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Alternative restocking strategy could reverse declines of a critically endangered sturgeon

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Report

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Summary

Demographic modelling can reveal options for improved conservation management, especially for rare or long-lived species not amenable to experimentation. Sturgeon (Acipenseridae) include many such species, endangered by demand for caviar, their unfertilized roe, and by dams blocking their migrations. Restocking of sturgeon populations with farm-raised individuals has probably prevented extinctions and widespread extirpations of some species, but it has rarely led to true recovery in Eurasia, given ongoing harvest. We used modified Leslie matrix models to test whether restocking with year-old juveniles instead of weeks-old fry could recover the critically endangered Amur sturgeon (*Acipenser schrenckii*), endemic to the Amur River basin along the Russia–China border. Without restocking, or even releasing an expert-recommended annual volume of young fry (10 million), we project that three of four Amur sturgeon populations will be nearly extirpated within 30 years. However, restocking with 5% as many (500 000) year-old juveniles annually could grow three populations (currently 0–425 mature females) and slow declines in another so that each has over 6400 mature females within 30 years. Retooling stocking efforts to use fewer juveniles that survive at higher rates than do small fry could buy time to reduce harvesting pressure on Amur sturgeon and for other related sturgeon species.

Introduction

Population viability analysis includes a series of modelling techniques developed in the last four decades to forecast the demographics and persistence of at-risk species (Boyce 1992, Beissinger & McCullough 2002). One use for these demographic models is to test the effects of alternative management strategies on conservation outcomes (Fantle-Lepczyk et al. 2018, Saunders et al. 2018), which can be especially fruitful for data-deficient (Tucker et al. 2021) or long-lived species that are difficult to experiment with *in situ* (Armbruster et al. 1999, King et al. 2014). For data-poor species, parameterizing multiple sets of models with a range of plausible demographic rates can reveal which aspects of their life history or anthropogenic impacts are most important for designing effective conservation strategies (King et al. 2014, McCusker et al. 2017, McGowan et al. 2017).

Sturgeon (Acipenseridae) are a family of 27 species of large, primarily anadromous fish distributed across north temperate regions (Billard & Lecointre 2000). Most sturgeon species are highly threatened due to dams that impede their migration between feeding and spawning grounds and by harvest for their meat and especially their unfertilized roe, which is used to make caviar (Birstein et al. 2006). The long generation times of sturgeon and their secretive demersal nature (Birstein et al. 2006) make them difficult to study and experiment on in the wild.

Amur sturgeon (*Acipenser schrenckii*) are native to the Amur River basin along the Russia–China border (Billard & Lecointre 2000, Zhuang et al. 2002) and have been classified as critically endangered on the International Union for Conservation of Nature (IUCN) Red List since 2010. Like most sturgeon, *A. schrenckii* is a late-maturing, long-lived species, able to survive up to 60 years (Krykhtin & Svirskii 1997), and beginning reproduction after 9–14 years (Wei et al. 1997). The species was historically abundant along the full length (*c.* 3000 km) of the Amur River and most or all of its large tributaries (Krykhtin & Svirskii 1997, Zhuang et al. 2002, Vaisman & Fomenko 2006). However, since at least the late 1800s, intensive fishing pressure to fulfil demand for caviar, coupled with the construction of large dams and excessive pollution in several Amur tributaries, has caused dramatic declines estimated to exceed 95% of the species' former abundance (Ruban & Qiwei 2010). Conservation efforts including restocking with farmed fry, regulation of international trade by the Convention on International Trade in Endangered Species (CITES) and fishery regulation by the range countries have failed to recover the species (Zhuang et al. 2002, Vaisman & Fomenko 2006).

We built age-structured population models (Caswell 2006) to test the potential of alternative restocking practices to reverse the declines in Amur sturgeon. Specifically, we compared a

Table 1. Initial population structures.

Parameter	Estuary/Lower/Middle Amur values	Justification with example for the Estuary population
Initial mature (9+ years old) population, females	28 860/425/85	Total estimated population >1 year old × percentage mature × percentage of mature fish female Estuary: 264 000 fish >1 year old × 32.8% mature × 33.33% mature fish female (Koshelev et al. 2014a, 2014b)
Initial population per juvenile age class (1–8 years old), females	11 088/1483/297	Total estimated population >1 year old × percentage immature × 50% female; evenly distributed across eight immature age classes Estuary: 264 000 fish >1 year old × 67.2% immature × 50% female; evenly distributed across eight immature age classes (Wei et al. 1997, Koshelev et al. 2014b)
Fry <1 year old, females	5.19194×10^7/764 575/152 915	Average fecundity, females × the fraction of females reproductive annually × initial number of females × spawner survival Estuary: 143 890 (average fecundity, females) × ¼ (fraction of females reproductive annually) × 28 860 (initial number of females) (Krykhtin & Svirskii 1997)

harvest-only scenario projecting population trajectories in the face of continued harvest without restocking to population projections with restocking efforts using either fry (fish of 2–3 g mass, just weeks old and the current standard procedure; Koshelev et al. 2014a, 2014b) or juveniles (>1 year old, *c.* 30 cm in length; Zhuang et al. 2002).

Methods

Model structure and parameterization

We used modified Leslie matrix models (Heppell et al. 2000, Caswell 2006) to simulate the future trajectories of the four Amur sturgeon populations. Although information on the population biology of Amur sturgeon is limited, the fish are believed to spawn within the same groups as those in which they feed throughout the year (Novomodny et al. 2004, Ruban & Qiwei 2010). Therefore, we follow the limited literature (e.g., Krykhtin & Svirskii 1997, Koshelev et al. 2014b) and consider fish from the following four river regions to be the populations for our models:

- Amur estuary, inclusive of the few individuals found in the Sea of Japan and Sea of Ohkotsk;
- Lower Amur, from Khaborovsk (Russia) to the mouth of the river where it meets the estuary;
- Middle Amur, from Heihe (China) to Khaborovsk, inclusive of the Zeya and Bureya rivers (northern tributaries of the Amur);
- Upper Amur, upstream of Heihe, inclusive of the Shilka and Argun rivers, the confluence of which forms the Amur headwaters.

Although the exact migration routes, spawning locations and levels of interbreeding among fish from these regions are not known, fish that feed and mature in different river regions generally migrate to and breed in separate locations. For instance, fish from the Zeya and Bureya rivers are believed to breed in the upper Middle Amur (Krykhtin & Svirskii 1997), whereas fish from the estuary and lower river migrate upstream to breed between Luobei, Xunke and Tongjiang counties along the lower Middle Amur (Wei et al. 1997).

All of our models proceed from an initial condition we define to represent the year 2021 and for which we specify a starting population size and age-class distribution based on the most recently published population surveys (Table 1). These surveys reported the estimated total number of fish greater than 1 year of age, the percentage reproductively mature and the percentage of mature individuals that were female (Koshelev et al. 2014a, 2014b). The Upper Amur population is extirpated, so for models simulating its restoration we used initial population sizes of 0. We assumed that 50% of 1–8-year-old fish (juveniles) were female and that the age distribution among these age classes was even.

To obtain a starting abundance of fry (fish ≤1 year of age) for each population, we multiplied the initial abundance of mature females by their average fecundity, divided by four because no more than 25% of females attempt to spawn annually (Krykhtin & Svirskii 1997), and we multiplied the result by 0.05, which represents the best estimate of the proportion of spawners that survive harvest for caviar (Simonov & Dahmer 2008). Thus, our models included 10 age classes (fry, juveniles 1–8 years old and mature fish). Following convention, we only modelled females (Heppell et al. 2000, Jarić & Gessner 2013).

We projected future population sizes and age distributions at successive annual time steps for 30 years. Future population sizes are computed by multiplying the population size for each age class by the probability that its individuals survive to the following age class (Table 2). Mature individuals add new fry to the population by reproducing at each time step. Fecundity was included as the per-female number of females produced in an average bout of spawning multiplied by the proportion of females spawning (0.25) and surviving harvest (0.05) each year (Table 2 & Supplementary Appendix S1, available online).

We employed consistent age-specific survival, maturation, fecundity and frequency of reproduction across populations and scenarios. Where there was uncertainty in demographic rates, we relied on published values for related *Acipenser* spp. and opted for more optimistic values (i.e., greater survival).

Because there was especially high uncertainty in the published values for juvenile *Acipenser* spp. survival rates (0.20–0.89), we used a calibrated value determined from iterative runs of the baseline harvest-only models with the aim of selecting the largest (most optimistic) survival rate that produced declining populations in each of the three extant populations. This matches our best understanding of the present condition of the species (i.e., it is declining; Ruban & Qiwei 2010) and yielded a value of 0.67.

Future scenarios

We ran models representing three future scenarios. The first represents a future with the status quo level of harvest and no restocking of Amur sturgeon. These models were run according to the parameters described above.

The second scenario represents a future in which the considerable aquaculture capacity in the Amur region is partially redirected

Table 2. Demographic parameters for all models.

Parameter	Values	Justification/citation
Annual survival of fish <1 year old	0.00053	Highest estimate from population viability analyses of related *Acipenser* spp. (Jager et al. 2002, Jarić & Gessner 2013)
Annual survival of fish aged 1–7 years	0.67	Reported range of 0.20–0.89 for annual survival of juvenile *Acipenser* spp. (Jager et al. 2001, 2002, Jarić & Gessner 2013, Wang et al. 2017) 0.67 is the highest value that produced declining population trajectories for the baseline *harvest-only* models (i.e., an optimistic value calibrated to our knowledge of current population trends)
Age at first reproduction	9 years	Low end from range of 9–14 years (Krykhtin & Svirskii 1997, Wei et al. 1997)
Average fecundity (production of females) per female, in years reproducing	143 890	Empirically determined mean from 317 females (Krykhtin & Svirskii 1997), halved to represent only female offspring
Proportion of mature females spawning each year	0.25	Spawning frequency at least every 4–5 years (Zhuang et al. 2002, Novomodny et al. 2004); spawning periodicity: 4–5 years in females (Ruban & Qiwei 2010)
Survival of spawners	0.05	Approximately 95% of spawning females are harvested (Simonov & Dahmer 2008)
Annual survival of mature fish	0.57	0.74 baseline adult survival × 0.75 proportion not breeding + 0.05 survival of spawning fish × 0.25 proportion spawning (Krykhtin & Svirskii 1997, Jager et al. 2001, Simonov & Dahmer 2008, Ruban & Qiwei 2010)

to help restore wild populations. At least 10–11 million Amur sturgeon has been suggested as the level necessary for rehabilitation of the species' abundance and range (Krykhtin & Gorbach 1994, cited in Koshelev et al. 2014b), although it is not clear how this number was determined. We tested the sufficiency of this proposed restocking strategy using fry, because the vast majority of fish used in restocking have been very young fry, *c.* 30 days old (Koshelev et al. 2014b). For each of the four populations, we simulated the addition of 2.5 million age-zero fish (1.25 million females) to each population annually between 2021 and 2051 (totalling the recommended range-wide total of 10 million/year). All other parameters were the same as in the harvest-only models. The Upper Amur model was built starting with a completely extirpated population.

In the third scenario, we simulated a future in which Amur sturgeon are farmed until at least 1 year of age before use in restocking. Annual survival of pre-reproductive sturgeon >1 year old is approximately three orders of magnitude greater than for fish in their first year (Table 2) (Jager et al. 2001, 2002, Jarić & Gessner 2013). Thus, introduction of many fewer 1-year-old fish than fry should be needed to recover Amur sturgeon. We modelled the annual addition of 125 000 year-old fish (62 500 females) to each population. This is 5% of the number of fry restocked in the second scenario. All other demographic parameters were held the same as in the harvest-only and fry-restocking scenarios. Again, the Upper Amur population was started from complete extirpation.

We ran simulations for 30 years. Although this only represents time for approximately two generations for Amur sturgeon (Ruban & Qiwei 2010), we chose this timeframe for its relevance to near-term management planning. For each scenario, we report the resulting projected abundance of mature females at the end of the 30-year window in 2051.

Our modelling framework includes several assumptions, which, if anything, bias the models in favour of positive population growth and persistence. We assumed that harvest rate would not change over time and that stocked and wild-born fish would have the same survival rates. Because we were primarily interested in testing the relative benefits of the two restocking strategies, we did not include any stochastic demographic or environmental processes in our models, which would likely increase extinction rates in small populations (Beissinger & McCullough 2002). We also did not include a carrying capacity because the populations are all so depleted that they are unlikely to approach such a limit within our simulation timeframe. Finally, adult fish in our model were not subject to senescence or maximum lifespan. This probably did not impose unrealistic outcomes because most spawners are recently matured and are harvested after reproducing only once or twice (Simonov & Dahmer 2008, Koshelev et al. 2014b).

Sensitivity tests

To test the sensitivity of our results to uncertainty in two demographic parameters, we ran the models for each of the three scenarios using altered parameter values. First, we tested a reduction of the harvest rate (using 90% annual mortality of spawning fish, which is 10% annual survival, instead of the best available estimate of 95% annual mortality of spawning fish or 5% annual survival; Simonov & Dahmer 2008). When coupled with our already high-end estimates for survival of fish in all immature age classes, this likely produces a highly optimistic set of projections. Second, because the range of juvenile survival rates reported in related sturgeon species was wide (Table 2) and our iterative procedure for selecting a juvenile survival rate to use in the baseline models likely produced an optimistic value, we repeated all projections using a moderate reduction in juvenile survival rate to 0.55 from 0.67.

Long-term population projections

In the short term, restocking efforts may maintain or enhance populations, but if managers ever wish to cease restocking without populations tending towards eventual extinction, then the long-term population trend must be positive. Therefore, in addition to 30-year simulations of population dynamics under alternative restocking scenarios, we also considered the long-run viability of the populations. In this analysis, we asked whether a population would be self-sustaining in the absence of restocking given the current rate of harvest and the best available estimates of Amur sturgeon demographic parameters. To answer this question, we determined whether the growth rate of a population at its stable age distribution and without restocking would be >1. Mathematically, the long-run growth rate of an unstocked population that has reached its stable age distribution is equal to the dominant eigenvalue of the Leslie matrix that governs population dynamics (Caswell 2006). The dominant eigenvalue is independent of fish abundance, dependent only on survival rates for the different age classes.

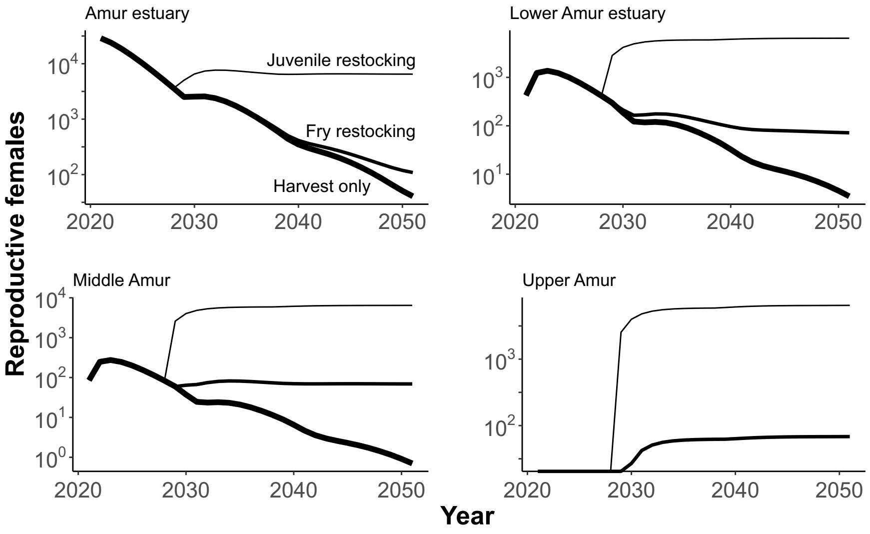

Fig. 1. Initial and projected abundances of mature female Amur sturgeon for alternative future scenarios for the years 2021–2051. The Upper Amur has no harvest-only model because the sturgeon is currently extirpated. Full data are available in Table S1.

Results

Harvest only

In the baseline harvest-only scenario, Amur sturgeon reproductive female abundance is projected to decline to near zero in all three extant populations (Fig. 1). The Estuary, Lower Amur and Middle Amur populations are all projected to decline by over 99% and to have 41, 3 and 1 mature females remaining, respectively. The long-term trajectory of these populations tends towards extinction, declining by 19% per year (dominant eigenvalue = 0.81).

Fry stocking

Restocking with fry only slightly moderated population declines (Fig. 1). In the Estuary population, the projected population decline was lessened by only tenths of a percentage point, and the population is projected to have 108 mature females in 2051. The abundance of mature females in the Lower Amur is projected to decline by 83%, leaving 72 individuals, and the Middle Amur is projected to decline by 19% and to contain 69 mature females. The restoration of the Upper Amur population is projected to yield 68 mature females by 2051 (Fig. 1).

Juvenile stocking

In contrast to the fry-stocking scenario, using many fewer year-old juveniles is projected to more strongly moderate, and in some cases reverse, declines (Fig. 1). The Estuary population is projected to decline by 78%, while the Lower and Middle Amur populations would grow by 1518% and 7587%, respectively. Including the restored Upper Amur, all four locations were projected to have between 6449 and 6490 mature females.

Sensitivity analyses

Doubling the best available estimate of spawning female survival rate in the reduced-harvest scenarios generally had only slight effects on population projections (96–99% decline in the harvest-only scenario; Fig. S1 & Table S1). No projected declines were reversed, although the small Middle Amur population was nearly steady with fry restocking (4% decline versus 19% decline in the baseline model).

Reducing juvenile survival from 0.67 to 0.55 per year sped projected population declines and strongly moderated growth with juvenile restocking (Fig. S2 & Table S1). The Middle and Lower Amur populations were projected to go extinct by *c.* 2040 in the harvest-only scenario. With juvenile stocking and the reduced juvenile survival rate, the four populations all reached *c.* 1200 mature females, *c.* 20% of the projected population in the baseline scenario.

Discussion

Sturgeon fry have very high mortality rates (over 99.9% in the first year; Jager et al. 2001, 2002, Jarić & Gessner 2013), and past restocking efforts using fry have not reversed the decline of Amur sturgeon (Zhuang et al. 2002, Ruban & Qiwei 2010). The same is true of other fry restocking efforts in other *Acipenser* spp. (McDougall et al. 2014). Our simulations indicate that even with the annual release of a recommended number of fry (10 million; Koshelev et al. 2014b) declines would continue. In contrast, a relatively efficient and effective method for recovering Amur sturgeon may be to restock populations using many fewer juveniles of at least 1 year of age because the older juveniles survive at per capita rates of up to 10 000 times greater than fry do (Table 2). Managers should carefully consider the decision to introduce differently aged fish, given that our projections indicate that by 2040 only the estuary is projected to have more than *c.* 100 mature females under harvest-only or juvenile-restocking scenarios. In an analogous situation, lake sturgeon (*Acipenser fulvescens*) has recovered comparably well where age-1 fish were released instead of age-0 fry (McDougall et al. 2014, 2020).

Our models also indicate that better restocking practices could arrest population declines and allow moderate recovery of Amur sturgeon. If continued indefinitely and at sufficient volume, well-planned restocking (e.g., using juveniles, not fry) could allow the species to persist despite high levels of harvest. However, if the goal is to eventually cease financially costly restocking efforts, the prevailing conditions must be favourable enough that once restocking ends the populations continue to recover and persist. Our analysis of the long-term growth rates of the populations indicates that persistence in the absence of restocking is only feasible given significant reductions from the present rate of harvest. This is in line with previous qualitative assessments of the species' status (Novomodny et al. 2004, Vaisman & Fomenko 2006, Simonov & Dahmer 2008, Ruban & Qiwei 2010).

Given that commercial aquaculture facilities in the region regularly raise fish to maturity for breeding and caviar harvest, there is already capacity to raise fish for a full year after hatching (Wei et al. 2011, Bronzi et al. 2019). In the early 2000s, less than 1% of sturgeon produced in China were released into natural habitats (Simonov & Dahmer 2008). This would have amounted to *c.* 600 000 sturgeon (of several species) per year between 2007 and 2009 (Wei et al. 2011) and suggests that the 500 000 we simulated introducing annually in our juvenile-restocking scenario is well within reach. Some restructuring of aquaculture facilities may be needed to provide more naturistic settings for fish to be prepared for wild settings. Where retrofitting might be necessary to raise these older juveniles rather than the fry primarily produced by non-commercial, restocking-focused farms, it is unlikely that raising fish for an additional year would cost substantially more per capita, especially since we show that 5% as many juveniles as fry could produce much more favourable outcomes.

Our models may be considered optimistic given the built-in assumptions (use of a high-end juvenile survival rate calibrated to yield marginally negative population growth in the baseline scenario, equal survival of wild-born and farmed fish and no stochasticity). Species-specific demographic studies could help narrow the uncertainty remaining in our models by obviating the need for a calibrated juvenile survival rate and by providing updated estimates of population abundance and age distributions (Koshelev et al. 2014a, 2014b).

Other limitations of our model stem from the scarcity of data on Amur sturgeon demographics. We were forced to use fry survival rates estimated from related species. However, because our intention was specifically to model differential outcomes among the three alternative management scenarios and not to forecast exact numerical outcomes for the species, our parameterizations provide a useful framework for future *in situ* conservation efforts and experimentation. We also included a constant proportional rate of harvest; there is the possibility of eventually decreased harvest, although corruption and poor law enforcement capacity make this unlikely in the Russian Amur region in the near future (Harris & Shiraishi 2018). On the other hand, successful restocking and eventual increased availability of adults may keep harvest rates high.

We also focused the reporting of our projections on adult females. For the baseline model set, there were between 1600 and 2800 times as many fry as mature females remaining in populations in 2051 – the end point of our simulations. Thus, a projected zero abundance of adult females in 2051 in our models does not mean that the population will be extirpated (Table S1).

Since the full Acipenseridae family was listed under CITES in 1998, nearly all Amur sturgeon (and all other Acipenserids) in legal international trade are reported to be aquaculture-derived products, not wild sourced (CITES & UNEP-WCMC 2021). However, the strong ongoing domestic demand for caviar and the ongoing illegal trade, especially in Russia, continue to imperil the species (Ruban & Qiwei 2010, Harris & Shiraishi 2018). The same is true of most Eurasian sturgeon, for which national economic interests, corruption, the large profits available from illegal trade, a failure to act before sturgeon stocks crashed, the largely voluntary nature of agreements and a lack of public awareness all conspire to handicap most national and multilateral conservation efforts (Vaisman & Fomenko 2006, Harris & Shiraishi 2018, WSCS et al. 2018). Although broader interventions are required to secure sturgeon populations from ongoing harvest, illegal trade and dam construction (Ruban & Qiwei 2010, Harris & Shiraishi 2018, WSCS et al. 2018), we demonstrate that restocking with careful attention to species' demography could improve species' viability in the interim.

Supplementary materials. For supplementary material accompanying this paper, visit https://doi.org/10.1017/S0376892922000017.

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