H's," hatcheries, harvest and habitat, as strategies to increase population size.

Methods

Species

Worldwide, there are perhaps 25 or 27 species of sturgeon depending on classification. Bemis and Kynard (1997) considered 27 Acipenseridae species, but this was revised by Birstein et al. (2000), who grouped three previously determined separate species into a single species. The taxonomy and phylogeny of sturgeons remains an active area of study today (e.g., Bemis et al. 1997). In the genus *Acipenser*, 16–19 species have radiated into some of the smallest and largest sturgeons. We have chosen three North American species that vary greatly in body size and life history, and that have relatively well-known biologies. We focus on females, and thus the demographic parameter values mentioned are for females. Males typically become sexually mature at an earlier age, have a shorter interval between successive spawnings, and do not live as long as females (Auer 1999). We assume that males are always available for fertilization and therefore do not limit population growth.

Shortnose - With a maximum female length and weight less than 1.2 m and 24 kg, respectively, the shortnose sturgeon is the smallest *Acipenser* in North America (Kynard 1997). Because of its small size, it has been of less commercial and recreational interest than other sturgeon, but populations have declined severely due to blockage of spawning runs by dams, bycatch harvest, dredging and regulation of rivers, and pollution (Kynard 1997; NMFS 1998a). The shortnose sturgeon was listed in 1973 on the endangered species list. The species is amphidromous, spending most of its life in fresh water, but with occasional exposure to marine or brackish waters in estuaries of its natal rivers (Bain 1997; Kynard 1997). Adults migrate in fall and concentrate on spawning grounds earlier than other sturgeon species, generally spawning every two to four years in late winter or spring, depending on latitude (Dadswell et al. 1984; Gilbert and Moran 1989; Bain 1997). Young of the year remain in fresh water, but 1-year-old and older juveniles join adults in similar patterns of freshwater and saltwater habitat use, including migration (Dovel et al. 1992; Kynard 1997). Female shortnose sturgeon typically mature at 6–10 years of age and live to a maximum of about 37 years (Table 1). The shortnose sturgeon's geographic range includes coastal rivers from New Brunswick to Florida (Gilbert and Moran 1989).

Atlantic - With a maximum female length of 4 m and weight of less than 350 kg, the Atlantic sturgeon is one of the largest fish in North American rivers, but intermediate in size among sturgeon (Magnin 1964; Scott and Crossman 1973; Dovel and Berggren 1983; Winemiller and Rose 1992). It was an important commercial species for both flesh and caviar (Waldman and Secor 1998). The combination of habitat destruction, pollution, and overharvesting has severely reduced its numbers, and fishery restrictions or closures are in place (Kahnle et al. 1998; NMFS 1998b; Secor and Gunderson 1998; Secor and Waldman 1999). The Atlantic sturgeon is anadromous. Adults migrate from marine to fresh water every three to six years in late winter and spawn in spring or early summer (Van Eenennaam et al. 1996). Young of the year remain on upstream spawning grounds for the first three months of life before migrating downstream to deeper estuarine waters (Dovel

Table 1. Demographic parameter values and references used for female shortnose, Atlantic and white sturgeon. YOY is the young-of-the-year age-class. Spawning date varies among systems; the spawning date used in the model is given with the representative system to which it refers (overall ranges of spawning dates for the species are listed in parentheses). YOY survival, as solved by the model for a population at equilibrium and spawning on the given date, is listed (parentheses indicate the ranges in YOY survivals corresponding to the ranges in spawning dates).

	Shortnose sturgeon	Atlantic sturgeon	White sturgeon
System	Kennebec River Connecticut River Hudson River	Hudson River	Lower Columbia River
Studies	Boreman 1997 Dadswell 1979	Magnin 1964 Stevenson 1997 Van Eenennaam et al. 1996 Van Eenennaam and Doroshov 1998	Beamesderfer and Rien 1993 Beamesderfer et al. 1995 Boreman 1997 Chapman et al. 1996 Tracy and Wall 1993
Lifespan (yr)	37	60	100
Age at maturity (yr)	8 (6–10)	16 (14–17)	26 (16–35)
Survival for ages ≥ 1	0.865	0.93	0.91
Spawning Date	1 May, Hudson (February–May)	15 June, Hudson (March–July)	1 May, Lower Columbia (April–June)
YOY survival (solved by model)	5.37×10^{-5} ($5.18 \times 10^{-5} - 5.44 \times 10^{-5}$)	7.56×10^{-7} ($7.41 \times 10^{-7} - 7.64 \times 10^{-7}$)	1.05×10^{-5} ($1.04 \times 10^{-5} - 1.06 \times 10^{-5}$)
Fecundity function (eggs/female)	4091 + 2864*AGE	−1,304,704 + 111,909*AGE	−279,991 + 23,371*AGE
Spawn interval (yr)	3	4.5 (3-6)	3 (2-4)

and Berggren 1983). Juveniles move between upstream freshwater areas during the warmer months and downstream brackish areas during the colder months for one to six years before migrating out to sea (Dovel et Berggren 1983; Secor et al. 2000b). Both adults and juveniles spend much of their lives in the marine environment, and may travel great distances (>1000 km), but they generally remain near the shore in depths of less than 20 m (Gilbert and Moran 1989; Bain 1997; Johnson et al. 1997). Female Atlantic sturgeon typically mature at 14–17 years of age and live to 60 years (Table 1). The Atlantic sturgeon is protected over much of its geographic range, which comprises the western Atlantic Ocean and coastal rivers from Labrador south to Florida (Gilbert and Moran 1989; ASMFC 1998). This range encompasses that of the shortnose sturgeon, and where the two species co-occur, they tend to segregate on the basis of habitat (Dovel and Berggren 1983; Bain 1997).

White - With a maximum female length greater than 6 m and weight of 600 kg, the white sturgeon is the largest North American sturgeon and probably the largest fish in North American fresh waters (Scott and Crossman 1973; Winemiller and Rose 1992; Birstein 1993). It is an important aquaculture species for flesh and caviar and is also popular as a recreational fish (McCabe and Tracy 1994; Chapman et al. 1996). Regulations on size limits in some areas may not be adequate to protect populations from overexploitation (DeVore et al. 1995). The white sturgeon is anadromous, with females migrating every three years or so in late winter to spawn in the spring (Chapman et al. 1996). Young of the year remain in fresh water, generally in the deeper areas of rivers (McCabe and Tracy 1994). Juveniles move upstream during the fall and early winter and downstream during late winter and early spring (Scott and Crossman 1973). Adults spend most of their lives in shallow, local estuarine and marine waters, but are known to move to depths of 30 m and distances of more than 1,000 km (Scott and Crossman 1973; Chapman et al. 1996). Contingents of white sturgeon are also landlocked, completing their life cycle in freshwater (Duke et al. 1999; Anders et al. 2001). Female white sturgeon typically mature at 16–35 years of age and live to be more than 100 years (Table 1). The white sturgeon's geographic range includes coastal Pacific rivers and estuaries from Alaska to California (Scott and Crossman 1973; Birstein 1993).

Data

Data on females of the three species were compiled from the literature (Table 1). There is little information about variation in parameter values within and among locations; therefore, our choice of parameter values should be viewed as approximate. For Atlantic sturgeon and white sturgeon, complete sets of life history attributes have only been documented for the Hudson River and Columbia River systems, respectively, which limited the choice of parameter values to these systems. We used natural mortality rates with no added anthropogenic mortality. Since young-of-the-year mortality rates are empirically unknown, we solved for the survival that gives the eigenvalue $\lambda = 1$ (i.e., a population at equilibrium). Although choice of spawning date affects the young-of-year survival solution, it does not change the elasticity calculations.

We recognized three female life stages: young of the year, juvenile, and adult. Young of the year is the interval (usually 7–8 months) between emergence and 1 January of the next calendar year. In some literature, young of the year is called "age 0" or is indicated by a "+" sign, as in age "X+." Juvenile (J) is from age 1 (1 January –31 December after the young-of-the-year phase) through each year before maturity. Adult (A) is the first year of maturity (reproduction or egg production) through the year of death.

Age at maturity occurs over a range of ages (e.g., 6–10 years for female shortnose sturgeon), and for the purpose of modeling convenience we have chosen a median value (e.g., 8 years for female shortnose sturgeon). For shortnose sturgeon, the natural mortality value of 0.135 corresponds to an annual survival without fishing mortality of 0.865. Constant mortality over all classes, in this case ages 1–37, is of course a crude assumption. However, many sturgeon biologists seem to agree that high mortality in the young of the year is substantially reduced to very low mortality in the juveniles and adults (e.g., Boreman 1997). In fact, year-class strength is probably established within the first two months of life (Kynard 1997; Nilo et al. 1997). By age 2, sturgeon are large enough to have escaped most natural predators (except humans), at which point the major sources of mortality become fishing, illnesses, food, habitat issues, and/or senescence (e.g., McCabe and Tracy 1994; Secor and Waldman 1999). The interval between successive spawnings is poorly documented for female sturgeons but is known to be more than 1 year and to vary significantly among and within species (Stevenson and Secor 2000). Fecundity schedules were calculated from published data that we reference in Table 1. Linear fits of fecundity (number of eggs per female) and age provided reasonable representation of fecundity schedules for the three sturgeon species.

Model

The models developed here are based on age-specific classes: we divide the life of the sturgeon into single age-classes. For the shortnose sturgeon, as an example, the information available suggests a maximum age of 37 years plus the time as young of the year, so we consider a life history model divided into 38 classes. The data in Table 1 were incorporated into a 38 × 38 matrix representing the change in population structure from one year to the next. Survival in the first year (young of the year) was unknown. The entry in the $(i+1)$th row and ith column is the proportion of the ith age-class that survives into the $(i+1)$th age-class. The entry in the first row in the jth column is the average number of female eggs produced by an individual female in the jth class. This is calculated from the fecundity function (Table 1), divided by spawning interval (e.g., three years for shortnose sturgeon), discounted by the mortality of females between the 1 January census and the spawning date, and then divided by two to count only those eggs that can mature into females. All other entries in the matrix are zero. The matrix has a maximum eigenvalue, λ, which represents the factor by which the total population changes in one year (population growth rate). If λ exceeds one, the population is growing; if it is below one, the population is declining. Under the assumption that the data apply to a population at equilibrium (i.e., $\lambda = 1$), it is possible to solve for first-year (young of the year) survival.

Most matrix projection models adopt either prebreeding (immediately prior to reproduction) or postbreeding (immediately following reproduction) census times (Caswell 2001). However, our model follows the aging convention used for fish and adopts 1 January in the calendar year as its census time. Each adult age therefore undergoes a specific fraction of its annual mortality before reproduction that is dependent on the spawning date of the species. Choice of census time, like choice of spawning date, affects the solved value for young-of-the-year survival but does not affect elasticity values.

With the matrix constructed as above, elasticities were calculated by standard methods (see Caswell 2001 and a special feature edited by Heppell et al. 2000 in Ecology 81(3):605–708; especially de Kroon et al. 2000). For each age-class, we can evaluate the effect on λ of changes in survival (S). We can also evaluate the effect of changes in fecundity (F) in adults (females alone). For example, if the elasticity of λ to the survival of four-year olds is 6%, then a change to their survival will result in a percentage change to λ that is 6% as large. Therefore, increasing S for four-year-olds by 10% would result in a 0.6% (6% × 10%) increase in the population growth rate, changing $\lambda = 1$ to $\lambda = 1.006$ (see Caswell, 2000, pp. 240–243, eq. 9.111). However, an S elasticity of 6% for each juvenile age-class (ages 1–7) would provide a total elasticity of 42% (7 years × 6%). A 10% increase to each juvenile age would then provide a 4.2% (42% × 10%) increase to λ, changing $\lambda = 1$ to $\lambda = 1.042$. Elasticities of λ to fecundity have a similar interpretation.

It should be emphasized that elasticities are derivatives and, as such, are localized analyses. Predictions of changes in λ become more accurate as the changes become smaller. Fortunately, in practice, λ is probably close to linear at the scale of changes we considered, and therefore, elasticities can provide reasonably accurate predictions of even relatively large perturbations (Caswell 2001).

Finally, although our analyses focus on increases to λ from the increases to survival or fecundity that might result from conservation initiatives, we note that our elasticity analyses will apply equally to decreases in survival or fecundity (e.g., because of fishing mortality). Thus, they can be used to interpret decreases to λ from negative impacts on these parameters.

Assumptions

The model makes a number of assumptions. The major ones are listed below:

1. The annual mortality rate is assumed to be the same for all juvenile and adult ages. Young of the year have their own mortality rate, which is very high. Many researchers appear to accept this assumption, and there are data to support it (Nilo et al. 1997; Secor et al. 2000a). However, we test the effect of changing mortality rates.
2. Female fecundity is assumed to increase linearly across all adult age classes. Published fe-

cundity data generally fit quite well to linear functions (see Table 1 for species-specific studies), but fecundity may not increase linearly in some systems (e.g., Boreman 1997). In addition, fecundity functions do not incorporate differences in quality of females of different ages, such as superior egg quality or spawning locations for older females. We therefore test the effect of varying female quality with age by letting fecundity increase either more or less rapidly than linearly with age.

3. Females are assumed to have a fixed spawning interval. In reality, females probably use environmental and physiological information to choose years for spawning, but spawning intervals are poorly known and vary among rivers. Fortunately, whether the spawn interval is 3, 5, or more years has no effect on the elasticity outcomes, and minimal effect on the rest of our analyses.
4. The model assumes an average proportion of individuals spawn every year (e.g.,1/3 for shortnose). Irregular spawning by individuals has no effect on the model. However, irregular but concurrent spawning by the entire population may affect the patterns of recruitment through density-dependent processes and thus possibly some outcomes of the model (see assumption 6).
5. The populations are evaluated at equilibrium and at a stable age distribution. As sturgeon are periodic species (Winemiller and Rose 1992), most populations are probably not in stable age distribution. Actual populations are known to have dramatic fluctuations in the size of each age-class. This means that a given age-class will constitute different proportions of the population in different years, which in turn means that elasticities will also fluctuate. However, the results obtained here are expected to be meaningful if they are interpreted in the sense of an "average." That is, if a given percentage change is imposed each year for a number of years, then the predicted effect should occur over the long term.
6. The model assumes no density dependence in population dynamics. While density-dependent growth and survival might be incorporated, these are difficult to include within the model framework (the deterministic matrix model is fundamentally linear and does not incorporate nonlinear effects). Since we are evaluating the potentials for recovery of depressed populations, it seems reasonable to ignore density dependence at this point.

Results

We first present the elasticity analyses for both the age classes and stages of the three sturgeon species. Next, we examine the robustness of the elasticity analyses to variation in the underlying data from which they were constructed. Third, we show how λ responds to the results found in the elasticity analyses. Finally, we summarize the study and discuss the maximum achievable gain in population growth from increasing the survival and fecundity of sturgeon.

Elasticity

Age-class - The elasticity analyses have remarkably similar shapes for each of the three species (Figure 1). Elasticity values are always greatest for annual survival in early life, drop at the onset of maturity, and are relatively small for fecundity of each age-class. An important feature of each analysis is the 'plateau' of survival elasticity values before maturity, a property common to elasticity analyses (e.g., Heppell et al. 2000a; Caswell 2001). All ages before maturity, including the young of the year (age 0) and juvenile ages, have exactly the same elasticity. Population growth rate is therefore no more affected by percentage changes to the young-of-the-year survival than it is by the same percentage changes to the survival of any other age before maturity (equal rates of return). Across species, the age-class elasticity values necessarily decrease as the number of juvenile and adult years increases. This is why the plateaus decrease from shortnose (5.8%) to Atlantic (2.9%) to white sturgeon (2.2%). Therefore, for a fixed percentage increase in survival of any age-class before maturity, the shortnose should show the largest response and the white sturgeon the least.

In contrast to the plateau in early life, the adult ages have declining elasticities (decreasing rates of return). Therefore, among adults, population growth rate responds best to improvement of survival in the early adult ages. There is low elasticity for each late adult age-class, and thus there will be little response in population growth rate to increasing the survival of older adults. It should be noted that while elasticities of adult age-classes decline, the reproductive value of individual females may increase; a single adult is worth more than a single young of the year.

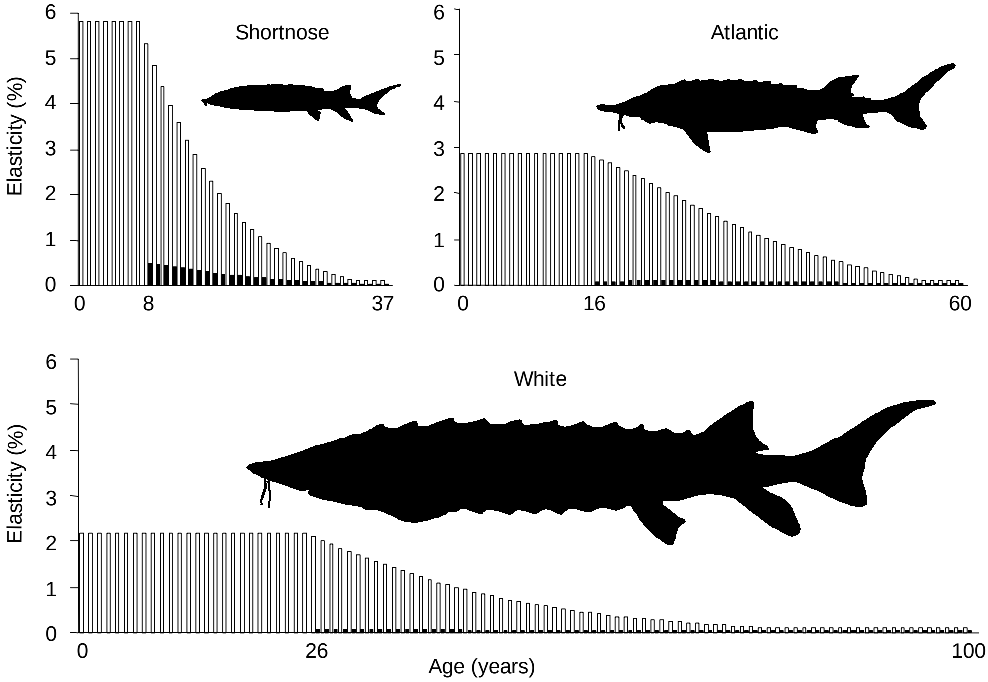

Figure 1. Age-class elasticity profiles for females of the three sturgeon species: shortnose, Atlantic, and white sturgeon. The elasticity scale represents the percentage contribution of each age-specific survival and fecundity parameter to population growth rate λ. The age of maturity and the final year of life are given for each species along the horizontal axis. Age 0 is the YOY (young-of-the-year) age-class; ages 1 to the year prior to maturity are the juvenile age-classes; and from maturity to final year of life are the adult age-classes. The short black bars represent the elasticity for fecundity; the longer open bars represent the elasticity for survival. The combined fecundity and survival elasticity bars total 100%. Sturgeon silhouettes were drawn from Scott and Crossman (1973) and are approximately to scale.

Compared with survival, fecundity has relatively low elasticity (low rate of return). Therefore, l will show relatively little response to improvements in fecundity. The highest annual fecundity elasticity among the three species is only 0.5% (at age 8 for the shortnose sturgeon). This is because the effects of fecundity are shared across all adult age classes and because high mortality in the young of the year devalues the contribution of egg number to population growth.

Life Stage - The elasticities of the life stages are calculated by summing across the ages in each stage (Figure 2). The young-of-the-year stage, being a single age, has much lower survival elasticity than the juvenile stage. But the juvenile stage, with many fewer ages than the adult stage, is comparable in total elasticity to the adult stage. This is because each juvenile age is worth more in elasticity than each adult age (i.e., the survival of each juvenile age has a greater influence on λ). Fecundity across all ages has much less elasticity than the survival of either the juvenile or adult stages. If the cumulative elasticity for fecundity across all adult age classes is considered, it is equal to the survival elasticity of the young of the year (Heppell et al. 2000a). This means that λ is affected equally by a percentage increase in overall egg production as by an equal percentage increase in the young-of-the-year survival.

The elasticity of life stage survival increases from young of the year to juvenile to adult in both shortnose sturgeon and Atlantic sturgeon. In contrast, it peaks at the juvenile stage in the white sturgeon. This difference among the species is largely due to differences in the number of years spent in the juvenile stage relative to the adult stage and in annual survival. As the number of

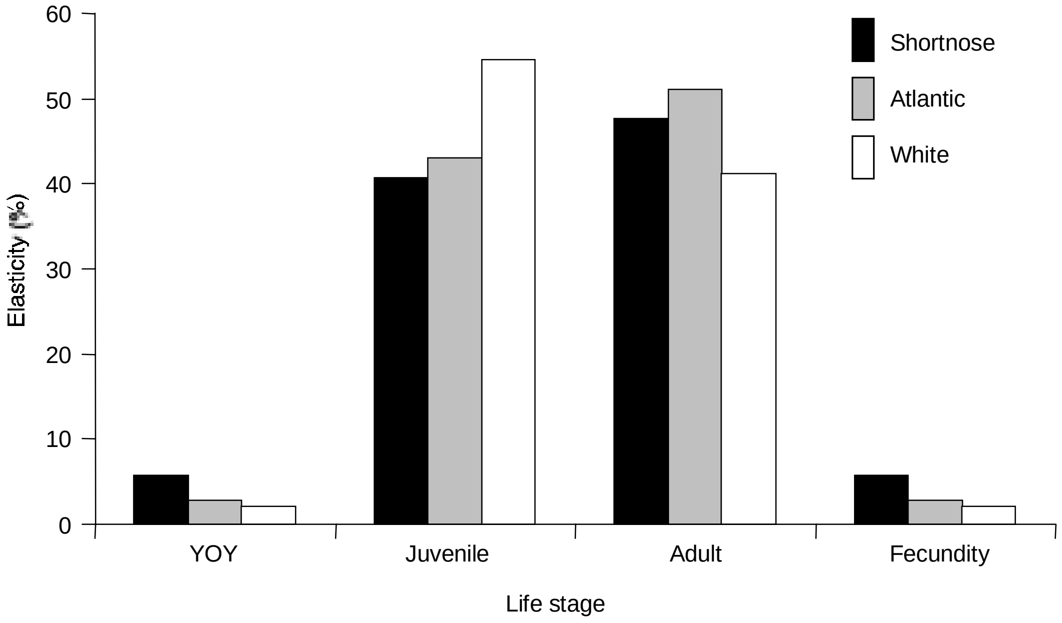

Figure 2. Combined elasticities for survival in the three life stages and fecundity for female shortnose, Atlantic, and white sturgeon. The sum of the bars for each species is 100%.

juvenile ages increases, the population becomes more sensitive to the survival of this life stage. As the annual survival of all age classes increases, the population becomes more sensitive to adult survival (see Figure 3).

Robustness of Elasticities

The matrix projection models are based on the data of Table 1; the data are approximations and can be expected to vary through time and among locations (e.g., Dadswell et al. 1984; Gilbert and Moran 1989). How robust are the results to variation in the underlying data? We address this by varying the underlying survival, age of maturity, and fecundity data and examining the resulting elasticity values. Since the outcomes are similar for the three species, we present only the results for the shortnose sturgeon (Figure 3).

For survival (Figure 3b), we contrast the average annual survival of 86.5% used in the base elasticity profile (Figure 3a) for juveniles and adults (Figure 1), with a reduced survival of 70%, and an increased survival of 95%. As survival decreases, survival elasticity shifts to the juvenile stage and to early adulthood, and decreases at later adult ages. Fecundity elasticity also shifts to early adulthood. With low annual survival of 70%, population growth becomes less than half as sensitive to improvements in adult survival (elasticity = 25%) as to juvenile survival (59%). This is because few adults remain at older ages, and thus the best improvements to population growth are obtained by getting more recruits into the first few adult ages. The same results would apply if there were a decrease in adult survival relative to juvenile survival, rather than a uniform decrease to both life-stages. The reverse is also true; as survival increases to 95%, survival elasticity shifts away from juveniles and toward the adult stage. Fecundity elasticity shifts to later adult ages and becomes more evenly distributed across years. With high annual survival of 95%, population growth becomes about half as sensitive to improvements in juvenile survival (elasticity = 30%) as to adult survival (61%).

For age of maturity (Figure 3c), we contrast the average age used in the base elasticity profile (age 8; Figure 3a), with the minimum bound (age 6; Table 1), and the upper bound (age 10; Table 1). As age of maturity increases from 6 to 10 years, the total elasticity of the juvenile stage also increases and that of the adult stage decreases. The rate of increase in total juvenile elasticity slows down, however, as age of maturity increases. Thus, there is a greater increase in juvenile elasticity when the age of maturity increases from 6 to 8

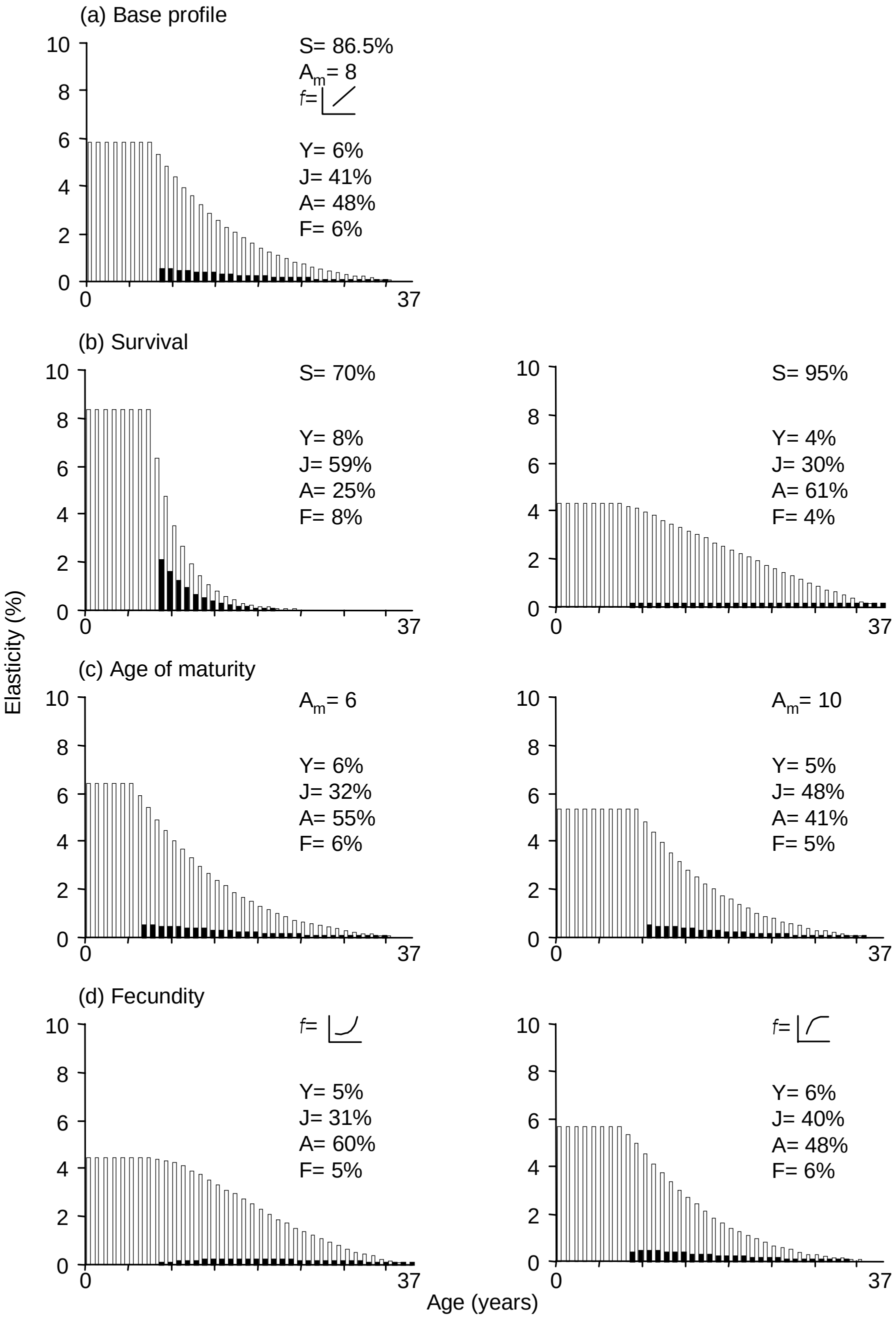

Figure 3. Changes in elasticity profiles of female shornose sturgeon in response to hypothetical changes in the underlying demographic data. (a) The base elasticity profile, as in Figure 1, including the survival (S), age at maturity (A_m), and fecundity function-type (f) used in its construction (Table 1). The stage-specific elasticity values for YOY (Y), juveniles (J), adults (A), and fecundity (F) are given. (b) Elasticities after changing juvenile and adult survival from 86.5% to 70% and 95%. (c) Elasticities after changing age at first maturity from 8 years to 6 and 10 years. (d) Elasticities after increasing fecundity (or offspring quality) of older females 30 fold and from representing sturgeon fecundity as a quadratic function with a negative leading coefficient.

(+9%) than when it increases from 8 to 10 (+7%). The relative importance of juveniles and adults flips between ages of maturity 8 and 10, with the latter more important when age of maturity is 8 and the former when it is 10. Thus, age of maturity is a strong determinant of total juvenile elasticity and the relative value of the juvenile and adult life-stages. Finally, the young-of-the-year and fecundity elasticities show only slight decreases with increasing age of maturity.

For fecundity (Figure 3 d), we contrast the linear increase in eggs with age, as used in the model, to a quadratic function that rises to 30 times as much at the oldest age-class. By increasing female fecundity in this manner, we emphasize the additional potential contributions of older females to recruitment that may not be captured by egg number alone. For instance, older females may also produce eggs or larvae of better quality, obtain superior spawning locations or spawn at better times within the year, or have greater genetic quality that is passed on to their offspring. All of these factors could increase recruitment and therefore increase the relative value of older females to population growth rate. The results show that an increase in the value of older females does shift elasticity toward them, and away from the juveniles, but the overall impact on elasticity is not very strong, and there is very little effect on the elasticity of young of the year (or fecundity). We also consider fecundity as a quadratic function with a negative leading coefficient. Here, the quadratic fecundity function was chosen to have the same values at ages 8 and 37 as the linear function used in the base profile, but to rise more quickly and flatten out at the end. Specifically, it was chosen to have a horizontal tangent at age 37, which, together with the values at ages 8 and 37, determines the function uniquely. This would correspond to a situation in which fecundity grows rapidly in early maturity but levels off in old age. We find that this quadratic function barely alters the values of the base profile.

In summary, the elasticity analyses are very robust to the data sets on which they were established, and thus the results from the analyses should be widely applicable to sturgeon. We find that the total elasticity of the juvenile stage survival increases with a decrease in juvenile and adult survival, an increase in age of maturity, or a decrease in the fecundity value of older females. However, these changes do not change the basic character of the elasticity results.

Constraints to Population Growth Rate (λ)

There is a ceiling to the increase in λ that can be obtained from improving survival (de Kroon et al. 2000). For example, in shortnose sturgeon, juvenile ages 1–7 already have an annual survival of 86.5%, so the increase in their survival is limited to 15.6% (100/86.5–1). As a consequence of this survival ceiling, the maximum possible increase to λ from increasing the survival at each age 1–7 is 1% (annual elasticity of 5.8% x 15.6%). Adult ages 8–37 also share the same annual survival, and therefore, they too are limited to 15.6% increases. However, they have even lower elasticities, and thus, their maximum survival improvements will achieve less than a 1% increase in λ. In contrast, when existing survivals are below 50%, increases in survival can exceed 100%, and λ can increase substantially. The extremely low young-of-the-year survival of perhaps 5×10^{-5} (about one egg in 20,000 survives to age 1) provides considerable opportunity for survival gains and thus large potential increases to λ.

The maximum increases in λ that can be realized in this model under the constraints of the demography and life history of sturgeon are summarized in Figure 4 for shortnose sturgeon. The maximum achievable increase in survival, ΔS, is capped by the 0.865 survival (Table 1) to 15.6% for ages 1–37 (Figure 4a, insert). The young-of-the-year age-class has a much lower survival (Table 1) and therefore a much higher cap, as indicated by the vertical arrow. The base elasticity profile of Figure 1 illustrates a survival elasticity of 5.8% for ages 0–7, and this falls rapidly after maturity (Figure 4a). The two functions, ΔS and elasticity, are multiplied to obtain the theoretical maximum increase in λ (%) for each class. This maximum increase is the largest percent increase in population growth rate that is possible (Figure 4b). The maximum increase in population growth rate obtained by improving survival in each of the ages 1–7 is less than 1% and declines rapidly across ages 8–37. In contrast, young-of-the-year age-class has a very high maximum potential contribution to λ because of its low survival. Improving juvenile survival can, in total, achieve a 6.4% increase to λ, and adult survival 7.4% (Figure 4c). The young of the year, by contrast, can theoretically achieve more than a 100% increase to λ (Figure 4c). Thus, the greatest potential for increasing sturgeon population size may be realized through changes to young-of-the-year survival.

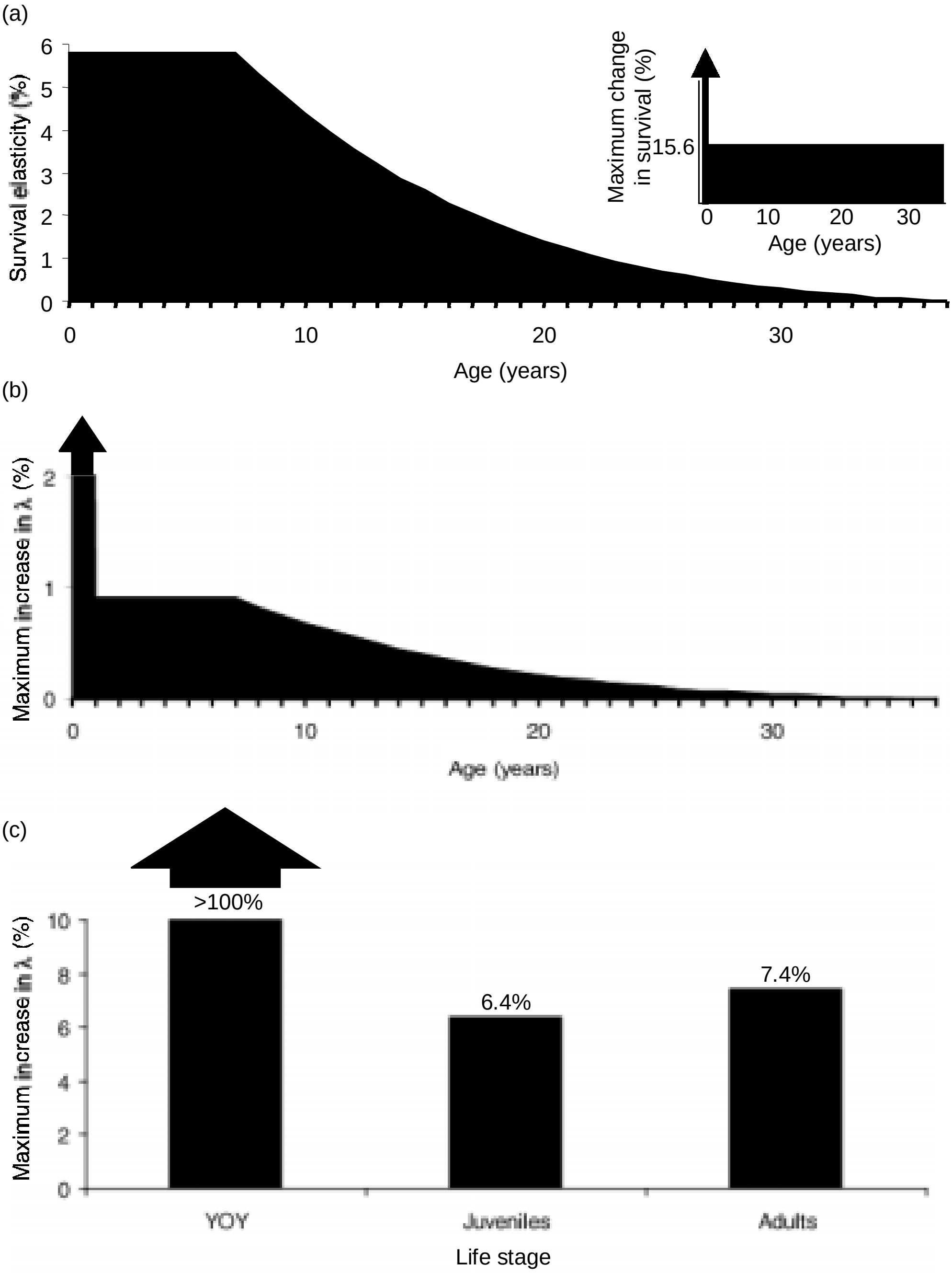

Figure 4. The maximun possible increases in λ through increasing the survival and fecundity of female shornose sturgeon. (a) Age-specific elasticity and annual mortality (insert). (b) Calculated maximum possible increase (Δλ) in λ for each age-class. (c) Maximum possible increase (Δλ) in λ for each life stage. Because the fecundity results are the same as for YOY, they are not redrawn.

Discussion

Our modeling results suggest that very different sturgeon species have similar elasticity profiles for population growth rate, which allows general interpretation of population growth for sturgeon. We find that population growth in sturgeon is (1) most sensitive to young-of-the-year and juvenile survival on an age-specific basis, (2) about equally sensitive to the survival in the entire juvenile stage and the entire adult stage, and (3) least sensitive to annual adult fecundity. Young-of-the-year and juvenile survival elasticities have the same value at all ages, whereas survival elasticity declines rapidly with age after maturity (Caswell 2001). We find that certain life history and demographic parameters strongly influence the potential for increasing population growth rate. In particular, the relatively high natural survival of juvenile and adult ages restricts their potential contributions to population growth. In contrast, the relatively low survival of young of the year means that recovery programs focused on this stage could be more efficient and realize much greater improvements in population growth rates than those that focus on juvenile or adult stages. Of course, our analysis of the three sturgeon species assumes that the populations are undergoing only natural mortality. With added anthropogenic mortality, such as harvest, the scope for improvement in survival rates will increase.

Our finding of high elasticity in young of the year and juvenile ages compared with adult ages differs from previous conclusions for long-lived species. Elasticity profiles of sea turtles (Heppell and Crowder 1998; Heppell et al. 2000a) differ considerably from those of sturgeon, probably due to the sturgeon's vastly larger fecundity. Heppell and Crowder (1998) infer from their results for sea turtles that the adult stage of sturgeon may also have greater influence on λ than the early life stages. We found that the relative contributions to λ of the two stages (juveniles and adults) when all ages are summed are roughly equivalent, with weighting dependent on both the length of each stage and annual survival values. A higher annual survival tends to shift weighting away from juveniles and towards adults. The differences between our results and those for sea turtles indicate that the results of elasticity analyses may vary considerably among "long-lived" species.

Sturgeon Conservation Strategies

We now interpret these results in terms of hatcheries, harvest and habitat strategies. We focus primarily on hatcheries, because the model results suggest that hatcheries may be a highly effective management strategy. It should be noted that this interpretation of management alternatives is limited to identifying the possibilities and constraints in affecting population growth rate through changes in specific portions of the life cycle. These analyses cannot weigh the ease with which a given change can be achieved. Such considerations must be address-ed by professional sturgeon managers, and we take caution not to overreach in attempting to draw management conclusions. We also point out that the changes to λ that result from extreme increases in survival are difficult to predict with accuracy since our model assumes a linear response in $\Delta\lambda$ while biological consequences, such as density dependence, become increasingly important with increasing magnitude of change. Our analyses also assume that ΔS is acting upon all individuals within a class. In some conservation initiatives, however, only a proportion of the individuals in a class will benefit. For instance, a hatchery that collects eggs from a sample of females will only increase the survival for that proportion of the young of the year. The contributions to λ will be influenced by the proportion affected.

Finally, there is a qualification to be made regarding the utilization of elasticity analyses in management. The analysis does not consider the unforeseen fluctuations and imperfect information that challenge management applications. Both the data entered into models and the applications of the results of models are subject to error. These uncertainties must of course be taken into account in management practice by precautionary decision-making.

Hatcheries - Hatcheries function primarily to increase survival in early classes, typically eggs and young of the year (Piper et al. 1982). Early hatchery survival rates of two orders of magnitude above natural are possible (Secor et al. 1992; Secor and Houde 1998; Secor et al. 2000a), although not always achieved. Managers may also attempt to increase 'fecundity' through stocking and translocation from other sources (this indirect increase in fecundity is not typical, but see Beamesderfer and Farr [1997] and Rien and North [2001]). In our analyses, any increase in fecundity is equivalent to an increase in young-of-the-year survival, so it increases the number of individuals within the young-of-the-year class. For example, a 10% increase in eggs in a population is equivalent to a 10% increase in young-of-the-year survival.

Survival of the young of the year in sturgeon is typically low (e.g., Nilo et al. 1997; Secor and Waldman 1999). This may be a consequence of the unpredictability of the environment and thus the evolution of small egg size and minimal parental investment (Roff 1992; Sargent and Gross 1993; Winemiller and Rose 1993). Hatcheries can avoid this unpredictability by providing the resources that the developing young require (Secor and Houde 1998). Provided that the sturgeon culture techniques exist (e.g., Smith et al. 1985; Conte et al. 1988; Gisbert and Williot 1997, Ireland et al. 2001), it is possible to increase survival manyfold, and this increase, together with the relatively large elasticity for young of the year, can achieve significant increases in population growth rate. Thus, hatcheries are manipulating a highly elastic component of the system.

However, there are several considerations regarding hatcheries. First, the proportion of the population that is affected may be very low in large populations (although it can be higher for small populations). Thus even large increases in survival for the individuals affected may have relatively little effect on overall population growth in an abundant population, i.e., there is a tradeoff between the proportion affected and the increase in survival (or fecundity) that will be necessary to obtain the desired λ.

Second, the value of hatcheries must be assessed against the contributions of adult fish left in the wild, and against the loss of their future production due to the impact they receive in the hatchery. Hatcheries typically operate at some cost to adults. Handling females and the physical removal of eggs typically involve some injury, which can decrease subsequent female survival and may in some cases cause death. Any gain from the hatchery must be discounted by any loss to the current and future wild production. The elasticities of young-of-the-year survival, and of fecundities, provide a mechanism for analyzing this tradeoff. Increasing one at the cost of the other may not provide any gain at all.

Third, elasticity is equally high in all juvenile ages, so focusing on ages 0 or 1 is not necessarily the ‘best’ hatchery strategy. In some situations, a percentage increase in survival may be easier at later ages, when there are fewer individuals to work with or when the effort is more readily accomplished. For example, in some populations it may be easier to catch and increase the survival of most of the juveniles in a later age-class because there are fewer of them. This strategy would improve a larger proportion of the population, perhaps more economically, and may thus override the constraints on survival increases after age 0. Another consideration is that hatcheries tend to maximize numbers, producing thousands or millions of young of the year, of which only a very small percentage will survive to maturity (e.g., Smith et al. 1995). In some cases, it may be more productive to put resources into a few hundred eggs or young of the year that can be reared for a longer time period, combining elasticity across several age classes.

Fourth, there are many ecological and evolutionary issues that must be considered when evaluating the contribution of hatcheries for any fish species. Hatcheries can and have caused developmental and genetic changes that reduce the fitness not only of hatchery-produced individuals, but also of those born in the wild (e.g., Schramm and Piper 1995; Gross 1998; Youngson and Verspoor 1998). Developmental changes immediately reduce survival and performance of hatchery-released individuals relative to their wild counterparts. For instance, when reared under traditional production-hatchery techniques, individuals lack information about predators, food sources, and habitat structure when they are released, and have modified morphologies (e.g., finshape), all of which reduce their own performance, but can also impact the performance of wild fish. Hatchery-induced genetic changes are responsible for the longer-term reduction in survival and performance that characterizes hatchery-produced fish (e.g., NRC 1996). Hatchery stocks can and have become increasingly domesticated to the hatchery, thereby losing their adaptations for the wild and the genetic variation that is important for future evolution. Hatchery stocks can also replace and alter wild gene frequencies. These genetic and developmental concerns restrict the potential for hatcheries to utilize the full elasticity response of sturgeon for population growth. For example, reducing the number of classes reared in hatcheries and specifically selecting adults involved in the hatchery program can minimize developmental and genetic changes, but both inevitably reduce the number of individuals that can benefit.

Finally, hatcheries rarely solve problems so much as provide a bandage to the symptom. The decline in sturgeon has almost always been due to habitat deterioration and harvesting practices (Birstein 1993); hatcheries do not reverse these problems. Many fish biologists have become increasingly outspoken against hatcheries because of the diversion of attention from the real issues (e.g., Kynard 1997; Lichatowich 1999). As we have shown, hatcheries can, in theory, significantly increase sturgeon numbers. However, it would seem that hatcheries should operate only with full awareness of the tradeoffs involved.

Harvest - Harvest regulations attempt to maximize or maintain yields through quotas, size (gear) limits, and season limits. Regulations are also directed at controlling poaching and bycatch, which can remove substantial fractions of the juvenile and adult stock (Collins et al. 1996; Kynard 1997; Secor et al. 2000b). It might seem that harvest regulations will have little effect on population growth because of the relatively low elasticity in adult age classes. However, the combined elasticity for adult survival is about equal to that of juvenile survival, and thus the mortality imposed on adults through fishing can have a severe effect on sturgeon population growth. Boreman (1997) has already shown the vulnerability of sturgeon populations to fishing impacts as a consequence of the number of years that long-lived adults spend in the fishery. Cochnauer (2001) presents a case where harvest restriction appears to have resulted in an improved age-class structure for a population of white sturgeon.

The relatively low survival elasticity of the older adult age classes, and their much larger body size, suggest some important management considerations. If fishers insist on capturing a fixed percentage of certain individuals, then all else being equal, this percentage should probably be taken from the very oldest fish, since these individuals contribute least to population growth (Figure 1; Figure 4). Even though an older female sturgeon contributes substantially more eggs, or progeny of better quality, her remaining lifetime contribution to population growth is still much less than that of even a middle-aged female. This is because the older fish is not going to contribute for as many additional years to production. Thus, its removal has less of an impact on sturgeon population growth than the loss of a younger individual with higher reproductive value. An important qualification is that older individuals in a population with nonstable age distribution (e.g., missing younger individuals) may be necessary to span recruitment gaps (Secor 2000).

In contrast, the smaller elasticity of fecundity relative to adult survival in any age-class suggests that egg exploitation for caviar may be less detrimental to population growth than adult harvest, providing that adults are not severely impacted in the process of harvesting the caviar. Based upon life table analysis (egg production per recruit), Kahnle et al. (1998) and Secor et al. (2000a) argued that only mature sturgeons should be harvested during their spawning runs using escapement targets. This recommendation complements well the elasticity analysis, which indicates that egg harvesting from old females (i.e., decreasing fecundity) is more sustainable than harvest of flesh from younger individuals (i.e., decreasing survival). Conservation of sturgeon would be further promoted if eggs could be removed from live sturgeon that were then released after recovery (e.g., Ireland et al. 2001). It might therefore be possible to encourage a shift in the target of harvest from flesh to the renewable production of eggs as a means to maintain sturgeon populations in the face of exploitation pressure.

In general, managers of harvest may benefit by considering the ratio of elasticities to determine the potential trade-offs that exist in exploitation. For instance, the ratio of total adult survival elasticity to total juvenile survival elasticity in shortnose sturgeon is 1.17 (48%/41%; Figure 2). Therefore, the effects on l of a 10% decrease in adult survival through fishing mortality can be nullified by a 12% increase in juvenile survival (10% × 1.17 = 12%). The 10% decrease in adult survival will cost population growth about 4.8% (48% × 10% = 4.8%), while the 12% increase in juvenile survival will benefit population growth about 4.9% (41% × 12% = 4.9%). Similar trade-off analyses can be done for all classes and stages of the sturgeon life histories.

Habitat - The elasticity analyses show that habitat improvements increasing survival of young of the year or any class within the juvenile life stage will make strong contributions to population growth. Conversely, habitat improvements that increase only fecundity or survival of a specific age-class, such as increased feeding opportunities for certain adults, will provide less of an increase in population growth. Habitat improvement can vary from relatively minor to quite expensive undertakings (Beamesderfer and Farr 1997). Fortunately, habitat improvements usually simultaneously influence the survival of multiple classes, such as all juveniles or all adults or even both. Thus, the costs of these conservation initiatives can be shared across the multiple elasticities that are affected. Beamesderfer and Farr (1997) recently surveyed more than 200 sturgeon biologists and management organizations and found that habitat improvement was considered to be the most important conservation undertaking for sturgeon, yet the least often employed. Instead, hatcheries and harvest regulations were the most frequent initiatives. Since hatcheries primarily affect the young of the year, and harvest regulations primarily affect the adults, habitat improvements that simultaneously affect young of the year, juveniles and adults may achieve a combined elasticity benefit that far exceeds any other management alternative.

Acknowledgments

We thank Raymond Beamesderfer and Selina Heppell for extensive and helpful comments, and Selina Heppell for correcting an error in our young-of-the-year calculation. We appreciate the help of Debby Repka in editing an early version of this paper. The Natural Sciences and Engineering Research Council of Canada (NSERC) has supported the work of Mart Gross, Joe Repka, and Cory Robertson.

References

Anders, P. J., D. L. Richards, and M. S. Powell. 2001. The first endangered white sturgeon population (*Acipenser transmontanus*): repercussions in an altered large river-floodplain ecosystem. Pages XXX–XXX *in* W. Van Winkle, editor. Biology, management, and protection of sturgeon. American Fisheries Society, Symposium XX, Bethesda, Maryland.

ASMFC (Atlantic States Marine Fisheries Commission). 1998. Review of the Atlantic States Marine Fisheries Commission Fishery Management Plan for Atlantic sturgeon (*Acipenser oxyrhynchus*), ASMFC, Washington, D.C.

Auer, N. A. 1999. Population characteristics and movements of lake sturgeon in the Sturgeon River and Lake Superior. Journal of Great Lakes Research 25(2):282–293.

Bain, M. B. 1997. Atlantic and shortnose sturgeons of the Hudson River: common and divergent life history attributes. Environmental Biology of Fishes 48:347–358.

Beamesderfer, R. C. P., and R. A. Farr. 1997. Alternatives for the protection and restoration of sturgeons and their habitat. Environmental Biology of Fishes 48:407–417.

Beamesderfer, R. C. P., and T. A. Rien. 1993. Dynamics and potential production of white sturgeon populations in three Columbia River Reservoirs. Pages 175–206 *in* R. C. Beamesderfer and A. A. Nigro, editors. Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, volume 1. Bonneville Power Administration, Portland, Oregon.

Beamesderfer, R. C. P., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the lower Columbia River. Transactions of the American Fisheries Society 124:857–872.

Bemis, W. E., E. K. Findeis, and L. Grande. 1997. An overview of Acipenseriformes. Environmental Biology of Fishes 48:25–71.

Bemis, W. E., and B. Kynard. 1997. Sturgeon rivers: an introduction to acipenseriform biogeography and life history. Environmental Biology of Fishes 48:167–183.

Birstein, V. J. 1993. Sturgeons and paddlefishes: threatened fishes in need of conservation. Conservation Biology 7(4):773–787.

Birstein, V. J., P. Doukakis, and R. DeSalle. 2000. Polyphyly of mtDNA lineages in the Russian sturgeon *Acipenser gueldenstaedtii*: forensic and evolutionary implications. Conservation Genetics 1:81–88.

Boreman, J. 1997. Sensitivity of North American sturgeons and paddlefish to fishing mortality. Environmental Biology of Fishes 48:399–405.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81(3):619–627.

Caswell, H. 2001. Matrix Population Models: construction, analysis, and interpretation, 2nd edition. Sinauer, Sunderland, Maryland.

Chapman, F. A., J. P. Van Eenennaam, and S. I. Doroshov. 1996. The reproductive condition of white sturgeon, *Acipenser transmontanus*, in San Francisco Bay, California. Fisheries Bulletin 94 (4):629–634.

Cochnauer, T. G. 2001. Response of catch and release regulations on a white sturgeon population—now what? Pages XXX–XXX *in* W. Van Winkle, editor. Biology, management, and protection of sturgeon. American Fisheries Society, Symposium XX, Bethesda, Maryland.

Collins, M. R., S. G. Rogers, and T. I. J. Smith. 1996. Bycatch of sturgeons along the southern Atlantic coast of the USA. North American Journal of Fisheries Management 16:24–29.

Conte, F. S., S. I. Doroshov, P. B. Lutes, and E. M. Strange. 1988. Hatchery manual for the white sturgeon *Acipenser transmontanus* Richardson with application to other North American Acipenseridae. University of California Publications, Oakland, California.

Dadswell, M. J. 1979. Biology and population characteristics of the shortnose sturgeon, *Acipenser brevirostrum* Le Seuer 1818 (Osteichthyes: Acipseridae), in the Saint John Estuary, New

Brunswick, Canada. Canadian Journal of Zoology 57:2186–2210.

Dadswell, M. J., B. D. Taubert, T. S. Squiers, D. Marchette, and J. Buckley. 1984. Synopsis of biological data on shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818. NOAA, Washington, D.C.

de Kroon, H., J. van Groenendael, and J. Ehrlen. 2000. Elasticities: a review of methods, and model limitations. Ecology 81(3):607–618.

de Meulenaer, T., and C. Raymakers. 2000. Report to animals committee on review of significant trade of Acipenseriformes. Submitted for Convention on International Trade in Endangered Species of Wild Fauna and Flora at 16th Meeting, Shepherdstown, West Virginia. TRAFFIC International.

DeVore, J. D., B. W. James, C. A. Tracy, D. A. Hale. 1995. Dynamics and potential production of white sturgeon in the Columbia River downstream from Bonneville Dam. Transactions of the American Fisheries Society 124:845–856.

Dixon, P., N. Friday, P. Ang, S. Heppell, and M. Kshatriya. 1997. Sensitivity analysis of structured-population models for management and conservation. Pages 471–513 *in* S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York.

Doroshov, S. I. 1985. Biology and culture of sturgeons, Acipenseriformes. Pages 252–274 *in* J. F. Muirs and R. J. Roberts, editors. Recent Advances in Aquaculture, volume 2. Westview Press, Boulder, Colorado.

Dovel, W. L., and T. J. Berggren. 1983. Atlantic sturgeon of the Hudson Estuary, New York. NY Fish and Game Journal 30:140–172.

Dovel, W. L., A. W. Pekovitch, and T. J. Berggren. 1992. Biology of the shortnose sturgeon (*Acipenser brevirostrum* LeSueur, 1818) in the Hudson River Estuary, New York. Pages 187–227 *in* C. L. Smith, editor. Estuarine research in the 1980s. State University of New York, Stony Brook.

Duke, S., and ten coauthors. 1999. Recovery plan for Kootenai River white sturgeon (*Acipenser transmontanus*). Pages 157–163 *in* Proceedings of the 3rd International Symposium on Sturgeon, Piacenza, Italy, July 8-11, 1997, Blackwell Scientific Publications Wissenschafts-Verlag, Berlin (FRG). Volume 15, No. 4-5, Journal of Applied Ichthyology/Zeitschrift fur angewandte Ichthyologie. Hamburg, Berlin.

Gilbert, C. R., and D. Moran. 1989. Atlantic and shortnose sturgeons. U.S. Army Corps of Engineers and U.S. Department of the Interior, Biological Report 82 (11.22), Washington, D.C.

Gisbert, E., and P. Williot. 1997. Larval behaviour and effect of the timing of initial feeding on growth and survival of Siberian sturgeon (*Acipenser baeri*) larvae under small scale hatchery production. Aquaculture 156:63–76.

Gross, M. R. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and aquaculture. Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl. 1):131–144.

Heppell, S., H. Caswell, and L. Crowder. 2000a. Life histories, and elasticity patterns; perturbations for species with minimal demographic data. Ecology 81(3):654–665.

Heppell, S. S., and L. B. Crowder. 1998. Prognostic evaluation of enhancement programs using population models and life history analysis. Bulletin of Marine Science 62(2):495–507.

Heppell, S., C. Pfister, and H. de Kroon. 2000b. Elasticity analysis in population biology: methods, and applications. Ecology 81(3):605–606.

Ireland, S. C., P. J. Anders, and J. T. Siple. 2001. Conservation aquaculture: an adaptive approach to prevent extinction of an endangered white sturgeon population (*Acipenser transmontanus*). Pages XXX–XXX *in* W. Van Winkle, editor. Biology, management, and protection of sturgeon. American Fisheries Society, Symposium XX, Bethesda, Maryland.

Johnson, J. H., D. S. Dropkin, B. E. Warkentine, J. W. Rachlin, and W. D. Andrews. 1997. Food habits of Atlantic sturgeon off the central New Jersey Coast. Transactions of the American Fisheries Society 126:166–170.

Kahnle, A. W., K. A. Hattala, K. A. McKown, C. A. Shirey, M. R. Collins, T. S. Squiers, Jr., D. H. Secor, J. A. Musick, and T. Savoy. 1998. Stock Status of Atlantic Sturgeon of Atlantic Coast Estuaries. Atlantic States Marine Fisheries Commission, Washington, D.C.

Kynard, B. 1997. Life history, latitudinal patterns, and status of the shortnose sturgeon, *Acipenser brevirostrum*. Environmental Biology of Fishes 48:319–334.

Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, D.C.

Magnin, E. 1964. Crossance en longueur de trois esturgeons d'Amerique du Nord: *Acipenser oxyrhynchus* Mitchill, *Acipenser fulvescens* Rafinesque, et *Acipenser brevirostris* Lesueur. Verhandlungen Internationale Vereinigung fur theoretische und angewandte Limnologie 15:968–974.

McCabe Jr., G. T., and C. A. Tracy. 1994. Spawning and early life history of white sturgeon, *Acipenser transmontanus*, in the lower Columbia River. Fisheries Bulletin 92(4):760–772.

NMFS (U.S. National Marine Fisheries Service). 1998a. Recovery plan for the shortnose sturgeon (*Acipenser brevirostrum*). Prepared by the Shortnose Recovery Team for the National Marine Fisheries Service, Silver Spring, Maryland.

NMFS. 1998b. Status review of Atlantic sturgeon (*Acipenser oxyrhynchus oxyrhynchus*). National Marine Fisheries Service, Gloucester, Massachusetts.

NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Nilo, P., P. Dumont, and R. Fortin. 1997. Climatic and hydrological determinants of year-class strength of St. Lawrence River lake sturgeon (*Acipenser fulvescens*). Canadian Journal of Fisheries and Aquatic Sciences 54:774–780.

Piper, R. G., and 5 coauthors. 1982. Fish hatchery management. U.S. Department of the Interior Fish and Wildlife Service, Washington, D.C.

Rien, T. A., and J. A. North. 2001. White sturgeon transplants in the Columbia River. Pages XXX–XXX *in* W. Van Winkle, editor. Biology, management, and protection of sturgeon. American Fisheries Society, Symposium XX, Bethesda, Maryland.

Roff, D. A. 1992. The evolution of life histories. Chapman and Hall, New York.

Sargent, R. C., and M. R. Gross. 1993. William's principle: an explanation of parental care in teleost fishes. Pages 333–362 *in* T. J. Pitcher, editor. Behaviour of teleost fishes, 2nd edition. Chapman and Hall, London.

Schramm Jr., H. L., and R. G. Piper, editors. 1995. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Symposium 15, Bethesda, Maryland.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, Ottawa.

Secor, D. H. 2000. Spawning in the nick of time? Effect of adult demographics on spawning behaviour, and recruitment in Chesapeake Bay striped bass. ICES Journal of Marine Science 57:403–411.

Secor, D. H., J. M. Dean, T. A. Curtis, and F. W. Sessions. 1992. Effect of female size and propagation methods on larval production at a South Carolina striped bass (*Morone saxatilis*) hatchery. Canadian Journal of Fisheries and Aquatic Sciences 49:1778–1787.

Secor, D. H., and T. E. Gunderson. 1998. Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic sturgeon, *Acipenser oxyrinchus*. Fisheries Bulletin 96:603–613.

Secor, D. H., and E. D. Houde. 1998. Use of larval stocking in restoration of Chesapeake Bay striped bass. ICES Journal of Marine Science 55:228–239.

Secor, D. H., and J. R. Waldman. 1999. Historical abundance of Delaware Bay Atlantic sturgeon and potential rate of recovery. Pages 203–216 *in* J. A. Musick, editor. Life in the slow lane: ecology and conservation of long-lived marine animals. American Fisheries Society, Symposium 23, Bethesda, Maryland.

Secor, D. H., V. Arevyev, A. Nikolaev, and A. Sharov. 2000a. Restoration of sturgeons: lessons from the Caspian Sea Sturgeon Ranching Program. Fish and Fisheries 1:215–230.

Secor, D. H., E. J. Niklitschek, J. S. Stevenson, S. Minkkinen, B. Florence, M. Mangold, A. Skjeveland, and A. Henderson-Arzapalo. 2000b. Dispersal and growth of yearling Atlantic sturgeon *Acipenser oxyrinchus* released into the Chesapeake Bay. Fisheries Bulletin 98:800–810.

Smith, T. I. J., and five coauthors. 1985. Spawning and culture of shortnose sturgeon, *Acipenser brevirostrum*. Journal of the World Mariculture Society 16:104–113.

Smith, T. I. J., L. D. Heward, W. E. Jenkins, and M. R. Collins. 1995. Culture and stock enhancement of shortnose sturgeon, *Acipenser brevirostrum*, in the southern United States. Pages 204–214 *in* A. D. Gershanovich and T. I.J. Smith, editors. Proceedings of the International Symposium on Sturgeons, 6-11 September 1993. VNIRO Publishing, Moscow.

Stevenson, J. T. 1997. Life history characteristics of Hudson River Atlantic sturgeon and an age-based model for management. Master's thesis. University of Maryland, College Park.

Stevenson, J. T., and D. H. Secor. 2000. Age determination, and growth of Hudson River Atlantic sturgeon (*Acipenser oxyrinchus*). Fisheries Bulletin 97:153–166.

Tracy, C. A., and M. F. Wall. 1993. Length at age relationships for white sturgeon in the Columbia River downstream from Bonneville Dam. Pages 185–200 *in* R. C. Beamesderfer and A. A. Nigro, editors. Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, volume 2. Bonneville Power Administration, Portland, Oregon.

Van Eenennaam, J. P., and S. I. Doroshov. 1998. Effects of age and body size on gonadal development of Atlantic sturgeon. Journal of Fish Biology 53:624–637.

Van Eenennaam, J. P., and five coauthors. 1996. Reproductive conditions of the Atlantic sturgeon (*Acipenser oxyrhynchus*) in the Hudson River. Estuaries 19(4):769–777.

Waldman, J. R., and D. H. Secor. 1998. Caviar trade in North America - an historical perspective. Pages 52–64 *in* D. Williamson, G. W. Benz, and C. M. Hoover, editors. Proceedings of the Symposium on the Harvest, Trade and Conservation of North American Paddlefish and Sturgeon. TRAFFIC North American/World Wildlife Fund, Washington, D.C.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196–2218.

Winemiller, K. O., and K. A. Rose. 1993. Why do most fish produce so many tiny offspring? American Naturalist 142:585–603.

Youngson, A. F., and E. Verspoor. 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl. 1):153–160.