"The face of Nature in a vast expanse was naught but Chaos uniformly waste. It was a rude and undeveloped mass, that nothing made except a ponderous weight; and all discordant elements confused, were there congested in a shapeless heap" (Ovidii, 2017)

Instability Stabilized: Mechanisms of Evolutionary Stasis and Genetic Diversity Accumulation in Fishes and Lampreys from Environments with Unstable Abiotic Factors

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Abstract—As studies have shown, individuals from well morphologically distinct groups often represent the same species and may even belong to one population in fishes and lampreys from environments with unstable abiotic factors (Arctic, mountain, and desert regions). Phenotypic plasticity ensures broad variation ranges of morphological traits in unstable conditions, which require rapid transitions from one morphogenetic variant to another. The choice of a morphogenetic pathway can be influenced by the level of individual heterozygosity, changes in the copy numbers of certain DNA sequences, heteroplasmy, and the presence of several allelic variants in the genes that strongly affect the phenotype. A cyclic character is often observed for evolutionary processes driven by these mechanisms, and speciation usually does not take place in unstable environmental conditions. However, mobilization reserve accumulate in a species with a broad reaction norm, and particular morphogenetic pathways may be genetically fixed when its population finds its way into stable environmental conditions, facilitating fast allopatric speciation.

INTRODUCTION

Evolutionary stasis (understood here as lack of irreversible evolutionary changes) seems, at first glance, impossible in taxa from regions with unstable environmental conditions because environmental changes are the factor that drives and directs evolutionary processes (Trubenová et al., 2019). However, note that a species usually changes in response to the evolutionary innovations that arise in its interaction partners, such as predators, forage organisms, competitors, and parasites; i.e., changes in a biotic component of the environment induce the fastest and most dramatic transformations in the gene pool (van Valen, 1973).

Abiotic environmental factors can certainly change as well, but their changes are often oscillatory or cyclic. Abiotic characteristics of the environment thus remain within the same limits for thousands or even millions of years, and a number of species manage to adapt to such changes. The number of these species is relatively small. However, once a species has adapted to abiotic factors of its unstable environment, the rate of its evolution may substantially decrease because species only rarely encounter new or greatly changed antagonist species in unstable environments with an invariably poor species composition.

Polyakov (1975, p. 147) was probably the first to describe this paradoxical phenomenon, noting that natural selection "stabilizes the instability" of a population by eliminating the individuals that fail to change as directed by their diverse living conditions.

Here we summarize the empirical data and theoretical studies that demonstrate the existence of evolutionary stasis in environments with unstable abiotic factors and help to understand how organisms adapt to these conditions, using fishes and lampreys as an example.

We focus on the mechanisms that ensure alternative morphogenetic variants, each of which is adaptive for certain environmental conditions. Unfortunately, there

is no conventional term to describe the organism groups that result from such processes. Different terms have been used by different researchers: life forms, ecological forms, life strategies, discrete adaptive norms, ecomorphs, life-history styles, alternative phenotypes, etc.

Organisms from Arctic, mountain, and desert regions were chosen because abiotic environmental factors are especially unstable in these regions, while the effect of biotic factors is lower because the species compositions of the flora and fauna are relatively poor. Alternative morphogenetic variants may arise almost in their pure forms in these conditions. It is not surprising that high morphological diversity was many times observed in species from northern regions (Dunbar, 1968) and fishes in particular (for a review, see: Nikol'skii, 1980; Mina, 1986; Bell and Andrews, 1997; Robinson and Schluter, 2000). Morphologically different forms are additionally known for many fish species from Mongolia (Dgebuadze, 2001).

However, before we consider the mechanisms that regulate the origin of morphologically different forms, their taxonomic statuses are important to discuss because many fish and lamprey forms from habitats with unstable abiotic conditions have been described as separate, closely related species of recent divergence. The evolutionary significance of the mechanisms described is considered in the last part of the article.

What remains outside the scope of this review includes an important and interesting, but quite separate problem of how living organisms adapt to extreme, but stable environmental conditions, such as deepwater lakes and seas, thermal springs, caves, and water bodies with unusual hydrochemical conditions. The problem has been considered comprehensively in other reviews (Birshtein, 1985; Bolotov et al., 2012, 2016; Kaufman, 2015; Berman and Leirikh, 2017; Wilkens and Strecker, 2017).

We additionally omit the interesting fish group that is adapted to environments where both abiotic and biotic factors are unstable. For example, the group includes the Amur sleeper *Perccottus glenii* (Reshetnikov, 2009), the topmouth gudgeon *Pseudorasbora parva* (Karabanov et al., 2010), fishes of the genus *Carassius* (Mezhzherin et al., 2009), and the genus *Nothobranchius* (Krysanov et al., 2016). Other mechanisms sustain adaptation in these fishes; in particular, alternative morphogenetic variants are absent. The fishes usually inhabit warmer (and, therefore, more abundant in organisms) regions as compared with the group under study.

Thus, we have three main objectives of this review: (1) to analyze the data on the taxonomic statuses of the fish and lamprey forms that differ morphologically and ecologically and are from environments with unstable abiotic factors, (2) to identify the main mechanisms of switching between alternative morphogenetic variants, and (3) to discuss the evolutionary role of the mechanisms.

THE PROBLEM OF TAXONOMIC STATUSES OF FORMS FROM UNSTABLE HABITATS

Starting from Darwin, it is broadly accepted in biology that every more or less distinct morphological form is a species or an incipient species. Total diversity of intraspecific forms is consequently often thought to represent various steps of speciation, while the most interesting phenomenon of evolutionary stasis is neglected.

The tendency of reducing microevolutionary processes to speciation is so strong that the term speciation is sometimes used to describe the origin of forms that have never been described as species and lack Latin names. Examples are provided by benthos- and plankton-feeding forms of the three-spined stickleback *Gasterosteus aculeatus* and resident and migratory forms of the sockeye salmon *Oncorhynchus nerka* (Schluter, 1996; Taylor, 1999). Concepts of parallel speciation, despeciation, and respeciation have been advanced to equate the forms with biological species understood as commonly accepted (Turner, 2002), but the underlying ideas clearly demonstrate that form generation, rather than speciation, is actually meant.

In the past years, new species were formally isolated in several groups from habitats with unstable abiotic conditions, for example, by assigning the species status to individual groups that morphologically differ from a "standard". To split a species, some researchers fail to analyze new materials or to examine available collections more comprehensively, but just mechanically elevate the forms described before to the species status; e.g., subspecies or ecological forms are made species. Moreover, almost any traits, including highly plastic ones, are used to isolate new species. Such trends have already been criticized in detail (Mina et al., 2006).

At the same time, methods to combine forms in one species are highly laborious. To demonstrate that forms belong to one species, it is necessary to observe how one form transforms into another in response to environmental changes in natural or artificial conditions or to obtain viable fertile hybrids of different forms and to estimate the heritability of their traits. Molecular genetic markers help in some cases to demonstrate the independent origin for forms with questionable status from different water systems (demonstration of polytopic form generation).

Studies with these methods have already shown for a number of fishes and lampreys that two or more morphologically different groups from habitats with unstable abiotic factors actually represent one species and, in some cases, even belong to one population (Table 1).

TRANSITION BETWEEN ALTERNATIVE MORPHOGENETIC VARIANTS DUE TO PHENOTYPIC PLASTICITY

Phenotypic plasticity is a main factor that ensures adaptation to rapid changes in environmental conditions during ontogeny in various groups of organisms

Table 1. Cases where forms with alternative morphogenetic variants are combined in one species

Species	Method used	Reference
Dwarf Altai osman *Oreoleuciscus humilis*	A transition from a river to a lake form was observed upon changes in environmental conditions in nature	Dgebuadze, 2001
European whitefish *Coregonus lavaretus*	A transition from one form to another was observed upon changes in environmental conditions in an artificial setting, viable hybrids were obtained, and form generation was shown to be polytopic in a study with molecular genetic markers	Reviews: Etheridge et al., 2012; Borovikova and Makhrov, 2013; Borovikova et al., 2020
Vendace *Coregonus albula*	A transition from one form to another was observed upon changes in environmental conditions in nature	Borovikova et al., 2013; Alekseeva and Makhrov, 2017
Three-spined stickleback *Gasterosteus aculeatus*	A transition from a marine to a freshwater form was observed upon changes in environmental conditions in nature	Review: Zyuganov, 1991
	Form generation was shown to be polytopic in a study with mitochondrial *COI* gene as a marker	Denys et al., 2015
Brown trout *Salmo trutta*	A transition from one form to another was observed upon changes in environmental conditions in an artificial setting	Makhrov et al., 2011
Rainbow trout *Parasalmo mykiss*	Form generation was shown to be polytopic via a microsatellite analysis	McPhee et al., 2007
	Individuals of one form were detected in offspring from another form by a chemical analysis of otoliths	Zimmerman et al., 2003, 2009
Arctic lamprey *Lethenteron camtschaticum*	Form generation was shown to be polytopic in a study with mitochondrial *COI* gene as a marker	Artamonova et al., 2015
River lamprey *Lampetra fluviatilis*	Viable hybrids were obtained, and form generation was shown to be polytopic by molecular genetic methods	Tsimbalov et al., 2018; see also references in Makhrov and Popov, 2015; Hume et al., 2018
Arctic char *Salvelinus alpinus*	Form generation was shown to be polytopic in a study with mitochondrial *COI* gene as a marker	Makhrov et al., 2019

(for a review, see: Schmalhausen, 1968; Pigliucci, 2001; West-Eberhard, 2003; Khlebovich, 2012; Markov and Ivnitskii, 2016). Adaptive phenotypic plasticity is naturally what is meant. Nonadaptive phenotypic plasticity arises when environmental parameters go beyond the limits to which the species is adapted genetically, leading to morphoses or increasing the developmental instability (Laius, D.L. and Laius, Yu.A., 2003; Lajus et al., 2003).

There are many cases where adaptive phenotypic plasticity underlies the transition from one alternative morphogenetic variant to another in species from water bodies with rapidly changing environmental parameters (for a review, see: Robinson and Parsons, 2002; McPhee et al., 2012).

For example, extremely high phenotypic plasticity is characteristic of Arctic char, a typical species of far northern and mountain water bodies. This plasticity is

to a great extent responsible for transitions between alternative morphotypes in the species (for a review, see: Knudsen et al., 2016).

High phenotypic plasticity is similarly observed in European whitefish (for a review, see: Borovikova and Makhrov, 2013), which is another species from Arctic and mountain water bodies, and brown trout, especially its populations from Caucasian water bodies (for a review, see: Makhrov and Bolotov, 2019). Phenotypic plasticity is extremely high in Altai osmans from the Mongolian lakes that dry up periodically (Dgebuadze, 2001). Highly plastic morphology is characteristic of minnows of the genus *Rhynchocypris* from small mountain water bodies of China (Park et al., 2001; Makhrov et al., 2019).

Schizothoracinae fishes, which also belong to the family Cyprinidae and are typical inhabitants of high-altitude Asian water bodies, seem to have similarly

high phenotypic plasticity. For example, new forms of the false osman *Schizopygopsis stolichkai* (Steindaechner) have already formed in the Pamir Yashil'kul' Lake, which arose only 800 years ago (Popov, 1968; Savvaitova et al., 1987). As expected, no genetic difference was detected between the original and new forms by molecular DNA hybridization (Timirkhanov et al., 1990). However, to convincingly demonstrate that all forms are genetically identical, it is necessary to employ a system of modern molecular genetic markers allowing a more detailed genome analysis.

The above examples fully agree with the theoretical concept that climatic oscillations lead to the formation of generalist species in various taxonomic groups (Dynesius and Jansson, 2000). Moreover, mathematic modeling has shown that phenotypic plasticity is expected for organisms from environments with variable parameters (see: Trubenová et al., 2019 and references therein).

It should be noted that, in terms of evolution, certain epigenetic mechanisms act similarly to the mechanisms that ensure a broad reaction norm in response to environmental conditions. In some cases, the offspring phenotype depends to a certain extent on the living conditions of the parents in fishes (as well as in other organisms) (for a review, see: Best et al., 2018). Thus, the size and swimming performance of larvae correlated with the temperature at which the paternal sperm was stored prior to fertilization in experiments with European whitefish (Kekäläinen et al., 2018).

It is unknown now what genome characteristics provide a species with a broad range of phenotypic plasticity. A noteworthy fact is that polyploidy is characteristic of many species from habitats with unstable abiotic conditions. The set includes salmonoids (Allendorf and Thorgaard, 1984), large barbs (Golubtsov and Krysanov, 1993), and Schizothoracinae (Dai and Han, 2018). Polyploidy probably ensured the fixation of heterozygous genotypes in the species, which consequently had an advantage over their diploid ancestors in unstable environmental conditions (Brochmann et al., 2004).

CHOICE OF THE MORPHOGENETIC PATHWAY AND THE INDIVIDUAL HETEROZYGOSITY LEVEL

Because individuals of different morphotypes or ecotypes may coexist in one population, the question arises as to how the developmental pathway is chosen in each particular case given that the reaction norm is the same in all individuals of a species. It should be noted here that the individual heterozygosity level is associated with many ontogenetic characteristics and, in particular, the development rate as a key parameter that determines many other parameters. The nature of the association is still unclear, but its existence is beyond doubt (for a review, see: Golubtsov, 1988; Chapman et al., 2009; Szulkin et al., 2010).

In male salmonids, high heterozygosity is characteristic of the most quickly growing males, which usually mature faster. They develop into dwarf males, which reach maturity in freshwater without migrating to the sea. This was observed in sockeye salmon, brown trout, and the Atlantic salmon *Salmo salar* (see references in: Artamonova and Makhrov, 2016).

A correlation between heterozygosity and the choice of the life strategy within the reaction norm makes it possible for individuals following different morphogenetic pathways to coexist in one population. Members of one species are consequently capable of colonizing different biotopes, and the capability is of extreme importance in unstable conditions.

Individuals with higher development rates often serve, in fact, as keepers of the population gene pool in unstable conditions. Dwarf males remain in the vicinity of the spawning grounds throughout their lives and have higher chances to survive. If a substantial portion of migratory fish dies from dramatic changes in environmental conditions, rapidly maturing heterozygotes are capable of reproducing the given morphotype within a short period of time. Thus, maintaining a relatively high heterozygosity level in populations increases the chances to survive for the species that inhabit regions with unstable abiotic conditions.

DIFFERENTIATION OF ECOLOGICAL FORMS AS A RESULT OF REPEAT COPY NUMBER VARIATION IN CERTAIN DNA REGIONS

The heterozygosity level provides a mechanism to regulate the phenotype within the lifespan on one generation. There are also mechanisms that ensure adaptation to local environmental conditions through many generations without leading to speciation.

One interesting, though poorly understood, mechanism is related to copy number variation of repetitive sequences (for a review, see: Lunt et al., 1998). Differences in copy number of repetitive sequences between the genomes of resident and migratory forms were observed in Arctic char individuals from the same population (Mednikov, 1977) and in sockeye salmon (Kosyuk and Borkhsenius, 1981; Chernov and Borkhsenius, 1987).

Recent studies showed that an increase in the copy number of the Fads2 gene always accompanies the formation of freshwater populations in sticklebacks of the genera *Gasterosteus* and *Pungitius*. The gene codes for a fatty acid desaturase, which is involved in fatty acid metabolism (Ishikawa et al., 2019).

An interesting example is provided by two coregonine fish forms from the Lake Stechlin, Germany. The forms have been described as separate species. One is common winter-spawning form known as *Coregonus albula*, and the other is a spring-spawning form that has been described as the endemic species *C. fontanae*. The endemic form differs from the common form in having

a greater copy number of the 45S pre-ribosomal RNA gene (Symonová et al., 2013). The same mitochondrial ND-3 gene haplotype was the most prevalent in samples of the two forms, providing indirect evidence that the forms belong to one species (Schulz et al., 2006).

Retrotransposons have been assumed to mediate the increase in 45S pre-ribosomal RNA gene (Symonová et al., 2013), in line with data on the role that mobile genetic elements play in adaptation processes (for a review, see: Casacuberta and González, 2013).

The length of the mitochondrial DNA control region is polymorphic as a result of the copy number variation of its fragments in European whitefish (Brzuzan, 2000; Borovikova et al., 2007). Differences in the copy number of internal transcribed spacer 1 (ITS1) of the ribosomal gene cluster were additionally detected between individuals from different populations of the species (Bochkarev et al., 2017).

Thus, changes in the copy number of certain DNA sequences provide a highly efficient mechanism that sustains adaptation to local conditions through generations and acts at the population level.

HETEROPLASMY

Heteroplasmy is the presence of two types of mitochondria (with different DNA variants) in all cells of an individual and has been detected in various taxa at an increasing rate (Kmiec et al., 2006). Currently available data are insufficient to conclude that a higher heteroplasmy frequency is characteristic of species from unstable environments, but heteroplasmy is certainly widespread in their populations. Heteroplasmy is common in Arctic lamprey (Artamonova et al., 2015), brown trout (Wetjen et al., 2017), three-spined stickleback (Stärner et al., 2004; our unpublished data), and guppy *Poecilia reticulata* (Taylor, Breden, 2002) and has been detected in one individual from an Atlantic salmon sample (Artamonova et al., 2008).

Discussions with colleagues and examination of the sequencing chromatograms from their studies have led us to think that heteroplasmy occurs as well in some other species from unstable habitats. However, this interesting phenomenon is neglected or escapes reliable detection in many cases. Yet heteroplasmy is most likely capable of contributing to long-term genetic adaptation to various environmental conditions.

HIGHLY HERITABLE TRAITS

While the majority of traits are each determined by a number of genes and usually have a low heritability in higher organisms, highly heritable traits are often observed in species from unstable environments.

For example, the number of gill rakers shows a high heritability in European whitefish (Svärdson, 1957). The time of spawning (Abadía-Cardoso et al., 2013) and smoltification-related traits (Thrower et al., 2004) are heritable to a substantial extent in rainbow trout.

Evidence has been obtained to date that the traits in question are highly heritable because different variants (alleles) of trait-determining genes occur in populations. For example, the *PGM-1r** regulatory gene influences the phosphoglucomutase synthesis in rainbow trout and Atlantic salmon. The development rate and several morphological traits differ between carriers of different *PGM-1r** alleles in rainbow trout (Leary et al., 1984), and dwarf males have a higher frequency of one of the *PGM-1r** alleles in Atlantic salmon (Pollard et al., 1994). The duration of feeding at sea to maturity depends to a great extent on the allelic variants of a single locus (Barson et al., 2015), which is subject to rapid selection in natural conditions (Czorlich et al., 2018).

An experiment performed to model the formation of a freshwater population from a migratory one in Atlantic salmon detected uncontrolled selection in favor of one allele of a malic enzyme gene. A higher frequency of the allele has earlier been observed in natural freshwater populations of the species (see: Artamonova et al., 2010 and references therein).

Parallel microevolution demonstrating the adaptive significance of a certain allele has been observed in other fish species as well. Three-spined stickleback was the subject of the most comprehensive studies of the parallel microevolutionary processes that accompany the formation of freshwater populations (for a review, see: Zyuganov, 1991; Bell and Aguirre, 2013).

Note that only a few fishes have morphogenetic traits that are controlled by single genes and consequently have a high heritability according to Kirpichnikov's summary (1979). The set includes sticklebacks, species of the families Poeciliidae (the genera *Astyanax* and *Aphanius anatoliae*) and Cichlidae (*Cichlasoma* (*Amphilophus*) *citrinellum* and *Pseudotropheus* (*Maylandia*) *zebra*), and the stone loach *Nemachilus* (*Barbatula*) *barbatula*. Tellingly, all of the fishes inhabit relatively unstable environments.

Another observation is also of interest. When more than one gene determine a highly heritable trait related to morphogenetic specifics, the genes are often located in one chromosome in the immediate vicinity of each other, as is the case in three-spined stickleback (Terekhanova et al., 2014).

This gene arrangement makes recombination less likely and helps to preserve the combination of the allelic variants that have been selected for high fitness to particular abiotic environmental conditions through generations, thus ensuring a high heritability for the respective traits (for a review, see: Neiman and Linksvayer, 2006). Moreover, a chromosome inversion is known in rainbow trout. The inversion involves large-effect genes and totally prevents recombination and, therefore, disruption of the set of adaptations they determine. Individuals with chromosomes carrying the inversion and individuals with inversion-free chromosomes are found in the same populations; i.e.,

alternative morphogenetic strategies can be used depending on the individual genotype (see: Arostegui et al., 2019 and references therein).

The presence of different alleles of genes having large effects on morphogenesis provides for rapid selection and allows the population to change the frequencies of individuals with different morphogenetic variants when this is necessary for its adaptation to quickly changing environmental conditions.

To consider the mutual relationships and mutual effects of phenotypic plasticity and the presence of large-effect genes, note that the genes include a group of regulatory sequences, which act essentially as switches between different morphogenetic pathways. Among the genes mentioned above, the *PGM-1r** regulatory gene of rainbow trout and Atlantic salmon belongs to the group (Leary et al., 1984; Pollard et al., 1994).

The following tendency is additionally noteworthy. The lower the stability of environmental conditions of a species (Arctic and high-altitude regions), the greater is the role of phenotypic plasticity and the less important is the role of the genetic component in species adaptation. Discrete morphotypes fit to particular environmental conditions are usually indistinct in such cases, and there are many intermediate variants between highly different forms. Such a situation is characteristic of Arctic char and brown trout (Savvaitova, 1989; Cucherousset et al., 2005).

It is therefore not surprising that parallel evolution at the genetic level is utilized to different extents by different species, based on genomics data (for a review, see: Bernatchez, 2016). As we go from extremely unstable to more stable conditions (e.g., northern regions of the temperate zone and submountain regions), an increase in frequency is observed for the species that rely on parallel microevolutionary processes (e.g., to develop freshwater forms from sea forms or lake forms from river forms). The set includes three-spined stickleback, Atlantic salmon, and rainbow trout.

The lake trout *Salvelinus namaycush*, which inhabits less stable water bodies, clearly differs from three-spined stickleback and Atlantic salmon. A study of identical ecotypes from different habitats has not detected any parallelism in genetic divergence of the ecotypes in lake trout (Perreault-Payette et al., 2017). Likewise, large-effect genes have not been found (at least so far) in Arctic char (O'Malley et al., 2019) and brown trout (for a review, see: Ferguson et al., 2019).

Three-spined stickleback provides a classical example of parallel genetic adaptation to freshwater environments. However, such adaptation was convergent in its populations found in northern Finland. Adaptation to freshwater environments is always convergent in populations of nine-spined stickleback, which inhabits more unstable environments (in particular, its species range extends farther northwards) as compared with three-spined stickleback (Merilä, 2013).

EVOLUTIONARY CIRCLES AND SWAMPS IN UNSTABLE ENVIRONMENTAL CONDITIONS: FAST ADAPTATION AND INHIBITED SPECIATION

Thus, the three above mechanisms—phenotypic plasticity, individual heterozygosity as a means to regulate morphogenesis, and the presence of alleles in genes exerting large effects on morphogenesis (heteroplasmy may conventionally be added to this category)—reliably ensure adaptation to unstable abiotic conditions by rapidly changing the proportion of different morpho-physiological forms.

It is of interest that many species with alternative morphogenetic variants are now efficiently colonizing new habitats and especially those affected by human activities. For example, brown trout and rainbow trout are classed with the most dangerous invasive species (Lowe et al., 2004).

However, none of the above mechanisms leads to speciation. Phenotypic plasticity and heteroplasmy are naturally incapable of changing the allele frequencies of any gene. Moreover, a low efficiency of selection is usually associated with phenotypic plasticity (Gause and Alpatov, 1941; Gause, 1942). Selection in favor of heterozygotes was aptly termed the Sisyphean cycle because allele combinations supported by selection are disrupted in the next generation (Mitton, 1997). A freshwater form always develops from a migratory one in three-spined stickleback. The same mechanisms usually sustain the generation of forms; i.e., the same gene alleles again and again ensure the formation of freshwater populations. The term allele recycling is even used to describe these processes (Bell and Aguirre, 2013).

In addition, a high level of migration, which shuffles local gene pools, is often characteristic of populations from environments with unstable abiotic conditions (Dynesius and Jansson, 2000). This has been observed, in particular, in brown trout (see: Makhrov et al., 1999 and references therein) and Arctic lamprey (Yamazaki et al., 2014; Shink et al., 2018). Migration combines populations into population systems, where average allele frequencies are maintained constant for long period of times on experimental evidence (Altukhov, 2003).

Thus, intraspecific forms may however long remain associated via mutual transitions in unstable environmental conditions, and the gene pool of the total species consequently remains unchanged; i.e., the species does not evolve at the macro level. The apt term "dumbbell-shaped structures" has been proposed for such associated forms (Kondrashov and Mina, 1986).

Savvaitova (1985) noted that intraspecific forms associated via transitions are more often observed in fish populations that live in extreme, unstable conditions, such as Arctic and subarctic regions, high-altitude water bodies, and ephemeral lakes of arid zones,

where communities are poor in species and free ecological niches exist.

Molecular genetic findings support decelerated evolution of Arctic char, which is the most typical species in water bodies with unstable abiotic factors (Artamonova et al., 2018).

Thus, form generation in unstable environmental conditions can euphemistically be described as the evolutionary cycling or even the evolutionary swamp. However, just as swamps sometimes give rise to great rivers, species associated with unstable habitats are capable of rapid evolution if they find their way into environments where conditions are more stable.

ACCUMULATION OF GENETIC DIVERSITY IN UNSTABLE ENVIRONMENTAL CONDITIONS AND ITS MOBILIZATION IN STABLE CONDITIONS

As mentioned above, the efficiency of selection decreases to a great extent when phenotypic plasticity is high (Gause and Alpatov, 1941; Gause, 1942), and various alleles of many genes can survive in the population. Genetic diversity, or mobilization reserve (Gershenson, 1941), thus accumulates under the shelter of phenotypic plasticity. The mobilization reserve can be used efficiently to sustain adaptation at the genetic level when a population of the species finds its way into an environment with stable conditions, where selection works to improve the fitness to the stable conditions rather than to increase the reaction norm. The process has been observed in African cichlids in nature (Gunter et al., 2017) and experimentally reproduced many times in model species (Bateman, 1959; Gause, 1984). It is important to note that the process is allele selection rather than mythic inheritance of acquired traits.

The transition from a form that arises anew in every generation to complete genetic determination is possible to observe in brown trout. Studies in Norway showed that several ecological forms, including a large-sized predatory form, coexist in brown trout populations from environments with unstable conditions. The predatory form occurs as a separate population in more stable large water systems (Wollebaek et al., 2018). On the British Islands, the predatory form occurs as an independent phylogenetic lineage, *ferox*, rather than arising independently in each water system (see: Verspoor et al., 2019 and references therein).

Both selection in favor of heterozygotes and heteroplasmy directly lead to an accumulation of mobilization reserve.

Although speciation does not take place in unstable environmental conditions, evolutionary circling thus often leads to an accumulation of genetic diversity, which provides a basis for speciation when environmental conditions are stabilized.

According to molecular genetic data, fishes that were similar to modern Arctic char and were likely as plastic gave origin to all other salmonid genera (Artamonova et al., 2018). Caucasian trouts, which are highly phenotypically plastic, are ancestors of all other forms of the genus *Salmo* (Makhrov and Bolotov, 2019).

It is important to note that mobilization reserve accumulated in unstable abiotic conditions provide well for subsequent adaptation, while speciation is prevented in this case because selection in unstable environmental conditions works against the gene alleles that allow postzygotic reproductive isolation to arise. As a result, highly divergent phylogenetic lineages often remain capable of introgressive hybridization even when the species range is discontinuous.

Many groups whose ancestors migrated from habitats with unstable abiotic factors are consequently the subjects of longstanding disputes among taxonomists. In particular, controversy rages as to how to classify the sympatric forms in the Arctic chars of the genus *Salvelinus* (for a review, see: Savvaitova, 1989; Jonsson, Jonsson, 2001; Klementsen, 2010; Knudsen et al., 2016; Esin and Markevich, 2017), whitefishes of the genus *Coregonus* (for a review, see: Kottelat and Freyhof, 2007; Etheridge et al., 2012; Borovikova and Makhrov, 2013), barbs of the genus *Barbus* (Dzerzhinskii et al., 2007; de Graaf et al., 2010; Mina et al., 2012; Nagelkerke et al., 2015; Shkil et al., 2015; Levin et al., 2019), and redfishes of the genus *Sebastes* (Cadrin et al., 2010; Makhrov et al., 2011; Artamonova et al., 2013).

Possibly because the alleles that can provide for postzygotic reproductive isolation are lacking, large chromosome rearrangements often mediate the formation of true species in such groups, as is the case in certain salmonoids (for a review, see: Makhrov, 2017) and three-spined sticklebacks (Yoshida et al., 2014). Speciation most likely occurs only in an allopatric manner. An example interesting in this respect is provided by three endemic char forms (*Salvelinus*) from the El'gygytgyn Lake (Chukotka). The forms differ in chromosome number (Frolov, 1993). An allopatric origin was shown for all of the forms in molecular genetic studies (Osinov et al., 2015).

The data support the idea that alternative morphogenetic variants play an important role in speciation (for reviews, see: Mednikov, 1963, 1987; Savvaitova, 1985; Mina, 1986; Wimberger, 1994; Smith and Skúlason, 1996; West-Eberhard, 2003; Khlebovich, 2009). However, allopatric, rather than sympatric, mechanisms mediate the divergence of forms, fixation of adaptive morphogenetic traits at the genetic level, and subsequent speciation, as is evident from recent findings.

CONCLUSIONS

(1) High morpho-ecological diversity is characteristic of fishes and lampreys from environments with unstable abiotic factors, and species with known alternative morphogenetic pathways belong predominantly to this group.

(2) Particular morphogenetic pathways are expressed as a result of phenotypic plasticity. Selection maintains higher phenotypic plasticity in populations from environments with unstable abiotic factors. The choice of a particular morphogenetic pathway is affected by the individual heterozygosity level, changes in the copy numbers of certain DNA sequences, (possibly) heteroplasmy, and the presence of certain allelic variants in large-effect genes.

(3) Because a broad reaction norm is maintained in species from environments with unstable abiotic factors by microevolutionary processes, speciation does usually not take place in these conditions. However, genetic diversity accumulated in such environments often facilitates speciation when a population of the species finds its way into an environment where abiotic factors are stable.

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COMPLIANCE WITH ETHICAL STANDARDS

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