

Population genetics of Atlantic salmon and brown trout and its relevance for management of genetic resources

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Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) are genetically highly structured species. The structuring on a broad distributional scale is the result of the glacial and postglacial history, therefore in Europe several main population groups of Atlantic salmon and anadromous form of brown trout, sea trout, have been identified and divergent sources of origin of these groups have been proposed. The pattern of substantial microgeographical differentiation results from the joint action of gene flow, genetic drift, mutation, and natural selection. It is important to understand the effects that the last glaciations have had on the distribution and genetic diversity of these species as well as how selection, genetic drift and gene flow can affect genetic variation within populations and genetic differences between populations in order to fully comprehend the genetic structure of populations and to implement the knowledge for conservation. Genetic management is an important component of strategies that ensure the conservation and recovery of salmon and trout populations. The major issues of genetic management are related with monitoring and conserving gene-level biodiversity, resolving spatio-temporal population structure as well as with genetic consequences of stocking practices. Studies of the population genetic structure are essential for providing estimates of the different sources of variation that determine species' genetic composition over the geographic area. Knowledge from studies describing spatial and temporal genetic structure is needed to identify and analyze changes of gene level diversity caused by human mediated harvest as well as enhancement practices. Ignoring or not knowing the genetic population structure may result in loss of genetic diversity, reduced productivity and ecological damage. In Lithuania, future management considerations should focus both on maintaining individual populations even at tributary level and ensuring natural levels of gene flow among populations.

Key words: Atlantic salmon, brown trout, population genetics, genetic management

INTRODUCTION

Genetic variation constitutes the basis for biological evolution and consequently influences all levels of biodiversity (Laikre et al., 2010a). Genetic components of biodiversity are essential for adaptation to environmental changes, sustainable use of resources and ecosystem recovery

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(Luck et al., 2003; Frankham, 2005; Reusch et al., 2005). Species are not genetically homogeneous, but structured into groups of individuals (or populations) that are genetically differentiated (Laikre et al., 2005). *Genetic population structure* of the species is a pattern of distribution of genetic variation within and between populations and genetic differences between them. Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo*

trutta L.) are genetically highly structured species. The brown trout has two alternative life stages: (i) resident form – fish spend their entire life in a river or a small stream, and often spawn in smaller tributaries of the area and (ii) anadromous form (sea trout) – fish migrate from the rivers or streams in which they were born to the sea where they forage until reaching sexual maturity and then return to their native rivers to spawn. (Elliott, 1994). There is a complete reproductive isolation between resident populations which are physically isolated (Moran et al., 1995; Bouza et al., 1999). Anadromous sea trout, as well as salmon populations, due to homing behavior and restricted gene flow, are also partly isolated from each other (Hansen et al., 2002) and it provides a possibility to genetically adapt to environmental conditions in their natal rivers and results in the formation of a pronounced genetic structure, where each river system contains at least one genetically distinct population (Hansen et al., 2002; Koljonen et al., 2002; Fraser et al., 2007; Apostolidis et al., 2008; Ozerov et al., 2010). Ignoring or not knowing the genetic population structure may result in loss of genetic diversity, reduced productivity, and ecological damage (Laike et al., 2005).

The objectives of this paper were to overview the key determinants of the genetic structure of Atlantic salmon and brown trout populations as well as molecular methods utilized in population genetic studies, also to summarize the major issues of genetic management and overview the current status and management measures of these species in Lithuanian rivers.

Phylogeography of Atlantic salmon and brown trout

Salmonid fishes exhibit complex patterns of genetic differentiation both at macro- and microgeographical levels (Garant et al., 2000; Spidle et al., 2003; Verspoor et al., 2005; Dillane et al., 2007; Vähä et al., 2007; Heggenes et al., 2009). The structuring on a broad distributional scale is the result of the glacial and postglacial history, therefore in Europe several main population groups of Atlantic salmon and brown trout have been identified and divergent sources of origin of these groups have been proposed (Koljonen et al., 1999; Consuegra et al., 2002; Säisä et al., 2005; Berna-

tchez 2001; Weiss et al., 2000). It is important to understand the effects that the last glaciations have had on the distribution and genetic diversity of these species in order to fully comprehend the genetic structure of populations and to utilize this knowledge for conservation.

Atlantic salmon. The distribution area of Atlantic salmon covers north Atlantic river system in North America and Europe. Nowadays its European distribution range extends from northern Portugal to the Pechora River in northwest Russia, including Iceland, the British Isles and the Baltic Sea (Tonteri et al., 2005). In the western Atlantic salmon is found in the rivers of USA, Canada and Greenland. The analysis of various classes of molecular markers showed clear genetic differentiation between western and eastern groups of Atlantic salmon populations (Ståhl, 1987; McConnell et al., 1995a, b; Verspoor et al., 1999; King et al., 2001) as well as between eastern Atlantic and Baltic salmon groups (Bourke et al., 1997; Verspoor et al., 1999; Nilsson et al., 2001; Consuegra et al., 2002; Säisä et al., 2005). Consequently, Baltic Sea salmon forms one of the three major groups of Atlantic salmon; the others are groups of western and eastern Atlantic.

For the Baltic Sea salmon, three hypotheses of postglacial origin have been proposed. One of the hypotheses is that the Baltic Sea could be colonized by salmon from eastern preglacial lakes before the Yoldia sea stage (Kazakov, Titov, 1991; Nilsson et al., 2001; Tonteri et al., 2005). Another hypothesis proposes a western origin from Atlantic populations via Närke Strait at the beginning of the Yoldia sea stage (Verspoor et al., 1999) and the third hypothesis suggests combination of both west and east origin of Baltic salmon (Koljonen et al., 1999). The hypothesis that the entire Baltic Sea was colonized from a western refuge (Verspoor et al., 1999) was based on the studies of salmon populations from the Gulf of Bothnia only, while other Baltic Sea areas and populations had not been covered by investigations (Säisä et al., 2005). However, knowledge on allozyme and mitochondrial DNA variation provides clear evidence of the genetic differences between southern Baltic populations (Main Basin and Gulf of Finland) and populations that belong to the Gulf of Bothnia (Koljonen et al.,

1999; Nilsson et al., 2001). It was proposed that these differences exist because the postglacial colonization of the Baltic Sea with different lineages from different glacial refuge: the present salmon stocks of Estonia, Latvia, Russia and southern Sweden are probably originated from the eastern glacial lakes (the Ice Lake lineage) and stocks of northern Finland and northern Sweden are of Atlantic origin (Atlantic lineage) (Koljonen et al., 1999).

Later it has been found that based on microsatellite DNA variation, there are genetic differences not only between southern and northern Baltic salmon populations, but also between populations within the southern group. Within the Baltic Sea, the anadromous salmon populations form three distinct groups, corresponding to the northern (Gulf of Bothnia), eastern (Gulf of Finland and eastern Baltic Main Basin) and southern regions (western Baltic Main Basin) (Säisä et al., 2005). These findings indicated that the Baltic Sea was colonized by at least three distinct lineages originating from different refuge areas: the Gulf of Bothnia from the Atlantic refuge, the Gulf of Finland from an eastern ice lake refuge and the southern Main Basin from a southern refuge that was presumably located in the basin of rivers Nemunas, Vistula, Odra and Elbe (Säisä et al., 2005).

Colonization hypothesis that the entire Baltic Sea has been colonized from eastern preglacial lakes (Kazakov, Titov, 1991; Nilsson et al., 2001; Tonteri et al., 2005) and uncertainty about the possibility of an immigration from Atlantic were based on the fact that one mtDNA haplotype, which is found in the majority of Atlantic populations, was absent in populations from the Gulf of Bothnia (Nilsson et al., 2001). However, Nilsson and co-authors (2001) found that populations from Gulf of Bothnia had several haplotypes that are attributable to Atlantic populations. Studies on allozyme data (Koljonen et al., 1999) as well as microsatellite data (Säisä et al., 2005) also showed a similarity between the northern Baltic Sea group and Atlantic populations. Consequently, although the original colonization lineage may later have admixed with other lineages to some extent (Säisä et al., 2005), theories regarding the origin of the Baltic salmon remain controversial.

Brown trout. Brown trout is naturally distributed in Europe, Western Asia and North Africa (Garcia-Marin et al., 1999a). Its natural distribution ranges from northern Norway and north-east Russia, southward to the Atlas Mountains of North Africa. From west to east, its distribution extends from Iceland to the headwaters of Aral Sea in Afghanistan (Apostolidis et al., 1996; Bernatchez, 2001). The analysis of mitochondrial DNA (mtDNA) sequence variation has revealed five major phylogeographic groupings among western and central European populations of brown trout: Atlantic, Adriatic, Danubian, Mediterranean and *marmoratus* (Bernatchez et al., 1992; Bernatchez, Osinov, 1995; Bernatchez, 2001). The Atlantic phylogeographic group is found throughout the Atlantic river systems from Iceland and Norway in the north to Iberia and the Atlas Mountains of Morocco and also in the Baltic and White Sea drainages. Danubian lineage is associated with drainages of the Black, Caspian and Aral Sea basins, as well as the Persian Gulf. The distribution of other three lineages – Adriatic, Mediterranean and *marmoratus* – slightly overlap with the other two and differ in distribution pattern within the Mediterranean Sea basin. The *marmoratus* lineage is almost strictly associated with the Adriatic basin. The Mediterranean lineage is predominantly found in tributaries draining in the western basin of Mediterranean Sea, whereas the Adriatic lineage is distributed in the eastern part of the Mediterranean basin (Bernatchez, 2001).

Considering that Atlantic lineage is associated with the Atlantic basin, the center of origin of this lineage is associated with drainages of this system. The northern part of the Atlantic region was ice-covered and thus many populations have existed only since postglacial times (Apostolidis et al., 1996a). However, in addition to the brown trout populations being present in unglaciated parts of the Atlantic region, one or more glacial refuge probably existed at the margins of the ice sheets (Ferguson, Fleming, 1983; Hamilton et al., 1989; Bernatchez, Osinov, 1995). This was supported by significant differences in nuclear and mitochondrial DNA markers between Atlantic Iberian populations and more northern Atlantic populations (Moran et al., 1995; Antunes et al., 1999; Garcia-Marin et al., 1999a; Weiss et al., 2000).

Studies based on variation of allozyme alleles and mitochondrial DNA have indicated that more than one postglacial colonization of northwestern Europe took place. On the basis of variation in allozyme alleles, Ferguson and Fleming (1983) proposed that the northwest Atlantic was colonized independently by two races of brown trout. Hynes et al. (1996) analyzed the pattern of distribution of mtDNA and suggested that the postglacial colonization of northwest Europe was more complex. Garcia-Marin et al. (1999a) contributed to the hypothesis of multiple colonization and proposed a postglacial recolonization model of the northwest Atlantic, based on allelic distribution at two enzymatic loci. According to this model, colonization occurred from (i) a northwestern migration from an eastern Mediterranean-Caspian refuge, (ii) a northern expansion from a refuge in Atlantic drainages of Iberia and southern France, and (iii) a northern and eastern migration from a refuge centered near the English Channel (Garcia-Marin et al., 1999a). They suggested that many current populations in the formerly glaciated area are combinations of these lineages. In the subsequent study, this hypothesis was re-evaluated and was argued that distribution of both mtDNA haplotypes and allozyme alleles do not support the contribution of two major glacial refuges (southwest Atlantic and Mediterranean-Caspian Basin) to the postglacial recolonization (Weiss et al., 2000). It was also suggested that distribution of mtDNA and nuclear gene markers in previously glaciated areas of northern Europe can be explained by postglacial dispersal from a refuge located northwards of the Iberian Peninsula, as well as the Black-Caspian-Aral basins (Weiss et al., 2000). Furthermore, Bernatchez (2001) reconciled previous interpretations of the origin and postglacial history of brown trout and supported the existence of a northwestern refuge as well as existence of a northeastern refuge and also provided evidence for the contribution of a southern refuge. Results of that study implied that northern colonization by this southern group occurred prior to the last glaciations; they also refute a contribution of a Ponto-Caspian lineage. It can be concluded that current genetic diversity in the North Atlantic region is the result of independent postglacial colonization by genetically distinct brown trout lineages (Bernatchez, 2001).

Factors affecting fine scale genetic differentiation of populations

The large microgeographical differentiation is mainly associated with reproductive isolation and homing behavior (Ferguson, 1989). In some cases genetic differentiation is the result of complete reproductive isolation – distinct populations have been found within the locations that are separated by impassable waterfalls and other geomorphological structures. Otherwise, if there are no physical barriers, strong homing behavior may be sufficient to maintain genetic differentiation (Ferguson, Mason, 1981; Ståhl, 1987). The pattern of substantial microgeographical differentiation may be the result of a combination of mutation, random genetic drift, gene flow and natural selection (Wright, 1931).

Genetic drift is a random change in allele frequency of a population, which occurs if a population size is not infinite. In populations that are not infinitely large, allele frequencies will change over time randomly. The effects of genetic drift are the strongest in small populations: the fewer individuals in the population, the stronger genetic drift affects the population. However, the effect is very small in large populations. In the short term, over a few generations, genetic drift would result in randomly increasing or decreasing of allele frequencies. In the longer term, the main result of genetic drift is the loss of genetic variation. This occurs because some alleles may not be passed to the next generation and over time the effect of genetic drift will be the loss of alleles by chance. Genetic drift also results in genetic differentiation of populations because different alleles will become more frequent or fixed in different populations.

Natural selection occurs because different genotypes have different fitness. Individuals with some genotypes (those with higher fitness) survive and reproduce more successfully than other individuals. As a result, these genotypes become increasingly more and more common in populations. In different populations, parents of different genotypes pass their genes unequally to the next generation, leading to genetic differences among isolated populations. Hence, genetic drift tends to make different populations genetically different from each other by chance, whereas natural selection tends to form genetically different populations due to environmental constraints.

Consequently, the traits that have high fitness in one population and evolve through natural selection will be different from the traits that have high fitness and evolve through natural selection in another population.

Mutation is a biochemical change in DNA and assumes changes of one allele into another, what creates new alleles. It is a very unusual process and typical mutation rates are about one mutation in a million genes passed from generation to generation. As a result, evolution through mutation is extremely slow – so slow that it is generally impossible to detect. However, mutation is important as a source of genetic variation. The process of mutation is the only way in which genetic variability is created, and without mutations there would be no biological diversity. Another important aspect of genetic mutation is its randomness – it may produce alleles that result in high or low fitness. What happens to those alleles, once they are produced, depends on the natural selection, genetic drift and gene flow.

Gene flow is a change in allele frequency that occurs due to migration of individuals among populations. When individuals move into a population they may bring new alleles which are not present in that population or occur in frequencies that differ from the allele frequencies of that population. Gene flow increases genetic variation within a population and tends to make populations genetically similar to each other. The more gene flow occurs, the more similar the populations will become. If less than one individual per generation moves between populations, i. e. the amount of gene flow is very low, populations will develop complete differences (differences in which alleles are fixed in different populations). In contrast, if large numbers of individuals migrate between populations, i. e. the amount of gene flow is very high, the populations will be like one single population and will have the same alleles in the same frequencies, even if they occur in different environments and differences could otherwise evolve through natural selection. Large amounts of gene flow will mask the effects of other forms of evolution and make populations similar. In between these two situations, the movement of at least one individual in each generation from population to population will prevent complete differences – the alleles found in one population

will also be found in the other. However, if levels of gene flow are fairly low, the populations may have large differences in allele frequency – an allele that is common in one population may be rare in another.

Generally, selection, genetic drift and gene flow affect genetic variation within populations and genetic differences between populations. Both drift and selection tend to decrease variation within populations and increase differences between populations, whereas gene flow increases variation within populations but makes populations similar.

Genetic management of salmon and trout populations

Large parts of the intraspecific variability of the salmon and brown trout have been lost due to environmental degradation, harvest and stocking (Parrish et al., 1998; Nilsson et al., 2005; Allendorf et al., 2008), whereas the remaining parts are threatened. Therefore, there is a need for increased conservation efforts on these species. An extensive proportion of the natural habitat of the salmon and brown trout has been affected by various activities (pollution, power plant construction, log floatways) that have altered the natural state of ecosystems. But it is not enough to consider habitat improvement and to ensure that future manipulations of the remaining unexploited areas are avoided as much as possible. To enable sustainable use and conservation of natural salmon and brown trout populations it is essential to incorporate genetic aspects into the management (Allendorf, Ryman, 1987). Furthermore, due to the species economic value, the remaining populations are threatened by activities such as releases of translocated or hatchery bred individuals (Laikre et al., 2010b). These activities are frequently considered harmless or even beneficial, but may be devastating from a genetic conservation standpoint (Laikre et al., 2010b). Therefore, genetic management is an important component of strategies that ensure the conservation and recovery of salmon and brown trout populations.

Genetic management deals with the genetic factors that affect extinction risk and conservation programs required to minimize these risks. The major issues of genetic management are related with monitoring and protection of gene-level biodiversity, resolving spatio-temporal population

structure as well as with genetic consequences of stocking practices.

Monitoring genetic diversity

It is recognized that genetic diversity is the basis of evolutionary potential of the species. The presence of genetic variation between populations as well as between individuals within populations is essential for their potential to survive and ability to evolve in response to both short- and long-term environmental changes (Allendorf et al., 2008). The two primary measures of genetic diversity are heterozygosity and allelic diversity. Allelic diversity refers to the number of different alleles at any given locus in the population. Heterozygosity is the percentage of heterozygous loci in a population or individual. Loss of heterozygosity can reduce viability of population by reducing individual fitness, hence it is important for immediate adaptation and loss of allelic diversity can affect the ability of populations to evolve in the future (Ryman et al., 1995). The population viability strongly depends on the effective population size which determines the rate of loss of genetic diversity in each generation as a result of genetic drift and inbreeding (Frankham et al., 2002). Smaller populations tend to lose more genetic variation than large, becoming less adaptable to a changing environment. It is broadly conceded that an effective population size of at least 500 is required for long-term viability (Laikre et al., 2009). The effects of small population size are of major concern because small populations suffer from inbreeding and loss of genetic diversity resulting in elevated extinction risks. Consequently, one of the major objectives of genetic management is to minimize inbreeding and loss of genetic diversity.

Resolving spatio-temporal population structure

A large proportion of the intraspecific biological diversity of the salmon and brown trout is represented by genetic differences between populations. Genetic studies help to identify discrete populations and their interactions. It was determined that each river system has at least one genetically distinct population (Ståhl, 1987; Carlsson, Nilsson, 2000; Hansen et al., 2002; Koljonen et al., 2002; Fraser et al., 2007; Apostolidis et al., 2008; Ozerov et al., 2010). Moreover, often there is a high degree of differentiation among populations even

at a very small geographical scale therefore it is impossible to detect if a particular water system contains one or more populations without the genetic studies of the population (Carlsson, Nilsson, 2000; Spidle et al., 2003; Ruzzante et al., 2001). Strong homing of Atlantic salmon and brown trout results in little genetic exchange between rivers, however occasional straying more likely occurs between adjacent rivers. This gene flow pattern results in association between genetic and geographic distance (or isolation by distance). Many empirical salmonid studies have revealed significant correlations between geographical and genetic distances (Bouza et al., 1999; Carlsson, Nilsson, 2000; Ruzzante et al., 2001; Campos et al., 2007; Palstra et al., 2007). Thus, even though individuals in each river should be considered as one separate population, genetic diversity in one of a population can be dependent on other geographically close populations (Vasemägi et al., 2005). Furthermore, gene flow between local salmon and brown trout populations often is asymmetric and individuals move preferably from large into small populations (Hansen et al., 2007). This pattern of gene flow may be important for maintaining the genetic diversity and viability of the small populations (Consuegra et al., 2005) and providing stability to regional population structure (Palstra et al., 2007). Thus, it is clear that genetic monitoring of contemporary connectivity of populations is necessary for conservation.

Whereas one of the fundamental aims of the conservation genetics is to maintain as much genetic variability within and between populations as possible, it is necessary to study and monitor the amount and distribution of biological diversity over time. Otherwise it would be impossible to detect negative changes and reductions of this diversity. Generally wild populations of salmon and brown trout are assumed to be genetically temporally stable (Ståhl, 1987; Koljonen et al., 1989; Hansen et al., 2002; Verspoor et al., 2005; Campos et al., 2007; Palstra et al., 2007; Vähä et al., 2008). However, some studies have shown temporal variation that includes significant allele frequency differences between temporally separated samples (Laikre et al., 2002; Østergaard et al., 2003; Jensen et al., 2005; Hansen et al., 2009). Several comparisons of originally wild and hatchery stocked populations indicated a clear loss of diversity and decrease of

allelic richness in hatchery stocked population (Säisä et al., 2003; Aho et al., 2006). Therefore genetic management must include collation of information on genetic population structure as well as changes of genetic composition over time in order to identify human mediated loss and change of genetic diversity.

Identifying genetic effects of stocking

Stocking–releasing into the wild of the fish that were bred in hatcheries or transferred from other location is a very common management practice. It is aimed to enhance the natural population and is generally regarded as beneficial. However, the studies of the efficiency of stocking programmes have shown that genetic introgression of the stocked fish on wild populations is variable and unpredictable. In some cases stocking programmes appear to have been inefficient or introgression is very low (<5%) (Moran et al., 1991; Martinez et al., 1993; Garcia-Marin et al., 1999b; Antunes et al., 2001; Aurelle et al., 2002; Almodovar et al., 2006). Other examples of stocking activities have clearly resulted in survival and reproduction of stocked trout, although the levels of introgression vary very broadly: from less than 25% to more than 70% (Apostolidis et al., 1996, 1997; Berrebi et al., 2000; Weiss et al., 2001; Jug et al., 2005). Harmful genetic effects of releases on native gene pools and the need of monitoring of such effects had been recognized several decades ago (Ryman, 1981) and more recent studies also emphasized the deleterious effects of farmed fish on genetic diversity of wild populations (Hindar et al., 1991; Moran et al., 2005; Vasemägi et al., 2005; Apostolidis et al., 2008; McGinnity et al., 2009; Hansen et al., 2010).

Genetic risks associated with releases of hatchery-reared fish can be direct and indirect. Indirect genetic changes can result from ecological impacts that arise through competition, introduction of diseases and parasites and increased predation. Stocked trout is often larger than wild, as a result of selection for faster growth together with favorable conditions for growth (such as diet and temperature) in the farm. Because of larger size and more aggressive behavior that is typical for domesticated fish, stocked fish can competitively displace wild fish (Weber, Fausch, 2003). Introduction of farm-reared salmonids can increase predation on wild

fish through the attraction of predators (Nickle-son, 2003). Introduced diseases and parasites can also increase mortality in the wild. Therefore, these ecological impacts can be the reason of lowered effective population size which in turn can cause the loss of genetic variability within populations through increased genetic drift and inbreeding.

Direct genetic impacts emerge when released fish is interacting and reproducing with the wild fish. Here the risks are dependent on the stocking type. There are two common types of farmed salmonid releases: 1) releases of genetically distinct (non-local) populations and 2) releases of local populations from which captive-bred individuals are derived (supportive breeding) (Laikre et al., 2010b). In the case of releases of genetically distinct populations, genetic variation of wild populations may be lost and unique gene pools can be destroyed due to a strong inflow of genes from non-local population (Moran et al., 2005; Apostolidis et al., 2008). In addition to genetic differences between wild and reared fish due to different origin, they can differ in their co-adapted gene complexes that are comprised of many genes and are involved in local adaptations. If fish with different co-adapted gene complexes interbreed, these gene complexes may be broken down resulting in loss of adaptations, the so-called outbreeding depression (Gharrett et al., 1999; Muhlfeld et al., 2009). Releases of genetically distinct populations can also result in a change of genetic composition of wild population. Several studies have shown wild local populations becoming genetically similar to non-native hatchery stocks (Araguas et al., 2004; Vasemägi et al., 2005).

A particular form of stocking, supportive breeding, is a type of breeding–release programme where the released fish descend directly from the receiving population (Hansen et al., 2000). A fraction of the wild parental fish is brought into a hatchery for artificial reproduction, and the offspring is released into the natural habitat where it mixes with the wild fish. The aim of the supportive breeding is to avoid genetic problems of supplemental stocking with farm-reared or non-native brown trout. Although exogenous genes are prevented from introductions to the wild population in case of supportive breeding, it may have strong negative genetic effects. Several studies have shown that even a short period in a hatchery can

result in a reduction of subsequent survival and reproductive success, because differential or relaxed selection in hatchery environment alter behavior, physiology and genetics of fish (Glover et al., 2004; Sundström et al., 2004). Moreover, inadvertent artificial mixing of stocks that inhabit the same water system but are spatially or temporally reproductively isolated, can break down the population structure and local adaptations, leading to a loss of productivity and fitness (Stewart et al., 2006).

Considering all possible threats, any stocking activity should always be preceded by analysis of potential genetic consequences and organized with aim to eliminate or minimize the negative genetic effects.

Relevance of population genetic studies for management of genetic resources

Studies of the population genetic structure are essential for providing estimates of the different sources of variation that determine species' genetic composition over the geographic area, e. g. between geographical regions, between distinct populations within regions, and among temporally spaced samples within populations (Laikre et al., 2005). The information obtained from population genetic studies can help to resolve the question whether or not two or more natural populations from different rivers or tributaries of the same river are genetically distinct and what are the patterns of genetic relationships between them. Knowledge from studies describing spatial and temporal genetic structure is needed to identify and analyze the changes of gene level diversity caused by human mediated harvest as well as enhancement practices. Lack of information on or ignorance of genetic population structure may result in underestimation of impacts of stochastic environmental fluctuations, risks of genetic diversity loss through genetic drift, extinction risks as well as underestimated fishing and stocking impacts (Dionne et al., 2009). On the other hand, this can determine unnecessary proliferation of management actions and ignoring potential impacts of management actions on the entire system (Dionne et al., 2009).

Current status and management measures of salmon and trout in Lithuania

There are 84 salmon rivers and around 1000 sea trout rivers and streams in the Baltic Sea (HEL-

COM, 2011). ICES has estimated that of these there are only 29 wild salmon rivers and up to nearly 500 wild sea trout populations in the Baltic Sea area (ICES, 2012). The status of these populations varies between different parts of the Baltic Sea. The sea trout populations in both Gulf of Bothnia and Gulf of Finland are in poor state, whereas populations in the Main Basin are in a good or moderate condition (HELCOM, 2011; ICES, 2012). Differences in the status of the wild salmon populations have become more apparent in recent years: most populations in Gulf of Bothnia have shown increases in abundance while many of populations in the Main Basin have shown either decreasing or stable abundance (ICES, 2012). Therefore, currently only 10 of 84 salmon rivers maintain self-sustaining wild natural populations in safe numbers (Palme et al., 2012).

In order to prevent the extinction of wild Baltic salmon and a further decrease of naturally produced populations, the International Baltic Sea Fisheries Commission (IBSFC) in 1997 adopted the Salmon Action Plan 1997–2010, which expired in 2010. The objectives of this plan were to enable wild Baltic salmon to recover, to maintain the genetic diversity of the river stocks, to re-establish salmon populations in potential salmon rivers and to keep the level of fishery as high as possible (IBSFC, 1997). As a consequence of the re-stocking target, the Baltic countries have for many years been releasing salmon fry, parr and smolt in rivers with extinct salmon populations. A considerable part of the releases constituted supportive releases in order to enhance weak natural populations. In some Baltic countries (e. g. Sweden and Finland) large-scale releases of salmon have been proceeded to compensate for the production losses caused by dam construction which prohibit natural migration of spawners to reproduction areas in rivers and migration of smolts to feeding areas in the Baltic Sea. As a result of all these activities, from 6 to 7 million smolts are currently released in the Baltic Sea region every year, which is almost three times the natural production of smolts. Therefore, hatchery produced and released salmon constitutes about 70% of the salmon in the Baltic Sea (ICES, 2011a).

In August 2011, the European Commission prepared a new "Proposal for a Regulation of the European Parliament and of the Council establishing

a multiannual plan for the Baltic salmon stock and the fisheries exploiting that stock” (European Commission, 2011). This proposal includes the provisions dealing with stocking to be conducted in wild salmon rivers; direct restocking to be conducted in potential salmon rivers and the phasing out of other type of releases of reared salmon. Also, a considerable part of the plan is designed of the requirements dealing with the member states’ obligations to monitor salmon rivers, provide information on releases of reared salmon and on their genetic information.

Sea trout is not included in the proposed multiannual salmon management plan. However, in 2007 ICES established the Study Group on Data Requirements and Assessment Needs for Baltic Sea Trout (SGBALANST) that was able to estimate the need for further assessment of sea trout populations in the Baltic Sea. This group reported that international agreements on management issues are strongly needed in the northern part of the Bothnian Bay, all round Finland and in the Gulf of Finland; in the rest of the Baltic Sea the need for international management actions is considered to be less urgent (Pedersen et al., 2012). This group also stressed that for the management it would be crucial to provide guidelines for management actions stating by which factors keeping stock status below “optimal” can be affected and stock status improved (ICES, 2011b). In order to improve the situation of the poor sea trout stocks, approx. 3 million of reared smolts are released in the rivers and river mouths or directly to the sea. It is a general agreement that genetically only local stock with sufficient variation should be used for the enhancement stockings (Pedersen et al., 2012).

In Lithuania there are 12 rivers inhabited by salmon populations and the status of these rivers differs. Based on historical data and today’s situation, salmon rivers can be divided into the following groups: 1 – inhabited by wild salmon; 2 – inhabited by artificially reared salmon; 3 – inhabited by mixed salmon population; 4 – “potential” rivers, i. e. where salmon occurs occasionally; 5 – rivers where salmon got extinct (Kesminas et al., 2003). A purely natural salmon population inhabits the Žeimena River and its tributaries – Mera and Saria, while mixed, i. e. natural and reared populations are in rivers Neris, Švento-

ji, Vilnia, Baltijos Šventoji, Dubysa, Siesartis, Širvinta and Vokė. Populations formed of reared salmon inhabit rivers Virinta, Jūra, Minija and some smaller tributaries of these rivers (ICES, 2011a).

The observed salmon parr densities in Lithuania are very low in relation to the observed parr densities in most other Baltic rivers (ICES, 2011a). There is also a remarkable variation in the annual parr densities, as well as between different rivers. The most abundant salmon populations were found in rivers Siesartis, Vilnia, Šventoji and Žeimena. 90% of total smolt production was originated from these rivers. Smolt production in other salmon rivers was significantly lower (ICES, 2011a).

In Lithuania the population of sea trout is greater than that of salmon. Sea trout populations inhabit 76 rivers that belong to 10 major basins: Neris, Žeimena, Šventoji, Minija, Jūra, Dubysa, Bartuva, Akmena-Danė, Šyša, Baltijos Šventoji. The highest densities of natural sea trout have been reported in western Lithuania – in Minija, Jūra and Dubysa river basins (Kesminas, Kontautas, 2011). According to experts’ evaluation, the current sea trout smolt production represents only 13% of the potential production (Kesminas, Kontautas, 2011).

Lithuania is engaged in the implementation of two relevant plans for the management of salmon: 1) IBSFC Salmon Action Plan 1997–2010 and 2) State program and action plan for salmon recovery and protection in Lithuanian waters 1997–2010. Lithuania also implements a state program for sea trout recovery and protection for 2001–2010. Through implementation of these plans, Lithuania carries out stocking of salmon and sea trout with the purpose of enhancing and restoring the natural populations of salmon and sea trout. Supportive breeding in Lithuania is carried out since 2000 and is based on wild breeders caught each year at the spawning sites and on migration pathways in some of the tributaries of the Lower Nemunas and the Curonian Lagoon. Due to limited technical possibilities, female and male spawners from different rivers are pooled together and thus, broodstock represents a mixture of several distinct populations. This practice is of great concern because the results of mitochondrial DNR analysis revealed statistically significant differences between Žeimena, Jūra and the Lower Nemunas sea trout populations (Leliūna, 2010)

and the analysis of microsatellite DNA showed that populations inhabiting different rivers and different tributaries of the same river are genetically differentiated (Samuiloviene et al., 2009). It is also evident that human mediated gene flow from stocked to wild populations alters hierarchical as well as spatial population structure of Lithuanian sea trout (Samuiloviene, 2012). Therefore, future management considerations should focus both on maintaining individual populations even at tributary level and ensuring natural levels of gene flow among populations.

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ATLANTO LAŠIŠOS IR ŠLAKIO POPULIACIJŲ GENETIKA IR JOS SVARBA GENETINIŲ RESURSŲ VALDYMUI

Santrauka

Atlanto lašišos (*Salmo salar* L.) ir šlakio (*Salmo trutta* L.) populiacijos pasižymi stipriai išreikšta genetinė struktūra. Genetinės populiacijų struktūros susiformavimas plačioje geografinėje skalėje priklauso nuo ledynmečio metu ir po ledynmečio vykusių įvykių, todėl Europoje yra nustatyta keletas pagrindinių Atlanto lašišos ir šlakio grupių bei skirtinga jų kilmė. Genetiniai skirtumai mažesnėje geografinėje skalėje priklauso nuo bendro genų dreifo, genetinio drifto, mutacijų ir natūralios atrankos poveikio. Siekiant išsiaiškinti genetinę populiacijų struktūrą ir pritaikyti šias žinias, kad būtų išsaugoti šių rūšių resursai, svarbu suprasti pastutiniojo apledėjimo poveikį jų pasiskirstymui ir genetinei įvairovei, taip pat natūralios atrankos, genetinio drifto ir genų dreifo poveikį genetinei įvairovei populiacijos viduje bei genetiniams skirtumams tarp populiacijų. Genetinių resursų valdymas yra labai svarbus metodų, kurie garantuotų lašišų ir šlakių populiacijų išsaugojimą ir atkūrimą, komponentas. Pagrindinės genetinių resursų valdymo problemos yra susijusios su genetinės bioįvairovės stebėseną ir išsaugojimu, populiacijų genetinės struktūros laike ir erdvėje ištyrimu bei veisimo programų genetinių padarinių nustatymu. Populiacijų genetinės struktūros tyrimai Lietuvoje yra būtini siekiant apskaičiuoti skirtingų šaltinių lemiamą įvairovę ir kaip nuo šios įvairovės priklauso rūšies genetinė sudėtis geografiniame regione. Genetinės populiacijų struktūros erdvėje ir laike tyrimų metu gautos žinios yra reikalingos siekiant nustatyti ir ištirti genetinės įvairovės pokyčius, kuriuos sukelia per didelis išteklių sunaudojimas ir įžuvinimo programos. Duomenų apie genetinę populiacijų struktūrą neturėjimas arba jų ignoravimas gali lemti genetinės įvairovės praradimą, sumažėjusį produktyvumą ir ekologinę žalą. Planuojant lašišų ir šlakių išteklių valdymą Lietuvoje, būtina užtikrinti individualių populiacijų išsaugojimą ir atsižvelgti į natūralų genų srautą tarp populiacijų.

Raktažodžiai: Atlanto lašiša, šlakis, populiacijų genetika, genetinių išteklių valdymas