

Management and Recovery Options for Ural River Beluga Sturgeon

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Abstract: *Management of declining fisheries of anadromous species sometimes relies heavily on supplementation of populations with captive breeding, despite evidence that captive breeding can have negative consequences and may not address the root cause of decline. The beluga sturgeon (Huso huso), a species threatened by the market for black caviar and reductions in habitat quality, is managed through harvest control and hatchery supplementation, with an emphasis on the latter. We used yield per recruit and elasticity analyses to evaluate the population status and current levels of fishing and to identify the life-history stages that are the best targets for conservation of beluga of the Ural River. Harvest rates in recent years were four to five times higher than rates that would sustain population abundance. Sustainable rates of fishing mortality are similar to those for other long-lived marine species such as sharks and mammals. Yield per recruit, which is maximized if fish are first harvested at age 31 years, would be greatly enhanced by raising minimum size limits or reducing illegal take of subadults. Improving the survival of subadult and adult females would increase population productivity by 10 times that achieved by improving fecundity and survival from egg to age 1 year (i.e., hatchery supplementation). These results suggest that reducing mortality of subadults and adult wild fish is a more effective conservation strategy than hatchery supplementation. Because genetics is not factored into hatchery management practices, supplementation may even reduce the viability of the beluga sturgeon.*

Keywords: Caspian Sea, caviar, CITES, hatchery, overfishing, reference points

Opciones de Manejo y Recuperación del Esturión Beluga del Río Ural

Resumen: *El manejo de pesquerías de peces anádromos en declinación a veces depende estrechamente de la suplementación de poblaciones mediante la reproducción en cautiverio, no obstante la evidencia de que la reproducción en cautiverio puede tener consecuencias negativas y no abordar la causa principal de la declinación. El esturión beluga (Huso huso), una especie amenazada por el mercado de caviar negro y por reducciones en la calidad del hábitat, es manejado mediante el control de la cosecha y suplementación de poblaciones, con énfasis en esta. Utilizamos análisis de producción por recluta y de elasticidad para evaluar el estatus de la población y los niveles de pesca actuales y para identificar las etapas de la historia de vida que*

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son los mejores blancos para la conservación del beluga en el Río Ural. Las tasas de cosecha en años recientes fueron cuatro a cinco veces mayores que las tasas que sustentarían la abundancia de la población. Las tasas sustentables de mortalidad por pesca son similares a las de otras especies marinas longevas como tiburones y mamíferos. La producción por recluta, que es maximizada si los peces son cosechados a la edad de 31 años, podría incrementar significativamente elevando los límites de talla mínima o reduciendo la captura ilegal de subadultos. La mejora de la supervivencia de hembras subadultas y adultas incrementaría la productividad de la población 10 veces más que la mejora obtenida incrementando la fecundidad y supervivencia de buevo a 1 año de edad (i. e., suplementación de poblaciones mediante reproducción en cautiverio). Estos resultados sugieren que la reducción de la mortalidad de peces silvestres subadultos y adultos es una mejor estrategia de conservación que la suplementación. Debido a que la genética no es considerada en las prácticas de manejo en los criaderos, la suplementación incluso puede reducir la viabilidad del esturión beluga.

Palabras Clave: caviar, CITES, criadero, Mar Caspio, puntos de referencia, sobrepesca

Introduction

Species conservation and restoration programs sometimes use captive-bred individuals to improve the status of wild populations (Fraser 2008). For fishes, hatchery-based supplementation programs, although potentially beneficial, can have negative genetic, ecological, and evolutionary effects, particularly when the abundance of wild populations is very small (Ryman & Laikre 1991). Moreover, restoration through hatchery supplementation can only be achieved if the root cause of decline (e.g., fishing, loss of habitat) is addressed. Results of some previous research suggest that hatchery supplementation should only be used in the short term to maintain extremely small populations and not as a primary tool for rebuilding fish populations (Philippart 1995; Fraser 2008; McClure et al. 2008). Therefore, alternative conservation actions should be evaluated to determine whether they could more effectively achieve recovery.

The beluga sturgeon (*Huso huso*) is an economically valuable species that is managed through harvest control and hatchery supplementation, with an emphasis on the latter. The historic range of this anadromous species and the rivers where a majority of fish spawned included the Caspian (Ural and Volga rivers), Black (Danube and Dnepr rivers), Azov (Don and Kuban rivers), and Adriatic seas (Po River) (Billard & Lecointre 2001; Pikitch et al. 2005). According to the International Union for Conservation of Nature (IUCN 2009), the beluga sturgeon is endangered. Its Adriatic population has been extirpated, and the population in the Azov Sea is critically endangered (IUCN 2009). Long lived (up to 100 years) and late maturing (9–13 years), beluga are particularly vulnerable to heavy levels of fishing (Babushkin 1964; Raspopov 1993; Billard & Lecointre 2001). International trade of beluga sturgeon products is regulated by the Convention on International Trade in Endangered Species (CITES) under Appendix II of the convention.

High demand for black caviar (unfertilized roe of sturgeon), fishing, and changes in habitat quality have negatively affected the beluga sturgeon, and commercial populations are currently limited to the Caspian Sea (Pik-

itch et al. 2005). The value of beluga caviar, which in 2009 sold for up to US\$8000/kg, is a source of incentive for poaching and intensive fishing. Dams have affected spawning habitat; 90% of the historic spawning grounds in the Caspian Sea have been destroyed or are inaccessible to the species (Secor et al. 2000). More than 12 hatcheries were established in rivers of the Caspian Sea in the 1960s to compensate for the effects of dams and have released millions of juvenile sturgeon (including beluga) annually (Secor et al. 2000; Chebanov et al. 2002). Only limited broodstock is used in most hatcheries, and no genetic management plans exist. The success of hatchery release for this or any other species of sturgeon has not been well assessed.

Beluga sturgeon landings in the Caspian Sea peaked at over 14,000 tons annually in the early 1900s, but harvest has not exceeded 2500 t annually since the late 1930s (Korobochkina 1964; Pikitch et al. 2005). For all nations except Iran, which has active fisheries in coastal areas, legal fishing of beluga occurs only in rivers during spring and autumn spawning periods (Bauer 1997; Levin 1997; Khodorevskaya & Krasikov 1999). The Ural River is the only major river in which no dams block access to spawning habitats and large spawning areas (981 ha) persist (Volkova 2007, unpublished manuscript). The two hatcheries on the Ural River operate by breeding reproductively mature fish captured during spawning runs and then harvesting these animals for their meat or occasionally retaining them for continued use in the hatchery. Landings of beluga sturgeon in the Ural River peaked at over 750 t in the mid 1960s and decreased to 27 t in 2007 (Mamina 1995; unpublished data of the Research and Production Center of Fish Industry). As of 2002, 2500 beluga sturgeon spawned in the Ural River, whereas historically tens of thousands spawned there annually.

Currently there is no accepted estimate of the number of individual beluga sturgeon in the Ural River or any other population in the Caspian Sea. Concerns have been raised regarding the methods used to estimate abundance and total allowable catch (TAC), which are the basis for CITES trade quotas, and the effectiveness of fisheries management practices (FAO 2004; Doukakis et al.

2005; Pikitch et al. 2005). Fishing quotas are highest for nations with the greatest hatchery output, which creates an incentive to focus on hatchery output. Quantifying the number of individuals in Caspian Sea populations and current rates of mortality from fishing and evaluating the impact of different conservation measures (i.e., limiting fishing vs. increasing hatchery output) are necessary steps toward creating an effective conservation and management plan for this species.

We used yield per recruit, spawner biomass per recruit, and demographic elasticity analyses (de Kroon et al. 2000) to determine current and sustainable fishing rates, estimate biological reference points, and evaluate the relative merits of focusing on hatchery output versus harvest control. Simple assessment methods were chosen because available data were limited (e.g., incomplete catch and abundance indices over time). Elasticity analyses have been used to evaluate management strategies for other species of sturgeon (Gross et al. 2002; Heppell 2007).

Methods

Yield per Recruit and Spawning Stock Biomass per Recruit

Data on maximum age, natural mortality rate, mean weight at different ages, age at maturity, and selectivity at age (i.e., the partial recruitment vector) were gathered from the literature. Because beluga sturgeon can live as many as 100 years (Petrov 1927; Babushkin 1964; Mitrofanov et al. 1986), we assumed 100 age groups for the base run in our analysis and a maximum age of 80 and 120 years in the sensitivity analysis of natural mortality. Males and females in the Ural River population begin to mature at 9 and 12–13 years, respectively, and most are mature at 12–15 years and 15–20 years, respectively (Mitrofanov et al. 1986; Mamina 1995). We used female maturity in the stock biomass per recruit (SSBR) analysis. The maturation schedule was approximated with a linear function that started with 0% of females mature at age 11 and 100% mature at age 20 and 0% of males mature at age 8 and 100% mature at age 15.

Direct estimates of natural mortality for beluga sturgeon were not available. Natural mortality is thought to be low due to the mean longevity of individuals (Hewitt & Hoenig 2005). We estimated natural mortality (M) at 0.04/year on the basis of maximum longevity of 100 years. An upper ($M = 0.05$ /year) and lower bound ($M = 0.034$ /year) of natural mortality were estimated with maximum ages of 80 and 120 years, respectively (Table 1)

Because legal harvest of beluga sturgeon occurs during the spawning run in the Ural River, we assumed that every fish in the spawning population has an equal probability of capture and fishing mortality can be applied equally to

Table 1. Parameter estimates or range of values used in the yield per recruit and spawning potential ratio analysis of Ural River beluga sturgeon.

Parameter ^a	Females	Males
t_{\max} , maximum age (range)	100 (80–120)	100 (80–120)
t_{\min} , fishery recruitment age	11	11
M , natural mortality (range)	0.04 (0.03–0.05)	0.04 (0.03–0.05)
t_0 , age at zero length	–5.66	–14.04
K , growth coefficient	0.03	0.01
L_{∞} , maximum length ^b	416.8	822.2
a , length-weight parameter	1.35×10^{-5}	2.34×10^{-4}
b , length-weight parameter	2.86	2.32

^aAge is in years, length in centimeters, and weight in kilograms.

^bThe L_{∞} for males is an asymptotic value estimated by the model and should not be confused with maximum observed value for male beluga. The L_{∞} is a parameter that provides the best model fit to the available range of size at age of entry into the fishery. For reference, if our parameters are used in the Von Bertalanffy model, the estimated mean total length of male beluga at age 100 years is 499.8 cm, which is similar to the maximum observed lengths in historical records.

the entire spawning population. In younger age groups, only mature fish are removed by fishing, whereas immature members of the same year class remain at sea. Partially mature age classes thus experience less fishing mortality than fully mature age groups. Therefore, partial recruitment at age or the fraction of fishing mortality experienced by a certain age group compared with fishing mortality experienced by fully mature ages (F) was calculated as

$$PR_a = PM_a \times RM_a + PF_a \times RF_a, \quad (1)$$

where PR_a is partial recruitment value for age a , PM_a is the proportion of mature males at age a , PF_a is the proportion of mature females at age a , and RM_a and RF_a are the corresponding proportions of males and females within age a . We assumed a 50:50 sex ratio. Under existing regulations the minimum legal size corresponds to age 11. Consequently, fish younger than age 11 were assigned a PR value of zero.

Direct estimates of weight (W_t) at age t were available for only a limited number of age groups, so we calculated W_t in two stages. We fitted theoretical growth curves for males and females to an average length (L_t) at age t . We used data from Mamina (1995) on the L_t of male and female beluga sturgeon for ages 10–38 in the Ural River. Values of L_t for younger ages were not available from the Ural River population, so we used L_t for beluga sturgeon at ages 2–9 in the northern Caspian region (populations of the Ural, Volga, and Kura rivers; Babushkin 1964). We fit the von Bertalanffy (1938) growth function to empirical data on length at age with nonlinear regression, which produced average fish sizes for the full range

of ages

$$L_t = L_\infty (1 - e^{-K(t-t_0)}), \quad (2)$$

where L_∞ is the maximum asymptotic length, K is the Brody growth coefficient, and t_0 is the hypothetical age at which the fish would be zero length. The von Bertalanffy growth function was fitted separately for data on males and females (Table 1).

We used an allometric growth function to convert L_t to W_t :

$$W_t = aL_t^b, \quad (3)$$

where a and b are parameters. The parameters a and b of the allometric growth model were estimated by fitting the allometric growth function to empirical weight and length data (Table 1).

We used a modified version of the Thompson Bell yield-per-recruit (YPR) model (Thompson & Bell 1934; Ricker 1975). We calculated yield per recruit as

$$\frac{Y}{R} = \sum_{a=1}^{t_{\max}} w_a \frac{F_a}{F_a + M} (1 - e^{-(F_a+M)}) e^{-\left(\sum_{b=1}^{a-1} (F_b+M)\right)}, \quad (4)$$

where Y/R is yield in kilograms per recruit, a and b are the age of fish, t_{\max} is maximum age, w_a is the mean weight at age a , F_a is fishing mortality at age a , and M is instantaneous natural mortality (Table 1).

We used the National Oceanic and Atmospheric Administration Fisheries Toolbox (NOAA 2004) to determine F_{\max} (fishing mortality value that generates the maximum YPR) for a range of fishing mortality values from 0 to 1.0 with a step of 0.01 and to select the F that generated the highest value of YPR. We also calculated $F_{0.1}$ (fishing mortality at the point on the YPR curve with slope equal to 0.1 of the slope at the point of origin). The $F_{0.1}$ is often used rather than F_{\max} because it is a more conservative parameter and presents a lower risk of fishing at unsustainable levels (Doubleday et al. 1984; Andrew & Butterworth 1987; Hilborn & Walters 1992).

We estimated spawning SSB $_a$ and spawning potential ratio (SPR) following Gabriel et al. (1989). The spawning stock biomass at each age is the number alive multiplied by the proportion mature multiplied by the weight of an individual as follows:

$$SSB_a = w_a N_a P M_a e^{-Z_a}, \quad (5)$$

where SSB $_a$ is the spawning stock biomass at age a , w_a is a mean weight at age a , N_a is the number of fish alive at the start of the year at age a , $P M_a$ is the proportion of fish mature at age a , and Z_a is the total mortality of fish at age a between 1 January of the year and the spawning time. We calculated Z_a as follows:

$$Z_a = (P R_a F + M) \Delta T, \quad (6)$$

where $P R_a$ is the partial recruitment for age a (fraction of full F applied to age a), M is the natural mortality, and ΔT

is the time between the start of the year and spawning (as a fraction of a year).

The total contribution of a cohort to the spawning biomass over the cohort's lifetime is the sum of the cohort's contributions at each age,

$$SSB_{\text{total}} = \sum_{a=1}^{t_{\max}} SSB_a, \quad (7)$$

and SSBR is

$$SSBR = \frac{SSB_{\text{total}}}{N_1}, \quad (8)$$

where N_1 is the number of recruits (fish at age 1).

An SPR is calculated as a ratio of SSBR at a selected level of F and the SSBR at zero fishing mortality:

$$SPR = \frac{SSBR_F}{SSBR_{F=0}}, \quad (9)$$

We used values of SPR from 35% to 45% as precautionary management targets and values from 20% to 35% as limit reference points, which defined unsustainable levels of fishing (Hilborn & Walters 1992; Mace & Sissenwine 1993; Mace 1994; Quinn & Deriso 1999).

Elasticity Analyses

Elasticity is the proportional change in population growth (λ) corresponding to a proportional change in one entry in the Leslie matrix (\mathbf{A}) describing the population's fecundity and survival at age (de Kroon et al. 2000; Heppell 2007):

$$\frac{\mathbf{A}_{ij}}{\lambda} \frac{\partial \lambda}{\partial \mathbf{A}_{ij}} = \frac{\mathbf{A}_{ij} \mathbf{v}_i \mathbf{u}_j}{\lambda \langle \mathbf{u}, \mathbf{v} \rangle}, \quad (10)$$

where v is the age-specific reproductive value, calculated as the first left eigenvector of the Leslie matrix (scaled to sum to 1.0), and u is the stable age distribution, calculated as the first right eigenvector of the Leslie matrix scaled to sum to 1.0. The inner product of the two vectors is denoted by $\langle \mathbf{u}, \mathbf{v} \rangle$. Elasticities were additive and summed to 1.0.

We performed the elasticity analysis once with the most likely values of each input parameter (Table 2) and then repeated the analysis with a Monte Carlo simulation to evaluate the effect of parameter uncertainty. Because no information was available to estimate survival of eggs to age 1, we used a value that resulted in $\lambda = 1.0$ given the other parameters. This value of λ implies that the population is in equilibrium with no fishing (Gross et al. 2002). We assumed survival of fish age 1 and greater was constant and used the natural mortality rate to calculate it ($M = 0.04$, corresponds to a survival of $\exp[-0.04] = 0.96$). We calculated fecundity for spawning females by fitting a linear relationship (Table 2) to egg production data from Mamina (1995). We assumed the proportion mature animals increased linearly from

Table 2. Data used for elasticity analysis for Ural River beluga sturgeon.

Parameter	Most likely value ^a	Distribution for simulation
Age at first maturity	13	12 and 13 equally likely
Age at 50% mature	16	15 to 20 all equally likely
Age all mature	22	22
Spawning interval	5	$p_4 = 0.25, p_5 = 0.5, p_6 = 0.25^b$
Lifespan with no fishing	100	normal, mean = 100 (SD 5)
Egg-to-age-1 survival (S_0)	6.0×10^{-7}	log survival uniform between -14 and -7 ,
Annual survival (S) for ages 1 and higher	0.96	M lognormal with mean = 0.04 (log SD 0.3), $S = \exp(-M)$
Fecundity at age	$49657 \times \text{age} - 531970$	same but multiplied by error, lognormal, mean = 1 (log SD 0.1)

^aAll ages are in years, survivals are in fraction of the population, and fecundity is in numbers of eggs.

^bThe p_x refers to the probability that the spawning interval is x years.

0% at age 12 years to 50% at the modal age of maturity (16 years). We assumed this increase was followed by a more gradual, linear increase to the age at which there was 100% maturity (22 years). The Leslie matrix was assumed to apply to only females, and the matrix included fish in the Caspian Sea and fish that move into the Ural River to spawn. Thus, f_i equaled one-half multiplied by the egg production per spawning female at a given age multiplied by the proportion mature at a given age divided by the spawning interval. The spawning interval was assumed to be five because females tend to spawn every 4 to 6 years (Mamina 1995). The fecundity was divided in half so as to include only female eggs.

For the Monte Carlo simulations, we gave each parameter a probability density function that described the plausible range of variability for the parameter (Table 2). Five thousand values of each parameter were then drawn randomly from these distributions and the resulting elasticities were summarized. We carried out all elasticity analyses in S-plus (version 8.0 for Windows; TIBCO Software, Palo Alto, California).

Results

Yield and Stock Biomass per Recruit

The maximum on the curve of YPR at $F_{\max} = 0.066/\text{year}$ (Fig. 1) was well defined. The more conservative reference point $F_{0.1}$ was 0.034/year. Spawning stock biomass and spawning potential ratio declined rapidly as F increased (Fig. 1). Spawning stock biomass per recruit declined to 40% of the unfished level at $F = 0.03/\text{year}$, 30% of the unfished level at $F = 0.04/\text{year}$ and 20% of unfished SSB at $F = 0.07/\text{year}$ (Fig. 1).

The mean age of fish in the population declined steeply for F between 0 and 0.1. The average age in an unfished population was 24 years. At a harvest level of $F_{0.1}$ or $F_{40\%} = 0.03$, the mean age is 16.2. At F_{\max} and $F = 0.2$, mean age was 12.4 years and about 8 years, respectively.

Fishing mortality affected population age structure. In the absence of fishing mortality, most spawner biomass (78%) was accumulated in fish ≥ 30 years old. As fishing mortality increased, the proportion of older and larger fish in the spawning stock declined rapidly. At $F = 0.2$, spawners of age 30 and older were practically absent. Average age in the spawning stock of the unfished population was 37.3 years. At $F = 0.1$, average age declined to 29.2 years, and at F_{\max} the average age of spawners was 24 years old.

The age of entry into the fishery affected maximum YPR and fishing mortality (Fig. 2). At an age of entry of 11 years (base run), $F_{\max} = 0.066$ and YPR was 28.2 kg. An increase in age of entry led to a higher YPR and increased F_{\max} . When fish entered the fishery at age 20, the YPR was higher (33 kg/recruit) and the F_{\max} was twice that of the base run ($F = 0.14$, Fig. 2). The YPR was maximized when age of entry was 31 years and asymptotic when YPR was 36 kg and F_{\max} was $\geq 0.3/\text{year}$ (Fig. 2). We repeated the YPR analysis for several estimates of natural mortality within the range of $M = 0.03$ – 0.05 , which corresponds to maximum age variation between 80 and 120. The F_{\max}

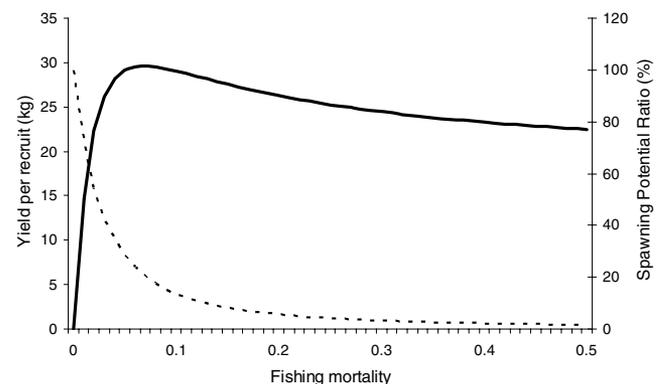


Figure 1. Yield per recruit (solid line) and spawning potential ratio (dashed line) for Ural River beluga sturgeon.

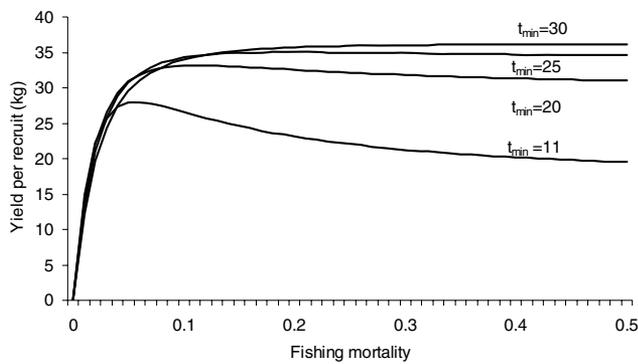


Figure 2. Yield per recruit at age of entry into the fishery for Ural River beluga sturgeon (t_{min} , minimum age of fish in years).

and the other reference points increased as the value of natural mortality increased (Table 3).

The distribution of cumulative age at different F values under equilibrium conditions of the YPR analysis showed that the age distribution shifted quickly to younger ages as F increased (Fig. 3). At $F = 0.1$, an estimated 4.6% of the fish in the spawning stock were over 30 years old. At $F = 0.2$ and $F = 0.3$, only 2.4% and 0.45%, respectively, were over 30 years old.

To arrive at the fishing mortality rate applicable to both male and female fish in the spawning population, we multiplied by a factor of 4 given that only about one-quarter of spawning-age fish migrate into the river and are subject to fishing mortality in any given year. An $F_{max} = 0.066$ applied uniformly to the entire population that is over 11 years was thus equivalent to the $F = 0.066 \times 4 = 0.264/\text{year}$ when applied to the spawning population each year. Assuming a natural mortality rate of $M = 0.04$, this corresponded to a catch of about 23% of the spawning population in the river. An $F_{0.1}$ of 0.034 would correspond to a mortality rate of $F = 0.136$ if it were applied to the spawning population (equivalent to a catch of about 13% of the spawning fish). For the analysis of cumulative age distribution, the F from YPR was estimated for the entire exploitable stock, so F on the spawning population in the river was 4–5 times greater (i.e., $F = 1.2\text{--}1.5$).

Table 3. Fishing mortality (F) reference points as a function of natural mortality estimates.

Natural mortality	$F_{0.1}$	F_{max}	$F_{20\%}$	$F_{30\%}$	$F_{40\%}$
0.03	0.028	0.049	0.059	0.039	0.028
0.035	0.031	0.058	0.064	0.042	0.030
0.04	0.035	0.068	0.071	0.046	0.032
0.045	0.038	0.081	0.077	0.050	0.035

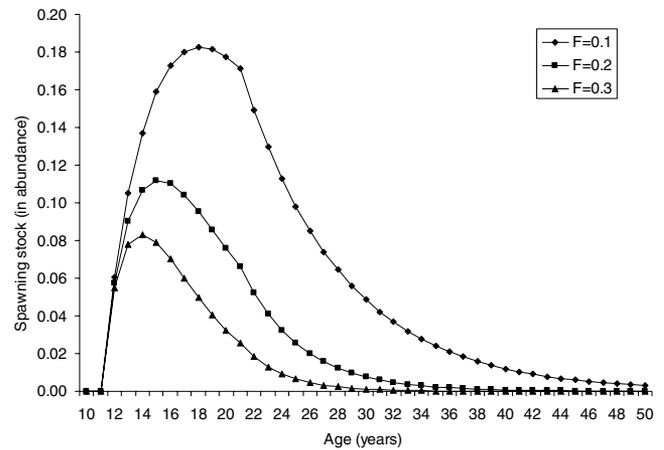


Figure 3. Cumulative age distribution of Ural River beluga sturgeon as a function of fishing mortality (F).

Elasticity Analyses

The elasticity of survival at age was highest (2%) for immature age classes and declined with age (Fig. 4a) because fewer fish survive to the older ages to contribute to the population's reproductive rate. Because beluga are long lived, the cumulative elasticity of survival of all the adult age classes was higher than that of immature (i.e., age 1 until the age of maturity) age classes (Fig. 4b). The elasticity of fecundity multiplied by egg-to-age-1 survival was low compared with the elasticity of immature and adult survival (Fig. 4b). The cumulative elasticity across all age classes of fecundity multiplied by egg-to-age-1 survival was around 2%, equivalent to the elasticity of a single immature age class (Fig. 4a). When parameter variability was included in the analysis (Fig. 4b), the mean elasticity of immature age classes was higher than that calculated at the most likely values of the parameters. Nevertheless, the result that fecundity multiplied by egg-to-age-1 survival had low elasticity relative to the survival of immature fish and adults was consistent in the simulations.

Discussion

We are the first to have calculated fishing mortality rate reference points for any Caspian Sea sturgeon fishery. Our results indicate that beluga sturgeon of the Ural River cannot be sustained at a consistent abundance under high levels of fishing mortality. Precautionary target-fishing mortality rates $F_{0.1}$ and $F_{40\%}$ are on the order of 0.03, whereas F_{max} and $F_{20\%}$ are around 0.07. The latter values are similar to those for long-lived species such as sharks and marine mammals but smaller than those for the productive teleost species that sustain large fisheries. The actual F_{max} and $F_{0.1}$ values also depend on the assumed natural mortality (Table 3). A lower assumed

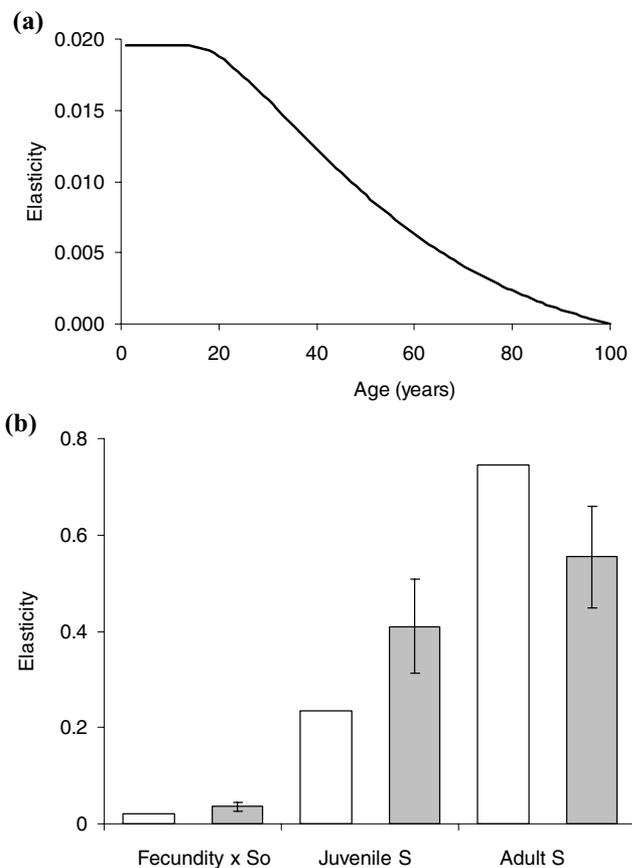


Figure 4. Elasticity of beluga sturgeon calculated with the parameter values from Table 2: (a) elasticity of annual survival (S) by age for the most likely values of the parameters and (b) elasticity of fecundity times egg-to-age-1 survival (So), survival across all immature age classes, and survival across all adult age classes for the most likely values of the parameters (white) and mean values (SD) from the Monte Carlo simulations (shaded).

natural mortality leads to lower target fishing mortality rates because abundance of a more long-lived population, which depends on the accumulation of fish in older age classes for much of population productivity, is less able to remain relatively stable under high levels of fishing. Thus, if the natural mortality of beluga is closer to the lower range of values considered here, a more conservative F_{max} value should be used to meet the objective of sustaining abundance. As with other sturgeon fisheries, where population crashes have been observed within 7–12 years of fisheries opening, fishing must be limited to a relatively low level to maintain long-term fishery productivity (Pikitch et al. 2005).

Two of our findings suggest that the beluga sturgeon fishery in the Ural River is being fished at an unsustainable level. The first is the age structure of the population. If the population were harvested at $F = 0.03$, the mean age

of the population would be 16 years, and the spawning stock would be dominated by fish 18–22 years old (average age 29.2). At F_{max} the average age of the spawning stock would be 24 years. Mean age of the spawning population was 21.8 years in 1996 and decreased to 17.4 years in 2006. Our cumulative-age distribution analysis (Fig. 3) and age distribution in 2006 suggests an $F = 0.2$ – 0.3 for the entire population and $F = 1.2$ – 1.5 for the spawning population. This amounts to a removal rate of more than 70%. Fishing rates may thus exceed F_{max} by four to five times. This is consistent with observations that the Ural River fishery is dominated by first-time spawners (P. Doukakis, unpublished), as is seen in other rivers of the Caspian Sea (Khodorevskaya & Novikova 1995). Lack of older age classes in a spawning population is a classical sign of unsustainable levels of fishing, as demonstrated for a large number of species globally (Hilborn & Walters 1992; Froese 2004).

Second, actual catch likely exceeds that calculated as sustainable. A sustainable fishery should catch <23% of the spawning fish in the Ural River, including males and females. Assuming a constant daily abundance of migrating beluga sturgeon throughout the season, this equates to a regime of fishing 1–2 days/week. Current fishing regulations allow for fishing 5 days/week. Combined with illegal fishing, estimated at 6–10 times legal fishing rates, current fishing pressure likely far exceeds sustainable levels.

Results of our demographic sensitivity analyses indicated that in a naturally reproducing population, adult fish have the most important cumulative contribution to increasing abundance. Along with the results of the YPR and SSBR analyses, this suggests that reducing fishing pressure on adults is the most effective conservation measure. Eliminating poaching in the sea is one way this could occur because it would essentially increase the age of entry into the fishery and yield and spawning stock biomass per recruit. Delaying the age of entry of fish into the fishery by increasing the minimum size limit would also increase yield and spawning production per recruit. Yield per recruit would be maximized at an age of entry into the fishery of 31 years, and at that time mean total length would be 259 cm for males and 269 cm for females. No individuals of 31 years of age were observed in the fishery in 2006. In the mid to late 1990s, 1.6–2.6% of fish were older than 30 years, which indicates age structure may be changing.

Because beluga sturgeon mature at 11–20 years and most fish now entering rivers are first-time spawners, the effects of high levels of fishing over the last 11–20 years on beluga sturgeon recruitment may now be evident. By the same token, it will take decades of reduced fishing pressure in the Ural River for the population to recover to a state in which older animals represent a greater portion of the spawning population. Examples from other sturgeons suggest at least a 40-year hiatus from fishing is

needed for recovery (National Marine Fisheries Service 1998; Pikitch et al. 2005; Bain et al. 2007).

The results of our demographic analyses strongly suggest that to sustain the population, the current management approach stressing hatchery output over fisheries management needs to be changed. Hatcheries increase egg-to-age-1 survival by allowing eggs to hatch and grow to juveniles in an environment with plentiful food and no predators (Gross et al. 2002). Our results show that a proportional reduction in fishing mortality on adults or immature fish would result in a population growth rate approximately 10 times greater than an equivalent proportional increase in fecundity multiplied by egg-to-age-1 survival. Fishing mortality appears to be at least as high as natural mortality, and possibly much higher, which allows for the possibility of increasing the survival of subadult and adult age classes by 50% or more if fishing were reduced substantially. This would translate directly into a higher growth rate in the wild population. A much larger increase in egg-to-age-1 survival would be necessary to achieve the same effect from hatchery production.

Because egg-to-age-1 survival is so low (i.e., 6.0×10^{-7}), there is some scope for hatcheries to improve survival by several orders of magnitude, which would increase the population growth rate (Gross et al. 2002). Nevertheless, hatcheries could only have a positive impact if hatchery-produced fish survive and reproduce as well or nearly as well as wild fish throughout their lives. Hatchery-produced individuals of other anadromous species may have lower fitness even if hatcheries maintain genetic diversity (Fraser 2008). Recommendations on the effective population size for captive breeding vary (e.g., Fraser 2008), but those for sturgeon have been set at 100/generation or 6/year class with a balanced sex ratio and a long-term captive-breeding program (St. Pierre 1999). Ural River hatcheries have no genetic management plans and generally use <6 effective breeders/year class. Thus, reductions in fishing mortality are almost certain to increase the population growth rate, whereas increased hatchery production may or may not be beneficial. Hatchery supplementation is increasingly being viewed as a last resort when trying to restore natural populations of sturgeons and other fishes (Philippart 1995; Pikitch et al. 2005; Fraser 2008; McClure et al. 2008). Known cases of recovery of sturgeon populations have occurred without hatchery supplementation and in the absence of fishing (e.g., Bain et al. 2007). Reduction of fishing mortality must, however, be combined with restoration or creation of spawning habitat.

The reference points we calculated here can be used to guide fisheries management. A necessary next step is to conduct a thorough stock assessment to more fully elaborate benchmarks for a sustainable fishery. Data are difficult to obtain, and the historic data collected prior to the early 1990s are not river specific. Furthermore,

estimates of illegal harvests are needed for an accurate mortality estimate. Our analyses included a number of assumptions that could be relaxed with a more detailed assessment. For example, we assumed natural mortality was constant from age 1 onward; mortality is likely to be greater for spawning fish. Estimates of age- or stage-specific natural mortality would improve the estimates of the management benchmarks. We also assumed the Ural River population was independent of those spawning in other rivers, which may not be the case (Doukakis et al. 2004, 2008).

Assessment of the population status of beluga sturgeon in all tributaries of the Caspian Sea is also needed. In the interim, reducing fisheries catches may help avoid unsustainable levels of fishing. Eliminating all fishing would not only reduce mortality, but also simplify harvest and trade enforcement because all fishing and resulting products would become illegal. If hatcheries are to be maintained as a conservation tool, genetic management plans are needed. Hatchery production should not, however, be given priority over reducing harvest of wild fish if the ultimate goal of management of Caspian Sea beluga sturgeon is preservation and restoration.

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