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Restoration of sturgeons: lessons from the Caspian Sea Sturgeon Ranching Programme

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Abstract

Depletion of sturgeon stocks world-wide has increased interest in aquaculture-based restoration programmes. The Caspian Sea Sturgeon Ranching Programme (SRP) of the former Soviet Union represents a unique opportunity to evaluate expense, benefits and potential ecological and genetic effects of such restoration programmes. The SRP was initiated in the 1950s to compensate for lost spawning habitat in the Volga River and elsewhere. After its completion in 1962, the Volgograd Dam reduced spawning grounds in the Volga River system, the principal spawning tributary of the Caspian Sea, by ~80%. For two of the three commercial sturgeon species (Russian sturgeon, *Acipenser güldenstädti*, and stellate sturgeon, *A. stellatus*), yields improved after the imposition of the 1962 moratorium on sturgeon harvests in the Caspian Sea. Volga River fisheries were managed for spawning escapement. Although imprecisely known, the contribution of the millions of stocked Russian and stellate juveniles during 1962–91 was most likely important to sustaining fisheries, although less so (contributing to <30% of the adult stock) than natural recruitment. Apparently, reduced spawning grounds, supplemented with artificial spawning reefs were sufficient to support reproduction and large fishery yields of Russian and stellate sturgeons. For beluga sturgeon, *Huso huso*, harvests in the Volga River were nearly all dependent upon hatchery stocking. Beluga sturgeon spawning grounds were mostly eliminated with the construction of the Volgograd Dam. Without the hatchery programme, beluga sturgeon in the Volga River and Caspian Sea would in all likelihood have been extirpated. Currently, sturgeons are severely depleted in the Volga River and Caspian Sea due to poaching and lack of co-operation between countries exploiting the species. Aquaculture-based restoration in Russia is now viewed a chief means of rebuilding stocks of Caspian Sea sturgeons.

Keywords Caspian Sea, caviar, hatchery, potential egg production per recruit, spawning escapement, sturgeon

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Introduction

Sturgeons (Acipenseridae) are depleted world-wide and several species are in jeopardy of extirpation (Waldman 1995; Birstein *et al.* 1997). As an example of threatened species, Atlantic sturgeon (*Acipenser oxyrinchus*) may now be extirpated for most subestuaries of the Chesapeake Bay (Secor 1996; Grogan and Boreman 1998; Waldman and Wirgin 1998). United States federal and state agencies are currently researching methods to culture and restore Atlantic sturgeon (ASMFC 1990; Waldman and Wirgin 1998). In a feasibility study, several thousand yearling Atlantic sturgeon juveniles were released during July 1996 into the Chesapeake Bay (Secor *et al.* 2000). The contribution of hatcheries to fisheries enhancement historically has been a controversial issue for scientists, managers and policy makers. Due to the length of time (i.e. decades) it would require to restore Atlantic sturgeon and other sturgeons to historic abundances (Secor and Waldman 1999), careful consideration should be given to the expense, benefits, and potential ecological and genetic effects of a restoration program.

Caspian Sea sturgeon fisheries have historically produced most of the world's supply of caviar. Yet the majority of natural spawning grounds for the three premier species, Russian sturgeon (*Acipenser güldenstädti*), stellate sturgeon (*A. stellatus*) and beluga sturgeon (*Huso huso*) were lost due to the construction of the Volgograd Hydroelectric Dam (Volga River). To mitigate the lost reproduction by the Volga River guild of sturgeons, the Soviet Union initiated a large hatchery-based restoration programme. A commonly held belief is that the Soviet Union's important exports of caviar were largely sustained by this hatchery programme (De Meulenaer and Raymakers 1996).

The Caspian Sea Sturgeon Ranching Programme (SRP) represents a unique opportunity to evaluate the feasibility of an aquaculture-based sturgeon restoration programme. Here we present (i) a history of the Caspian Sea SRP, (ii) an evaluation of the SRP in supplementing natural reproduction and increasing harvest yields, (iii) a review of ecological and genetic considerations of the SRP, and (iv) recommendations for aquaculture-based programmes of sturgeon restoration.

History of the Caspian Sea Sturgeon Ranching Programme

Artificial reproduction of sturgeons

Ovsjannikov in 1869 (Milstein 1971) developed artificial fertilization of Caspian Sea sturgeons. This was followed by innovations in sturgeon egg incubation and artificial rearing of larval stages. Due to its small size and freshwater life-cycle, Volga River sterlet (*Acipenser ruthenus*) was initially used to develop these techniques. Similar artificial reproduction techniques were developed for North American lake sturgeon (*A. fulvescens*) in 1875, for stellate sturgeon (*A. stellatus*) by Borodin in the Ural River in 1884 (Leach 1920; Milstein 1971), and for Atlantic sturgeon in the Delaware River in 1887 (Ryder 1890). Methods for artificial reproduction remain largely unmodified since their development in the 19th century. A notable advance was made by Gerbilsky, who in the late 1940s developed a method of inducing final egg ripening through injection of hormones extracted from the hypophysis of sturgeons (Gerbilsky 1956).

From the late 19th century to the 1930s, trials were conducted releasing hatchery-produced sturgeon larvae into natural habitats (Berezovsky 1933). Overall, more than 250 million stellate sturgeon larvae were released during the period 1902–41, and 17 million Russian sturgeon larvae were released from 1922 to 1941 (Derjavin 1947). Survival of released larvae was believed to be quite low (Milstein 1971). Chalikov (1936) recommended releasing young-of-the-year fingerlings between 1 and 10 g in weight. However, it remained infeasible to stock fingerlings until the mid-1950s, by which time large-scale rearing methods for fingerlings had been developed (Veltitischeva 1955). By 1960, Soviet scientists had developed and adapted the principal methods of artificial reproduction and fingerling culture that were to be used in the Caspian Sea SRP (Gershanovich *et al.* 1987).

Threat to Caspian Sea sturgeons

Abundance of sturgeons in the Caspian Sea dwarf those elsewhere in the world. During the late 19th and early 20th centuries, harvests often exceeded 20 000 tonnes (Fig. 1). These levels were 7-fold greater than peak Atlantic sturgeon harvests along the entire eastern coast of North America (3100 tonnes in 1880; Waldman and Secor 1998). (Historically, Atlantic sturgeon supported the highest North American sturgeon landings.)

Since World War II, hydroelectric dam construction and increased industrial pollution resulted in some loss of sturgeon spawning and nursery habitats (Shagaeva *et al.* 1993; Barannikova *et al.* 1995). After construction of the Volgograd Dam in 1962, the upriver extent of the Volga River spawning grounds was curtailed from river km 3350 to km 400 (Fig. 2). Attempts to engineer effective fish lifts failed, and today, spawning grounds upriver of Volgograd are only used by the land-locked sterlet sturgeon. A major research effort in the 1950s and 1960s sought to precisely map sturgeon spawning grounds, prior to construction of the Volgograd Dam. For Russian sturgeon, historical spawning habitat occurred between river km 200 (100 km below Volgograd) and km 1500 (85% loss). Stellate sturgeon spawned between river km 200 and km 1000 (*c.* 80% loss; Kozhin 1964). Beluga spawned up to river km 3000, using large tributaries of the Volga. Total areal extent of sturgeon spawning grounds was estimated at 3390 ha prior to the Volgograd Dam construction. With the addition of artificial spawning reefs, approximately 372 ha – about one-tenth of spawning habitat – remains (Raspopov *et al.* 1995). Similar problems associated with construction of dams and, additionally, industrial pollution, exist for other spawning tributaries of the Caspian Sea (Barannikova 1995). Although the Ural River has remained un-impounded by hydroelectric dams, about 50% of spawning grounds were lost due to sedimentation and pollution (Verina and Peseridi 1979). The region around the Ural River is heavily industrialized with steel mills, and mining operations cause metal concentrations (Fe, Cu and Zn) in the River to periodically occur at unsafe levels. Large collective farming operations have historically contributed substantial loads of fertilizers and pesticides to the Ural River.

With the construction of hydroelectric dams on the Volga River, particularly the one at Volgograd, conservation of Russian sturgeons became a national priority. The Caspian Sea SRP was initiated in 1953 under the direction of Minister Kosygin, who later became Prime Minister of the Soviet Union

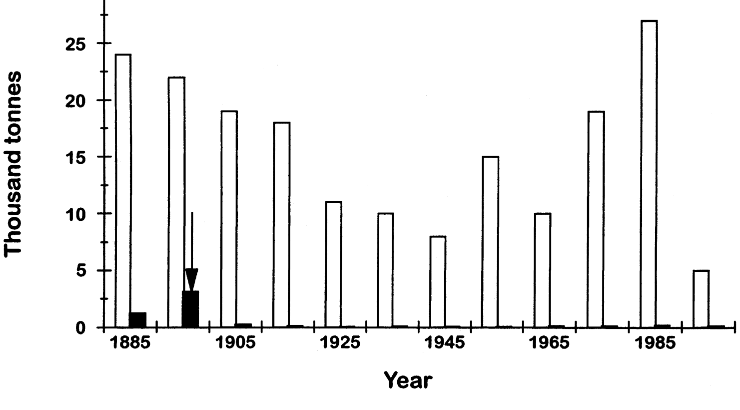

Figure 1 Time series of total Caspian Sea sturgeon harvests (open bars). Each bar represents a 10-year mean. For reference US Atlantic sturgeon harvests are also shown (solid bars). Arrow indicates peak in landings for Atlantic sturgeon. Data from VNIRO and Murawski and Pacheco (1977).

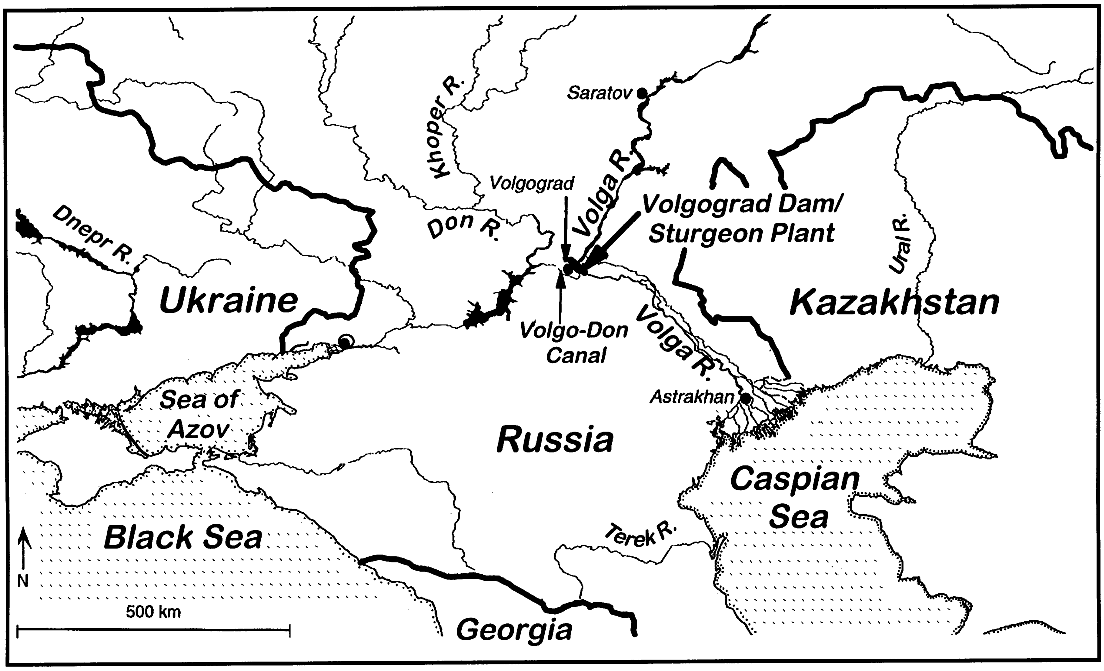

Figure 2 Map of the Volgo-Caspian Basin showing Volograd Dam and Volgograd Sturgeon Plant. Modified from Khodorevskaya *et al.* 1997.

during the 1960s. The main goal of the SRP was to supplement natural reproduction of all Caspian sturgeon species. Even with reduced spawning grounds, natural reproduction was expected to remain sufficient below the Volgograd Dam to sustain Caspian Sea sturgeon stocks. Thus, Soviet scientists believed that significant enhancement of natural propagation by the SRP was unlikely. Moreover, replacement was an undesired goal. The sturgeon specialist Kozhin (1964) argued that natural reproduction should be preserved because hatcheries cannot replace all properties of the natural populations that are characterized by complex age structure, and migration and feeding behaviours (see also Barannikova *et al.* 1995).

Sturgeon plants

During the late 1950s, 11 sturgeon 'plants' (e.g. hatcheries) were built; their main goal was the artificial propagation of Russian, stellate and beluga sturgeon (Kozhin *et al.* 1963). In 1953, Minister Kosygin signed the order which initiated construction of sturgeon plants (including four plants in the Volga region) and provided support for research on the problems related to sturgeon stocking (Letichevsky 1954). Ultimately, eight sturgeon plants were constructed on the Volga River, and five others in Caspian Basin. Fingerling releases into the Caspian Sea increased from 1.15 million juveniles (species combined) in 1955 to more than 90 million in 1990 (Fig. 3).

Sturgeon plants were public works projects. They employed large numbers of staff (80 to more than 100 persons), many of whom were not directly involved in sturgeon production. Sturgeon plants were operated throughout the year, despite production periods that lasted 6 months or less. Plants were quite large. For instance, the *c.* 500 ha plant at the Volgograd Dam, designed to produce tens of millions of fingerlings per year, comprised numerous hatchery buildings and ponds that exceeded 300 ha in total area. Because of their remote locations, the Soviet Union provided plants with substantial infrastructural support (e.g. transportation, markets and entire towns). After 1991, lack of continued state support resulted in plant closures and reduced production (Birstein *et al.* 1997). In 1996, seven plants (in the Volga region) remained open; these were supported by the Russian government.

As the SRP developed, it was believed that a realistic goal would be for sturgeon production to exceed historical levels. It was envisaged that the Caspian Sea could provide large and productive nursery and feeding grounds for juvenile and adult sturgeon; scientists thought that reproduction and

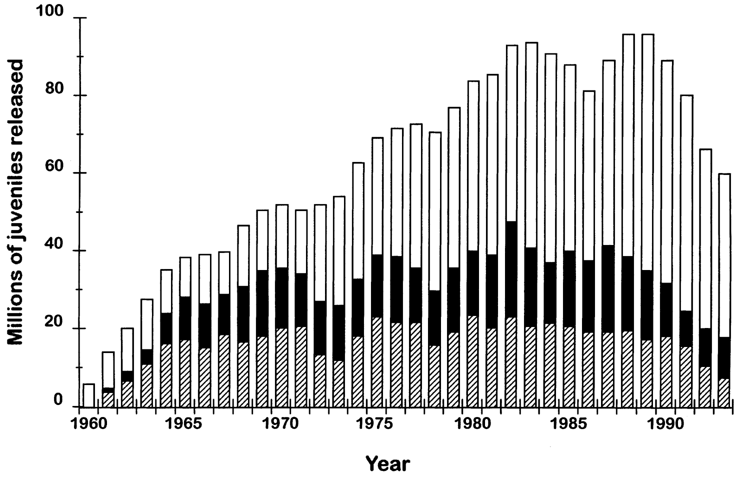

Figure 3 Number of hatchery-produced Russian (open bar), stellate (filled bar), and beluga sturgeon (cross-hatched bar) juveniles released into the Volga River. Data from VNIRO records.

early survival limited fishery yields (Shorygin 1952). The belief that sturgeon species would not compete with each other was supported by trophic ecology studies in the Volga River and Caspian Sea (Soldatova and Rykova 1979; Polyaninova and Molodtseva 1995). Beluga sturgeon is a piscivore, Russian sturgeon feed predominantly on molluscs, and stellate sturgeon prefer crustaceans and annelids (Derjavin 1947). Indeed, in 1952 a *Nereis* spp. (Polychaeta) from the Azov–Black Sea system was deliberately introduced to further enhance the carrying capacity of the Caspian Sea (Polyaninova 1979). Recently, biomass of benthos in the Northern Caspian Sea was 25–43 g per m^2, a level above the forage demand estimated for sturgeons (Polyaninova and Molodtseva 1995).

Efficacy of the Caspian Sea Sturgeon Ranching Programme

The Caspian Sea SRP was initiated without a formal plan for evaluation of its economic revenue, nor were there specific goals for enhancement of natural stocks. Rather, goals were set for production quotas from the hatcheries. In addition, fishery management of sturgeon stocks included strict harvest regulations, water flow management, and the creation of artificial spawning grounds. Here we concentrate on biological rather than economic effects of the SRP. Calculation of real economic values was not possible due to the Soviet Union's central market economy and many unknown costs, such as government support for fishers (sometimes including boats and fishing equipment), and depreciation of hatchery facilities and equipment.

Caspian Sea sturgeon fisheries' trends and management

Trends in Caspian Sea sturgeon harvests since 1940 can be characterized by two periods of high yields (Fig. 1). After 1946, a 20-year period of increasing yield occurred. The increase in landings was probably due to the cessation of fishing during World War II and an increase in sturgeon stocks during 1941–46. A reduction in harvests occurred in the early 1960s. From 1962 to 1991, the USSR enforced a moratorium on the harvesting of open sea sturgeons. In 1967, harvesting other anadromous fishes (e.g. *Caspialosa* sp., Clupeidae) was prohibited in the open sea to eliminate by-catch mortality of juvenile sturgeon. These moratoria were followed by dramatic increases in landings during the 1970s (Khodorevskaya *et al.* 1995, 1997). Total sturgeon landings were 27 200 tonnes in 1977, a level similar to early 20th century harvest levels. Harvests declined after 1980 due to declining juvenile survival in the early 1970s (Khodorevskaya *et al.* 1997) and high levels of pollution that affected egg and larval viability (Barannikova *et al.* 1995). Total Russian landings fell to 14 000 tonnes in 1988, 4700 tonnes in 1993 and 2500 tonnes in 1997 (1998 United Nations Food and Agriculture Organization Fisheries Statistics).

From 1961 until the dissolution of the USSR, strict limits were placed on landings, which were taken with haul seines and drift gill nets at specific locations during spawning runs. Dates of the fishery were determined using data on migration dynamics of spring and autumn runs. Minimum size limits were strictly enforced to curtail harvest to mature females. Typically, harvests were not permitted to exceed $> 60\%$ of the total spawning population, allowing 40% escapement. The approach for regulating escapement was to release a fixed fraction of spawning run fish captured by fishers using fixed nets. These nets were deployed across major portions of the river width from land-based sites called 'tonya.' VNIRO scientist believed that these nets were capable of capturing most individuals of a spawning run at least once. Scientific organizations (e.g. the Caspian Sea Institute, Astrakhan) monitored natural populations and provided management information to appropriate ministries. Unfortunately, effective tagging methods were never developed to improve fishery statistics. Fishery independent surveys of spawning runs used fixed site deployments of gill nets stretched across major portions of the river width. Khodorevskaya *et al.* (1995) reported demographic trends in spawning populations of Volga River sturgeon since 1961. In the recent period of environmental degradation (1980–90), total escapement in the Volga River was about 12–18 thousand breeders per year (Khodorevskaya *et al.* 1995). This level was believed to be too low to guarantee natural reproduction and also supply broodstock for the sturgeon ranching programme.

Estimation of hatchery contribution

The efficacy of the SRP has been determined by means of an index, 'commercial returning rate', originally conceived by Tikhij (1925) to index the recruitment of hatchery fish to the fishery. Kozhin (1951) formulated this index for stellate sturgeon as the ratio between the abundance of a year-class harvested divided by the number of hatchery-produced sturgeon released into that year-class. There have been numerous modifications to the index that differ from each other in the formulation of the denominator in Kozhin's ratio. Most indices consider probable early survival of released fingerlings. Such indices are biased by changes in the environment, year-class strength and exploitation rate. Therefore, commercial returning rate has been used in parallel with other parameters, such as level of natural reproduction, natural recruitment and fishing intensity.

During the 1953–76 period, return rates were low but stable between years, ranging 0.52–0.74% and 0.82–1.02%, for beluga and stellate sturgeon, respectively (Veshchev *et al.* 1993). For Russian sturgeon the commercial return rate has been much higher but decreased markedly from 14.3% in 1956–60 to 1.6% in 1968–75. The main reason for this decrease is believed to be ineffective stocking strategies that resulted in poor survival of released fingerlings. Early survival and return rate indices are highly dependent on high river discharge rates (Makarov 1970; Veshchev 1998). A mean commercial return rate of 3% for stocked juveniles (*c.* 3 g at stocking) has been accepted as a 'typical' value in the Caspian SRP, regardless of sturgeon species (Kozhin 1964). Limited tagging experiments have supported this value, taking into account that survival at 1 year after release was about 20% for beluga and 12–15% for stellate and Russian sturgeons (Barannikova *et al.* 1979).

The optimal size for releasing sturgeon fingerlings was believed to be 3–10 g. Choice of a more precise weight within these limits is dependent upon economic aspects, taking into account the expected commercial return rates. Returning rate for stocked fingerling sturgeon (~ 3 g of weight) was estimated to be one order of magnitude higher than that of stocked larvae ($< 0.3\%$). Three grams was believed to be the minimal size at which juveniles can evade predation. In the Caspian Sea tributaries, the main predator of sturgeon eggs and fingerlings is walleye (*Stizostedion* spp., Percidae). As a rule, stocking should take place in freshwater, but sturgeon species can acclimate well to a range of lower salinities (< 20 p.p.t.). For example, fingerlings of stellate are characterized by highest salinity tolerance and some scientists (Barannikova *et al.* 1979) have recommended rearing fingerlings in brackish water (8–12 p.p.t.). As mentioned above, conditions of flow will influence survival of stocked fingerlings.

Unfortunately, the contribution of SRP sturgeons as a proportion of the entire population has never been estimated directly. Based upon estimated commercial returning rates, contribution rates were believed to range from 10% to 30% for Russian and stellate sturgeons, and $> 90\%$ for beluga (due to loss of spawning habitat). No effective method was developed for the long-term identification of released fish as adults. The most popular method for marking hatchery fish was removing barbels or scutes but this was not effective because mutilation of small sturgeons resulted in increased mortality, and barbels and scutes may regenerate. An attempt was made to use isotopes as short-term markers. Oligochaetes were incubated in ^{32}P and ^{45}Ca solutions and then fed to Russian sturgeon. Recaptures of radioactive juveniles demonstrated rapid dispersal of juveniles from release sites (Vodovozova 1971). Other tagging methods (e.g.

microchip or coded wire internal tags, biochemical, chemical and genetic tags) have not been used in recent years due to inadequate funding.

To further investigate the effects of the SRP, we tested whether enhancement of early vital rates in the hatchery could be sufficient to increase spawning stocks following the general approach given by Secor and Houde (1998). In order to produce at the hatchery a number of young fish equal to that produced by the wild population, the following condition should hold:

$$B_W J_W = B_H J_H \tag{1}$$

or

$$B_W / B_H = J_H / J_W \tag{2}$$

where B_W = spawning run abundance of males and females (including those used by hatchery), B_H = number of breeders (males and females) used in the SRP, J_H = early stage survival in the hatchery, and J_W = early stage survival in the wild. Thus, knowing the number of females used in the hatchery and in the spawning population, we can estimate a required level of survival enhancement (E) where

$$E = J_H / J_W = B_W / B_H. \tag{3}$$

Early stage survival was estimated for the first 40 days in the hatchery including fertilization rate, larval and juvenile survival during rearing, and stocking survival. Equation 3 was then solved for J_W for levels of 25%, 50%, and 100% stock enhancement ($E_{1.25}$, $E_{1.5}$, $E_{2.0}$). Daily instantaneous mortality rate (M day^{-1}) was calculated from J_W to facilitate comparison to published values for other fishes. Few natural rates of larval mortality are available for teleosts and none are published for sturgeons. In a comparison of larval mortality rates between freshwater and marine taxa, Houde (1994) reported that large egg sizes (> 200 μg dry weight) and lower mortality rates (mean = 0.16 day^{-1}) typified freshwater fishes. Smaller egg sizes (< 100 μg) and high mortality rates (mean = 0.24 day^{-1}) were reported for marine fishes. Although Caspian Sea sturgeons could be considered marine, their anadromous life history and large eggs indicate that their early life history attributes are more appropriately classified as typical of freshwater taxa.

In 1968, a year we chose as typical in the SRP, necessary rates of enhancement of early survival to increase yields two-fold were estimated to be 96-fold for beluga, 149-fold for stellate sturgeon and greater than 2000-fold for Russian sturgeons (Table 1). The relatively high proportion of beluga spawning females taken from the natural population for the SRP (1%) drove differences between the beluga and the other two species. Two-fold enhancement ($E_{2.0}$) translated into natural mortality rates of 0.15, 0.20, and 0.27 day^{-1} for beluga, stellate and Russian sturgeons, respectively. Under the scenario of hatchery fish contributing 25% to fishing yields ($E_{1.25}$), estimated mortality rates for stellate and Russian sturgeons (0.17 and 0.23 day^{-1}) were similar to mortality rates typical of large-egg freshwater fishes (0.20 day^{-1}; Houde 1994). Although we have no direct estimates of natural larval mortality rates for sturgeons, the above analysis suggests that enhancement of hatchery early survival rates could be sufficient to achieve substantial enhancement ($> 25\%$) of yields in Caspian Sea sturgeon stocks. Important untested assumptions remain, however; not least of which is accuracy in estimates of J_H. For instance, Secor and Houde (1998) observed that for striped bass hatcheries this estimate was poorly measured and documented despite its importance in evaluating hatchery-based enhancement.

Biological and genetic considerations

A common debate in aquaculture-based stocking programmes is that stocked fish may only replace natural production, rather than supplement it (Cuenco 1994). Sturgeons in the northern Caspian Sea have been shown to cause local and seasonal depressions in macrobenthos biomass (Polyaninova and Molodtseva 1995). Nevertheless, VNIRO scientists believed that the Caspian Sea's potential for sturgeon production was underutilized over the period of the SRP (Berdichevskij and Petrenko 1979). Interactions among stocked sturgeon may be limited due to discrete ecological niches (see above).

No studies exist on possible inbreeding depression as a result of the Caspian Sea SRP.

Genetic parameters of breeders (excluding precise species identification because sturgeon are highly hybridogenic) used in artificial propagation were not taken into account. Investigations have demonstrated high genotypic, and phenotypic plasticity among sturgeons (Gerbilsky 1972). Until recently, high numbers of broodstock and low indices of

Table 1 Evaluation of enhancement of early survival rates in the hatchery necessary to achieve increases of 25%, 50% and 100% to Caspian Sea sturgeon stocks of beluga, stellate and Russian sturgeon; B_H = number of adults (males and females) removed from spawning run by the hatchery; $E_{1.25}$, $E_{1.5}$, $E_{2.0}$ = multiple of increase in early hatchery survival (egg–prerelease juvenile) required to attain levels of 25%, 50% and 100% stock enhancement. J_H = estimated early hatchery survival (rearing survival′ stocking survival); M day$^{-1} \times E_{1.25}$, M day$^{-1} \times E_{1.5}$, M day$^{-1} \times E_{2.0}$ = theoretical early mortality rate in wild fish required to balance enhancements of early hatchery survival associated with 25%, 50% and 100% increases to sturgeon stocks. See text for further details.

Parameter	Beluga sturgeon (*Huso huso*)	Stellate sturgeon (*Acipenser stellatus*)	Russian sturgeon (*Acipenser güldenstädti*)	Reference
Spawning run (B_W) estimated as midpoint for years 1970–72	2.0×10^4	5.0×10^5	1.6×10^6	Khodorevskaya *et al.* (1997)
Hatchery breeders per 10^6 juveniles	26	186	62	VNIRO records
Total released juveniles (1968)	8×10^6	18×10^6	12×10^6	VNIRO records
No. hatchery breeders (B_H)	208	3348	744	Estimated
$E_{1.25}$	24	37	538	Estimated
$E_{1.5}$	48	75	1075	Estimated
$E_{2.0}$	96	149	2150	Estimated
Rearing survival hatchery-pond	50%	50%	50%	Saldlaev and Kipper (1964)
Stocking survival	10%	10%	10%	Marakov (1964); Levin (1995); VNIRO records
J_H	5%	5%	5%	Estimated
M day$^{-1} \times E_{1.25}$	0.15	0.17	0.23	Estimated
M day$^{-1} \times E_{1.5}$	0.17	0.18	0.25	Estimated
M day$^{-1} \times E_{2.0}$	0.20	0.20	0.27	Estimated

commercial return rates indicated that inbreeding in Caspian Sea sturgeons was unlikely to be due to the SRP. Typical broodstock numbers for 1 million live fingerlings were 26 breeders (including 10 females) for beluga sturgeon, 62 breeders (31 females) for Russian sturgeon, and 186 (93 females) for stellate sturgeon. Assuming equal survival among broods of offspring, effective population size (Gall 1987) per million juveniles would be 25, 62 and 186 for beluga, Russian and stellate sturgeon, respectively. Because broodstock numbers available to hatcheries are now in steep decline, recent concerns have emerged about the need to conserve genetic and behavioural variability in breeders used in the SRP (Barannikova *et al.* 1995).

Deterioration of Caspian Sea sturgeon stocks

Loss of spawners

Fingerling releases into the Volga River and Caspian Sea increased from 1.15 million juveniles (species combined) in 1955 to more than 90 million in 1990 (Fig. 3). Despite the large increase in stocking levels, Russian sturgeon landings and presumably abundances declined during this period (Figs 4 and 5). For the relatively rare beluga, recruitment is apparently controlled by hatchery releases. Overall, the SRP may have only partially compensated for processes that have contributed to stock declines. In recent years, however, the role of SRP in merely conserving spawning stocks has become critical.

After the dissolution of the USSR in 1991, the sturgeon fishery has become essentially unmanaged. A moratorium is in place for all open-sea harvests but it cannot be enforced. Using recent (albeit imprecise) estimates, greater than 50% of all sturgeon have been caught by poachers (De Meulenaer and Raymakers 1996). The increase in illegal harvests has corresponded with a large decline in spawning stock because poachers typically select mature females for harvest of caviar.

To evaluate the potential for reproductive failure in current Caspian Sea sturgeon stocks, an egg production per recruit model was constructed for the three principal sturgeons. This is a life-table approach based upon fecundity and natural mortality schedules. First, a value of lifetime egg production under no exploitation is computed. Lifetime egg productions under varying exploitation rates and scenarios are then compared to this value as a fraction, termed '% of maximum eggs

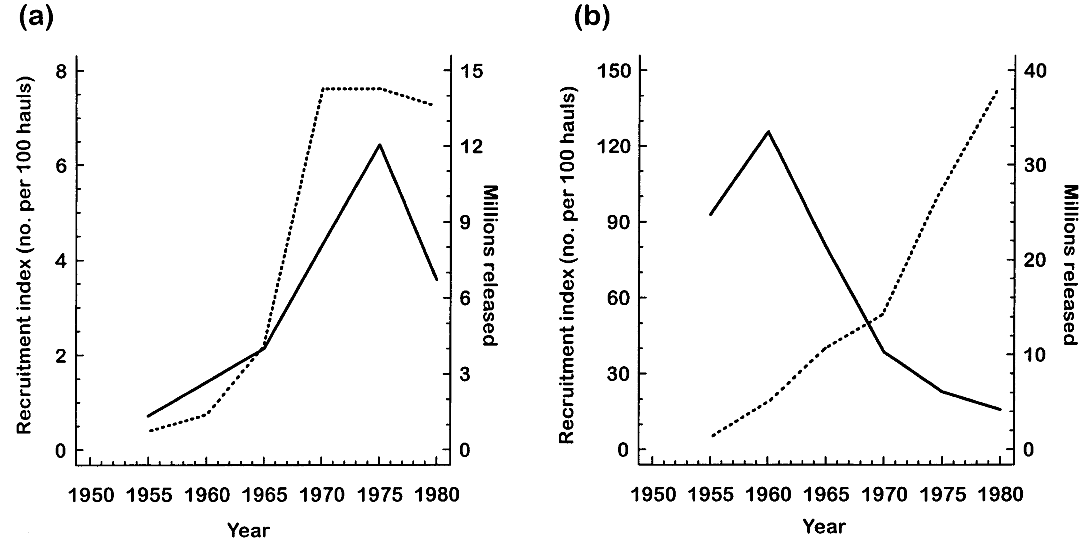

Figure 4 Recruitment index (solid line) and number of juveniles released into the Volga River (dotted line) for (a) beluga and (b) Russian sturgeon. No similar data records were available for stellate sturgeon. Data from VNIRO records.

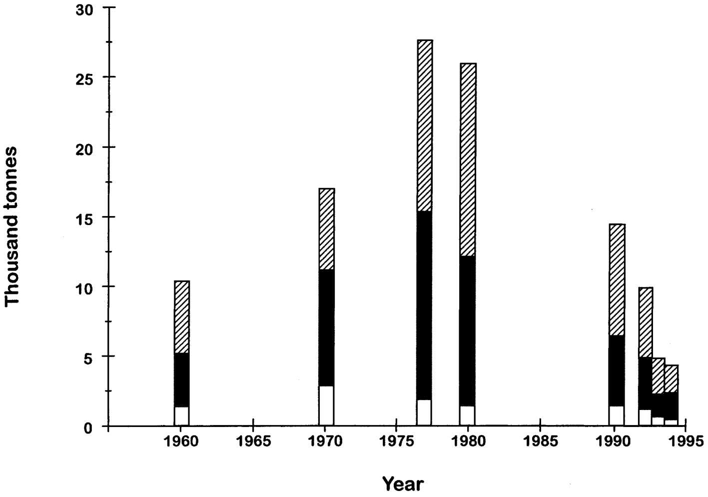

Figure 5 Recent harvest records for produced beluga (open bar), stellate (filled bar) and Russian sturgeon (cross-hatched bar) from the Volga River. Data from VNIRO records.

per recruit', %$\mathrm{EPR}_{\max}$ (Boreman 1997). Parameters for the model are shown in Table 2 and Fig. 6. Two scenarios were examined to evaluate the effects of exploitation rate on egg production by spawners: (i) exploitation of only ripe individuals, and (ii) exploitation of all adults, whether spawning or not. The first and second scenarios are meant to represent exploitation of sturgeons before and after the dissolution of the Soviet Union. Because sturgeons do not spawn every year, the first scenario includes a refuge from exploitation in non-spawning years. For instance, if exploitation is 60% (instantaneous fishing mortality rate (F) = 0.9 year^{-1}) for each spawning run of beluga sturgeon, yet an individual female spawns only once every 4 years, then realized exploitation for the population would be 15% (F = 0.16 year^{-1}). Boreman (1997) recommended that at least 50% (F_{50}) of an unexploited population's egg production should be conserved for long-lived, late-maturing species such as sturgeons. The Atlantic States Marine Fisheries Commission has adopted this standard for US Atlantic sturgeon (Kahnle *et al.* 1998).

Potential egg production ratio sharply declined with increased exploitation rates (Fig. 7). In regulated fisheries for ripe females, F_{50} was estimated at 0.09, 0.1, and 0.2 year^{-1} for beluga, Russian and stellate sturgeon, respectively. These values are in the range of F levels associated with

Table 2 Female life history traits for three principal Caspian Sea sturgeons.

Trait	Beluga sturgeon (*Huso huso*)	Stellate sturgeon (*Acipenser stellatus*)	Russian sturgeon (*Acipenser gldenstdti*)
Natural mortality (year^{-1}) (Hoenig 1983)	0.05	0.14	0.07
Age at maturity	16 years (range 15–18)	10 years (range 8–15)	14 years (range 10–20)
Fecundity	–	133 000 x 10 years	–
	350 000 x 16 years	229 000 x 16 years	160 000 x 16 years
	1 000 000 x 30 years	430 000 x 30 years	400 000 x 30 years
	2 400 000 x 50 years	–	1 200 000 x 50 years
Longevity	> 80 years	30 years	60 years
Spawning Interval	4 years	2 years	4 years

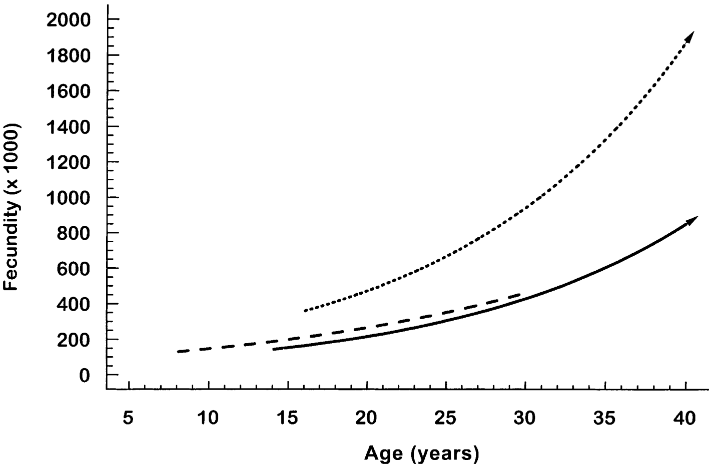

Figure 6 Fecundity vs. age relationships for beluga (dotted line), stellate (dashed line) and Russian sturgeon (solid line). Arrow heads indicate that beluga and Russian sturgeon continue to reproduce beyond 40 years. Data from VNIRO and Doroshov 1985.

past management strategy of conserving 40% of each spawning run. Based upon different spawning frequencies, this practice would result in realized *F*-values of 0.16 for beluga and Russian sturgeon and 0.22 year^{-1} for stellate sturgeon. Under an unregulated situation where no spawning refuge from exploitation is allowed, F_{50} values were estimated at 0.03 for beluga and Russian sturgeon and 0.1 year^{-1} for stellate sturgeon. Because poachers are believed to be removing 50% of all mature sturgeon per year ($F = 0.9$ year^{-1} under an assumption of negligible natural mortality), population crashes are imminent for all three species. This is a conservative prediction because the model does not consider the harvesting of immature sturgeons, which is well known to occur (Barannikova *et al.* 1995; De Meulenaer and Raymakers 1996).

Increased dependence upon hatcheries

The rapid decrease in spawning stock has developed into an ironic tragedy. Historically, with the exception of beluga, hatchery contributions were small compared with natural reproduction; however, today artificial reproduction is believed critical to conservation of the three principal stocks of Caspian Sea sturgeons. Unfortunately, spawning females have become so scarce that they can no longer supply the needs of the remaining sturgeon plants. Rough estimates of the current rate of contribution of hatchery-produced sturgeon to overall stocks are 26–28% for Russian sturgeon, 30% for stellate sturgeon and > 90% for beluga sturgeon (A. Ivanov, VNIRO, Moscow, unpublished data).

The outlook for sturgeon fisheries in the Caspian Sea is unpredictable. Five countries (Russia, Kazakhstan, Azerbaidzhan, Iran and Turkmenia) have been unable to engage in effective negotiations to control harvests in the Caspian Sea (De Meulanaer and Raymaker 1996). Despite exploitation of sturgeon by all countries, only Russia (11 plants) and Iran (one known plant) support the population through hatchery stocking. Effective (enforceable) laws against poaching are absent in all countries. If all poaching could be halted, an unlikely event, we predict that harvest levels similar to those taken in

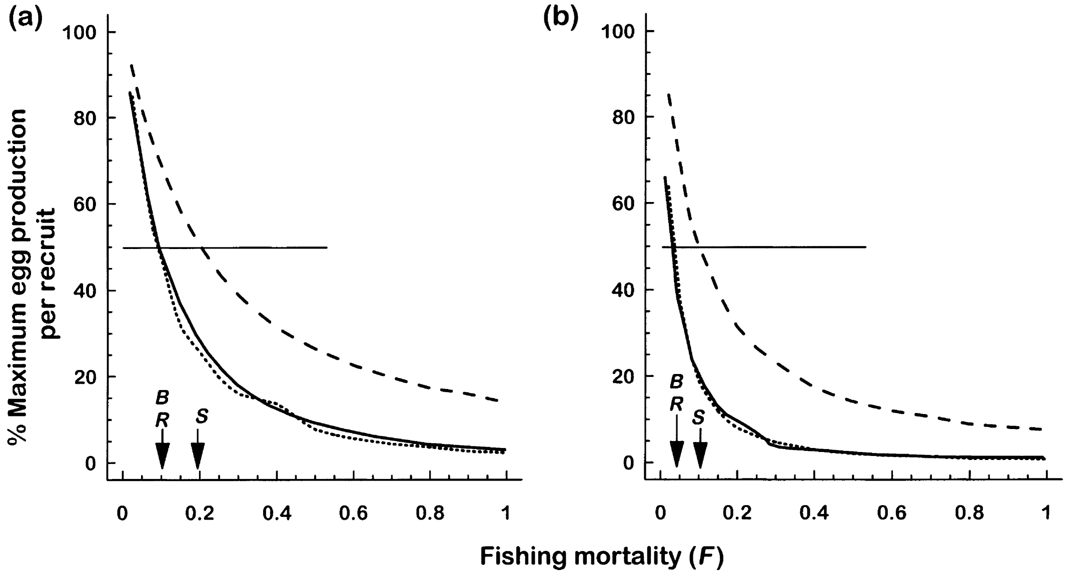

Figure 7 Percent of maximum egg per recruit vs. instantaneous fishing mortality rate (F) for two fishing scenarios for beluga (dotted line), stellate (dashed line) and Russian sturgeon (solid line). (a) Scenario 1 is for exclusive exploitation of spawning run females. (b) Scenario 2 is for exploitation on all segments of the mature population (e.g. exploitation in the Caspian Sea). Criteria for sustainability, 50% of unexploited population egg production, is shown by the horizontal line in each plot. Arrows indicate F_{50} (F resulting in 50% of maximum eggs per recruit (EPR) that would occur in unexploited stock) for beluga (B), Russian (R) and stellate (S) sturgeons. See text and Table 2 for further details.

the 1960s would only be attained after a greater than 30-year period of population recovery (Secor and Waldman 1999). Since 1998, exports of caviar have been regulated under the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES) (US Federal Register 1999, Vol. 64 (233): 68113). Regulations require the country of origin to certify that exported caviar is not harming local stocks. In all likelihood, this will not halt the decline of Caspian Sea sturgeons. In particular, beluga sturgeon are imperilled by the combined factors of historical loss of spawning grounds and current overexploitation. The current SRP for beluga is completely dysfunctional due to the unavailability of broodstock (Birstein *et al.* 1997). No longer can the SRP replace individuals at the same rate as they are being harvested.

Aquaculture-based sturgeon restoration

Development of commercial sturgeon aquaculture has been pursued internationally, particularly for Siberian sturgeon (*A. baeri*), white sturgeon (*A. transmontanus*) and a hybrid of beluga and sterlet sturgeon, the bester (De Meulanaer and Raymakers 1996). White sturgeon commercialization has been extremely rapid over the past decade (Anonymous 1997). Production of white sturgeon by two US companies in 1997 exceeded 900 tonnes, an equivalent level to peak historical landings for this species. White sturgeons are cultured intensively for 2 years until they attain a size of 2–4 kg. Their flesh is marketed as a gourmet item to restaurants. Rearing white sturgeon for caviar production is also quite feasible and, in some cases, profitable (Logan *et al.* 1995). Cultured bester roe and Siberian sturgeon roe also supplies caviar markets (Nikolaev 1985; Hjul 1996). The success of the white sturgeon aquaculture industry required government support for research and development and multimillion-dollar start-up costs by the companies involved. Despite these constraints, it is quite clear that aquaculture represents a powerful means to supply sturgeon meat and caviar markets, and to achieve conservation aims through broodstock maintenance and hatchery programmes.

The American alligator provides a useful case study on the possible benefits of aquaculture to conservation of endangered species. The alligator is highly valued for its skin and meat. Although protected by US federal laws since 1967, populations experienced considerable poaching. By the mid-1970s, the alligators began to rebound and in the 1980s tightly controlled programmes of harvesting and farming were initiated. Rapid recovery of alligator populations in the south-east US is attributed to a dual policy of controlling harvests while promoting alligator farming as a means of satisfying the demand of skin and meat markets. In 1995, alligator farming in Florida yielded more than 26 000 skins (Anonymous 1996). Conceivably, culture of sturgeon could also alleviate demand for illegally harvested caviar (Burtsev 1997).

Beyond benefits for commercial and conservation aims, aquaculture also conveys risks related to transmission of disease, accidental release and interactions of cultured fish with wild ones, and environmental damage due to aquaculture plant construction and discharges. Additionally, aquaculture conveys great economic risk because fish production is strongly related to maintenance of water quality conditions and plant failures can result in large losses of fish despite previous investments in their production. Disease and accidental releases are key problems identified for alligator, salmon and other aquaculture industries. The white sturgeon for instance harbours two *Herpes* viruses in culture (Watson *et al.* 1995). Should white sturgeon aquaculture develop in regions where depleted populations of sturgeons reside, transmission of the disease could contribute to further declines in those populations.

Interactions of accidentally released cultured sturgeons with wild sturgeon can result in hybridization if the two sturgeons are separate species. Hybridogenesis is well known for sturgeons, and many hybrids are reproductively viable. If the species is the same, releases could cause deleterious effects to the endemic population due to ecological and genetic interactions. For instance, the Hudson River (US) has been ecologically altered through the accidental introduction of zebra mussel (Strayer *et al.* 1998, 1999), which have not yet invaded other US Atlantic estuaries. Federal scientists have undertaken careful measures to quarantine and treat Hudson River sturgeon used for broodstock culture to reduce the risk of zebra mussel introduction into other systems.

Hatchery-based stocking programmes

The Caspian Sea SRP demonstrated that aquaculture can yield millions of 0+ juveniles for stocking into natural systems. Beyond the technical and economical issues of hatchery production of juveniles, lie principal and often neglected questions of the efficiency with which stocked fish recruit into an endemic breeding population or initiate their own spawning population. There are also important issues related to the ecological and genetic consequences of their interactions with wild sturgeon.

In systems where sturgeons are depleted or extirpated, the primary issue is whether the system contains sufficient habitat for spawning, feeding, environmental and predation refugia, and migration. In the former Soviet Union, concern about spawning habitat prompted a large survey of available spawning habitat prior to construction of the Volgograd Dam. Spawning grounds were later enhanced by construction and maintenance of large bars of cobble below the Volgograd Dam. Careful selection of times and places can reduce loss of released juveniles due to predation. For instance, by stocking Russian sturgeon directly in brackish ‘nursery’ areas of the Caspian Sea rather than in the Volga River, predation by large riverine walleye perch *Stizostedion lucioperca* and giant catfish *Silurus glanis Siluridae* was precluded. An important consideration in North American systems is the past introduction of exotic piscivores in many systems. In the Chesapeake Bay, introduced largemouth bass *Micropterus salmoides Centrarchidae*, and channel catfish *Ictalurus punctatus Ictaluridae* could cause large mortalities on stocked sturgeons if released at a small size. Migration corridors are a principal problem in restoring sturgeons because fish ladders are ineffective in passing sturgeons through dams. A fish ladder appropriately scaled in size for sturgeons was constructed for the Volgograd Dam. With the exception of sterlet sturgeons, very few sturgeons utilized the passage.

Perhaps the most difficult ecological issue related to restoration is homing. With the exception of salmonids (Hasler and Scholz 1983), homing mechanisms and behaviours are poorly understood in fishes. Due to long generation times, homing will be especially difficult to understand for sturgeons. It is as yet unknown whether hatchery-produced juveniles will return as adults to systems into which they were originally stocked 5–25 years previously. Biochemical markers of parentage would be a particularly useful means to identify the progeny of the relatively few individuals used by hatchery programmes.

For large releases of juveniles from limited parentage, negative impacts due to competition or future genetic contributions should be considered (Tringali and Bert 1998). Protocols for

Atlantic and white sturgeon stocking programmes have been promulgated by government agencies to ensure that stocked sturgeon represent sufficient genetic diversity to reduce the probability of inbreeding (St. Pierre 1994; Kincaid *et al.* 1997). Potential ecological effects can be evaluated through bioenergetic modelling, potential habitat inventories and experimental stockings (Secor *et al.* 2000). For large releases of juveniles, straying could contribute to genetic and ecological impacts to adjacent depleted populations.

Recommendations for aquaculture-based sturgeon restoration

Aquaculture cannot be viewed as a risk-free solution to sturgeon restoration. Nevertheless, there exists very strong justification to pursue aquaculture-based restoration for many sturgeon populations. Sturgeon abundance has been depleted historically through overfishing and habitat degradation. The former Soviet Union showed prudent management of its sturgeon fisheries by escapement-based regulation. Exploitation is now tightly restricted in North America and Europe, and caviar imports from the Caspian Sea and elsewhere are controlled under CITES (Appendix II listing). Despite these restrictions many species and populations remain extremely depressed in abundance and may not be capable of recovery without the aid of deliberate releases of hatchery-produced sturgeons. As indicated above, exploitation is largely unregulated in the Caspian Sea and throughout most of the former Soviet Union and hatcheries are now viewed as essential for conservation (Birstein *et al.* 1997).

Initiation of a hatchery-based restoration programme must occur concomitantly with research on, and recovery of, lost habitats. As an extreme example, it would be a waste of resources to stock millions of juveniles, yet not to have spawning habitats for those fish to return to as adults. In many developed countries, there have been positive trends in habitat improvement, brought about by waste water and pollution abatement programmes which have significantly improved water quality (Waldman 2000). On the other hand, sedimentation, river barriers and pollution have substantially reduced spawning habitats for sturgeons worldwide, and in some systems spawning habitats may need to be artificially enhanced.

Risks of negative ecological, genetic or economic impacts of aquaculture can be reduced by a careful survey of genetic inventories of systems into which stocking occurs. Historical documentation of sturgeon populations should be undertaken together with interview- and fieldwork-based studies to determine if reproduction might still occur. If natal fish can be identified, biochemical studies should be undertaken to catalogue genetic diversity within the population (Waldman and Wirgin 1998). Whether water quality and forage base in a system is capable of supporting stocked fish can initially be examined through bioenergetic assessments. Initial small-scale 'experimental' releases are especially valuable to assess losses of stocked fish due to predation, competitive interactions with endemic sturgeons and other fishes, and possible habitat constraints (Secor *et al.* 2000). Indeed, in systems where sturgeons are extirpated, deliberate releases will be the only means to evaluate whether sturgeons can continue to undertake feeding, migration, homing and spawning.

Despite the historical controversy on use of aquaculture in maintenance and restoration of fish stocks, catalyzing restoration through deliberate releases of hatchery-produced sturgeons merits serious consideration. By learning from past mistakes and understanding what is feasible, risks can be minimized through precautionary approaches that: (i) inventory biological and genetic resources prior to initiation of a recovery programme; (ii) assess whether suitable habitat still remains through bioenergetic models and small-scale feasibility stockings; (iii) maximize genetic diversity of stocked juveniles as much as possible; (iv) undergo concomitant programmes of habitat restoration and harvest control; and (v) monitor the efficiency with which hatchery-produced fish recruit into a spawning population. It should be apparent that for these aims to be fulfilled, greater resources of finance and effort will be needed than those required for the production of the thousands of juveniles alone. Beyond considerations of the important lessons from the Caspian Sea SRP, these aims represent a principal lesson from the history of stocking programmes in general: best begun well or not begun at all.

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References

Anonymous (1996) Good money from skins for U.S. alligator farms. *Fish Farming International* **23**, 12.

Anonymous (1997) California joint venture project will produce sturgeon caviar. *Fish Farming International* **24**, 6.

ASMFC (1990) *Atlantic States Marine Commission Fishery Management Plan for Atlantic Sturgeon.* Atlantic States Marine Commission Fishery Management, Washington DC.

Barannikova I.A (1995) Measures to maintain sturgeon fisheries under conditions of environmental changes. In: *Proceedings of the International Symposium on Sturgeons, Moscow, September 1993* (eds A.D. Gershanovich and T.I.J. Smith). VNIRO Publishing, Moscow, pp. 131–136.

Barannikova I.A., Berdichevskij L.S. and Sokolov L.I (1979) Scientific basis of sturgeon reproduction and culture and prospects of its development in the USSR seas. In: *Biological Basis of Sturgeon Culture in USSR Water.* Nauka Press, Moscow, pp. 5–22. (in Russian)

Barannikova I.A., Burtsev I.A., Vlasenko A.D., Gershanovich A.D., Makarov E.V. and Chebanov M.S (1995) Sturgeon fisheries in Russia. In: *Proceedings of the International Symposium on Sturgeons, Moscow, September 1993* (eds A.D. Gershanovich and T.I.J. Smith) VNIRO Publishing, Moscow, pp. 124–130.

Berdichevskij L.S. and Petrenko I.N (1979) Biological basis of species composition in the Caspian Sea and its regulation. In: *Biological Basis of Sturgeon Culture in USSR Water.* Nauka Press, Moscow, pp. 34–48. (in Russian)

Berezovsky A.I (1933) On the problem of effectiveness and methods of stock reconstruction in anadromous fish. *Fisheries (Rybnoye Khozyastvo)* **2**, 5–17. (in Russian)

Birstein V.J., Bemis W.E. and Waldman J.R (1997) The threatened status of acipenseriform fishes: a summary. *Environmental Biology of Fishes* **48**, 427–435.

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

Burtsev I.A (1997) *Bester in aquaculture*, Vol 17. In: *Sturgeon Stocks and Caviar Trade Workshop Proceedings* (eds V.J. Birstein and A. Bauer). Occasional Paper. IUCN Survival Commission, Gland, Switzerland, pp. 35–43.

Chalikov B.G (1936) Modern statue of sturgeon culture in the lower Volga River. In: *First all Caspian Fish Culture Conference,* Part I. Moscow, pp. 67–68. (in Russian)

Cuenco M.L (1994) A model of an internally supplemented population. *Transactions of the American Fisheries Society* **123**, 277–288.

De Meulenaer T. and Raymakers C (1996) Sturgeons of the Caspian Sea and the international trade in caviar. TRAFFIC International, Cambridge, UK.

Derjavin A.N (1947) *Reproducing of the Sturgeon Stocks.* Izdatelstvo Akademii Nauk Azerbijanskoi SSR (Azerbijan Academy of Science Press), Baku, 247 pp. (in Russian)

Doroshov S.I (1985) Biology and culture of sturgeons, Acipenseriformes. In: *Recent Advances in Aquaculture,* Vol 2. (eds J.F. Muirs and R.J. Roberts), Westview Press, Boulder, pp. 251–274.

Gall G.A.E (1987) Inbreeding. In: *Population Genetics and Fishery Management* (eds N. Ryman and F. Utter), Washington Sea Grant, University of Washington, Seattle, pp. 47–87.

Gerbilsky N.L (1956) Histological analysis of transfers between ontogeny stages in fishes. In: *Problems of Modern Embryology.* Leningrad St University of Publishers, Leningrad, pp. 122–128. (in Russian)

Gerbilsky N.L (1972) The theory of biological progress of acipenserids and its application for sturgeon management practice. In: *Sturgeons and Problems of Sturgeon Culture* (eds Y.Y. Marti and I.A. Barannikova), Pitschevaya Promyshlennost Publishers, Moscow, pp. 101–111. (in Russian)

Gershanovich A.D., Pegasov V.A. and Shatunovskij M.I (1987) *Ecology and physiology of sturgeon fingerlings.* Nauka Press, Moscow. (in Russian).

Grogan C.S. and Boreman J (1998) Estimating the probability that historical populations of fish species are now extirpated. *North American Journal of Fisheries Management* **18**, 522–529.

Hasler A.D. and Scholz A.T (1983) *Olfactory Imprinting and Homing in Salmon.* Springer-Verlag, Berlin.

Hjul P (1996) French farms are to market fish of kings. *Seafood International* **11**, 60–62.

Hoenig J.M (1983) Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* **82**, 898–902.

Houde E.D (1994) Differences between marine and freshwater fish larvae: implications for recruitment. *ICES Journal of Marine Science* **51**, 91–97.

Kahnle A.W., Hattala K.A., McKown K.A. *et al.* (1998) *Stock Status of Atlantic Sturgeon of Atlantic Coast Estuaries.* Atlantic States Marine Fisheries Commission, Washington, DC.

Khodorevskaya R.P., Dovgopol G.F., Zhuravleva O.L. and Vlasenko A (1995) Formation of commercial sturgeon (Acipenseridae) stock. In: *Proceedings of the International Symposium on Sturgeons, Moscow, September 1993.* A.D. Gershanovich and T.I.J. Smith, eds. VNIRO Publishers, Moscow, pp. 137–150.

Khodorevskaya R.P., Dovgopol G.F., Zhuravleva O.L. and Vlasenko A (1997) Present status of stocks of sturgeons in the Caspian Sea basin. *Environmental Biology of Fishes* **48**, 209–219.

Kincaid H.L., Gray M.J., Mengel L.J. and Brimm S (1997) *National Fish Strain Registry. Species Tables of Reported Strains and Broodstocks.* Biological Resources Division, U.S. Geological Service, Wellsboro, Pennsylvania. NTIS Accession no. PB98142441.

Kozhin N.I (1951) The coefficient of commercial returning rate. In: *Reproduction of Anadromous and Semi-Anadromous Fish of the Caspian Sea.* VNIRO Proceedings 19. Pitschevaya Promyshlennost Publishers, Moscow, pp. 128–133. (in Russian)

Kozhin N.I (1964) Sturgeons of the USSR and their reproduction. In: *Sturgeons of the Southern Seas of the USSR.* VNIRO Proceedings 52. VNIRO Publishers, Moscow, pp. 32–59. (in Russian)

Kozhin N.I., Gerbilskij N.L. and Kazanskij B.N (1963) Biotechnology of sturgeon reproduction and principal scheme of sturgeon plant. In: *Sturgeon Culture in the USSR*. Academic Nauk Publishers, Moscow, pp. 14–31. (in Russian)

Leach G.C (1920) *Artificial propagation of sturgeon, review of sturgeon culture in the United States.* Report to US Fish Commission 1919, 3–5.

Letichevsky M.A (1954) *Commercial fish culture in the Volga-Caspian district.* Newspaper Volga-Publisher, Astrakhan. (in Russian)

Levin A.V (1995) Russian sturgeon, *Acipenser güldenstädti* Brandt, stocking in the Volgo-Caspian basin. In: *Proceedings of the International Symposium on Sturgeons, Moscow, September 1993*. A.D. Gershanovich and T.I.J., eds. VNIRO, Moscow, pp. 178–188.

Logan S.H., Johnston W.E. and Doroshov S.I (1995) Economics of joint production of sturgeon (*Acipenser transmontanus* Richardson) and roe for caviar. *Aquaculture* **130**, 299–316.

Makarov E.V (1970) Estimation of dynamics and structure of Azov Sea sturgeons. *VNIRO Proceedings*.

Moscow **71**, 96–156. (in Russian)

Marakov E.V (1964) Evaluation of the productive activity of the hatcheries of Acipenseridae reared at the hatcheries of the Don River. In: *Sturgeons of the Southern Seas of the USSR*. VNIRO Proceedings 56. VNIRO Publishers, Moscow, pp. 141–170. (in Russian)

Milstein V.V (1971) Centenary of sturgeon culture. In: *Sturgeons of the USSR and Their Reproduction*, Nauka Press, Moscow (in Russian), pp. 5–13.

Murawski S.A. and Pacheco A.L (1977) Biological and fisheries data on Atlantic sturgeon, *Acipenser oxyrhynchus* (Mitchill). National Marine Fisheries Service, NOAA, Highlands, NJ.

Nikolaev A.I (1985) *Growth, Survival and Physiologo-biochemical Characteristics of Selected Forms of the Bester*. PhD Thesis, University of Moscow. (in Russian)

Polyaninova A.A (1979) Circadian feeding rhythm and rations of Russian sturgeon and Stellate in the Northern Caspian Sea. In: *Biological Basis of Sturgeon Culture in USSR Water*. Nauka, Moscow, pp. 170–180. (in Russian)

Polyaninova A.A. and Molodtseva A.I (1995) The benthos-sturgeon feeding relationship for the Caspian Sea. In: *Proceedings of the International Symposium on Sturgeons, Moscow, September 1993*. A.D. Gershanovich and T.I.J. Smith, eds. VNIRO Publishing, Moscow, pp. 151–157.

Raspopov V.M., Vershchev P.V. and Novikova A.S (1995) The relationship between sturgeon fecundity and reproduction in the Volga River. In: *Proceedings of the International Symposium on Sturgeons, Moscow, September 1993*. A.D. Gershanovich and T.I.J. Smith, eds. VNIRO Publishing, Moscow, pp. 158–163.

Ryder J.A (1890) The sturgeon and sturgeon industries of the eastern coast of the U.S., with an account of experiments bearing upon sturgeon culture. *Bulletin of the US Fisheries Commission* **1888**, 231–281.

Sadlaev K.A. and Kipper Z.M (1964) The present state of the artificial reproduction of Acipenseridae and new solutions of the technical problems. In: *Sturgeons of the Southern Seas of the USSR.* VNIRO Proceedings 56. VNIRO Publishers, Moscow, pp. 237–254. (in Russian)

Secor D.H (1996) *Chesapeake Bay Atlantic sturgeon: Current status and future recovery.* Chesapeake Biological Laboratory, Solomons, MD.

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

Secor D.H., Niklitschek E.J., Stevenson J.S. *et al.* (2000) Dispersal and growth of yearling Atlantic sturgeon *Acipenser oxyrinchus* released into the Chesapeake Bay. *Fisheries Bulletin* **98**, 800–810.

Secor D.H. and Waldman J.R (1999) Historical abundance of Delaware Bay Atlantic sturgeon and potential rate of recovery. In: *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals. American Fisheries Society Symposium* **23**, 203–216.

Shagaeva V.G., Nikol'skaya M.P., Akimova N.V., Markov K.P. and Nikol'skaya N.G (1993) Investigations of early ontogenesis of the Volga River sturgeons (Acipenseridae) influenced by anthropogenic activity. *Journal of Ichthyology* **33**, 23–41.

Shorygin A.A (1952) *Feeding and Trophic Relationships of Fishes in the Caspian Sea*. Pitschevaya Promyshlennost Publishers, Moscow. (in Russian)

Soldatova E.V. and Rykova T.I (1979) *Data on Feeding of Russian Sturgeon and Use of Food Supply in the Middle Caspian Sea*. VNIRO Publishers, Moscow. (in Russian)

St. Pierre R.A (1994) *Breeding and Stocking Protocol for Cultured Atlantic Sturgeon.* Atlantic States Marine Fisheries Commission, Harrisburg, PA.

Strayer D.L., Caraco N.F., Cole J.J., Findlay S. and Pace M.L (1999) Transformation of freshwater ecosystems by bivalves. *Bioscience* **49**, 19–27.

Strayer D.L., Smith L.C. and Hunter D.C (1998) Effects of the zebra mussel (*Dreissena polymorpha*) invasion on the macrobenthos of the freshwater tidal Hudson River. *Canadian Journal of Fisheries and Aquatic Science* **76**, 419–425.

Tikhij M.I (1925) On the fish-culturing coefficient. *Proceedings of the Federal Institute of Agronomy, Moscow*, **3**, 17–24. (in Russian)

Tringali M.D. and Bert T.M (1998) Risk to genetic effective population size should be an important consideration in stock-enhancement programs. *Bulletin of Marine Science* **62**, 641–659.

Veltitischeva I.F (1955) *Feeding of Sturgeon Fingerlings During Artificial Rearing and Prospects for Increase of Pond Productivity.* PhD Thesis, University of Baku. (in Russian)

Verina I.P. and Peseridi N.E (1979) On the sturgeon spawning grounds conditions in the Ural River. In: *Sturgeon Culture of Inland Waters.* Caspian Fisheries Institute, Astrakhan, pp. 33–34. (in Russian)

Veschev P.V (1998) Influence of principal factors on the efficiency of natural reproduction of the Volga Stellate sturgeon *Acipenser stellatus*. *Russian Journal of Ecology* **29**, 310–315.

Veshchev P.V., Vlasenko A.D. and Dovgopol G.F (1993) Analysis of the commercial return coefficients of the Stellate Sturgeon, *Acipenser stellatus*. *Journal of Ichthyology* **3**, 56–62.

Vodovozova M.A (1971) Data and sturgeon fingerling tagging at the Kurinsk sturgeon plant. In: *Sturgeons of the USSR and their Reproduction,* TsNiorKh Publishers, Moscow **3**, 114–119. (in Russian)

Waldman J.R (1995) Sturgeons and paddlefishes: a convergence of biology, politics, and greed. *Fisheries* **20**, 20–21.

Waldman J.R (2000) *Heartbeats in the muck: a Dramatic Look at the History, Sea Life, and Environment of New York Harbor.* The Lyons Press, New York.

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

Waldman J. and Wirgin I (1998) Status and restoration options for Atlantic sturgeon in North America. *Conservation Biology* **12**, 631–638.

Watson L.R., Yun S.C., Groff J.M. and Hedrick R.P (1995) Characteristics and pathogenecity of a noval herpesvirus isolated from adult and subadult white sturgeon *Acipenser transmontanus*. *Diseases of Aquatic Organisms* **22**, 199–210.