



Interspecific hybridization in natural sturgeon populations of the Eastern Black Sea: the consequence of drastic population decline?

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Abstract

The eastern part of the Black Sea and its tributaries are suitable habitats for several sturgeon species, among which *Acipenser gueldenstaedtii*, *A. stellatus*, *A. nudiventris*, *A. persicus*, *A. sturio*, and *H. huso* are well documented. However, different threats have led these species to a dramatic decline, all of them are currently listed as *Critically Endangered*, and some *Locally Extinct*, in that area. We tested 94 wild sturgeon samples from the Black Sea and Rioni River by analyzing the mitochondrial Control Region and nuclear markers for hybrid identification. The data analyses (1) assessed mitochondrial diversity among samples, (2) identified their species, as well as (3) indicated instances of hybridization. The data collected, besides confirming a sharp decrease of catches of Beluga and Stellate sturgeon in recent years, also revealed four juvenile hybrids between Russian and Stellate sturgeon, providing the first evidence of natural interspecific hybridization in the Rioni. The present communication raises concerns about the status of sturgeon species in this area and underlines the urgent need for conservation programs to restore self-sustaining populations.

Keywords Sturgeons · Interspecific hybrids · *Acipenser gueldenstaedtii* · *Acipenser stellatus* · Rioni · Black Sea

Introduction

Sturgeons are among the most endangered species groups in the world according to the International Union for Conservation of Nature (IUCN 2010), with some of the most

imperiled species distributed in the Palearctic region. The Eastern part of the Black Sea and a major tributary in the Caucasus, the Rioni River, are known to have hosted in historical times at least five sturgeon species. The Russian sturgeon (*Acipenser gueldenstaedtii*), the Stellate sturgeon (*A. stellatus*), the Beluga sturgeon (*Huso huso*), the European sturgeon (*A. sturio*), and the Ship sturgeon (*A. nudiventris*) (Variadilis et al. 1998; Guchmanidze 2009). All of these are listed by IUCN as *Critically Endangered*, with European and Ship sturgeons also believed to be *Locally Extinct*, with wild populations considered to be extirpated from the Black Sea basin (Gessner et al. 2010; Muge et al. 2016).

The population decline is mainly caused by habitat degradation, including river damming and consequent high sediment flushing, overfishing, and pollution. Accurate historical or present assessments of population sizes are not available, but there are indications that sturgeon populations in the region have been in steep decline since the early 20th century (Beridze et al. 2021). Historically, the Rioni River in Georgia is known as one of the main sites for sturgeon spawning in this area (IUCN, 2010, www.iucnredlist.org) and it currently is the only remaining functional sturgeon

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spawning river of the Eastern Black Sea. This was confirmed by monitoring research on sturgeon recruitment in the Rioni conducted by Fauna & Flora International (FFI) between 2018 and 2020. Intensive field surveys, annually held from March until October, led to the discovery of multiple juvenile sturgeon specimens of various species. In addition, data collection with associated anglers on the Rioni led to the discovery of eight specimens of *A. nudiventris* in 2020. Their possible origin from an ongoing captive breeding program in Krasnodar (River Kuban) has been excluded, supporting the hypothesis of a relict reproductively active population of *A. nudiventris* in the Rioni River (Beridze et al. 2021).

This study reports the results of the genetic characterization of sturgeons collected within the first three years of these monitoring activities. Monitoring is ongoing, with the aim of evaluating the state of sturgeon populations of this area and verifying abundance of the different species, the purity of the animals and whether the sampled individuals

come from restocking activities or if they result from natural reproduction.

The collected data has unexpectedly indicated the occurrence of interspecific hybrids between two species of sturgeon historically known to reproduce in the Rioni River. The occurrence of interspecific hybridization events is discussed in light of implications for the conservation of natural sturgeon populations.

Materials and methods

Between 2018 and 2020, a sturgeon sampling campaign was carried out in the Georgian part of the Black Sea (BS) and Rioni River (RR = Rioni River; RM = Rioni mouth) (Fig. 1A) by FFI. A total of 94 tissue samples were collected (Table 1); captured animals, mostly juveniles, were immediately released after sampling.

Fig. 1 Study area, sampling locations, and haplotype relationships. **A** Geographic locations of sampled individuals (green = *A. stellatus*, yellow = *A. gueldenstaedtii*, and blue = *H. huso*). The inset map shows a continental view where the sampling area in the south-eastern Black Sea is framed. Satellite image obtained from Google Earth Pro V. 7.3.3.7786 (Google LLC, California, USA). **B–D** Haplotype networks, obtained with PopART 1.7 software, showing relationships among haplotypes in the three species detected. The size of pie charts is proportional to the corresponding haplotype frequency while colours indicate the sampling origin (Yellow = BS – Black Sea; Blue = RR – Rioni River, Red = RM – Rioni Mouth). Capital letters B, C, and D show haplotype relationships of *A. gueldenstaedtii* (GUE), *A. stellatus* (STE), and *H. huso* (HUS), respectively. **E** Schematic NJ tree representing haplotypic distances between species

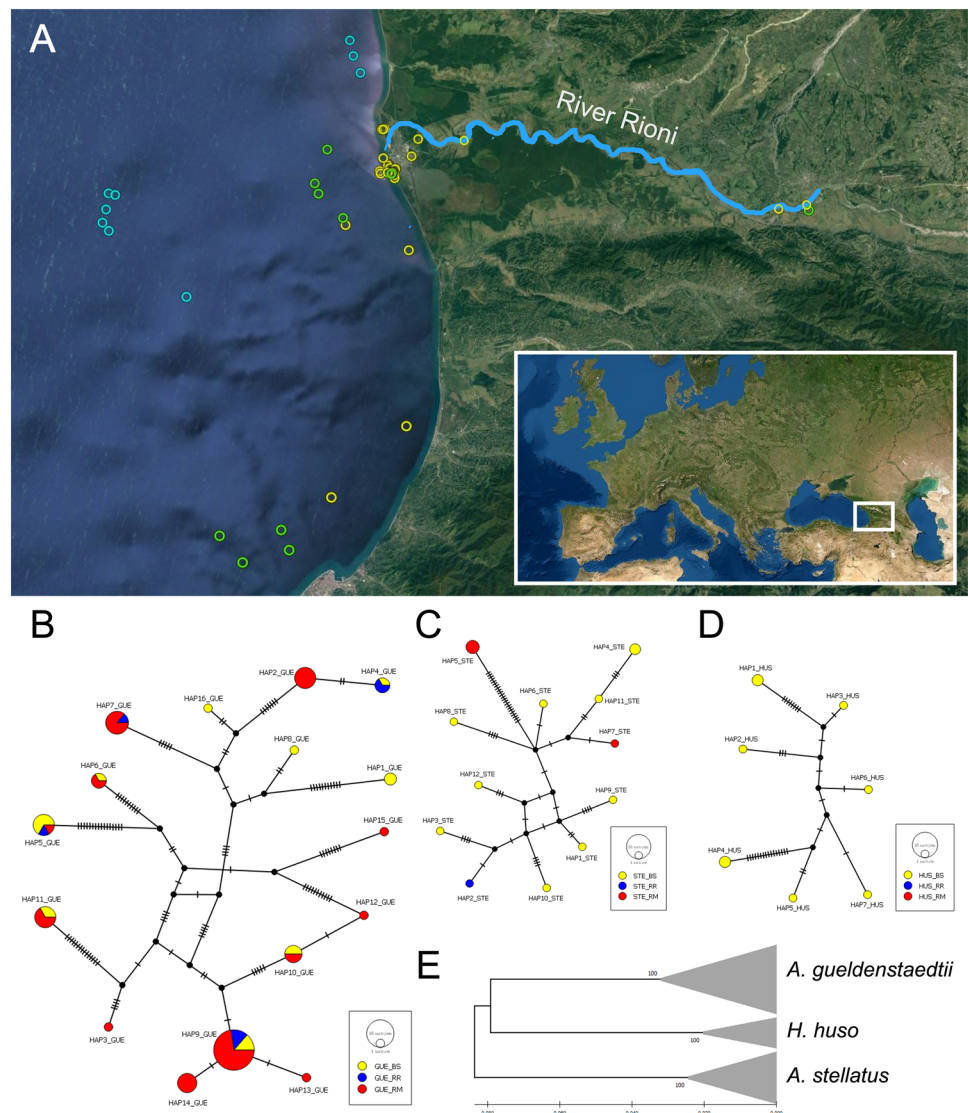


Table 1 Summary of the results from mitochondrial control region and diagnostic nuclear markers which specifically identify *A. stellatus* (ste), *A. gueldenstaedtii* (gue) and *H. huso* (hus)

Year	SampleID	mtDNA (present study)	Match with previously known haplotypes		Nuclear markers		
			Hap/Acc.n.	Occurrence	ste	gue	hus
2018	Ac91_BS	ste_Hap1	STE-HAP21	AS			
	Ac86_RR	ste_Hap2	STE-HAP108	CS			
	Ac89_BS	ste_Hap3	/	/			
	Ac92_BS, Ac105_BS	ste_Hap4	/	/			
	Ac94_RM, Ac114_RM	ste_Hap5	STE-HAP83	AS			
2019	Ac137_RM	ste_Hap5	STE-HAP83	AS			
	Ac101_BS	ste_Hap6	AF168525*	/			
	Ac115_RM	ste_Hap7	STE-HAP62	AS			
	Ac123_BS	ste_Hap8	AF168528*	/			
	Ac139_BS	ste_Hap9	AF168535*	/			
	Ac157_BS	ste_Hap10	STE-HAP15	CS/UR			
	Ac156_BS	ste_Hap11	STE_HAP64	DR/UR			
2020	Ac193_BS	ste_Hap12	STE_HAP9	AS			
2018	Ac70_BS, Ac76 ^h _BS	gue_Hap1	/	/			
	Ac93_RM, Ac95_RM	gue_Hap2	GUE_HAP137	BS			
	Ac96_RM	gue_Hap3	/	/			
	Ac112_RR	gue_Hap4	/	/			
	Ac113_RR	gue_Hap5	HQ7304710° GUE_HAP195	BS/CS			
2019	Ac125_BS	gue_Hap4	/	/			
	Ac120_BS	gue_Hap5	HQ7304710° GUE_HAP195	BS/CS			
	Ac116_RM, Ac136_RM	gue_Hap6	GUE_HAP101	AS/BS			
	Ac118_RR, Ac144_RM, Ac145_RM	gue_Hap7	/	/			
	Ac119_BS	gue_Hap8	GUE_HAP1	BS/CS			
	Ac121_BS, Ac135_RR, Ac143_RM, Ac146_RM, Ac147_RM, Ac148_RM	gue_Hap9	AF238725° GUE_HAP11	AS/BS			
	Ac127_BS	gue_Hap10	GUE_HAP140	DR			
	Ac128_BS, Ac140_RM	gue_Hap10	GUE_HAP140	DR			
	Ac133_BS	gue_Hap11	GUE_HAP135	BS			
	Ac150_RM	gue_Hap11	GUE_HAP135	BS			
	Ac198_RM, Ac200_RM, Ac203_RM, Ac205_RM	gue_Hap2	GUE_HAP137	BS			
	Ac196_RM	gue_Hap4	/	/			
	Ac189_BS, Ac194_BS, Ac210_BS, Ac201_RM	gue_Hap5	HQ7304710° GUE_HAP195	BS/CS			
Ac199_BS	gue_Hap6	GUE_HAP101	AS/BS				
Ac171_RM, Ac182_RM, Ac185_RM, Ac188_RM	gue_Hap7	/	/				
Ac204_BS, Ac209_BS, Ac165_RR, Ac161_RM, Ac163_RM, Ac168_RM, Ac172_RM, Ac174_RM, Ac177_RM, Ac179_RM, Ac181_RM, Ac183_RM, Ac187_RM, Ac202_RM, Ac208_RM	gue_Hap9	AF238725° GUE_HAP11	AS/BS				
Ac160_RR	gue_Hap9	AF238725° GUE_HAP11	AS/BS				
Ac197_RM	gue_Hap10	GUE_HAP140	DR				
Ac175_BS	gue_Hap11	GUE_HAP135	BS				
Ac162_RM, Ac164_RM, Ac173_RM	gue_Hap11	GUE_HAP135	BS				
Ac167_RM	gue_Hap12	GUE_HAP140	DR/UR				
Ac169_RM	gue_Hap13	/	/				
Ac170_RM, Ac176_RM, Ac180_RM, Ac186_RM, Ac192_RM	gue_Hap14	GUE_HAP185	CS				
Ac207_RM	gue_Hap15	/	/				
Ac212_BS	gue_Hap16	GUE_HAP141	DR/CS				
2018	Ac72_BS, Ac90_BS	hus_Hap1	HUS_HAP60	DR/CS			
	Ac73_BS	hus_Hap2	HUS_HAP73	DR			
	Ac74_BS	hus_Hap3	/	/			
2019	Ac98_BS, Ac99_BS	hus_Hap4	/	/			
Ac100_BS	hus_Hap5	HUS_HAP12	AS/BS/CS				
Ac102_BS	hus_Hap6	/	/				
Ac104_BS	hus_Hap7	HUS_HAP75	DR				

Table 1 (continued)

Samples are sorted by collecting year and by haplotype. Any correspondence with known haplotypes and their distribution is also reported. Codes in italics indicate haplotypes detected in the Russian sturgeon broodstocks. For each sample, the amplification of diagnostic nuclear markers is shown in grey-filled cells. Amplification of nuclear markers from four individuals failed, indicated in the table by the empty cells
BS Black Sea, *RR* Rioni River, *RM* Rioni mouth, *AS* Azov Sea, *DR* Danube River, *CS* Caspian Sea
 *Doukakis et al 1999; °Birstein et al. 2000; #= *A. gueldenstaedtii* baerii-like haplotype

Genomic DNA was purified using the Qiagen DNeasy Blood & Tissue Kit. All samples were genetically analyzed for species and hybrid identification by amplifying and sequencing the mitochondrial control region, and by checking the presence/absence of sturgeon diagnostic nuclear markers.

Primer pairs, PCR amplifications, and thermocycler conditions for the control region are as reported in the original reference by Congiu et al. (2011). PCR reactions were performed on Applied Biosystem GeneAmp®PCR System 9700 and MJ Research PTC-225 thermal cyclers. All PCR products were purified with ExoSAP-IT® according to the manufacturer's protocol, and directly sequenced on an ABI Prism 3730XL or an ABI 3100 automatic sequencer at Eurofins Genomics (Germany) or an ABI Prism 3730XL automatic sequencer at MacroGen Europe B.V. (Netherlands).

Mitochondrial sequences were aligned using ClustalW in MegaX (Kumar et al. 2018) and BLAST (Basic Local Alignment Search Tool, Altschul et al. 1990) searches were performed to determine the maternal species; most individuals were juveniles, making morphological identification more difficult. Mitochondrial genetic variation among collected samples was also evaluated. Haplotype diversity (h) and nucleotide diversity (π) were estimated with ARLEQUIN ver.3.5 (Excoffier and Lischer 2010) for each group of species detected by the BLAST searches.

Haplotypes and their relationships (i.e., representation of gene genealogies based on a maximum parsimony approach) were organized in networks with the PopART 1.7 software (Leigh and Bryant 2015; <http://popart.otago.ac.nz>) based on TCS network inference methods (Clement et al. 2000). A schematic neighbor-joining tree based on p-distance was generated by MegaX. Haplotypes were also compared with available datasets, including information on haplotype diversity of wild and captive sturgeon populations collected over the past years (personal communication by N. Mugue).

Focusing on sturgeon species that more likely could hybridize in the Black Sea and Rioni River, available diagnostic nuclear markers for *A. stellatus* (Ste_RP1F and RP1_LocusA_R, Boscarì et al. 2014), *A. gueldenstaedtii* (395_AB_for and 395_uni, Havelka et al. 2019), and *H. huso* (RP2S6_huso-F and RP2S6_groupA_R, Boscarì et al. 2017) were also used to test samples for interspecific

hybridization. Experimental protocols were as reported in the original references.

The presence/absence of diagnostic products (479 bp for *A. stellatus*, 395 bp for *A. gueldenstaedtii*, and 194 for *H. huso*) was checked on 1.8% agarose gel stained with GelRed (BIOTIUM, GelRed™ Nucleic Acid Stain).

Results and discussion

BLAST performed with mitochondrial data revealed three species: *A. gueldenstaedtii* (Accession numbers: MZ665962-MZ665977), *A. stellatus* (MZ665978-MZ665989), and *H. huso* (MZ665990-MZ665996) (Table 1), with 74% of haplotypes indicating *gueldenstaedtii* species identification. Among samples collected from the Black Sea (BS), 10 animals presented *A. stellatus* haplotypes, 17 *A. gueldenstaedtii*, and nine *H. huso*. In the Rioni River and its mouth (RR and RM) only *A. stellatus* (one RR samples and four RM samples) and *A. gueldenstaedtii* (six RR samples and 47-RM samples) haplotypes were found.

For each sample, Table 1 shows year of collection and the previous detection of each haplotype in wild populations or captive stocks; results of tests for interspecific hybridization performed with diagnostic nuclear markers are also indicated. Table 2 describes mitochondrial diversity for the three species. Figure 1B–E shows the relationships among haplotypes in the three species (12 haplotypes for *A. stellatus*, 16 for *A. gueldenstaedtii*, and seven for *H. huso*). For the three species, two, nine, and three haplotypes respectively were never observed before.

Four individuals with *A. gueldenstaedtii* haplotypes (one young of the year caught in 2018 and three 1 year olds caught in 2020), were positive for the diagnostic nuclear marker for *A. stellatus*, strongly pointing to their hybrid

Table 2 Summary data based on control region sequences

Control Region summary basic statistics					
Maternal species	N	N_h	P_s	h	π
<i>A. stellatus</i>	15	12	52	0.962 ± 0.040	0.019 ± 0.010
<i>A. gueldenstaedtii</i>	70	16	87	0.867 ± 0.029	0.023 ± 0.011
<i>H. huso</i>	9	7	36	0.944 ± 0.070	0.017 ± 0.009

N number of individuals, N_h number of haplotypes, P_s Polymorphic sites, h haplotype diversity, π nucleotide diversity

origin. It is worth noting that, for one of these animals, an informal identification as *A. stellatus* was provided before release by the FFI team members who collected it. The clear discordance between this *a priori* morphological classification and the haplotype sequence likewise indicates hybrid origin of that individual. Moreover, even though morphological indications for the other three detected hybrids were not provided, the *A. stellatus* diagnostic marker has never given false positive amplification in 11 other sturgeon species, including amongst 41 specimens of *A. gueldenstaedtii* from outside of the Black Sea (Boscari et al. 2014), strongly corroborating the reliability of this result. Given the underrepresentation of reference Russian sturgeons from the Black Sea, we cannot exclude that the allele frequency differs across locations such that *A. gueldenstaedtii* in the Black Sea might naturally carry the *A. stellatus*-diagnostic allele. However, commercial controls for species purity we routinely performed also included many *A. gueldenstaedtii* caviar samples from the Black Sea which have never shown the *A. stellatus* allele (data not shown).

The four haplotypes of the hybrid animals were not detected in the Russian sturgeon broodstocks used to generate juveniles for restocking in North Eastern Black Sea (Nikolai Mugue, pers. comm), suggesting that the hybrids found in this study were likely the offspring of wild breeders. Additionally, the four putative hybrids exhibited different haplotypes, indicating that each had a different *A. gueldenstaedtii* mother, and that hybridization involved at least four females. Sturgeons are known for their ability to hybridize in captivity and several species combinations have been generated in aquaculture for production purposes (Boscari et al. 2014). To our knowledge however, hybrids between *A. gueldenstaedtii* and *A. stellatus* are not used in aquaculture, and this species combination is not produced. Furthermore, no hatchery producing *A. stellatus*, either as pure species or as hybrids, is present in the area, excluding the possibility that the detected hybrids represent accidental escapees from aquaculture plants. This is not the first evidence of interspecific hybridization in nature between sturgeon species; for example, natural interspecific hybrids between *A. ruthenus* and *A. baerii* were found in the Danube River following careless release of the allochthonous *A. baerii* (Ludwig 2009). In this instance, it appears that hybridization occurs between indigenous species.

Although, a certain rate of hybridization may have always occurred, the present low density of populations (in particular of the Stellate sturgeon) might increase this phenomenon. Population decline may in fact promote interspecific hybridization due to the scarcity of conspecific mates. This phenomenon, known as Hubb's 'desperation' hypothesis (Hubbs 1955), adduces the urgent need for sturgeon conservation measures in the Eastern Black Sea and Rioni drainage. Additional concerns are raised by the possible impact that the

presence of interspecific hybrids might have on the already seriously compromised natural populations (Havelka et al. 2011). In our specific case, the two parental species have respectively about 240 (Russian sturgeon) and 120 chromosomes (Stellate sturgeon) and the resulting hybrids, having an intermediate chromosomal set, are expected to be sterile (Birstein 2002; Linhartová et al. 2018). However, the sterile condition does not prevent the animals from taking part to spawning as adults, competing with breeders of pure species with adverse effects on their reproductive success (Arcella et al. 2014; Fjelldal et al. 2014). Furthermore, a relict population of Ship sturgeon (*A. nudiventris*), whose chromosomal set is compatible with the Stellate sturgeon (*A. stellatus*), also inhabits the Rioni River (Beridze et al. 2021). An interspecific admixture between these species would result in fertile hybrid which might backcross with the parental species, potentially compromising their genetic integrity. This would be particularly harmful for the Ship sturgeon, on the verge of being classified as extinct in the wild, and for which a last spawning site of the entire distribution area was recently recorded in the River Rioni (Beridze et al. 2021).

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Authors' contributions TB and EB equally contributed to this study. FS, CA substantially contributed to the design of the work. TB and EB performed all the experiments and data analyses. TB, EB and LC contribute to results interpretation and wrote the manuscript. All the authors critically revised the manuscript and accepted the final version for publication.

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Availability of data and material Accession numbers available upon acceptance.

Code availability Not applicable.

Declarations

Conflicts of interest/Competing interests No conflict of interest.

Ethical approval Not applicable.

Consent to participate All authors have given consent to participate.

Consent for publication All authors have given consent to publication.

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