



Genetic monitoring for the successful re-stocking of a critically endangered diadromous fish with low diversity

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ABSTRACT

The success of conservation programs for genetically depleted species is challenging because survival and adaptive potential are thought to be promoted by genetic factors. Such programs are thus generally designed to minimize the risks associated with the loss of genetic diversity and inbreeding. However, few empirical studies have explored the outcomes of these strategies in released individuals once they are in the wild. The only remaining population of the critically endangered European sturgeon, *Acipenser sturio*, is located in the Gironde estuary (France) after continued demographic decline over the last century. A restoration program that was initiated 20 years ago has resulted in more than one and a half million individuals being stocked in the last decade. Because the captive broodstock is composed of a small number of breeders ($N = 78$ in 2007, which decreased to $N = 21$ in early 2017), maintaining genetic diversity and minimizing inbreeding are crucial for the successful recovery of this species. Based on the analysis of 18 microsatellite markers, we examined the patterns of genetic diversity of fish from the last wild cohorts and broodstock as well as of captive-born fish recaptured after stocking. Our results support the hypothesis of a genetic bottleneck with low genetic diversity and a highly reduced effective population size in wild-born *A. sturio*. While the original diversity is depleted, clearly challenging conservation strategies, we found that genetic erosion has been limited during re-stocking (96% of the broodstock and 90% of the wild fish original diversity has been maintained in recaptured individuals). Results further suggest that the genetics of the parents is not the main factor explaining recapture probability: progeny issued from both related and not related parent pairs were found in recaptures years after their release. For broodstock management, kinship between parents is identified as a relevant parameter to be considered to avoid inbreeding. This study suggests that a multi-year stocking strategy associated with sufficiently high numbers of unrelated parent pairs may be the best strategy for the successful reintroduction and preservation of genetic diversity for *A. sturio*. These findings are encouraging for the species and further highlights the relevance of careful genetic monitoring for the long-term conservation of genetically depleted species, which are more vulnerable to genetic effects.

1. Introduction

Captive breeding and re-stocking have become important tools for the conservation of populations and species facing high extinction risks in the wild. Conservation programs for such species are especially challenging because of the accumulation of genetic effects usually associated with small and declining populations (Ralls and Ballou, 1986; Caughley, 1994; Frankham, 1996; Lacy, 1997; Frankham, 2010; Rosenfeld, 2014). The subset of founders used to build a captive broodstock is often genetically impoverished by losses of genetic diversity due to past demographic bottlenecks and by posterior founder effects associated with captivity (Gilpin and Soulé, 1986; Frankham,

2005). This reduced diversity, along with a low initial number of breeders, an unequal sex ratio and a generally low probability of obtaining additional founders issued from the wild, tends to further reduce the effective population size (N_e), increasing the chances of inbreeding depression through drift (Jamieson, 2011; Naish et al., 2013). While such programs typically aim to supplement wild remnant populations, genetic issues in captive stocks may therefore compromise the survival and adaptive potential of individuals once they are released into the wild (Franklin and Frankham, 1998; Lynch and Lande, 1998; Bijlsma et al., 2000).

For these reasons, most ex situ captive breeding programs have seriously considered the significant role of genetic features, and several

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management options have been considered essential to minimize genetic effects. For genetically-depleted species, the most commonly used strategies for the success of such programs include preserving the original genetic diversity of the wild population as much as possible, maintaining the effective population size as high as possible, and minimizing kinship and inbreeding (i.e., favoring unrelated mating pairs) to maximize adaptive potential after stocking (Pollard and Flagg, 2004; Russello and Amato, 2004; Frankham, 2010; Witzemberger and Hochkirch, 2011; Allendorf et al., 2013; Duong et al., 2013; Fisch et al., 2015; Willoughby et al., 2015). The effects of re-stocking on the genetic diversity of the wild population can be influenced by several factors, such as the effective population size of the captive population and the relative contribution of breeders to progeny (Fraser, 2008). The effective breeding number (Neb) and the kinship between breeders are therefore among the most widely used parameters to monitor genetic variation in conservation programs (Alderson, 1991; Wang, 1997; Caballero and Toro, 2000). In addition, the genetic characteristics of released progeny at the time of mating may be quite different from the characteristics just after release due to natural selection pressures in the wild and differential post-release mortality. Reproductive and re-stocking success are thus usually assessed indirectly by comparison of the genetic composition of broodstock and progeny after re-stocking and by estimating the relative survival of progeny once in the wild (Naish et al., 2008; Darden and Denson, 2013; Perrier et al., 2013; Schreier et al., 2015; Welsh et al., 2015).

While most studies have described the genetic patterns of the captive population, there have been only a few empirical studies that tested how post-release mortality affects genetic diversity and how breeding strategy may be translated into the effective survival of future generations through re-stocking (Schwartz et al., 2007; Williams and Hoffman, 2009; Schreier et al., 2015; Attard et al., 2016). In an extensive review, Witzemberger and Hochkirch (2011) noted that most assessments remain incomplete, lacking some important demographic (e.g., size of the captive and wild populations or number of founders for captive populations), genetic (e.g., effective population size or inbreeding coefficient) or breeding (number and genetic characteristics of breeders, pedigree information, or mating schemes), information that is required to reach thoughtful conclusions. Often, comparisons with the original populations are not possible. More research is needed to quantify the potential benefit of genetic management options and to identify potential proxies of post-release survival in the wild (Moyle et al., 2003; Fraser, 2008; Hedrick and Fredrickson, 2008; Jager et al., 2008). The assessment of genetic effects is particularly relevant for species with low diversity and reduced population size for which long-term persistence will depend on how these effects impact the next released generations.

Sturgeons are one of the oldest families of fishes in existence, valued around the world for their precious roe. They are long-lived species, and some species are anadromous and do not reproduce annually, which makes them particularly vulnerable to population decline (Jager et al., 2008). Eighty-five percent of sturgeon species are currently at risk of extinction, making them the most threatened taxon on the IUCN Red List of Threatened Species™. The latest update of the Red List assessed the status of 17 sturgeon species from all over Europe and Asia and found that all of them were threatened (Birstein et al., 1997). Although most populations have low chances of survival without breeding and re-stocking plans, ex situ conservation programs are challenging, because efforts must continue for a long period of time. Conservation efforts for these species have therefore mostly focused on in situ conservation and the supplementation of natural populations through the artificial reproduction of wild breeders and re-stocking (Gesner et al., 2010), while only a few species are under ex situ conservation programs *sensu stricto* (i.e., *A. sinensis*, Qiwei (2010); *A. oxyrinchus*, Kolman et al. (2011); *A. naccarii*, Boscari and Congiu (2014); and *A. sturio*, Williot et al. (2007)). Numerous studies have genetically characterized captive sturgeon populations, but only a few have examined the genetics of released

cohorts after years of re-stocking. However, this is relevant for re-introduction efforts to estimate the survival rates and to optimize ex situ stock management (Drauch and Rhodes, 2007; Boscari and Congiu, 2014; Marranca et al., 2015; Schreier et al., 2015; Welsh et al., 2015).

Although it was one of the most widespread sturgeon species historically found in Western Europe (Lassalle et al., 2010), the European sturgeon (*Acipenser sturio* L.1758) is now one of the most threatened fish species in Europe (Rochard et al., 1990), being classified as critically endangered by the IUCN since 1992 (Gesner et al., 2010). *A. sturio* has suffered a precipitous decline during the second half of the twentieth century due to anthropogenic factors such as pollution, over-exploitation, and degradation of its natural reproduction habitats as well as its complex life cycle in different environments (Rochard et al., 1990). At present, only one natural population survives in the Gironde estuary in France (Atlantic coast). The last wild reproduction was observed in 1994 (Rochard et al., 1990; Williot et al., 2002; Lochet et al., 2004) and, having seen the rarity of its natural spawning (Castelnaud et al., 1991), efforts to reestablish the population have been initiated. An ex situ stock was constituted in the early 1990s from wild-captured specimens to secure the future of this species and to support the natural population (Williot et al., 1997; Williot et al., 2007; Chassaing, 2010). A re-stocking program was started in 1995 (Williot et al., 2005) and has expanded intensively since 2007 when the understanding of handling problems (i.e. rearing conditions, ovary maturation) for successful breeding has resulted in greater reproduction success (Williot and Chèvre 2011). Reproduction is assisted so that records are kept on all the breeders mating pairs that are performed. More than one and a half million larvae and juveniles have been released in the Gironde-Garonne-Dordogne watersheds since 1995. To assess the survival and re-stocking success, the stocked population has been intensively monitored from 2009 until now by sampling and individual marking campaigns in the Gironde Estuary (Acolas et al., 2011c). The genetic diversity of a small number of individuals of the current population of *A. sturio* was previously assessed using microsatellites (Ludwig et al., 2004; Berrebi and Cherbannel, 2011; Roques et al., 2016), while the genetic diversity of past samples was assessed using microsatellites and mtDNA markers (Ludwig et al., 2000; Chassaing, 2010; Chassaing et al., 2016; Chassaing et al., 2018). These previous studies documented low diversity through the last two centuries and an even lower current diversity in the Gironde remnant population. While these preliminary studies are limited in their abilities to precisely assess which future genetic-based strategies should be used, they put forward the challenging issue of a successful rescue for a species with such low genetic diversity.

To explore how careful genetic monitoring may help to enhance re-stocking success in species with reduced genetic diversity, we present this case of the European sturgeon. The fact that the entire captive breeding history is available for *A. sturio* makes it an ideal example for the evaluation of captive broodstock genetic diversity and the testing of predictions about the genetics of released cohorts after years of re-stocking. Using a set of 18 microsatellite loci (Roques et al., 2016), we aimed to 1) characterize the amount and genetic structure of the original genetic diversity available in the broodstock, which is composed of fish from the last natural cohorts (1970s-1994) and siblings from the first captive-born cohort (1995); 2) explore the genetic changes that occur with re-stocking by contrasting the patterns of genetic diversity between brood fish and captive-born progeny recaptured in the Gironde Estuary; 3) test how optimum breeding strategies may maintain genetic diversity and avoid inbreeding in progeny by testing the relationships of selected parameters (i.e., effective population size and relatedness between parents) on either inbreeding or recapture probability; and 4) address the implications and relevance of these results to the long term conservation and management of *A. sturio*.

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