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Failed protective effort of ex situ conservation of River Vistula trout (*Salmo trutta*) in Sweden

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Abstract Ex situ conservation comprises some of the oldest and best-known conservation methods and it has been applied for different fish stocks. This study describes attempts undertaken to preserve the long-migrating River Vistula (Poland) brown trout by a sea-ranching programme in the River Dalälven (Sweden). This focal strain was threatened in its native river and a major reason for selecting the River Dalälven was that its river mouth faces north as does that of the River Vistula. In the Swedish river, the Vistula trout in the 1970s and early 1980s returned early in the autumn and were generally large-sized (compared to the native strain of the River Dalälven). Over the study period (1978–2012), the size of returning adult fish declined, the return date becoming later in the year, and the number of spawners also declined. The reasons for these changes were probably caused by several interacting factors: (1) the most likely being high mortality of early returning fish which were held for longest in captivity before being used in the artificial spawning process; (2) the fact that the hatchery process was adapted to the Dalälven strain and not the Vistula one; (3) that the Vistula fish were marked by removing both pelvic fins (possible reducing subsequent survival); and (4) low genetic variation (as a result of few returning individuals). Thus, for several reasons, this ex situ conservation attempt for Vistula trout in Sweden is thought to have failed.

Keywords *Salmo trutta* · Strains · Ex situ conservation · Sea ranching · Artificial reproduction · Poland

Introduction

The process of protecting an endangered plant or animal species outside its natural habitat, for example by removing part of the population from a threatened habitat and placing it in a new location, is often referred to as ex situ conservation; another term referring to the same process is 'gene banking'. This process comprises some of the oldest and best known conservation methods (Fischer and Lindenmayer 2000) and the ex situ area may be a wild area or within the care of humans (such as zoos, aquaria,

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large enclosures). However, to date, the best strategy for the long-term conservation of the biological diversity of wild species and populations has been in situ conservation, through enhancement of the degree of protection or definition of new protected areas (Frankel and Soule 1981; Primack 2002) for instance.

Both in situ and ex situ conservation are regularly discussed in governmental plans for conserving biodiversity (e.g. Safont et al. 2012; NordGen 2012). Today, for many species, total habitat loss and increasing extinction rates are common and the situation is most likely exacerbated by climate change (Bellard et al. 2012). In the view of this, in situ strategies do not appear to be feasible in all cases (Pritchard et al. 2011; Zippel et al. 2011) and so ex situ conservation may be the only way to reduce or avoid the extinction of some species or populations (cf. Young and Harig 2001). Among the ex situ techniques that are applicable, germplasm banks, living plant collections and managed relocation are of particular interest for several reasons (McLachlan et al. 2007).

No successful methods for cryopreservation fish eggs and embryos are available, although cryopreservation of fish spermatozoa has been developed (Diwan el al. 2020). Recently transplantation of germ cells (primordial germ cells, spermatogonia and oogonia) into suitable recipients (Okutsu et al. 2007; Yoshizaki et al. 2011) has been suggested but it might take years for such methods to be applied in the field. Traditionally, the conservation and protection of native fish populations has often relied on stocking and/or translocation with hatchery-reared fingerlings originating from purebred wild animals (i.e. with no evidence of admixture of other strains) (Allendorf et al. 2001).

Sea- or lake-migrating brown trout (*Salmo trutta*) populations like populations of many other diadromous species suffer from different anthropogenic activities, for example land use, acid precipitation, other kinds of water pollution, riparian and flood plain habitat degradation, altered hydrology, migration barriers, fisheries exploitation, environmental (climate) change and introduction of invasive species (c.f. Cooke et al. 2012). In Finland 70% of the original migratory stocks of trout are threatened to some degree (Koljonen and Kallio-Nyberg 1991) and in south-west Sweden at least 54 out of 80 investigated lakes have lost their large-sized migratory trout populations during a period of about one century (Ros 1981). Native populations of trout generally show large genetic differentiation where the sea-migrating form has higher genetic variation than of the resident and lake-migrating forms (Hansen and Mensberg 1998; Apostolidis et al. 2008; Kohout et al. 2012; Östergren and Nilsson 2012). In addition, there is apparently also variation in the ecological traits of these three trout forms (Rogell et al. 2012, 2013). Although local adaptation seems to be more important at the scale of regions (such as close drainage areas) as compared with individual populations (individual rivers; Meier et al. 2011), the common view is that individual populations represent unique gene pools that are worth preserving (Apostolidis et al. 2008).

This paper describes attempts made to preserve the long-migrating Vistula trout through ex situ conservation techniques. The Vistula trout were taken to Älvkarleby as part of an ex situ hatchery-release programme because it was under conservation threat in its native river. According to the hatchery staff in Älvkarleby, the Vistula trout in the 1970s and early 1980s were early spawning migrators and generally large-sized (compared to the native strain from River Dalälven), just as the Vistula strain appeared in its native river. The two strains were separated by marking them through removing pelvic fins: the Vistula strain by removing both pelvic fins and the Dalälven strain by removing the left pelvic fin.

Here we present and analyse catch data from the trap catching spawning migrating adult fish in River Dalälven. We asked whether the hatchery programme could maintain (1) the characteristics of the Vistula strain, such as size and timing of migration, and (2) a sufficient number of spawners in order to preserve enough genetic variation. If not the ex situ conservation efforts have to be regarded as a failure.

Material and methods

The Vistula trout and its way to Sweden

The River Vistula is a river flowing to the Bay of Gdańsk (Baltic Sea) and is the largest river in Poland. The source of the Vistula is in southern Poland 1220 m above the sea level in the western part of the Carpathian Mountains. Before the river was dammed at Włocławek in 1968, the main spawning migration occurred in two periods every year. During the first spawning migration, in late autumn and winter, a year before spawning occurs, winter trout with immature gonads used to move upstream towards the spawning grounds, and there was a second run of fish between June and September when summer trout (almost ready to spawn) entered the river (Żarnecki 1963).

The winter trout population migrated upstream all the way to the mountain tributaries located almost a 1000 km from the sea. In the 1950s, and even in the 1960s, the Vistula winter trout still had good status. However, this collapsed following the building of the Wloclawek dam in 1968. Despite the intensive stocking that has been conducted for over a century in the River Vistula, the total catches of trout have declined from over 100 tons to nearly zero in recent years (Dębowski 2018). To alleviate this situation, for nearly a decade the hatchery-reared smolts originating from the Pomeranian rivers (including Rivers Rega and Parsęta, all situated west of River Vistula) were used to supplement the River Vistula population (Borzęcka 1998). Since 1976, this large, long-migrating winter trout from Poland has been subject to ex situ conservation measures in the River Dalälven in Sweden, although, initially at least, the aim of this programme was not exclusively conservation of the Polish stock but also an attempt to introduce this particular trout strain to Sweden for stock enhancement purposes. For a more detailed description, see Supplementary Information.

By the end of the 1960s, 'eyed' trout eggs (i.e. developing, fertilised eggs) from an unknown number of females (and males) were moved to the fishery research station in Kälarne (about 410 km north of Stockholm). Kälarne is an inland facility with no connection to the Baltic Sea and the strain was reared here in outdoor ponds for two or three generations. Thereafter the decision was made to move the trout to the fishery research station in Älvkarleby (about 160 km north of Stockholm), situated on the River Dalälven 10 km from the river mouth. This river is the only river in Sweden that runs north, which was regarded as beneficial because it was thought to mimic the situation in River Vistula. In the mid-1970s, eyed trout eggs from an unknown number of female and male parents were translocated from Poland to Älvkarleby and the first 2-year old smolts were released into the river in 1976. All stocked Vistula fish were marked by removing both pelvic fins. In 1978, the first returning Vistula trout was caught in the River Dalälven and the number, sex, size and catch date of all returning Vistula trout have been recorded since then.

Other trout strains in River Dalälven

Besides the Vistula trout, four other strains of trout have occurred in the River Dalälven. Two of these evolved from the same native population; one strain was established in 1967, when a large number of trout were caught and used in an artificial breeding programme for sea ranching. The Dalälven sea-ranched (DSR) strain has subsequently been kept separated from the other strains. The released offspring of DSR trout are marked by removing the left pelvic fin whilst another strain propagated in the River Dalälven, a landlocked one from Lake Vänern (also in Sweden), was marked by removing the right pelvic fin. However, the sea-ranching programme for this strain declined and was terminated in 1991. The fourth strain comprises the offspring of adult fish spawning in the wild (and thus is an admixture of all strains) and these wild trout are identified because both pelvic fins are intact (see Petersson et al. 1996 for more details about the two Dalälven strains). Thus, at the artificial breeding process only males and females with similar marking were crossed, i.e. there were no introgression between strains. In the wild, all strains probably interbred, and spawners originating from wild (natural) crossings returned to the hatchery with both pelvic fins intact, and these individuals were never mixed with marked individuals. One or two months before the smolt migration, most of the hatchery fish were stocked in two nearby ponds which have a continuous through flow of river water and an open outlet making it possible for the fish to leave the ponds and initiate seaward migration whenever it is triggered by internal or environmental conditions. This trout smolt migration normally peaks in the third or last week of May (Petersson et al. 2014).

Data collection of fish at spawning migration

In the River Dalälven, diadromous fishes are prevented from following their natural migration route because of a hydropower dam at Älvkarleby. Adult trout migrating upstream are thus caught, by means of a trap, and taken to a sorting hall, where they are kept and used for artificial breeding. These adult trout are caught from 1 June until mid-October each year. The intention is to keep fish from the entire period and 'surplus' fish have been stocked upstream the dam, killed or tagged and restocked at the river mouth, depending on the current policy. All fish that are caught in the trap at the research station are measured (length and weight), sexed, finclipping and the arrival date recorded. During the period 1978–1987, all individuals that were kept for artificial breeding were marked with week-specific combinations of dark-blue dots anterior of the pectoral fins. These marks were made by injecting a dye solution subcutaneously. This marking method made it hard to track individuals as the fish get more pigmented closer to spawning, and the data from these years cannot be used to estimate survival rates based on knowledge of their arrival date. During 4 years in 1987–1990, returning adults that were kept for artificial breeding were individually marked with self-piercing clamp tags in the operculum (such tags usually are applied to the lower jaw of the fish, e.g. Phelps and Rodriguez 2011).

Statistical treatment of data

The data differed from normal distribution; in order to adjust for this we used PROC TRANSREG in SAS statistical software for finding the optimal Box-Cox transformation ($Y(\text{transformed}) = Y^{\lambda}$). For date of spawning migration, $\lambda = 2.545$ and for length $\lambda = 1.540$. All calculations, except the logistic regression on lengths larger or shorter than 77 cm (see below), have been made on transformed data.

For length data and data on arrival date (converted to Julian data) as a function of study years, we calculated linear regressions for each strain using PROC REG in SAS statistical software. The regression coefficients (slopes) were compared according to Sokal and Rohlf (1995). However, it becomes apparent when visually evaluating the graphs (Figs. 1 and 2) that linear regression might not be the best fit, especially not for the Vistula strain. Therefore, we also used the programme TableCurve® and processed about 80 'simple functions' (see Table S1 in Supplementary Information). The best fit according to this process are viewed in Figs. 1 and 2.

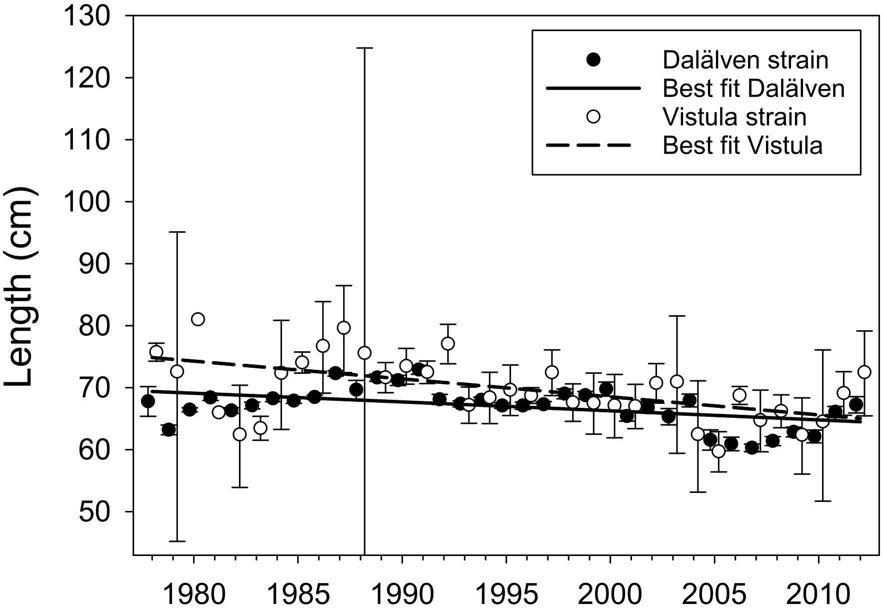

Fig. 1 Length (cm) as a function of year of recapture of returning adults of trout (*Salmo trutta*) at the fishery research station in Älvkarleby, Sweden, for Dalälven strain and Vistula strain. The circles show the mean values and the error bars 95% confident levels. The regression lines show the best fit among 80 different functions (see text for more information). All calculations were made on Box-Cox-transformed values; in the figure back-transformed values are shown. The lower confidence limit for Vistula strain in 1988 was below zero based on transformed values, which is not shown in the figure

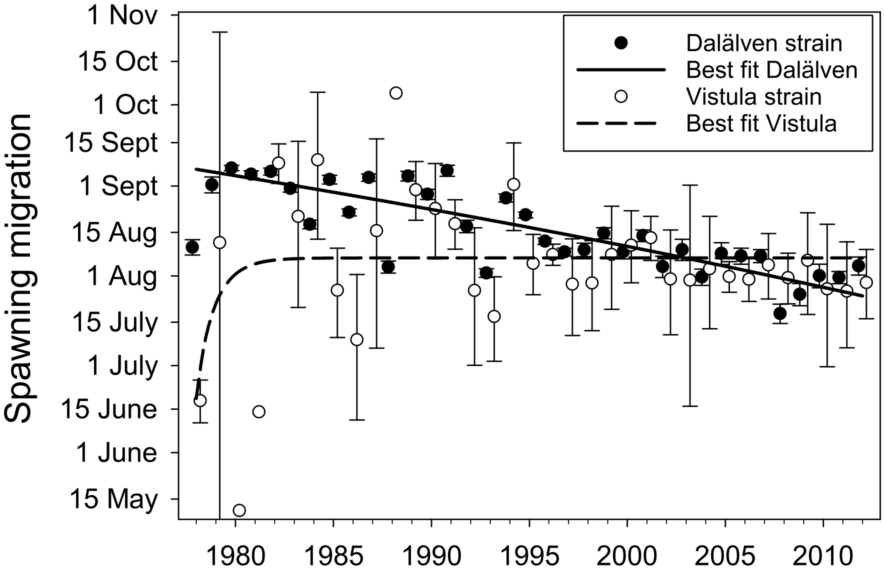

Fig. 2 Spawning migration (arrival dates to the trap at the fishery research station in Älvkarleby, Sweden) as a function of year of recapture for Dalälven strain and Vistula strain. The circles show the mean values and the error bars 95% confident levels. The regression lines show the best fit among 80 different functions (see text for more information). All calculations were made on Box-Cox-transformed values; in the figure back-transformed values are shown. The lower confidence limit for Vistula strain in 1979 was below zero based on transformed values, which is not shown in the figure

Logistic regressions were calculated using PROC GENMOD in SAS statistical software. First, we used the data set of individual fish to calculate the probability that an adult trout had a length greater than 77 cm, using logistic regression, year being predictor and strains being class variable. Second, we calculated the probability for an individual surviving until the onset of artificial breeding, arrival date being the predictor and the strains being class variable. For estimate of effective population sizes, we used harmonic means (Wright 1931).

Mean values, standard deviations and numbers of observations are given in Table S2 (Supplementary Information). Results are given as mean ± standard deviation, if not otherwise stated.

Results

The total sample size for DSR was 17,548, ranged from 68 to 1221; for Vistula strain total sample size was 579, ranged from 1 to 69 (see Supplementary Information, Table S2).

The average length of returning adults of DSR was 67.39 ± 21.74 cm and for Vistula 69.65 ± 22.47 cm (back-transformed values). The length of the returning adults of both strains decreased during the period 1978–2012 (see Fig. 1), and the decrease was steeper for the Vistula strain (DSR: length = 4891.18 − 2.13 × year, $F_{1,17546} = 516.3$, $r^2 = 0.029$, $p < 0.001$; Vistula strain: length = 9490 − 4.41 × year, $F_{1,577} = 69.5$, $r^2 = 0.108$, $p < 0.001$; slope difference: $t = 4.29$, $p < 0.001$). It is clear from Fig. 1 that during the first 10 years the largest individuals caught in the trap at Älvkarleby were of the Vistula strain. The probability that an adult trout was larger than 77 cm (the 9th percentile) was 0.136 ± 0.014 (S.E.) for Vistula trout and 0.081 ± 0.002 (S.E.) for DSR trout ($z = 4.59$, $p < 0.001$). The probability for a migrating adult trout (both strains combined) to be larger than 77 cm declined over the study period (estimate = − 0.022, Wald $\lambda = 53.1$, $p < 0.001$).

The average arrival Julian arrival date for DSR was 233.59 ± 138.82 and for Vistula 216.59 ± 145.27 (back-transformed values); the mean values correspond to 21st August and 4th August, respectively. The arrival date at the trap in Älvkarleby for returning adults as a function of study years decreased for DSR but not so for Vistula strain, and the slopes differed

(DSR: Julian date = 29,722,127 − 14,387 × year, $F_{1,17550} = 477.4$, $r^2 = 0.214$, $p < 0.001$; Vistula: Julian date = − 2,710,928 + 1798.5 × year, $F_{1,570} = 1.486$, $r^2 = 0.0026$, $p = 0.225$; slope difference: $t = 13.50$, $p < 0.001$). However, as can be seen in Fig. 2 the difference between the strains in arrival date was most pronounced in the earliest years. There was a difference between the strains during the first 10 years of the study (1978–1987) (DSR: 242.2 ± 20.7; Vistula: 198.4 ± 42.4, $t = 10.67$, $p < 0.001$) but during the last 10 years (2003–2012) no such difference was apparent (DSR: 208.9 ± 31.0; Vistula: 210.7 ± 23.1; $t = 0.35$, $p = 0.351$; back-transformed values; both *t*-tests adjusted for unequal variance (Satterhwaite 1946)). The harmonic mean of number of individual that could be used in the breeding programme was 10.3 for the period 1990–2012 (Vistula strain).

The tagging undertaken between 1987 and 1990 made it possible to investigate in detail the survival probability of fish held in the tanks from the time they were trapped until the start of the artificial spawning season which commenced on 1st October each year (although a few individuals were trapped after this date). As can be seen in Fig. 3, the survival probability during the holding period was lower for fish that returned early in the season.

After 2012 only single individuals of Vistula trout were caught in River Dalälven, the last individual was caught in 2015.

Discussion

In this study, we have showed that the Vistula trout propagated in River Dalälven in Sweden have experienced changes over time, a decline in size and a later arrival date. Initially, Vistula trout arrived earlier than did those of the Dalälven strain, but during later years there was no difference between the two trout strains (i.e. Dalälven versus Vistula). One of the characteristics hoped to be preserved was the early start of spawning migration in the Vistula trout strain, but this typical feature has become less pronounced during the study period. The observed changes in fish size

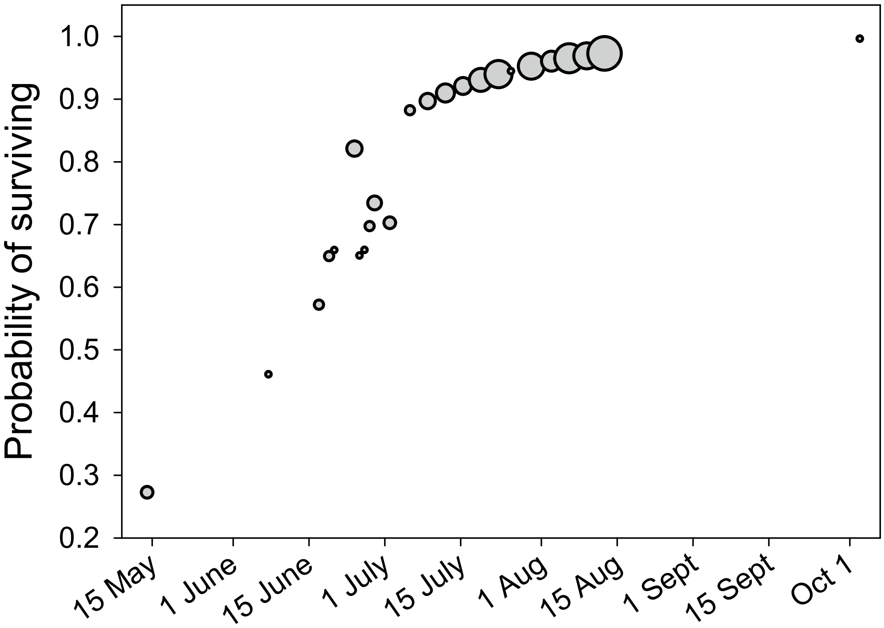

Fig. 3 Predicted probabilities (cross-validated from logistic regression) for survival of trout (*Salmo trutta*) depending on arrival date to the trap in Älvkarleby (River Dalälven). Survival here means that the fish survived from being caught in the trap till the start of artificial breeding (1st October each year). A few individual fish were caught after this date. The diameter of the circles in the figure is proportional to the logarithm of the number of observations each day. The values are combined data from 1987 to 1990. The effect of year was not significant (Wald $X^2 = 1.05$, $p = 0.31$) but the effect of arriving date was significant (Wald $X^2 = 4.33$, $p = 0.04$; $n = 203$)

and arrival date might be due to phenotypic plasticity, i.e. the fish stocks change in response to inputs from the environment, such as temperature and nutritional levels. But this does not explain the early arrival dates in the early years of the study. Another explanation might be that the mortality in the tanks where the returning adult trout were kept after being caught; the earlier a trout arrived the higher the probability that it should die before the onset of the spawning season. This means that fewer 'early trout' were surviving to spawning time and hence contributing less to subsequent returners. There is also an additional possible explanation; the Vistula trout juveniles were marked by cutting off both pelvic fins before being released and a study on native River Dalälven trout (Petersson et al. 2014) showed that such a marking caused a 30% reduction in the return rate of fish when compared to trout marked by the removal of a single pelvic fin or the adipose fin. In addition, the removal of both pelvic fins might affect the timing of migration in Vistula trout. However, the data indicate a gradual change (over several years) in timing of migration and none of the studies summarised in Petersson et al. (2014) mentions timing of migration as an effect of fin removal, rather growth and survival.

It is also notable that the timing of spawning migration of DSR trout changed over the year, on average arriving 1.3 days earlier each year. Similar changes have been observed also for some other salmonid populations: Atlantic salmon (*S. salar*; Juanes et al. 2004), sockeye salmon (*Oncorhynchus nerka*; Quinn and Adams 1996, Quinn et al. 2007, Hinch et al. 2012, Tillotson et al. 2019) and pink salmon (*O. gorbuscha*, Kovach et al. 2012, 2013). The proposed reasons for such changes vary. The hatchery rearing process as such might contribute by selection for early migrants (Tillotson et al. 2019). Kovach et al. (2012) suggested that warmer river temperatures may have caused reproductive overlap (and hence gene flow) between early- and late migrating individuals, resulting in evolutionary changes due to outbreeding depression. Timing of migration is phenological traits and such generally show high heritability in salmonids (Carlson and Seamons 2008), and thus it is likely that microevolutionary changes in migration timing would allow salmon populations to persist under climate warming (Reed et al. 2011) . In the River Dalälven, the trout spawning migration shows a large variation; river and sea temperatures and river discharge explain little of the variation in run date (Dahl et al. 2004). Trout females arrive about 1 week earlier than males. The sea and river temperatures are highly correlated during the spawning migration, indicating that large climate processes determine the temperature regimes in the Baltic Sea and its tributaries. Time of arrival to the river was not correlated with ovulation date; a female trout arriving late could ovulate almost immediately, whereas a female arriving early waits to ovulate (Dahl et al. 2004, cf. Hinch et al 2012). However, this does not explain the change in spawning migration observed for Vistula strain. As this strain experienced high mortalities among early migrants during the 1970s and 1980s (cf. Fig. 3), genes coding for early migration might have been almost wiped out from the population, giving less variation left for responding in the same way as the DSR strain. Another contribution factor might be that the low number of returning individuals complicates the statistically confirmation of such a change. Without doubt, more investigations are needed in order to understand this complex, multifactor phenomenon in general. Unfortunately, it is too late to apply such findings on the Vistula strain in River Dalälven.

These changes of the Vistula trout propagated in River Dalälven are not surprising when considered in the light of recent advances in conservation biology. Researchers commonly argue that populations may undergo evolutionary changes under captive conditions, leading to traits that are adaptive in artificial captive situations but which may be non-adaptive in the wild (Frankel and Soule 1981; Price 1984; Lacy 1994; Phillipart 1995; Sutherland 1998; Bryant and Reed 1999; Frankham 2008; but see Sgro and Partridge 2000). In this context, there are differences between animal taxa, with large vertebrate species (common zoo animals) having relatively long generation times and thus evolutionary changes in captive populations might well not yet have become apparent. In contrast, some species of insect have now been reared in captivity for 100 generations or more and evolutionary changes are reported in such populations (e.g. Morton 1991; Lewis and Thomas 2001). In addition, an extensive review (Martin-Wintle et al. 2018) provides good evidence that free mate choice and mating with preferred partners are beneficial in ex situ conservation programmes. For the Vistula trout reared in Sweden, this was not practised, rather, crossings (i.e. artificial matings) were as random as possible.

The conservation of species and strains is a challenging task due to the ongoing threats to biodiversity (c.f. Butchart et al. 2010). Most researchers and managers are aware that in situ conservation represents the most effective way to protect endangered species and strains, but it is evident that not all of these can be efficiently preserved in their natural habitats (Pritchard et al. 2011; Zippel et al. 2011). Therefore, ex situ conservation programmes and reintroductions of captive bred animals have become widespread measures to protect endangered species (Fischer and Lindenmayer 2000; Storfer 1999). One important factor here is the numbers of individual parents ('founders') that are used to start an ex situ population. In an analysis of 188 ex situ programmes, Witzenberger and Hochkirch (2011) concluded that the minimum number of founders was 15 and the minimum size of a captive population was 100 individuals. This is necessary in order to minimise a loss of genetic diversity. Optimally, founders should be unrelated and new ones should be integrated into the captive population successively. These authors also recommend that genetic analyses should generally precede and accompany ex situ conservation projects in order to avoid inbreeding and outbreeding depression. This was not done for the Vistula trout when it was first translocated to Sweden, nor is the number of founders known. In addition, the sea-ranched stock of Vistula trout in the River Dalälven was not a pure captive population, as part of its life cycle took place in the wild in the Baltic. This situation is incontestably more natural than a complete life cycle in captivity but makes it almost impossible to monitor of the size of the population. Nevertheless, the numbers of returning adult Vistula trout to the River Dalälven were far from what was recommended by Witzenberger and Hochkirch (2011).

Several studies show that inbreeding and loss of genetic diversity are risks in captive breeding programmes, and fish populations in stocking programmes as described for Vistula and DRS most likely are exposed to such effects. The genetic consequences of captive breeding are highly variable depending on a number of factors, such as the number and relatedness of founders or the period for which breeding has been conducted (Witzenberger and Hochkirch 2011). Experimental studies on fruit flies (*Drosophila melanogaster*) showed that unintentional adaptation during captive breeding programmes may seriously compromise the success of reintroduction programmes (Gilligan and Frankham 2003). Other studies show that several characteristics might be affected by the artificial breeding programme, such as egg size (Heath et al. 2003), reproductive success (e.g. Koch et al. 2022) and juvenile behaviour (Petersson and Järvi 2003). Such changes in the hatchery can occur in a single generation (Christie et al. 2012, 2016) and in addition captivity favours domesticated genotypes (Hagen et al. 2019). Thus, the hatchery process as such might contribute to the failure of ex situ conservation programmes.

Another issue is important when retrospectively evaluating the ex situ conservation of the Vistula trout. Apart from randomly choosing parents, nothing in line with the preservation of genetic diversity was ever applied to the sea-ranching programme of Vistula sea trout in Sweden. This is despite the fact that it would be possible during the process of artificial fertilisation to equalise the number of eggs from each female. Thus, new techniques and results may change the understanding of conservation biology, and thereby the management and actual actions for the focal species or stocks. Despite many efforts to maintain the genetic diversity of a captive population, the degree of genetic diversity is likely to decrease, highlighting concerns for the progression of inbreeding (cf. Willoughby et al. 2015). For example Yamazaki et al. (2017) predicted that the captive population of a rare fish the Itasenpara bitterling (*Acheilognathus longipinnis*) under the current rearing conditions are likely to be extinct in 50 years. There are thus evolutionary risks with artificial propagation programmes and they generally work best if implemented as a short-term, rather than as a long-term approach. Artificial propagation programmes can also have out-of-population impacts (e.g. countering natural patterns of variation or local adaptation) that should be considered in conservation planning (McClure et al. 2008).

Interestingly, in 1996, eggs of the Vistula strain of sea trout from Dalälven were sent from Älvkarleby to the hatchery of the Inland Fishery Institute in Rutki near Gdańsk. Experiments were subsequently carried out to compare these trout and the actual Vistula trout strain. Some parr from the Vistula-Dalälven trout from Sweden and some from the Polish hatchery brood stock in Rutki

(F2 and F3 of spawners) caught in the Vistula were PIT tagged then and kept for the next 3 years in tanks to monitor growth, smoltification and maturity. Generally, no differences were recorded in growth but Dalälven fish on average smoltified and matured a little earlier than did the Rutki fish from the Vistula (Dębowski 2002).

In conclusion, we surmise that the selective regime exposed to the fish stocks as a consequence of anthropogenic activities (the artificial spawning process) altering the Vistula sea trout in the River Dalälven and the conservation intentions subsequently failed.

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Author contribution Erik Petersson initiated the study, made all statistical analyses and wrote the first draft of the manuscript. Piotr Dębowski added the Polish knowledge and view, thus adding information in 'Material and methods', as well as having input in the 'Discussion'. Jörgen Rask compiled all data files needed for the analyses and also extracted other necessary information from the records at the hatchery.

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Data availability All data and materials have been reviewed to ensure congruency with the results and discussion points of this paper. Catch data and parental survival data are included as electronic supplementary material.

Code availability Not applicable.

Declarations

Ethics approval The hatchery in Älvkarleby runs according to a verdict from a Swedish Land and Environment Court, the purpose is to compensate for the loss of natural salmonid production due to the hydroelectrically power plant. The hatchery, its results and the health of fish, are surveyed by Fishery Investigation Board (Fiskeutredningsgruppen). Inspectors visit the hatchery each year and check the condition of the reared fish, noting such things as fish length, weight, fin erosion, other injuries and signs of diseases. The hatchery rearing and the stocking of fish is not regarded as animal experimentation according to Swedish legislation; thus, no ethical permit is needed for the hatchery. Nevertheless, the hatchery has to follow the Swedish regulation regarding aquaculture (SJVFS 2019:6) as well as EU Commission regulation No 710/2009. The fish are anaesthetized with tricaine methanesulphonate before being handled for the artificial spawning process. After this, as is standard practice, fish were either euthanized by brain destruction when still anaesthetized or allowed to recover and thereafter returned to the river.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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