RESEARCH PAPER

Population viability analysis of the Danube sturgeon populations in a Vortex simulation model

I. Jarić · T. Ebenhard · M. Lenhardt

Abstract Populations of six sturgeon species in the Danube River (beluga, Russian sturgeon, stellate sturgeon, sterlet, ship sturgeon and Atlantic sturgeon) have experienced severe decline during the last several decades, mostly due to the unsustainable fishery, river fragmentation and water pollution. Present lack of knowledge on basic sturgeon demography, life history and relative effects of different negative factors is further hindering implementation of efficient policy and management measures. In the present study, population viability analysis in a Vortex simulation model has been conducted in order to assess the state of the six Danube sturgeon species, their future risk of extinction and to determine the most suitable conservation and management measures. Population viability analysis has revealed a large sensitivity of the Danube sturgeon populations to changes in the natural mortality, fecundity, age at maturity and spawning frequency. It was also confirmed that the sturgeons are highly susceptible to even moderate levels of commercial fishery, and that their recovery is a multi-decadal affair. Stocking with adult individuals was shown to produce considerably greater effect on population persistence than stocking with juveniles, but the latter approach is probably still preferable since it avoids many inherent problems of aquaculture cultivation. This study represents the first population viability analysis of the Danube sturgeons.

Keywords Acipenser · Huso · PVA · Extinction risk · Life history · Modelling

I. Jarić (✉)
Institute for Multidisciplinary Research, Kneza Viseslava 1, 11000 Belgrade, Serbia
e-mail: ijaric@imsi.rs

T. Ebenhard
Swedish Biodiversity Centre (CBM), Swedish University of Agricultural Sciences, Box 7007, 750 07 Uppsala, Sweden

M. Lenhardt
Institute for Biological Research, Despota Stefana 142, 11000 Belgrade, Serbia

Introduction

Sturgeons (family Acipenseridae) are a group of 27 extant species that inhabit the northern hemisphere. They represent an old group of fish that has evolved for more than 250 million years, and that has successfully survived several mass extinction events throughout the history (Nikcevic et al. 2004). However, sturgeons have experienced the same fate as the majority of other economically important fish worldwide that are being either fully exploited,

overharvested or completely depleted (Birstein et al. 1997; Botsford et al. 1997). It is generally considered that the same life history strategy, involving long lifespan, delayed maturation, large size and anadromy, which has made them resilient to global environmental changes in the past (Bemis et al. 1997), is at the same time making them highly susceptible to extinction under anthropogenic impacts (Jager 2001).

The Danube River basin and the Black Sea are considered as the key habitat of European sturgeons (Williot et al. 2002). However, due to a whole spectre of anthropogenic impacts, such as over exploitation, habitat fragmentation and pollution, all six sturgeon species that have originally inhabited this region have experienced severe decline (Lenhardt et al. 2006a). Atlantic sturgeon (*Acipenser sturio*) is nowadays considered as extinct in the Danube, while the ship sturgeon (*Acipenser nudiventris*) might be on the verge of extinction (Jarić et al. 2009a). Populations of beluga (*Huso huso*), Russian sturgeon (*Acipenser gueldenstaedtii*), stellate sturgeon (*Acipenser stellatus*) and sterlet (*Acipenser ruthenus*) are considered as endangered and facing different levels of extinction risk (Reinartz 2002; Williot et al. 2002; Lenhardt et al. 2006b).

Assessments of the state of Danube sturgeon populations that have been the object of the commercial fishery (beluga, Russian sturgeon, stellate sturgeon and sterlet) have so far mostly relied on the assessment of catch statistics (Lenhardt et al. 2006b), which can be significantly biased by social and economic dynamics, and which does not consider illegal fishery that at certain points represented up to a 90% of the actual total catch in the Danube in the past (Bacalbasa-Dobrovici and Patriche 1999; Navodaru et al. 1999). The development of population models that are able to assess its viability and the extinction risks could be that tool that would bridge existing gaps in knowledge and understanding of sturgeon ecology and life history. Population viability analysis (PVA) is the method that has become the mainstream and indispensable tool in conservation biology during the last two decades (Boyce 1992), especially since it explicitly deals with uncertainties in ecological data and processes (Akçakaya and Sjögren-Gulve 2000). This approach has, however, not been applied to sturgeons in the Danube River basin.

The main objective of this study was to use Vortex simulation model to conduct population viability analysis of all six Danube sturgeon species, in order to assess the state of their populations in the Danube River, their future risk of extinction and existing measures for protection and sustainable use of their populations.

Materials and methods

This section contains only brief overview of the model development. Full description of the model parameterization is presented in the Appendix in Electronic Supplementary Material.

Population viability analysis of the six Danube sturgeon species was performed in Vortex software package (version 9.72). Vortex is a PVA computer model that makes an individual-based Monte Carlo simulation of a population, through the action of deterministic factors and environmental, demographic, and genetic stochasticity (Lacy 1993). For a more detailed description of Vortex, see Lacy (1993, 2000) and Miller and Lacy (2005).

In order to define population parameter values for each of the six Danube sturgeon species, a literature survey was conducted, and data sheets were made for each Danube sturgeon species, with the values for each of the basic parameters that are necessary for scenario building in Vortex (Chap. 3 in the Appendix).

In general, for parameters that were provided by different authors as ranges or that were inconsistent in provided values, a most probable mean value was determined, and ranges were included in the model as environmental variation through establishing a standard deviation for the mean value. If ranges provided by different authors were inconsistent, values that were given in the majority of the publications were applied, and the other values were included in the sensitivity analysis (for details see the Appendix).

The available data on deterministic growth rate (the r value) for sturgeon populations is poor, especially for the populations in the Danube River. Based on the limited information that is available, we have applied three different population growth rates for each species: 0.05, 0.10 and 0.15. In order to acquire such growth rates, age specific natural mortality was fitted so that each of these r values

was met in different scenarios (see Chap. 3 in the Appendix for the natural mortality rates). All scenarios and simulations were tested against each of the three defined population growth rates. As was proposed by a number of authors (Beissinger and Westphal 1998; Akçakaya 2000), pseudo-extinction criterion was applied in this study, instead of scoring the risk of reaching absolute extinction.

The age 0–1 natural mortality was incorporated in the model through the proportional reduction of number of offspring produced, so young-of-the-year that have not survived up to the age 1 were not considered in the simulation. Therefore, it is important to note that in the future text, population size (N) does not include embryos and young-of-the-year that will not survive up to the age 1. For example, the population size of 2,000 individuals applied in some scenarios represents a much larger actual population, since the number of offspring that will succumb to natural mortality during the first year of life can be up to few thousand times larger.

In order to test the dependence of the model behaviour on changes in each of the life history parameters, as well as to span the ranges of life history parameter values provided by different authors, a sensitivity analysis was conducted. In order to test the effect of change in any single parameter, only one parameter was being changed at a time. The age distribution of the initial population was kept constant in all scenarios that were compared, to avoid the effect of change in age distribution when life history parameters are being modified. The tested change in each parameter was either reflecting the ranges provided for that parameter by different authors, or some general amount of change was applied (e.g. ±50%). Ranges of values applied for each life history parameter are presented in the Chap. 4 of the Appendix. Output variables that were tracked during the sensitivity analysis simulations were the pseudo-extinction probability, deterministic and stochastic population growth rates, expected heterozygosity, and the mean time needed for population to reach half of the carrying capacity. Results of the sensitivity analysis were assessed through the use of two distinct approaches, a ranking technique and regression analysis.

Relationships between the deterministic population growth rate and the both probability of pseudo-extinction and the expected heterozygosity were assessed for each studied species with Spearman's non-parametric correlation test, in order to determine the potential of the deterministic growth rate as a general predictor of the overall population viability.

The basic questions that were addressed in harvest scenarios were the determination of the threshold level of the harvest pressure below which population viability would still be preserved, as well as to compare the vulnerability of different sturgeon species to harvest. The harvest was introduced in the model as the percentage of adults taken every year. Special scenarios were developed where the two oldest age groups of subadults were also harvested, with the same harvest pressure applied as for the adults.

Additional scenarios were developed to test effectiveness of supportive stocking, since this approach has been widely applied in the Danube River basin (Reinartz 2002; Williot et al. 2002; Vassilev 2006). The main goal was to test different approaches in supportive stocking, and their influence on the population viability. In general, stocking dynamics (e.g. time of the release, number of releases) varied between different scenarios along three main dimensions: total number of individuals that were released, age of released individuals (whether they were juveniles or adults), and the temporal scale of stocking (whether the same number of individuals was released in a single year, or during several years).

As proposed by a number of different authors (Ebenhard 2000; Beissinger 2002; Hanski 2002; Reed et al. 2002), results of all scenarios were used more to compare their relative effects, for instance to compare different management scenarios, than to use them as the absolute predictions. An extinction risk of $P < 0.05$ is commonly applied as the threshold to evaluate viability (Beissinger and Westphal 1998), so it was used in this study as well.

Results

Basic scenarios with the same total population size applied to all species have shown, as was expected, a high sensitivity of the model to the population size. In general, populations had a significant probability ($P > 0.05$) of going extinct at the population size of 50 individuals, and the probability was close to, or even at the absolute value ($P = 1.00$) for almost all

species, and across all of the three assessed population growth rates. In general, it was only at the population sizes above 1,000 individuals that long term viability became more likely. However, comparisons among the six studied species have shown that they substantially differed in the population viability and the other output model variables. There was an apparent pattern that the species which had the lowest proportion of the adults in a population, such as the ship sturgeon and the Atlantic sturgeon (see Chap. 2 in the Appendix), were also much more vulnerable than the other species at the same population size. An exception to this rule was the sterlet, which at the same time belonged to the more vulnerable species and to those with the highest proportion of adults in a population.

In order to check the effect of the absolute number of adults in a population on the risk of extinction, basic scenarios of each species were compared again, but this time with the same number of adult females kept in each population. In such setup of the basic scenario models, the Atlantic sturgeon and the ship sturgeon have produced results more similar to the other species, than it was in the model setup with the same total number of individuals. In general, there was a greater similarity among species, in both simulation results and their vulnerability. These results are indicating the importance of the adult individuals in the population, and the lesser usefulness of the total population size as the predictor of the population viability. However, the sterlet has remained vulnerable in such model setup as well, which might be explained by the ecology of this species, which is very different from all other Danube sturgeons (e.g. lower offspring number, frequent spawning, and short time to maturity).

Both methods that have been applied to the assessment of the results of the sensitivity analysis, the regression analysis and the ranking technique, had a high concordance in their results. Results of both approaches are presented in Chap. 5 of the Appendix. According to the results of the sensitivity analysis, the most influential life history parameters on the overall model behaviour were the age at which females reach the maturity, mean number of offspring, natural mortality of the 0–1 and 1–4 age groups, sex ratio, spawning frequency of females and the natural mortality of adults. The influence of the age at which females reach maturity on population

persistence was higher for early maturing species than for those with delayed maturation (i.e. this parameter was the most influential for sterlet and the least influential for beluga).

Maximum age of reproduction and the maximum number of offspring had a low or no influence at all on the model behaviour, probably because the values that have been applied to these parameters were too high to interfere with, respectively, the longevity defined by the distribution of the age specific natural mortality and the variation in the average number of offspring. Even a substantial decrease in the maximum reproductive age was able to produce only a moderate impact on the population viability. Male-related traits, such as the age at which males reach maturity or the spawning frequency of males, had also a weak effect on the population viability.

Environmental variation in life history traits had only moderate to low influence on model behaviour, and the environmental variation in natural mortality was the only one that had somewhat larger influence on the model. Carrying capacity and its environmental variation had significant influence on the population viability, and the impact of the environmental variation in carrying capacity was especially pronounced at the higher population growth rates (0.10 and 0.15).

Both population growth rates (deterministic and stochastic) that were assessed as model output variables were generally influenced by the same model parameters as the probability of pseudo-extinction. Since the male-related traits and environmental variation-related parameters are not included in the estimation of the deterministic population growth rate, these parameters had no influence on this output variable. The same ratio of change in the mean number of offspring, natural mortality of the 0–1 age group and in the sex ratio produced the same amount of change in the deterministic population growth rate, but the influence of the sex ratio on the stochastic population growth rate was always slightly weaker than the influence of the other two parameters.

The relationships between the deterministic population growth rate and the probability of pseudo-extinction for each of the studied species are presented in Fig. 1, and the relationships between the deterministic population growth rate and the expected heterozygosity in Fig. 2. As can be seen in both figures, the r value had a high degree of
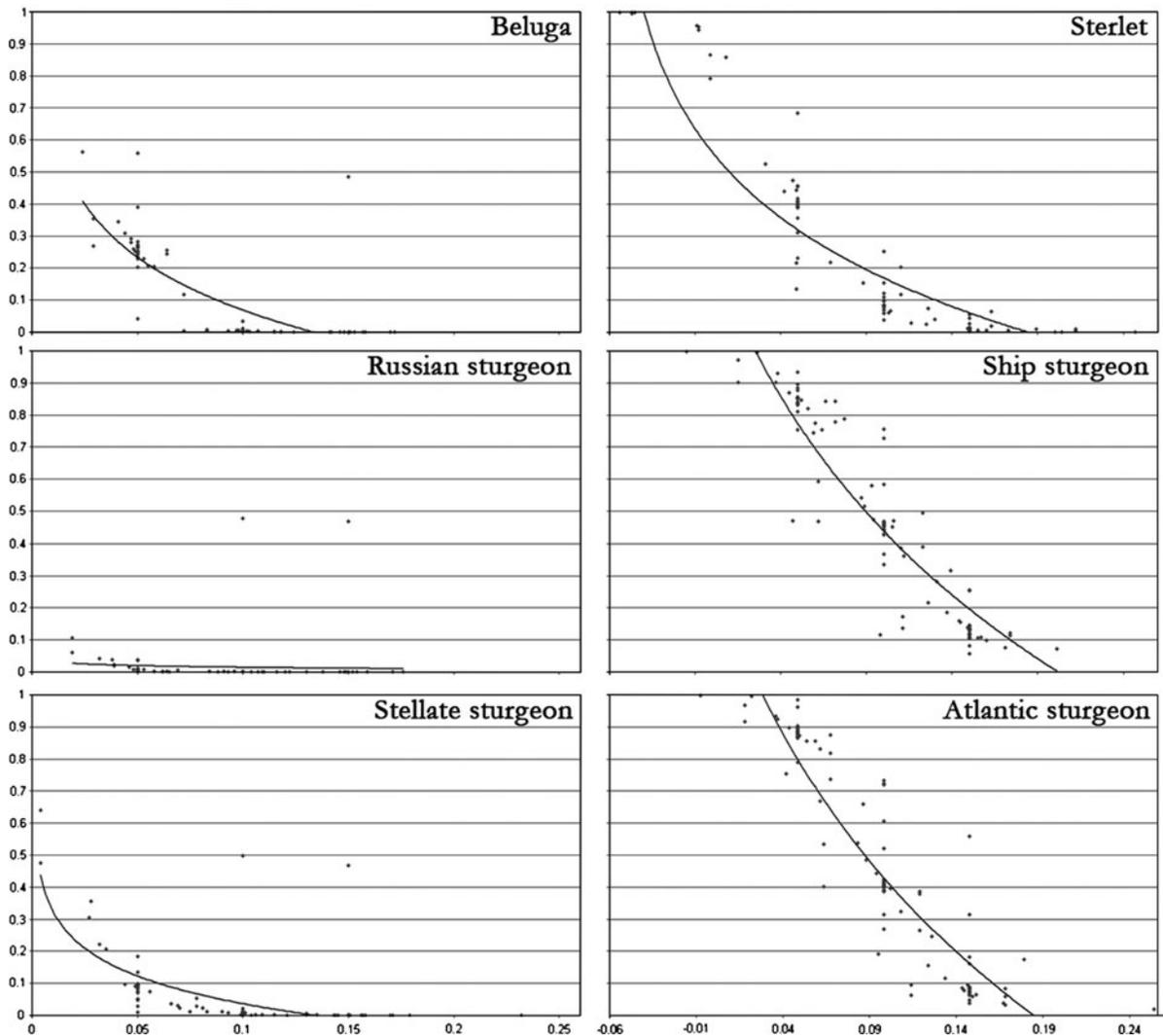
Fig. 1 Relationship between the deterministic population growth rate (*X* axis) and the probability of pseudo-extinction (*Y* axis) in the sensitivity analysis performed on the six Danube sturgeon species. Initial population size in all scenarios was set to 50 and the carrying capacity to 2,000 individuals

correlation with the probability of pseudo-extinction and the expected heterozygosity, but the exact relationship differed among species. Spearman's non-parametric correlation test confirmed high correlation between the *r* value and the both pseudo-extinction probability and expected heterozygosity (Table 1).

It is important to emphasize that many figures that will be presented contain only the average values among all iterations that have survived (1,000 iterations were applied in all simulations), while the individual iterations were always experiencing large

variations in population size and were never able to reach such stable behaviour as the average values (e.g. as it is presented in the Fig. 5). Results shown as average values of all simulated iterations are always associated with a large stochasticity expressed in each of the single iterations. Figure 3 shows two simulations with identical input data except in the environmental variation included in the model. As can be seen in the figure, the actual development of population dynamics can follow many different patterns, but variations are proportional to the total amount of stochasticity included in the model.
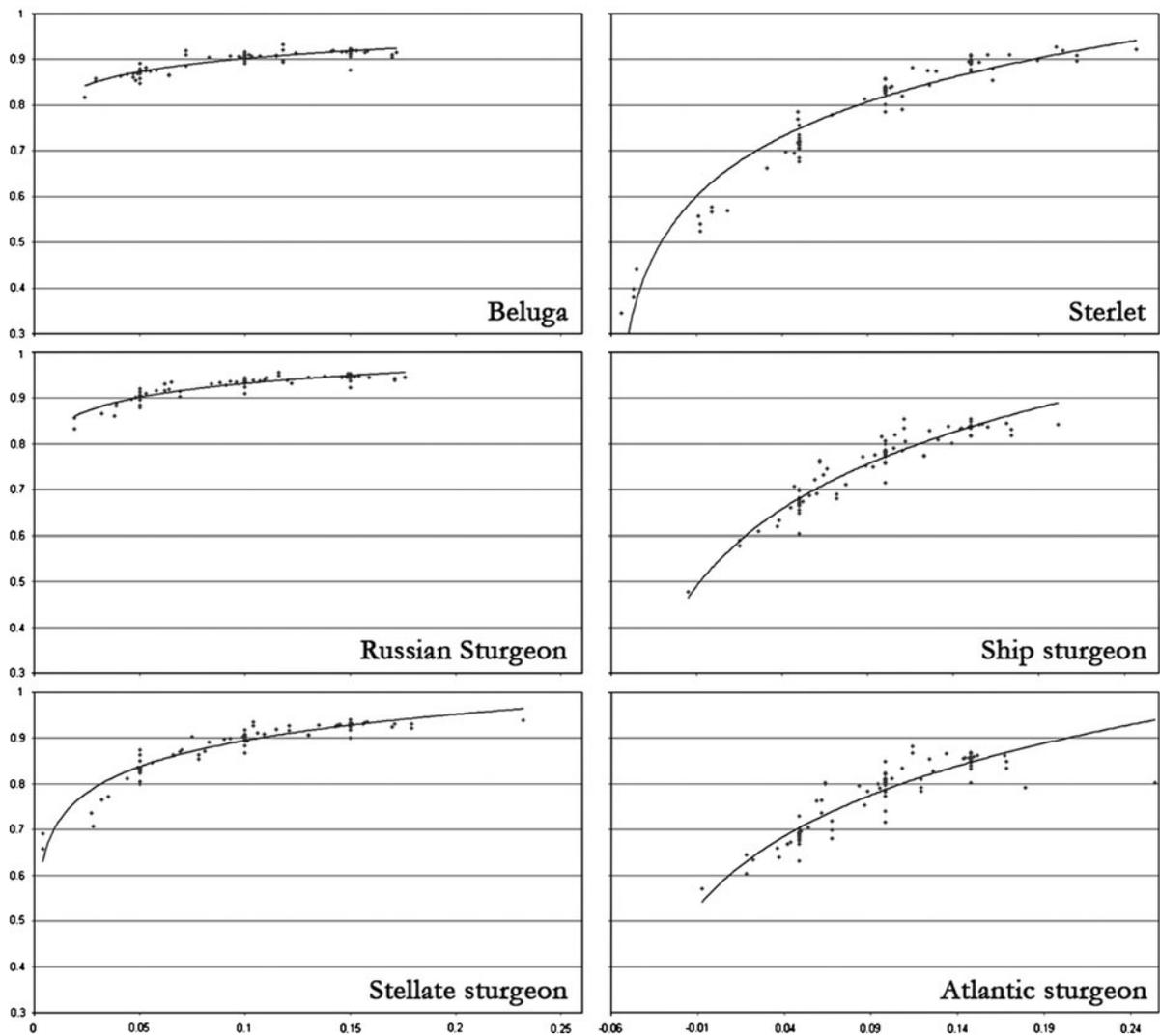
Fig. 2 Relationship between the deterministic population growth rate (X axis) and the expected heterozygosity (Y axis) in the sensitivity analysis performed on the six Danube sturgeon species. Initial population size in all scenarios was set to 50 and the carrying capacity to 2,000 individuals

Average values can present only the most probable general direction of change, and the actual result in a particular case may diverge from this central value.

Harvest scenarios showed high sensitivity of Danube sturgeon species to fishing pressure. Maximum harvest levels at which population remained viable were dependent on the population growth rate, and higher growth rates allowed higher harvest to be performed without causing the drop in population viability. Maximum harvest levels with preserved viability for each species and each population growth rate are presented in the Fig. 4.

At the harvest levels above those presented in the Fig. 4, populations were experiencing significant decline in population size (Fig. 5), and the extinction risk increased dramatically. A series of scenarios with different initial population sizes and carrying capacity levels was conducted, to check the effect of the carrying capacity and population size on these established thresholds of the maximum sustainable harvest levels. The results revealed that the maximum sustainable harvest level was not sensitive to the carrying capacity or the initial population size, probably since it was expressed in the percent of

Table 1 Correlations between the deterministic growth rate, pseudo-extinction probability and heterozygosity level in the sensitivity analysis of six studied sturgeon species (Spearman's non-parametric correlation test)

	r/P		*r/H*	
	Correlation coefficient	Significance	Correlation coefficient	Significance
Beluga	−0.888	0.000	0.844	0.000
Russian sturgeon	−0.760	0.000	0.893	0.000
Stellate sturgeon	−0.891	0.000	0.937	0.000
Sterlet	−0.949	0.000	0.952	0.000
Ship sturgeon	−0.939	0.000	0.940	0.000
Atlantic sturgeon	−0.936	0.000	0.881	0.000

r/P correlation between population growth rate and the pseudo-extinction probability, *r/H* correlation between population growth rate and the level of expected heterozygosity

the adult population that is being taken, so the harvest pressure was always relative to the population size. At the unsustainable levels of harvest, population size was always reduced to half of its initial size in no more than 50 years of the simulation, whatever the size of the initial population. Populations always declined to a low population size, where the harvest pressure also became low (since it is set to be relative to the population size), and then remained at those low population numbers, but with a high risk of extinction (i.e. with a high number of iterations going extinct).

In some cases, the maximum harvest pressure at which population viability was still preserved was not the level that was at the same time ensuring the maximum total number of harvested individuals. In such cases, depending on the species, the maximum total number of harvested individuals was reached at the harvest level that was either 5% units above or below the maximum viable harvest level. In other words, the maximum amount of harvested adults was reached for some species at the harvest pressure that was already above the acceptable risk of extinction ($P > 0.05$, ship sturgeon at population growth rates $r = 0.05$ and 0.10, sterlet at $r = 0.05$ and 0.10, and Atlantic sturgeon at $r = 0.05$), while for some species this occurred at the harvest pressure that was below the maximum viable one (Russian and stellate sturgeon at $r = 0.10$). Furthermore, in some cases the harvest level where the maximum number of harvested individuals was reached was not the same for both males and females, and in such cases the maximum number of males was harvested at 5% lower harvest pressure than for the females.

When the harvest of subadults was added to the harvest of adults, maximum viable harvest levels were dramatically reduced (Fig. 6). Even though the subadults comprised less than 50% of the number of adults in a population, the viability of populations when both subadults and adults were harvested was reduced twofold, so the effect of inclusion of subadults in the harvested part of the population on the sustainability of harvesting was manifested as more than simply additive.

In stocking scenarios, the largest differences were found between scenarios with releases of juvenile and adult individuals. In general, even the release of a small number of adults (in most cases even ten individuals) was sufficient to move the population out of the high risk of extinction. On the contrary, a high number of juveniles (even above 1,000) was often necessary to ensure population survival. Effects of these two stocking strategies seem to be inversely related. For example, the highest positive effect of stocking with juveniles was manifested in the sterlet population, while the same species also had the weakest effect of the stocking with adults. The cause probably lies in the life history of each species, mainly in relative juvenile and adult mortality, but also in the age at which females reach their maturity. The sterlet has higher adult mortality than the other sturgeon species, which probably reduces the positive effects of the stocking with adults. On the other hand, a short time to maturity enables the larger portion of stocked sterlet juveniles to survive to maturity and consequently increase the population size through reproduction. Due to the same reason, stocking with juveniles had smaller effect in species that need
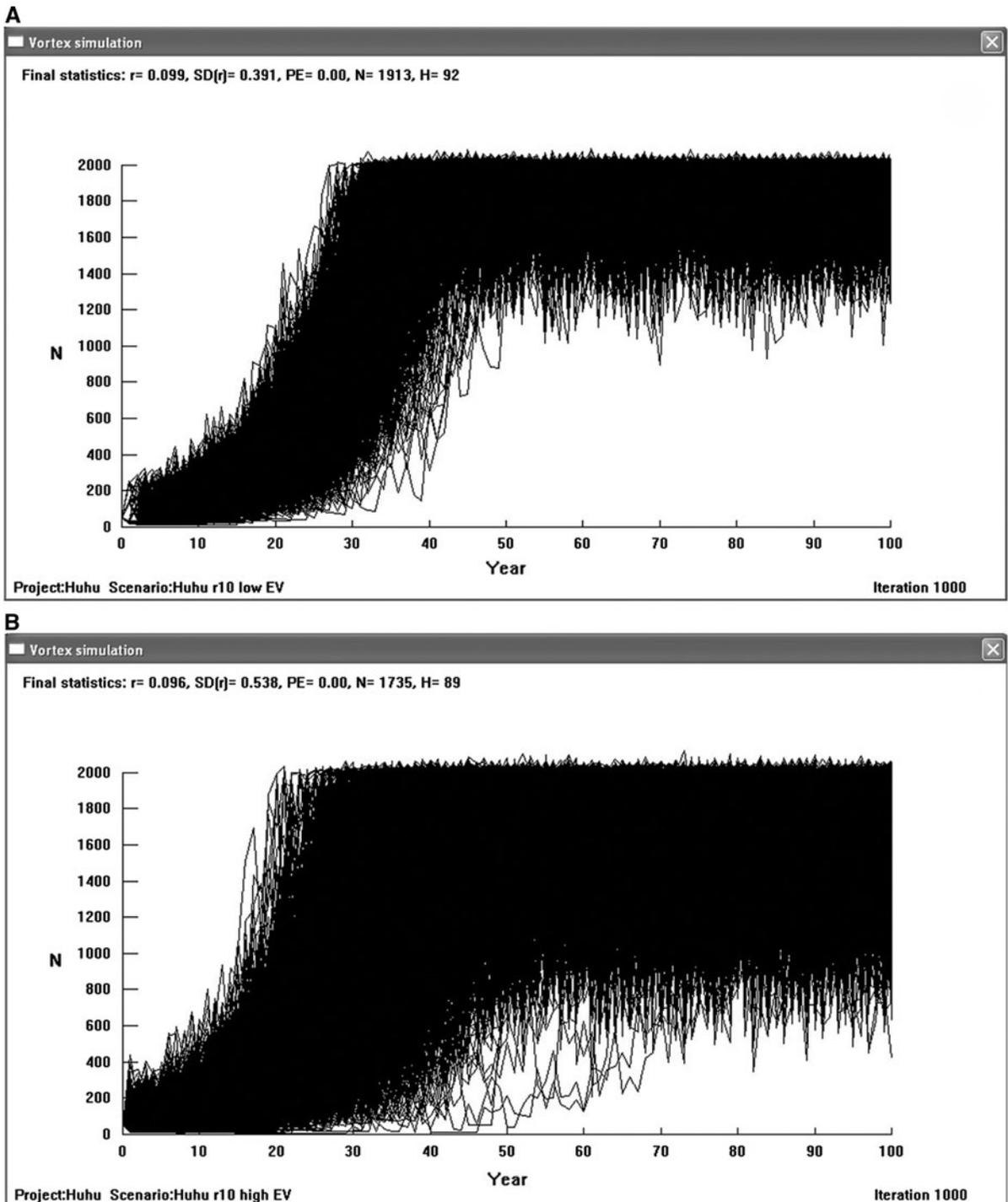
A

B

Fig. 3 Two scenarios with identical input data, except the larger amount of environmental variation that was applied in the scenario B. Images represent simulation screens from the Vortex program, with 1,000 iterations simulated in each scenario and population growth rate $r = 0.10$. **a** All environmental variation in the model (female spawning frequency, mean fecundity and natural mortality) reduced to zero; **b** environmental variation in all three variables increased by 50% over those applied in basic scenarios
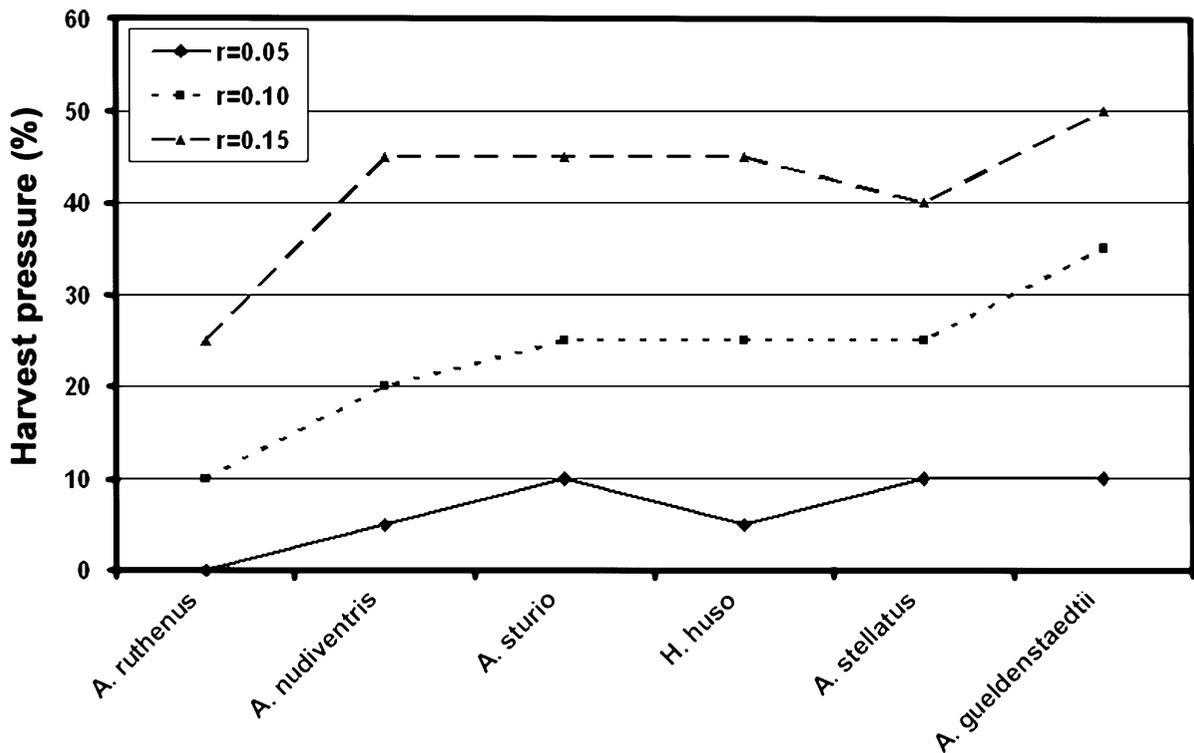
Fig. 4 Maximum harvest pressures at which the populations of six studied Danube sturgeon species remained viable (pseudo-extinction probability $P < 0.05$), given three different population growth rates ($r = 0.05$, 0.10 and 0.15)

longer time to mature, since the juveniles of those species have thus less chance to survive to maturity. Examples of the effect of the stocking with the adults and juveniles are, respectively, presented in Fig. 7.

As can be seen in the Fig. 7, stocking with juveniles always produces a lag in the increase of population, when compared with the immediate effect of stocking with adult individuals. The initial population increase, caused by the release of individuals in the population, is quickly followed by a significant decline, due to the high mortality of juveniles, and the actual population recovery occurs only after a lag of a certain number of years, that is equal to the time needed for females to reach maturity.

Observed differences between scenarios with different temporal dynamics of releases were smaller than expected (Fig. 8). In general, a release of all individuals in the first year of the simulation produced a shorter time for the population to recover, in comparison to scenarios where the same total number of individuals was released during a number of years. On the other hand, multiple release events reduced the risk of extinction, in comparison to single release scenarios. However, both outcomes should probably be expected, since the earlier release of an individual means that it will have more time to reproduce and thus help the population recovery, while the annual release of individuals during the period of 10 years would mean that the population cannot go extinct during that period, since new individuals are arriving in the population every year.

Discussion

The population viability analysis that was performed in the present study has shown in practice that the individual-based models, such as the Vortex simulation program, can be applied to species with life histories similar to those of the six studied Danube sturgeon species. It is important to emphasize that Vortex is a computer package developed primarily for the simulation of small populations of mammals,
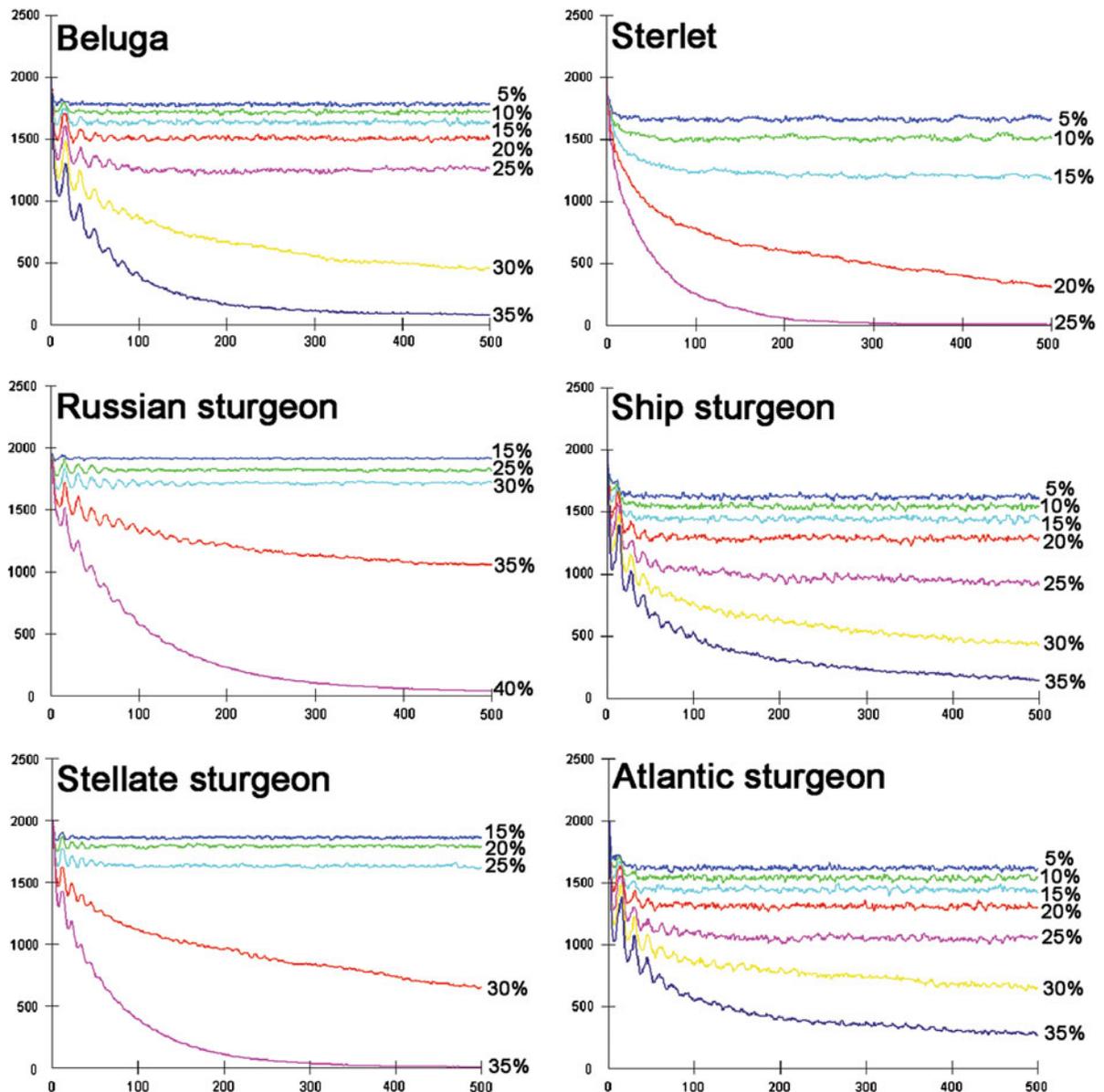
Fig. 5 Result of different harvest pressures applied on the six studied Danube sturgeon species (population growth rate $r = 0.10$). Y axis—average population size among all iterations in a simulation; X axis—years of the simulation; percentage values represent different harvest pressures. Initial population size and carrying capacity in all scenarios were set to 2,000 individuals

reptiles and birds (Miller and Lacy 2005), and that fish species have been so far rarely modelled in this program. Species with large populations and a life history similar to those of sturgeons (e.g. large fecundity) are not ideal objects of IBMs, since it is demanding for a computer to simulate such a large number of individuals. The limitations of the model do not allow simulation of the actual population sizes of sturgeons (measured in hundreds of thousands of individuals), so only theoretical populations could be simulated (e.g. 2,000 individuals).

On the other hand, there are also several advantages in using a model such as Vortex for the species in question. Some aspects of population dynamics,
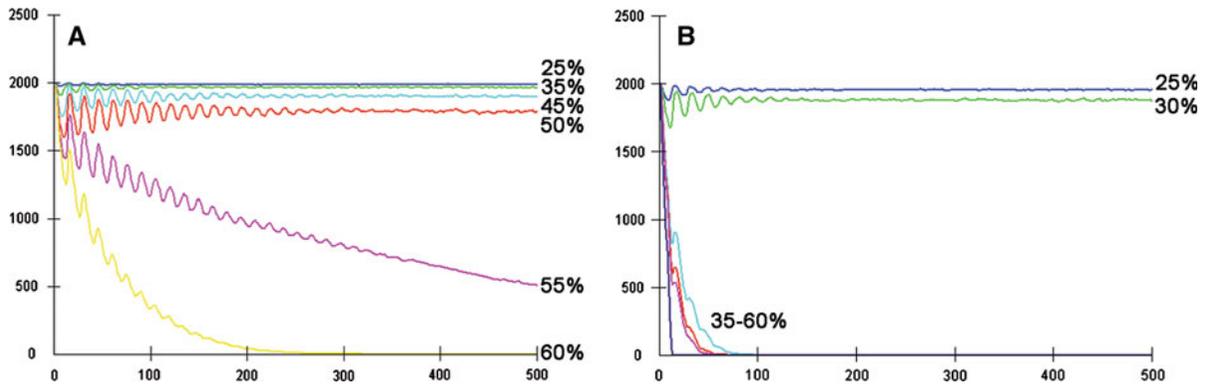
Fig. 6 Result of different harvest pressures applied on the Russian sturgeon (population growth rate $r = 0.15$). **a** Harvest of adults only; **b** harvest of both adults and the two oldest subadult age groups; Y axis—average population size among all iterations in a simulation; X axis—years of the simulation; percentage values represent different harvest pressures. Initial population size and carrying capacity in all scenarios were set to 2,000 individuals

such as stochasticity, and the inclusion of genetic considerations have rarely been addressed in PVAs of sturgeon species so far, and Vortex represents a tool with the ability to deal with these issues and thus provide new insights in sturgeon ecology. Furthermore, while the real population sizes could not be included in the model, absolute prediction was never a goal of this study, so the model was still expected to be capable to provide meaningful comparisons of relative differences among scenarios. The only situation where this study could provide certain power in the absolute projections is the case if sturgeons would drop to such small population sizes, in other words when the simulated population size would reflect the actual one, which may be the case for the Atlantic and ship sturgeon. Finally, this study could be a valuable case study for improvement of our knowledge and understanding of Vortex as a PVA model, since this is probably one of the rare cases when this widely used model has been applied to species with such a specific ecology and life history.

Most sturgeon PVAs have been based on age-structured models, and except for few examples of IBM applications (Jager et al. 2000, 2001; Jager 2001, 2005, 2006a, b), sturgeon PVAs have mostly lacked considerations of demographic and environmental stochasticity and genetics (Jarić et al. 2009b). The majority of models applied to sturgeons so far have been developed specifically for the purpose, and the software packages for IBMs, such as Vortex, have not been used previous to this study.

This study has revealed considerable sensitivity of sturgeon populations to changes in a number of life history parameters. Population viability was most strongly influenced by changes in the age at which females reach maturity, in the mean fecundity, egg to age 1 natural mortality and juvenile mortality (age groups 1–4), as well as by sex ratio, spawning frequency and adult mortality. These results are in accordance with PVAs performed on North American sturgeon species (Pine et al. 2001; Beamesderfer et al. 2007; Kennedy and Sutton 2007), that have found that the most influential parameters were egg mortality, age at maturity of females, spawning frequency and the overall natural mortality. Kennedy and Sutton (2007) estimated that the egg mortality was the single most influential population parameter, and an increase of 0.0001% units in mortality rate (from 0.9998 as the average value) caused as much as a 95% decline in population abundance and biomass. Bajer and Wildhaber (2007) have found that the egg, juvenile and young adult mortality were the most influential parameters on the population growth rate, while the fecundity was a less sensitive parameter. This differs from the findings in the present study, where the fecundity had the same effect on population persistence as the egg to age 1 mortality and belonged to the most sensitive parameters. However, it is important to note that these two life history parameters have been combined in this study (see Chap. 2 in the Appendix), so it was not really possible to make distinction between their effects.

It was determined in both the present study and by Kennedy and Sutton (2007) that the mortality of eggs and the youngest age classes were much more influential than the mortality of adult individuals.
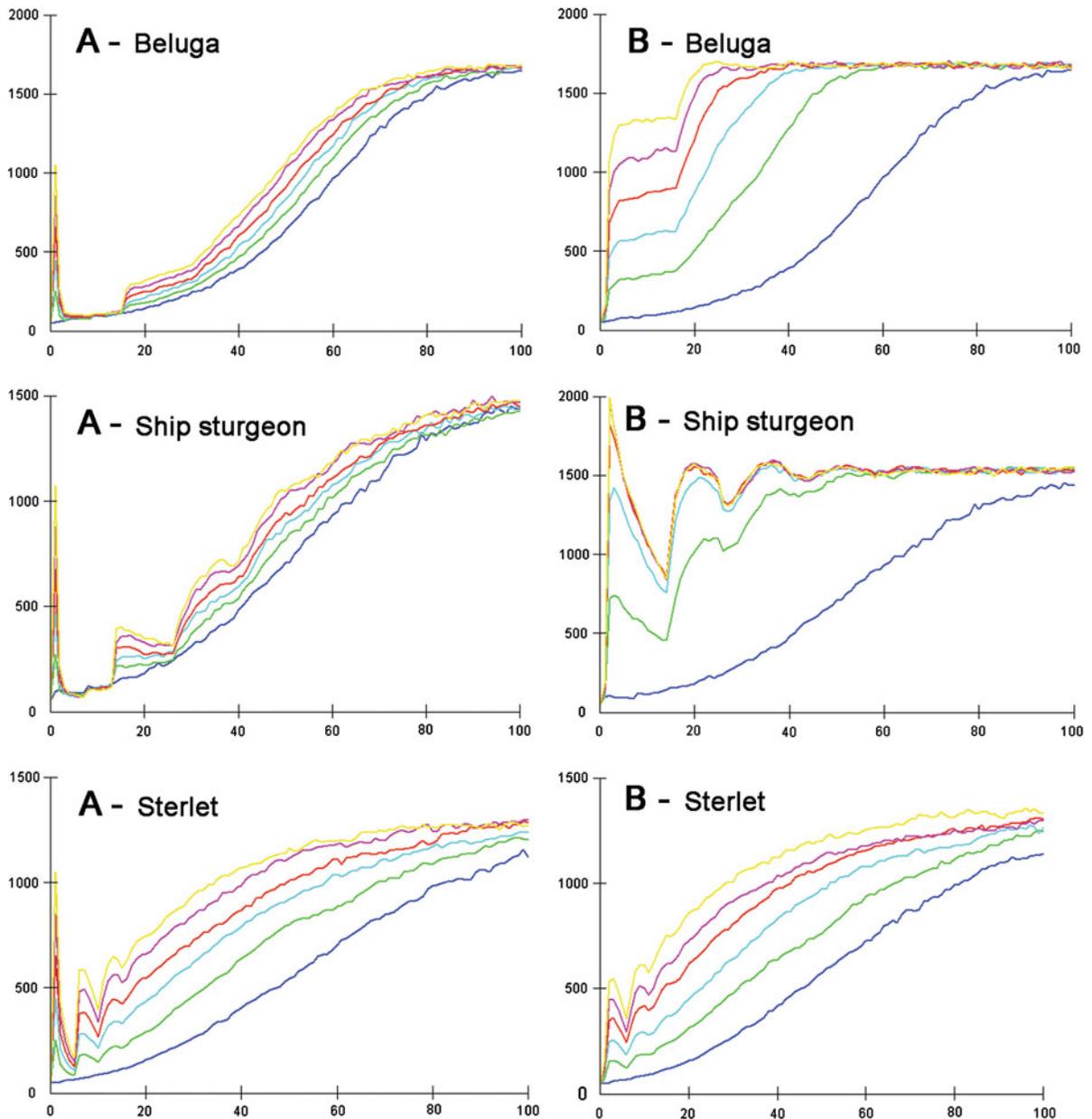
Fig. 7 Recovery of a small population of beluga, ship sturgeon and sterlet with different number of juvenile (**a**) or adult (**b**) individuals released in the first year of the simulation (population growth rate $r = 0.05$). From the lowest to the highest one, respectively, full lines in each graph represent: **a** the basic scenario and the release of 200, 400, 600, 800 and 1,000 juvenile individuals; **b** the basic scenario and the release of 20, 40, 60, 80 and 100 adult individuals; *Y* axis—average population size among iterations with surviving populations in a simulation; *X* axis—years of the simulation. Initial population size in all scenarios was set to 50 and the carrying capacity to 2,000 individuals

On the other hand, Pine et al. (2001) have established that the population of *A. oxyrinchus desotoi* was sensitive to even small changes in the adult mortality, and Boreman (1997) and Heppell (2007) have claimed that a small reduction in mortality of the adults could balance a relatively large increase in egg to age 1 mortality. Boreman (1997) supported this claim with the explanation that the fish are exposed to
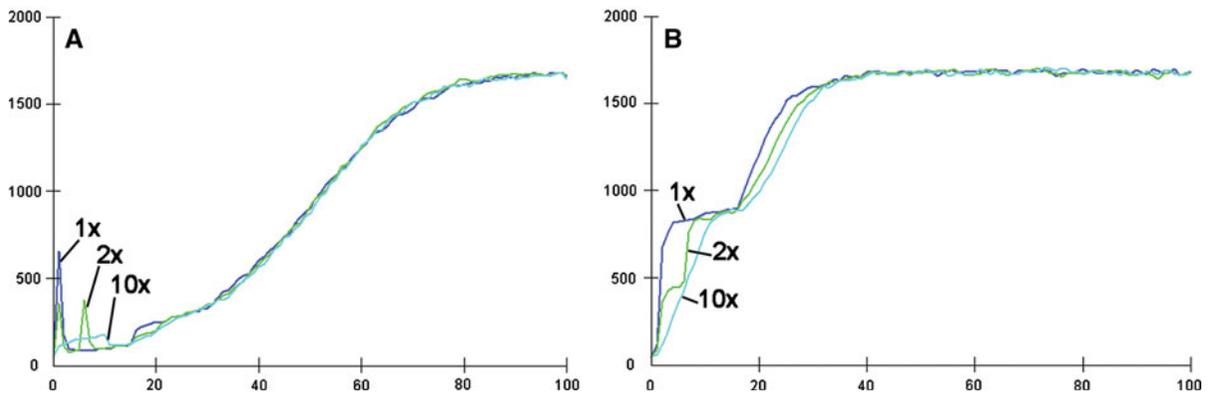
Fig. 8 Recovery of a small population of beluga, with the same number of juvenile (a) or adult (b) individuals released in three different patterns (population growth rate $r = 0.05$). 1×—All individuals released at once in the first year of the simulation, 2×—equal portions of individuals released two times, in the first and sixth year of the simulation, 10×—equal portions of individuals released each year during the initial 10 years of the simulation; Y axis—average population size among iterations with surviving populations in a simulation; X axis—years of the simulation. Initial population size in all scenarios was set to 50 and the carrying capacity to 2,000 individuals

a high mortality rate of age 0–1 during only 1 year of their life, while the mortality in adults encompasses many age groups. While we recognize the importance of the adult mortality on population viability, we have to disagree with such an explanation. High influence of the egg to age 1 mortality on the population persistence is caused by the fact that this age group comprises the major part of the population, so any change in their mortality will have an impact on a large number of individuals. The adult mortality indeed extends its impact on many age groups, but there are few individuals, so the total number of fish that are impacted by adult mortality will not be so large. In sturgeon populations, adults comprise only a small part of the total population. Beamesderfer et al. (2007) have estimated that the adults of A. medirostris have represented only 12% of the total population at equilibrium. In the present study, the proportion of adults in populations of different sturgeon species at stable age distribution varied between 2.7 and 15.1%, with the average value between 7.5 and 8.7%, depending on the population growth rate.

However, the importance of adults in a population has been confirmed in this study as well. It was indicated by the behaviour of scenarios where the six studied species were first compared at the same total population size and then at the same number of adults, with the latter approach leading to a greater similarity between species in result parameters. Since there are so few adults in a population, each adult

individual is important to the population persistence. Importance of adult individuals is further pronounced by their high survival rate, which enables them to reach older age and have multiple spawning events. It is generally considered that populations of long-lived organisms are sensitive to adult survivorship (Boyce 1992; Beissinger 2002). According to Colombo et al. (2007), harvested populations are likely to collapse due to the removal of reproductively viable adults, and age-specific maternal effects on offspring survival may emphasize the importance of maintaining large, old females in the population (Heppell 2007). However, the influence of adult mortality in the present study was found to be inversely related to the age at which individuals reach maturity, and not strongly related to the longevity of the species. In other words, species that matured early, such as the sterlet and stellate sturgeon, were more influenced by the adult mortality than those species that mature late, such as the beluga, even though the beluga has much greater longevity and thus has significantly greater number of adult age groups. The reason lies in the fact that species such as the sterlet have larger relative number of adult age groups than species with great longevity—i.e. the proportion of age classes that belong to adults, not their absolute number, is larger.

Life history parameters related to males have weak influence on the population viability, as long as there are enough males to fertilize the eggs in each

spawning event. Indeed, due to this fact, many sturgeon PVA models have been restricted only to females (Bajer and Wildhaber 2007; Kennedy and Sutton 2007).

The life history parameters that are most influential on population viability are usually proposed for the highest management or research priority (Mills and Lindberg 2002). However, as it was stated by Mills and Lindberg (2002), parameters that are influential can often have low level of actual variation, so this issue has also to be addressed with certain caution.

The present study has confirmed a high correlation between the population growth rate (deterministic and stochastic) and the population viability and rate of genetic loss. This confirms the value of the population growth rate as the overall predictor or indicator of the population state. Population growth rate has been used in many studies as one of the main simulation parameters for the assessment of the population viability (Pine et al. 2001; Bajer and Wildhaber 2007). However, any such use of the population growth rate should be conducted with the awareness that this parameter does not consider certain aspects, such as stochasticity, genetically linked demographic traits and the male-related traits, and that it is thus unable to register changes in these traits that might impact population viability.

What is the real value of population growth rate in the Danube populations? Surprisingly, this demographic parameter seems to be rarely touched upon or discussed in existing literature on the demography of sturgeons, and estimates of the rate were presented in few sources. Sturgeon PVAs generally produce the conclusion that slow physical growth and discontinuous spawning of sturgeons result in low intrinsic population growth rates (Heppell 2007), but the actual value of this parameter is seldom determined or presented. According to the scarce literature that is available, it can range from 0.05 (Bruch 2008) to 0.10 (Secor and Niklitschek 2002), or vary between 0.05 and 0.15 (Balnath et al. 2008). However, the present study has confirmed that the model behaviour and its sensitivity to changes in vital rates were particularly dependent on the population growth rate. The importance of this parameter was revealed by both the comparison of the scenarios with the three different population growth rates employed (0.05, 0.10 and 0.15), and by a strong correlation of the

population growth rate with the population viability and the amount of genetic loss. As it was shown in harvest scenarios, maximum harvest pressure (expressed as relative to population size) was dependent on population growth rate and not on the initial population size. The apparent lack of understanding of the real population growth rate in the six studied species may significantly hinder development of the effective management in the future, so the assessment of the intrinsic population growth rate of the Danube sturgeon populations should represent one of the highest research priorities. However, it is important to emphasize that, while the population growth rate is indeed an important population parameter, there are other parameters as well that might be used instead as good indicators of population state, which are at the same time more simple to measure, such as the population age structure.

Comparisons of the PVA results for the six studied sturgeon species have revealed that the sterlet population model was showing large differences compared to the other five species. This was shown through the different relative sensitivity to the life history parameters, lower general viability of the population in both types of basic scenarios (that were comparing species through the same population size and the same number of adult females), and by the extreme sensitivity to harvesting at low population growth rates ($r = 0.05$). Such model behaviour seems to be counterintuitive when compared to the actual situation in the field where, despite the high harvest pressure, this species has remained the least affected one—this is the only sturgeon species in the Danube River that is still an object of the commercial fishery. According to the IUCN Red List of Threatened Species (IUCN 2008), the sterlet is globally categorized as a vulnerable species, while the stellate, Russian, ship sturgeon and beluga are categorized as endangered and the Atlantic sturgeon as a critically endangered species. Based on these facts, it seems likely that the sterlet actually has a higher intrinsic population growth rate than the other five Danube sturgeon species. At higher population growth rates the model of this species behaves like the other five species at lower growth rates (e.g. if the population growth rate $r = 0.10$ is applied to the sterlet and $r = 0.05$ to the other five species). This difference can also be noticed at the maximum viable harvest levels in Fig. 4. Furthermore, while most

sturgeon species resemble to a certain extent the *K*-selected type of species (Pianka 1970)—great longevity, large body size, delayed reproduction, infrequent spawning (the exception to this is their high fecundity), the sterlet is less evolved in this direction than the other sturgeons and more towards the *r*-selected type of species—significantly shorter longevity, earlier maturation, frequent spawning and smaller body size. One of the common distinctions between those two types of selection is the larger population growth rate of the *r*-selected species. However, the question of the actual intrinsic population growth rate of the sterlet and other Danube sturgeons will be only resolved through future research efforts.

The present study has confirmed that the natural mortality rates of Danube sturgeon species, beside their intrinsic population growth rate, should probably represent the single most important object of any future study on Danube sturgeon populations. While the data on the actual natural mortality rates of sturgeons is almost non-existent, it is even more so regarding the Danube populations. Although it is generally acknowledged that it is probably the most difficult life history parameter to determine (Boyce 1992; Beissinger and Westphal 1998), it is at the same time one of the key parameters for any PVA scenario building, so it is likely that the lack of data on the sturgeon natural mortality will represent one of the main hindering factors for future development of Danube sturgeon PVAs.

Another issue that has been poorly addressed within the present literature on sturgeon ecology is the existence of senescence in sturgeons, the maximum reproductive age that occurs before the maximum longevity has been reached. In most of the studies performed so far, as well as in review studies dealing with the sturgeon ecology, this issue has not been raised or touched upon, not even regarding the North American sturgeon species that are generally considered as well studied. The only available reference that confirms existence of senescence in sturgeons is that of Lagutov and Lagutov (2008). A study by Williot et al. (2005) registered senescence in aquaculture populations, and it was hypothesized by Williot (personal communication) that it should be also present in the nature. On the other hand, most of the interviewed sturgeon experts were either uncertain whether senescence exists in sturgeons, or they

were even certain that sturgeons can spawn throughout their whole life. Sulak and Randall (2002) have argued against the widely accepted paradigm in sturgeon ecology that sturgeons can commonly attain those reported large body sizes and long age, and claimed that such large individuals are rare and their contribution to the population only minor. The sensitivity analysis has indicated that the existence of senescence would not have large influence on population viability, except if the maximum reproductive age is reached a long time before their maximum reported longevity. This issue, however, needs to be studied further.

All models that have been developed within the present study have dealt with a single small population of each species. This could correspond to an isolated subpopulation in a fragmented ecosystem, or a depleted population within a large distribution area. For some of the species this may be a realistic scenario at present, for other species the models are used to assess minimum viable population sizes, although the populations today are larger. The scenarios employed do not capture the case of several subpopulations partly linked through gene flow between them, but such scenarios should be an important object of further studies.

All studied sturgeon species have shown a relatively high susceptibility to harvest pressure. While it differed among different species and among different population growth rates applied (Fig. 4), the general pattern was that, at population growth rate of $r = 0.05$, the maximum viable harvest pressure was within the range of 0.05–0.10 of the adult population size, at $r = 0.10$ it ranged from 0.20 to 0.30, and at $r = 0.15$ from 0.40 to 0.50. As already discussed, the only exception was the sterlet, whose maximum harvest pressure was always more similar to that of other species at the lower population growth rate (e.g. the threshold harvest pressure at $r = 0.10$ was similar to the harvest threshold of other species at $r = 0.05$). These threshold levels fall within those determined by other PVAs, performed mostly on North American sturgeon species—reported threshold values were below 0.10 (Quist et al. 2002), 0.05–0.15 (Beamesderfer et al. 1995), 0.15–0.20 (Colombo et al. 2007), 0.35 (Kennedy and Sutton 2007). Although these PVAs have not presented the growth rates of simulated populations, comparison of these threshold values with those obtained in the present study shows

that they are mostly similar to the threshold ranges obtained at $r = 0.05$ and 0.10, which are also the more realistic population growth rates for sturgeons (as was previously discussed). It is important to note, however, that the harvest threshold levels that are expressed in such relative terms (i.e. in percentage of adults taken from the population) are difficult to be implemented in practice, since they would require a good knowledge of the actual population size, thus demanding constant efforts of making population censuses, that would be certainly both time and money consuming.

In harvest assessment scenarios developed by Kennedy and Sutton (2007), the model was not significantly influenced by the initial population size, and the harvest pressures, expressed as ratios, had the same influence on different sizes of population. The model in the present study had the same behaviour, and whatever initial population size was applied, the harvest threshold levels remained the same. At unsustainable harvest rates, populations in general needed less than 50 years to be reduced to the half of their initial size. If compared with results of harvest scenarios obtained in the present study, the actual rate of decline of the total sturgeon catch in Romania (Bacalbaşa-Dobrovici 1991 citt. in Patriche et al. 1999) would correspond to harvest pressures that are far above the threshold levels (Fig. 5).

Cases of harvest pressure that ensures maximum total yield being above the maximum viable harvest pressure (within the simulated period of 500 years), that were observed in the present study, represent additional problem in reaching the management goal of maximum sustained yield. Since the exploitation is always directed at levels that maximize yield on short term, in such cases they might tend to pass over the viable harvest thresholds, and reach a level with an unacceptable risk of extinction ($P > 0.05$). According to Ludwig and Walters (2002), maximum sustained yields are an inefficient and rarely achieved goal, which belongs more to the convenient political fiction than to the actual science. Botsford et al. (1997) have stated that the two main reasons for the failure of the approach of maximum sustained yield are the lack of political will to implement it and the imprecise predictions of harvest levels, due to an intrinsic uncertainty of the system. Kennedy and Sutton (2007) have proposed that the optimum harvest levels should always be 0.10 below the value

that represents the maximum viable harvest level, in order to allow natural variation in life history parameters such as the age at maturity. Such an approach would reduce the potential risk that harvest becomes a selection pressure towards the maturation at younger age and smaller body size (Kuparinen et al. 2008).

Fishing pressure that is at the same time directed at both adult and subadult age groups was shown to significantly reduce population viability, as well as the threshold of maximum viable harvest. The large impact of subadult harvest most likely originates from the fact that the subadult individuals that are taken from the population have thus failed to have at least one successful reproduction and in that way to compensate for the individuals that have been harvested. Currently, the sterlet population in Serbia is still considered to be under significant pressure of commercial fishery that is, due to illegal fishing practices, also comprised of subadults (Lenhardt et al. 2006a), which is likely to further reduce the population viability.

Stocking scenarios have shown significantly higher relative effect of stocking with adults, when compared to juveniles. This issue was the object of many debates in the field of conservation ichthyology, and there are many pros and cons for both approaches. The majority of sturgeons used for stocking worldwide are fingerlings (Chebanov and Billard 2001; Shahifar 2006). It is important to note that the juveniles released in stocking scenarios in the present study (Fig. 7) consisted of 1 year old individuals, while the most commonly released individuals in real cases are often only a few weeks or 1 month old. Since only a small number of fingerlings would survive to age 1, each released fish of age 1 would correspond to an actual release of several hundreds of fingerlings. Therefore, if the rough relationship between the effect of one released adult and the release of 1 year old fish is more than 1:10, the relationship between stocked adults and fingerlings would be then more than 1:1,000 or even 1:10,000. However, although stocked juveniles have a low survival when released in the natural environment (Chebanov and Billard 2001), stocking with adults comprises a number of other problems, such as the domestication and other selection processes caused by aquaculture conditions, as well as substantially reduced fitness when compared with fish from natural populations (Reisenbichler and Rubin 1999).

Rearing individuals up to their maturity is both time and money consuming, so it is usually not practiced, except in the commercial aquaculture for caviar production and in the case of permanent brood-stock. The only exception is probably the sterlet, due to its early maturity, and some countries like Austria have been also releasing sterlet adults (Williot et al. 2002). The pattern of lower effectiveness of juvenile stocking for late maturing species, that is caused by the lower chances of survival of stocked individuals if they need longer time to reach maturity and reproduce, indicates that this aspect of life history has to be always taken into consideration when deciding on the amount of juvenile individuals that should be released.

Another important pattern that was revealed in juvenile stocking scenarios is the delayed effect of stocking on the population recovery, proportional to the time of maturity (Fig. 7). This lag, caused by the time that released individuals need to wait before they start reproducing, has to be included in management planning. For instance, the release of large numbers of beluga juveniles will produce effect on population dynamics and recovery only after 15 years, which is the average time that females of this species need to reach the maturity.

The stocking scenarios within the present study have not dealt with the important question of the effect of supportive stocking on the inbreeding (and out-breeding) depression (Ludwig 2006), and there is a need for wider use of genetic models which could provide information on the costs and benefits of supplementing fish populations with hatchery-reared stock (Jager et al. 2000). As claimed by Hedrick (2002), effective population size of fish species with a high number of offspring can be surprisingly small, since there is a large variance in contribution to the next generation, which is even more visible in supportive stocking, when few adults are used to produce a large number of stocked individuals. It is a common practice to use no more than ten sturgeon individuals of each sex to produce hundreds of thousands of offspring that will be released (Patriche pers. comm.).

Conclusions

The population viability analysis performed in the present study has revealed a large sensitivity of the

Danube sturgeon populations to changes in life history parameters, especially in the natural mortality, fecundity, age at maturity and spawning frequency, so any anthropogenic impact that has an influence on these vital rates can also significantly increase their risk of extinction. It was also confirmed that the sturgeons are highly susceptible to even moderate levels of commercial fishery, and that the pressures that are above the thresholds of population viability can reduce a population to less then half of its initial size in only a few decades. Slow recovery of sturgeon populations, observed in no-impact scenarios, confirms the claim of Lenhardt et al. (2006a) that the recovery of sturgeons, especially of those long-lived species like the beluga, is a multi-decadal affair. This fact is important to take into consideration for any management planning in the present situation of established moratoria on sturgeon fishery in the Danube.

Stocking will probably remain one of the main conservation measures in the Danube basin. While the present study has shown that the stocking with adult individuals produces considerably greater effect on population persistence than the stocking with juveniles, the latter approach can be still considered as preferable, since it avoids many inherent problems of aquaculture cultivation. The significant lag in positive effects of stocking on population persistence and recovery, which was revealed in juvenile stocking scenarios and especially in slow maturing species, has to be considered in future conservation and management policy planning activities.

Nevertheless, due to a lack of data on life history parameters of Danube sturgeons, there were many assumptions and "rules of thumb" made in development of model input data, so there is a certain level of caution needed when interpreting obtained results. Indeed, although the development of PVA models for Danube sturgeons could improve our ability to implement efficient conservation strategies for these species, this process might be slowed to an extent by lack of exact data on sturgeon life history parameters. There is a present need for extensive studies on sturgeon ecology and life history that would provide better estimation of their life history parameters. However, the future development of PVA should not wait for better data, since it can provide insights regarding the parameters that have the strongest impact on population persistence, and thus endow

researchers with directions to research activities of greatest importance (Jarić et al. 2009b). Based on the results of this study, future research efforts should be oriented towards the estimation of the inherent population growth rate of each Danube sturgeon species, natural mortality rates of the each age group, and better assessment of the average fecundity, age at maturity and spawning frequency of females.

If used with ample precaution and thoroughness and taking into account present uncertainties, PVAs could significantly improve our knowledge about these remarkable species and possible ways of their protection.

References

Akçakaya HR (2000) Population viability analyses with demographically and spatially structured models. Ecol Bull 48:23–38

Akçakaya HR, Sjögren-Gulve P (2000) Population viability analyses in conservation planning: an overview. Ecol Bull 49:9–21

Bacalbasa-Dobrovici N, Patriche N (1999) Environmental studies and recovery actions for sturgeons in the Lower Danube River system. J Appl Ichthyol 15:114–115

Bajer PG, Wildhaber ML (2007) Population viability analysis of Lower Missouri River shovelnose sturgeon with initial application to the pallid sturgeon. J Appl Ichthyol 23:457–464

Balnath C, Gessner J, Rosenthal H (2008) Sturgeon conservation and aquaculture. XXXII scientific conference on fisheries and aquaculture. In: Proceedings of the international workshop on sturgeon conservation and breeding, Szarvas, Hungary, 15–16 May 2008. Available via http://hakinapok.haki.hu. Accessed 15 Apr 2009

Beamesderfer RCP, Rein TA, Nigro AA (1995) Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the Lower Columbia River. Trans Am Fish Soc 124:857–872

Beamesderfer RCP, Simpson ML, Kopp GJ (2007) Use of life history information in a population model for Sacramento green sturgeon. Environ Biol Fish 79:315–337

Beissinger SR (2002) Population viability analysis: past, present, future. In: Beissinger R, McCullough DR (eds) Population viability analysis. The University of Chicago Press, Chicago, pp 5–17

Beissinger SR, Westphal MI (1998) On the use of demographic models of population viability in endangered species management. J Wildl Manage 62(3):821–841

Bemis WE, Findeis EK, Grande L (1997) An overview of Acipenseriformes. Environ Biol Fish 48:25–71

Birstein VJ, Bemis WE, Waldman JR (1997) The threatened status of acipenseriform species: a summary. Environ Biol Fish 48:427–435

Boreman J (1997) Sensitivity of North American sturgeons and paddlefish to fishing mortality. Environ Biol Fish 48:399–405

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277:509–515

Boyce MS (1992) Population viability analysis. Annu Rev Ecol Syst 23:481–506

Bruch RM (2008) Modelling the population dynamics and sustainability of lake sturgeon in the Winnebago system, Wisconsin. Dissertation, University of Wisconsin-Milwaukee

Chebanov M, Billard R (2001) The culture of sturgeons in Russia: production of juveniles for stocking and meat for human consumption. Aquat Living Resour 14:375–381

Colombo RE, Garvey JE, Jackson ND, Brooks R, Herzog DP, Hrabik RA, Spier TW (2007) Harvest of Mississippi River sturgeon drives abundance and reproductive success: a harbinger of collapse? J Appl Ichthyol 23:444–451

Ebenhard T (2000) Population viability analyses in endangered species management: the wolf, otter and peregrine falcon in Sweden. Ecol Bull 48:143–163

Hanski I (2002) Metapopulation of animals in highly fragmented landscapes and population viability analysis. In: Beissinger R, McCullough DR (eds) Population viability analysis. The University of Chicago Press, Chicago, pp 86–108

Hedrick PW (2002) Application of molecular genetics to conservation: new issues and examples. In: Beissinger R, McCullough DR (eds) Population viability analysis. The University of Chicago Press, Chicago, pp 367–387

Heppell SS (2007) Elasticity analysis of green sturgeon life history. Environ Biol Fish 79:357–368

IUCN (2008) 2008 IUCN Red List of threatened species. International Union for Conservation of Nature and Natural Resources. Available via www.iucnredlist.org. Accessed 9 Apr 2009

Jager HI (2001) Individual variation in life history characteristics can influence extinction risk. Ecol Model 144:61–76

Jager HI (2005) Genetic and demographic implications of aquaculture in white sturgeon (*Acipenser transmontanus*) conservation. Can J Fish Aquat Sci 62:1733–1745

Jager HI (2006a) Chutes and ladders and other games we play with rivers. I. Simulated effects of upstream passage on white sturgeon. Can J Fish Aquat Sci 63:165–175

Jager HI (2006b) Chutes and ladders and other games we play with rivers. II. Simulated effects of translocation on white sturgeon. Can J Fish Aquat Sci 63:176–185

Jager HI, Lepla K, Chandler J, Bates P, Van Winkle W (2000) Population viability analysis of white sturgeon and other riverine fishes. Environ Sci Policy 3:S483–S489

Jager HI, Chandler JA, Lepla KB, Van Winkle W (2001) A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. Environ Biol Fish 60:347–361

Jarić I, Lenhardt M, Cvijanović G, Ebenhard T (2009a) *Acipenser sturio* and *Acipenser nudiventris* in the Danube—extant or extinct? J Appl Ichthyol 25:137–141

Jarić I, Lenhardt M, Cvijanović G, Ebenhard T (2009b) Population viability analysis and potential of its application to Danube sturgeons. Arch Biol Sci 61(1):123–128

Kennedy AJ, Sutton TM (2007) Effects of harvest and length limits on shovelnose sturgeon in the upper Wabash River, Indiana. J Appl Ichthyol 23:465–475

Kuparinen A, O'Hara RB, Merilä J (2008) The role of growth history in determining age and size at maturation in exploited fish populations. Fish Fish 9:201–207

Lacy RC (1993) VORTEX: a computer simulation model for population viability analysis. Wildl Res 20:45–65

Lacy RC (2000) Structure of the VORTEX simulation model for population viability analysis. Ecol Bull 48:191–203

Lagutov V, Lagutov V (2008) The Ural River sturgeons: population dynamics, catch, reasons for decline and restoration strategies. In: Lagutov V (ed) Rescue of sturgeon species in the Ural River Basin. Springer, Berlin, pp 193–276

Lenhardt M, Jarić I, Bojović D, Cvijanović G, Gačić Z (2006a) Past and current status of sturgeon in the Serbian part of the Danube River. In: Proceedings 36th international conference of IAD. Austrian Committee Danube Research/IAD, Vienna, pp 148–151

Lenhardt M, Jaric I, Kalauzi A, Cvijanovic G (2006b) Assessment of extinction risk and reasons for decline in sturgeon. Biodivers Conserv 15:1967–1976

Ludwig A (2006) A sturgeon view on conservation genetics. Eur J Wildl Res 52:3–8

Ludwig D, Walters CJ (2002) Fitting population viability analysis into adaptive management. In: Beissinger R, McCullough DR (eds) Population viability analysis. The University of Chicago Press, Chicago, pp 511–520

Miller PS, Lacy RS (2005) VORTEX: a stochastic simulation of the extinction process. Version 9.50 user's manual. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley

Mills LS, Lindberg MS (2002) Sensitivity analysis to evaluate the consequences of conservation actions. In: Beissinger R, McCullough DR (eds) Population viability analysis. The University of Chicago Press, Chicago, pp 338–366

Navodaru I, Staras M, Banks R (1999) Management of the sturgeon stocks of the Lower Danube River system. In: Stiuca R, Nuchersu I (eds) The Delta's: state-of-the-art protection and management. Conference proceedings, Tulcea, Romania, pp 229–237

Nikcevic M, Lenhardt M, Cakic P, Mickovic B, Kolarevic J, Jaric I (2004) Historical review and new initiatives for sturgeon fisheries, aquaculture and caviar production in Serbia and Montenegro. In: Oddmund O (ed) Releasing

development potentials at the Eastern Adriatic. Norwegian University of Science and Technology (NTNU), Trondheim, Norway. Available via www.easternadriatic. com. Accessed 15 Apr 2009

Patriche N, Pecheanu C, Billard R (1999) Sturgeon fisheries, caviar production in Romania and possible measures of rehabilitation in the Lower Danube. Riv Ital Acquacolt 34:83–91

Pianka ER (1970) On *r*- and *K*-selection. Am Nat 104(940): 592–597

Pine WE III, Allen MS, Dreitz VJ (2001) Population viability of the Gulf of Mexico sturgeon: inferences from capture–recapture and age-structured models. Trans Am Fish Soc 130:1164–1174

Quist MC, Guy CS, Pegg MA, Braaten PJ, Pierce CL, Travnichek VH (2002) Potential influence of harvest on shovelnose sturgeon populations in the Missouri River system. N Am J Fish Manage 22:537–549

Reed JM, Mills LS, Dunning JB Jr, Menges ES, McKelvey KS, Frye R, Beissinger SR, Anstett M-C, Miller P (2002) Emerging issues in population viability analysis. Conserv Biol 16(1):7–19

Reinartz R (2002) Sturgeons in the Danube River. Biology, status, conservation. Literature study. International Association for Danube Research (IAD), Bezirk Oberpfalz, Landesfischereiverband Bayern, e.V

Reisenbichler RR, Rubin SP (1999) Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES J Mar Sci 56:459–466

Secor DH, Niklitschek EJ (2002) Sensitivity if sturgeons to environmental hypoxia: a review of physiological and ecological evidence. In: Thurston RV (ed) Fish physiology, toxicology and water quality. Symposium proceedings, La Paz, Mexico, EPA/600/R-02/097, pp 61–78

Shahifar R (2006) Economic comparison between sturgeon fishery yield and releasing efforts of fingerlings in the Southern Caspian Sea (1972–2003). J Appl Ichthyol 22(Suppl 1):119–124

Sulak KJ, Randall M (2002) Understanding sturgeon life history: enigmas, myths, and insights from scientific studies. J Appl Ichthyol 18:519–528

Vassilev M (2006) Lower Danube—the last refuge for surviving of sturgeon fishes in the Black Sea Region. In: Hubert P (ed) Water observation and information system for decision support. Conference proceedings, Balwois, Ohrid, Macedonia. Available via http://balwois.org. Accessed 15 Apr 2009

Williot P, Arlati G, Chebanov M, Gulyas T, Kasimov R, Kirschbaum F, Patriche N, Pavlovskaya LP, Poliakova L, Pourkazemi M, Kim Y, Zhuang P, Zholdasova IM (2002) Status and management of Eurasian sturgeon: an overview. Int Rev Hydrobiol 87(5–6):483–506

Williot P, Brun R, Rouault T, Pelard M, Mercier D, Ludwig A (2005) Artificial spawning in cultured sterlet sturgeon, *Acipenser ruthenus* L., with special emphasis on hermaphrodites. Aquaculture 246:263–273