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REVIEW
GENETICS

Mechanisms of Sex Determination in Fish: Evolutionary and Practical Aspects

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Abstract—The mechanisms of sex determination in fish are extremely diverse, changeable, and labile. This review analyzes the possible variants of sex determination in fish, as well as the mechanisms that underlie quick changes in sex. The available data suggest that the ability to quickly change the molecular mechanisms of sex determination may frequently be adaptive in evolution and contribute to the formation of "biological" (non-crossing) species during a short time of isolation. Sex changes under the influence of external factors, even in the presence of the chromosome mechanism of sex determination, can also be regarded as aimed at the adaptation of populations and species to changing environmental factors. The implications of sex changes for fish aquaculture and for fish abundance assessment in natural populations are discussed. This is also essential to creating monosex fish cultures that are characterized by accelerated growth rates. Knowledge of the sex-determination mechanisms can also be useful for invasive species control.

Keywords: fish, sex-determining mechanisms, sex-determining genes, sex evolution

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Sexual reproduction, which appeared during the evolution of organisms, has evident advantages over asexual reproduction due to faster variations in the hereditary material as a result of recombination processes. The study of evolutionary mechanisms of sex determination in various groups of animals is of major interest, as these mechanisms are known to differ significantly.

The complex and multistage processes of sex formation are relatively well studied in vertebrates, which have the growth and differentiation of their gonads controlled by the endocrine pituitary gland; this process varies significantly between males and females, [20]. The endocrine control of sex differentiation is a complex interaction between the brain and gonads through hypophysis-produced gonadotropins and steroids synthesized in gonad cells. Steroid sex hormones exert a local and direct effect on the development of sex cells, but they also act as endocrine hormones by influencing other types of gonad cells and organs involved in sex differentiation. Thus, sex formation is controlled at several levels and includes biochemical, physiological, and neurohumoral pathways, which provide plasticity of gonad development during interactions with internal and external factors [9, 20]. It is obvious that triggering of this complex multi-level system via the activation of a few genes at early stages of development is the primary and crucial moment in most cases.

An immense amount of empirical material that testifies to the significant variations of the sex-determination mechanism in vertebrates has been collected in recent decades. At the same time, it is well known that at the biochemical level this process in vertebrates is due to the synthesis of several hormones, among which steroids are considered as the primary ones, which are synthesized in the following sequence: cholesterol → pregnenolone → progesterone → testosterone → estradiol. Cholesterol is transformed into steroid hormones through a cascade of biochemical reactions, when testosterones (androgens), which determine the formation of males, are synthesized at the first stage, and then estrogens, which determine the formation of the female phenotype, are formed from testosterones. In these transformations, the enzymes of the aromatase pathway and the activity of genes the encode them are of primary significance [31].

In mammals and birds, sex is rather strictly determined by the chromosomal mechanism. In most mammal species, males are the heterogametic sex (XY system): two homologous X chromosomes (the XX combination of sex chromosomes) exist in the female genome; in the male genome, these are X chromosome and the partially or completely non-homologous to it Y chromosome, which is poor in functional genes and enriched in repetitive non-functional DNA and transposons. Owing to this degeneration, any recombination between sex chromosomes is almost impossible.

Primary sex differentiation is determined by the presence and activation of the *sry* gene on the Y chromosome, which triggers a cascade of biochemical reactions, resulting in the formation of the male phenotype [24]. The *sry* gene is a member of the group of *sox* genes, which code high mobility gel (HMG) proteins that play an important role in the regulation of transcription. The *sry* gene originates from the *sox3* gene, which is found on the X chromosome of placental mammals. The phosphorylated nuclear protein, which is a product of the *sry* gene, forms a complex with the LIF1-like transcription factor, which is bound to specific sites in DNA and changes its superhelicity. This, in turn, causes local conformational variations in the chromatin structure and differential transcription of genes [24].

Unlike mammals, females in birds are most frequently the heterogametic sex (the WZ combination of chromosomes); males are, on the contrary, homogametic and bear two Z chromosomes (the ZZ combination of chromosomes). There is experimental evidence that sex in this case is determined by the dosage of the master gene [62].

About 20% of reptile species are viviparous; most of them lay eggs. The genetic mechanism of sex determination (GMSD) is typical for many reptile species. In some of them, sex formation is known to depend on environmental factors (most frequently on temperature). After studying 94 reptile species, Organ et al. [43] showed that the sex-determination mechanism and type of reproduction co-evolved in the history of amniotic animals; sex in viviparous species is usually determined genetically, whereas oviparous ones have both GMSD and sex determination that depends on external factors.

In all 1500 studied amphibian species, sex is determined genetically [56]. Both the XY and ZW systems of sex determination occur in this group, but morphologically differentiated sex chromosomes have been revealed in very few species (about 20) [56].

The most complex pattern of sex structure formation is observed in fish, which manifest very diverse types of reproduction and genetic mechanisms of sex determination.

Genetic Mechanisms of Sex Determination in Fish

Gynogenesis and different variants of hermaphroditism, along with the most-frequently occurring gonochoric reproduction, have been found in fish. Many fish species are constitutive and facultative hermaphrodites. Diverse variants of the sex-determination mechanism are observed in gonochoric species. Males are heterogametic in some fish species, whereas females are in other ones; even if sex chromosomes are present, autosomal loci may substantially influence sex determination. Sex chromosomes may be completely absent and multi-locus sex determination is observed in this case. There may be several sex chromosomes and even several pairs of sex chromosomes; in some fish species sex can be determined by temperature, social behavior, or other factors, such as the pH of the environment [20, 42].

Mank et al. [36] analyzed 591 species among 25 bony fish families. In 15 of the families, they found only bisexual species and did not observe hermaphroditic ones. However, gonohoric species were observed in all the families, where hermaphroditism occurred, i.e., it was not associated with some phyletic taxon. Bisexual species with male heterogamety occurred almost 2 times as frequently (in 22 families) as species with female heterogamety did (in 10 families). Sex control under the influence of external factors was recorded for seven families, but six of them also included species with GMSD. Single-sex species were found in three families, two of which are distantly related phyletic lines. Thus, the authors came to the conclusion that types of reproduction have a polyphyletic origin [36].

The structure and expression of genes that are involved in the determination and differentiation of sex in fish have been poorly studied. The sex-determining gene, *dmrt1* (*dmy*), was identified only in one fish species (medaka, *Oryzias latipes*) with the XX/XY chromosome system of sex determination [30, 40]. The family of *dmrt* genes received this name due to the presence of the highly conserved DNA-binding and transcription regulating domain (DM) in the amino-acid sequence of proteins that are encoded by this gene. The gene *dmy* is a copy of one of the *dmrt* genes, which has been transferred from the autosome to the Y chromosome, duplicated, and subsequently diverged [26, 37]. The other central gene that participates in sex determination in fish is *cyp19a1*, which encodes the aromatase enzyme, which irreversibly turns androgens into estrogens [31].

The active study of sex-determination mechanisms in various taxonomic groups of fishes has revealed a multitude of interesting facts. A sex-determining system with three sex chromosomes, viz., X, Y, and W, was found in the platyfish, *Xiphophorus maculatus*. Males of this species can be either XY or YY; females can be XX, XW, or YW. WW females were obtained during laboratory studies. It is worth mentioning that *X. maculates* has lines with heterogamety both in males (XX/XY) and in females (YW/YY) with a lack of influence of autosomal genes or environmental factors on sex determination. There are two models to explain the unusual sex-determination mechanism in platyfish. The first one postulates that genes that determine the male sex are located on the Y, X, and W chromosomes. According to this model, the only active gene is the one that is located on the Y chromosome, whereas the genes in the X and W chromosomes are repressed by autosomal suppressors [28]. According to the second model, sex is determined by gene dosage. The gene that determines the male sex is absent on the W chromosome and is represented by two copies on the Y chromosome and by one copy on the X chromosome. The larger number of genes in the XY or YY combinations of chromosomes cause the male phenotype to form [67]. The viability of YY males and WW females proves that sex chromosomes in this species are insubstantially degenerate and crossing over is probable along almost the entire length between X and Y chromosomes. Sex-related loci for XY and ZW are shown to be located in the same L24 linkage group, but the master gene has not been identified [10, 72].

In the guppy, *Poecilia reticulata*, which is a species with XY heterogamety in males, the genes the encode highly polymorphic genes for body and fin color are related to the X, Y, or X/Y chromosomes. The Ma (*Maculatus*, pigmentation), Ar (*Armatus*, pigmentation and color of the caudal fin), and Pa (*Pauper*, pigmentation) loci are examples of Y-related loci. Male guppies with two equivalent Y chromosomes are nonviable, unlike medaka and platyfish, which serves as evidence of a significant degeneration of the Y chromosome. At the same time, males with combinations of different Y chromosomes, such as $Y_{Ma}Y_{Ar}$, $Y_{Ma}Y_{Pa}$, and $Y_{Pa}Y_{Ar}$, are viable and fertile [4], which indicates various degrees of degeneration of Y chromosomes in different lines. The recent studies have shown that there are three regions in the sex chromosome of male guppies: the non-recombining MSNR1 (60% of the entire sex chromosome), the freely recombining FR (10–20%), and the non-recombining MSNR2 (20–30%), whereas all three regions recombine in females. The length of MSNR2 varies within guppy populations and the 25Y gonadosomal region varies with the sex-determining gene; Y-related genes for coloration are contained in this segment [65].

The nuclear genome of the zebrafish, *Danio rerio*, has been decoded completely [27]. Experiments with crossing provide indicate that sex in this species is determined genetically; however, attempts to reveal the sex-determining genes have failed. Sex is thought to be determined by a number of genes and, in part, by environmental factors [34]. Anderson et al. confirmed that sex in *D. rerio* is determined by many genes; moreover, sex in different lines can be formed by combinations of various genes and sex determination is influenced by environmental factors. It was shown that the main genes are located mostly in one arm of chromosome chr-4 [6].

Cichlid fishes (family Cichlidae) serve as a popular model object for elucidating the genetic and molecular fundamentals of sex determination [33]. A number of homologous genes that are involved in sex determination in other vertebrates have been found in the tilapia, *Oreochromis niloticus*; however, it is not obvious that any of them is sex determining for this species [13]. Cnaani et al., when studying the heritability of microsatellite loci, analyzed nucleotide sequences of fragments of sex chromosomes that had been cloned in bacterial artificial chromosomes (BACs) and determined the position of sex-related sites by using the FISH method [13]. The experiments included analysis of eight lines in six species of tilapia. The reported highly significant relationship between sex and segregation of some microsatellite loci in progeny indicates the strict genetic sex determination in these species. Moreover, a relationship with one of the linkage groups (LG1 or LG3) or with both groups is found in different species. Thus, sex-determining genes in various species are located on various chromosomes and differ in their type of influence. In species with the XY-chromosome sex-determination system, the locus in LG1 dominates and determines the formation of the male phenotype. In other species, the dominant locus is in the LG3 linkage group, which determines the female phenotype (WZ heterogamety of females) [13]. Nevertheless, the simple genetic model does not explain all the sex ratios that are observed in progeny that are obtained from crossing under experimental conditions; therefore, an additional interaction with autosomal loci is assumed [13].

A comparison of three related cichlid species, *Oryzias latipes, O. curvinotus*, and *O. luzonensis* that have the XY sex-determining systems showed that functional *dmy* genes can be identified for the former two species, although in orthologic chromosomes [37]. In the third species, *O. luzonensis*, the functional *dmy* gene was not identified [30], but its non-functional homolog, a pseudo-gene, was found instead, which means that the function of the master gene in *O. luzonensis* is performed by another gene [64]. A search for the sex-determining gene in *Oryzias dancena* has not revealed the homology of the sex chromosome in this species with the sex chromosome in *O. latipes*, but it showed a high level of synteny with one of the autosomes [63].

In the three-spined stickleback, *Gasterosteus aculeatus*, sex is also determined by the XY-chromosome system. The genome mapping allowed the identification of a single sex-determining sequence that is located on the distal arm of the LG19 linkage group [45]. The fact that males are constitutively heterozygotic due to unique alleles that are located in this region serves as evidence of the existence of GMSD; recombination in males in this chromosome is decreased as compared to that in females and the analysis of nucleotide sequences reveals numerous differences between X and Y chromosomes with transposons and duplications being accumulated in the latter one [45]. These researchers showed that other stickleback species have other types of sex determination [54]. In the nine-spine stickleback, *Pungitius pungitius*, the heteromorphic XY pair of chromosomes corresponds to the LG12 linkage group. In the male black-spotted stickleback, *Gasterosteus wheatlandi*, one copy of LG12 merges with the LG19 derivative of the Y chromosome, thus forming the X1X2Y sex-determining system. At the same time, it was shown that neither the LG12 linkage group nor the LG19 group is related to sex determination in the other two species, the brook stickleback *Culaea inconstans* and four-spine stickleback *Apeltes quadracus*. In the latter species, the sex is determined by the ZW chromosome pair [54]. Shikano et al.[60] also noted the high level and diverse types of chromosome differentiation in sticklebacks.

The sex-determination mechanisms in a number of salmon species, including the charr *Salvelinus alpinus*, Atlantic salmon *Salmo salar*, and trout *Salmo trutta*, as well as Pacific salmon of the genus *Oncorhynchus*, have also been studied. All these species are characterized by the chromosomal mechanism of sex determination with the XY heterogamety of males [20, 48]. However, heteromorphic sex chromosomes were found in only a few species. This serves as evidence that sex chromosomes in the studied species are at the early stages of differentiation. This is also confirmed by the viability of individuals with the YY combination of chromosomes. The sex-determining segment of Y chromosome is small; in various species it is located in different groups of chromosome linkage that are in contrast to the significant synteny in autosomes, which are not involved in sex determination in these species. Recently, Yano et al. [74] reported the finding of a gene associated with the Y chromosome that is designated *sdY* in salmon fishes. The amino-acid sequence of this gene is conserved in most salmon species. In various species, it is located in different linkage groups and its transfer is probably determined by transpositions [74]. This agrees with the previously hypothesized mechanisms of sex-chromosome formation in fish [73].

Thus, a major portion of the published data support the idea that processes of sex-chromosome formation and even variations of molecular mechanisms of sex determination in the evolution of fish may occur very rapidly, unlike those in mammals [35, 36, 57, 66]. In most fish species, heteromorphic sex chromosomes are not revealed even when chromosome sex determination has been proven [20]. Unlike sex chromosomes in mammals, those in fish are obviously "young," being at various stages of divergence. Moreover, significant degeneration, which is typical of heteromorphic sex chromosomes, is frequently not observed. Nevertheless, there are some common properties for sex chromosomes of mammals and fish; for example, a suppression of recombination in sex-determining and adjacent sites is often observed in fish, as in other animals whose sex chromosomes are heteromorphic.

The Evolutionary Significance of the Variability of Sex-Determination Mechanisms

It is still unclear why fish typically manifest such unusual chromosomal mechanisms of sex determination in which the sex-determining gene is frequently found in various chromosomes. In the homochromosome sex (XX or WW) of mammals, one of the chromosomes becomes inactivated, thus compensating for the gene dosage. There is no evidence that a similar mechanism of gene-dosage compensation exists in the sex chromosomes of fish [20, 66]. Volff et al. hypothesized that the periodic variations in location of sex-determining genes in fish are related to this fact. The suppression of recombination near the sex-determining gene causes an increase of degeneration in the newly formed Y chromosome, a disturbance in the dosage of neighboring genes in homo- and heterogametic sex, and a decline in the viability of heterogametic individuals. The dosage of genes in former sex chromosomes is gradually restored as a result of movement of the sex-determining gene into the autosome [66]. The cycle is then repeated. Thus, the emergence of new sex chromosomes and new sex-determination systems enable fish to avoid losing heterogametic sex and, eventually, the loss of populations and species.

The origination and maintenance of the genetic mechanism of sex determination provides rapid adaptive radiation of species [43]. Indeed, the chromosomal mechanism of sex determination in higher vertebrates, birds, and mammals appeared and has been supported for at least 180 million years; this apparently promoted their rapid divergent evolution. In spite of the much longer time of fish evolution and the existence of chromosomal sex determination in species from all the branches of the phylogenetic tree of this group, the mechanism of sex determination is not highly conserved in them [35, 36]. The vast diversity of fish species supports the idea that the strict and single-type of GMSD is not necessary for rapidly divergent evolution within taxa. The lability of sex-determination mechanisms is probably due to the environment of fish, which requires adaptation to its varying factors. This adaptation, while determining the lack of the necessity to fix and enhance seemingly advantageous mechanisms in other taxa, can be termed as the "principle of evolutionary sufficiency." Below, we will discuss the probable causes of this phenomenon.

The most important difference between fish and mammals and birds is the body homeothermy in the two latter clades. It is probably the stability of biochemical reactions in warm-blooded organisms that determines the constancy of chromosomal sex determination in mammals and birds. The dependence of body temperature on environment temperature can be the main factor of the retention of the labile genetic sex determination in fish evolution. The cascade and multi-stage pathway of biochemical reactions, when sexes are formed under varying temperature of the environment and, consequently, the temperature of an organism, may cause failure in the implementation of these mechanisms and also in the formation of single-sex populations.

Changes in sex-determination mechanisms are probably related to other features of evolution and adaptations in fish and play a leading role in the vast species diversity of this group of animals. The lack of natural barriers in the aquatic environment, particularly in lakes and oceans, as well as external fertilization in most fish, impede the formation of the population-genetic structure and the emergence of evolutionary significant populations that are potentially able to form new species. According to the existing evolutionary concepts, isolated populations are thought to gradually accumulate genetic changes, resulting in the formation of morphologically and genetically differing forms; in such a way, individuals from different populations cannot cross (the "biological concept of a species") as time passes [5]. This process may be too long and not always successful if the time interval is insufficient to form isolating mechanisms. We may assume that the possibility of rapid variation of the sex-determination mechanism allows the creation of reproductive isolation during a short period of time. Rapid variations of GMSD (for example, replacement of the XY system in one population by the ZW system in another population, and vice versa) may lead to a decisive moment for the accelerated formation of isolating mechanisms. Quinn et al. [51] developed a model, according to which rapid variations of sex-determining systems are possible without substantial changes in genetic material. They believe that the obligatory factor in this process is the ability of species to change sex under the influence of environmental factors, such as temperature, which is typical for many fish species with GMSD (see below).

Cichlid species are one of the most interesting model groups for the study of evolutionary processes [29, 55]. Representatives of the family Cichlidae inhabit waters off Asia, Madagascar, Africa, and South America. The first stage of divergence in this family was determined by the separation of continents after the breakup of Gondwana. This taxon receives even more attention due to the fact that over 2000 cichlid species have formed in large African lakes (such as Victoria, Tanganyika, and Malawi) in a short period of less than 1 million years [18, 22, 29]. This "burst-like" radiation of species supports the idea that not only allopatric speciation, but also sympatric speciation was of major importance in this case [7, 55, 59]. The cichlid species in these lakes probably diverged through two stages. At the first stage, the species separated depending on adaptation to sandy or rocky bottoms. At the second stage, divergence by food spectrum, with corresponding morphological changes, took place in each of these groups. In both cases, the ecological selection and adaptation to a narrow ecological niche were probably the main driving force behind evolution. The isolation factors were the preference for an ecological niche (philopatry) and the high level of "sedentariness" due to maternal care for offspring, as females of most cichlid species brood fertilized eggs in their mouths, while females of some other species do this with newly-hatched larvae. Males contribute nothing, except for their genes, to the reproduction process; this asymmetry results in sex selection, sexual dimorphism, and, respectively, in variations of historical aspects of the lifecycle and dispersal of forms [18, 32, 52]. Sex selection begins with the choice of a preferable female in mating with a male. In cichlid species, this can be due to variations in the color of males or females, i.e., by origination of new alleles of coloration genes. The theory predicts that origination and fixing of a new sex-determining gene can be regulated by antagonistic sex selection [32, 68]. The occurrence of an allele that increases the viability of one of the sexes and, simultaneously, decreasing the reproductive success or viability of the other sex, creates a genetic conflict, which can be resolved by activation of a new sex-determining gene that is linked with the gene that bears this allele [53, 57]. However, the existence of two sex-determination systems within a species creates conditions for the manifestation of another genetic conflict, which can be resolved either through the inactivation of the genes of one sex-determination system or through decreasing the viability in some combinations of crossing. Both variants have been found in cichlid species [44, 59]. A transient state like this, i.e., the simultaneous existence of two genetic systems, was reported for some cichlid species [59]. Subsequently, this conflict may result in postzygotic and prezygotic isolation, but these stages of divergent evolution are still poorly confirmed by experimental data.

One more cause of the variability of sex-determining systems probably consists in peculiarities of the evolution of fish. As is known, polyploidization events repeatedly took place during the evolution of fish [41], which apparently was followed by duplications of the entire genome or its larger portion. Duplication of the sex-determining gene, i.e., origination of two or more genes that participate in sex determination in the genome of one animal, must entail more complex consequences than the duplication of a common gene that codes for some enzyme. If sex is heterogametic, the occurrence of two genes whose products participate in the synthesis of steroid hormones in one genome may complicate the formation of one of the sexes. Consequently, there must be a mechanism that prevents situations like this in the case of the duplication of chromosomes and sex-determining genes. In this case, either repression of the duplicated copy of the gene or its inactivation through mutations are probable. These numerous sex-determining genes obviously do not vanish from the genome and remain inactivated in the chromosomes of duplicated genes. However during certain periods (for example, during transposition within the genome) they may become dominant over the prior sex-determining gene. Both variants have been found in cichlid species. The most interesting evidence for these processes in cichlid fishes was collected from Lake Malawi [59]. To clarify the sex-determination mechanisms, individuals of 19 species were crossbred; most of them belonged to the genus *Metriaclima*. The sex ratio and segregation of microsatellite loci related to some sex chromosome, LG7 in the case of the XY sex-determination system and LG5 in case of the WZ system, was analyzed in the offspring. It was found that sex is determined by the XY system in the largest portion of the species (in nine species). In four species, sex is determined by the WZ system linked to OB (orange blotch), which is a morphological coloration character in females that is determined, in turn, by the dominant locus on the W chromosome [59]. At the same time, some species, such as *M. pyrsonotos*, were found to have both sex-determination systems, XY and WZ. The WZ system epistatically suppresses the expression of the XY system and sexes in progeny are distributed according to Mendel's law (1 male : 3 females). However, in some of crossings (as in *M. pyrsonotos* and in *M.* "*kompakt*"), it is possible to explain the sex-determination mechanism if we admit the existence of one more dominant sex-determining gene that is located in another linkage group; to interpret other results, the influence of environmental factors should be assumed [59].

Thus, the plasticity of mechanisms of genetic sex determination and the possibility of a rapid switchover between types of sex determination may be of major importance in the evolution of fish, as they determine the possibility of rapid divergent evolution due to accelerated formation of mechanisms for non-crossability with the lack of barriers for the dispersal of individuals within the species range.

The Intraspecific Adaptability of the Plasticity of Sex-Determination Mechanisms

As noted above, the sex-determination process in many fish species is influenced by environmental factors. Moreover, it has been shown that a shift in sex ratio may occur, apparently, as a result of sex inversion under the effects of some environmental factors even in species with GMSD [20]. This phenomenon is thought to be adaptive. The Atlantic silverside, *Menidia menidia*, can be used as an example. Populations of fish of this species, which inhabit waters at high latitudes, have a very short season of growth and feeding and are characterized by GMSD. In low latitudes, sex determination in *M. menidia* is influenced by the environment: mainly females are formed at low temperatures. The adaptivity of this phenomenon consists in the following fact: since the period of growth is longer in the lower latitudes, the early occurrence and prevalence of females in populations enables them to achieve a larger body size and higher fertility [14]. A similar situation is observed in other representative of poikilothermic animals, e.g., the skink *Niveoscincus ocellatus*, which lives in Tasmania [46]. In near-shore populations, under relatively stable conditions, sex in this species is determined mainly by temperature; at the same time, in mountain areas, where climatic conditions are harsh and the lifecycle short, GMSD prevails. This is related to the different viability of sexes under unsteady temperatures and the genetic mechanism of sex determination appears to be preferable to the environmental one [46].

In tilapia, *O. niloticus*, which have genetic sex determination (the XY system), sex may change as well under the influence of temperature: an experimental short-term increase in temperature over 32°C during embryonic growth resulted in a significant shift in the sex ratio towards males. Furthermore, selection by this factor in generations may be fixed at the genetic level [8]. In three other species of African cichlids, *Oreochromis aureus, O. mossambicus,* and *Pseudocrenilabrus multicolor*, a shift in the sex ratio also occurred as a result of sex inversion, under the influence of temperature, in spite of the existence of GMSD [42].

A number of interesting observations on the discrepancy of genetic and morphological characters of sex were made during the study of another experimental species, *Oryzias latipes*. As noted above, the sex-determining gene *dmy* was revealed and the genetic system of sex determination was best studied in this species [30, 40]. However in natural populations of *O. latipes* there is a discrepancy between morphological and genetic sex identification: individuals with the XX combination of sex chromosomes were found among males and with the XY combination among females at various frequencies [39, 61]. Subsequently, females with the XY genotype from natural populations were crossed with normal males (XY) of laboratory inbred lines. The genetic analysis used in the work allowed the differentiation of the Y chromosome inherited from the mother (Y^p) or from the father (Y^m) in progeny. The offspring of crossed individuals with the XX combination of sex chromosomes was represented only by females; the offspring of individuals with the combinations XY^p and Y^pY^m were males, whereas all or most of the individuals that received an X chromosome from the mother in combination with a paternal Y chromosome (XY^m) proved to be females [61]. The causes of this deviation were explained for 2 of 12 females with the XY genotype, in whose offspring all individuals proved to be females: a mutation with a reading-frame shift that results in untimely termination of DMY protein synthesis was found in one of the females, while other female showed a low level of expression of this gene [44].

One more interesting result was obtained when single-sex populations of *O. latipes* were created. In order to have single-sex populations, induction of sex with steroid hormones was used. In this case, occurrence of males with the XX combination of sex chromosomes and females with the XY and YY combinations is probable. They were crossed, both with one another and with normal individuals. In most variants predictable results were obtained; at the same time, when normal females (XX) were crossed with an inverse by sex male (XX), in many lines of progeny males appeared at rates of 3.6 to 18.5%, although they had not been expected to occur [58]. This spontaneous sex reversion, which was recorded earlier in natural populations, is determined by a combination of unknown genetic factors [58].

The experiments with crossing showed that sex in Pacific salmon of the genus *Oncorhynchus* is determined by the XY chromosome system, whereas sex chromosomes in all species, except for sockeye salmon, are not differentiated morphologically [20, 48]. The *sex* sex-determining gene in these species is still unidentified and remains hypothetic. An approach to establishing sex in salmon specimens based on the identification of genomic DNA sequences that are located on the Y chromosome has been developed in the recent years. The sequences located on the Y chromosome and linked to the sex-determining gene were identified in chinook, chum, pink, cherrymasu, and coho salmon [11, 19, 48]. To reveal sequences like these, the method of DNA polymerase chain reaction (PCR) was used. The amplification of sequences in individual DNA preparations indicates existence of Y chromosome in genome of the individual (genetic males); the lack of amplified fragment means the absence of Y chromosome (genetic females).

The early works on chinook salmon showed a good congruence between the sex of an individual that was identified by using morphological characters and molecular markers. However according to some published data, this relationship is not always evident [1–3, 12, 19, 21, 38, 70, 75]; sequences specific for Ychromosome are sometimes found in the genome of morphological females, whereas these sequences may be absent in some males. The causes of the discrepancy remain unknown. There are several supposed mechanisms to explain this phenomenon. The mechanisms can be conventionally considered as either genetic, i.e., conditioned by internal factors, or physiological, i.e., determined by external factors.

Researchers who used chinook salmon in their experiments believe that the mechanism of the discrepancy is determined by chromosome rearrangements, translocations of DNA fragments from the Ychromosome to the X chromosome and autosome and/or by unequal crossingover [69, 70]. In North American chinook populations the discrepancy is found mainly in females, whose sequence of the Ychromosome is identified in 80% of the cases in some populations; researchers consider chromosome reorganizations to be the main cause of this discrepancy [48, 69, 70]. Some evidence of the fact that Y-linked segments in female chinooks can be found on the X chromosome is provided in a work by Williamson et al. [71].

The causes of the existence of males with a lack of Y-linked segments are almost not discussed. The genetic mechanism in this case is thought to be due to mutations in the target sites for primer DNA sequences. This prevents amplification, in spite of the presence of this sequence in the genome. At the same time, it was shown for the cherry salmon *O. masou* that the Y-specific sequence is actually absent in the genome of these males [75]. The lack of the sequence in this case may be explained by the deletion of a DNA fragment with neighboring segments or by its loss as a result of unequal crossing over. The authors believe that the discrepancy phenomenon in cherrymasu salmon can be due to physiological causes, i.e., by sex inversion [75].

The physiological possibility of sex inversion presumes other interpretation of the obtained data. The complexity of sex determination caused by a long chain of biochemical reactions, hormonal and cellular interactions, suggests that sex formation can be disturbed at one or several stages under the influence of external factors. For this reason, a different discrepancy mechanism, which has also been confirmed experimentally, can be hypothesized for many species, including salmon species. It was shown that in spite of the existence of the genetic mechanism of sex determination, the sex ratio in a number of fish species, including salmon, may vary up to complete prevalence of one of the sexes as a result of sex inversion (reversion) under the effects of such factors as hormones, temperature, or pollution [17, 47, 49, 50].

We studied the congruence of morphological characters and molecular markers of the Y chromosome in populations of sexually mature individuals of five species of Pacific salmon within the vast range of their distribution [1–3]. In a number of cases it was shown that the discrepancy can be related to sex inversion and has adaptive significance for populations and the entire species [3]. When the state of a population worsens under the effects of natural or anthropogenic factors, an increase in the proportion of males with the female genotype (the XX combination of sex chromosomes and feminization of individuals) in the population must result in the growth of the proportion of genetic and probably physiological females in subsequent generations. Correspondingly, an increase in the proportion of females causes the reproductive potential of the population to grow. Cotton and Wedekind [16], after analyzing the consequences of feminization and masculinization in populations of animals with the

XYchromosome system under the effects of external factors came to the conclusion that a moderate feminization (which we observed in most of the populations of the species) can be advantageous for the subsequent population growth. In natural populations, the fluctuation of the hormone level at spawning grounds, depending on the density and sex ratio of spawners, can be assumed as the primary trigger of sex inversion.

Thus, the accumulated data support the idea that the plasticity of sex-determination mechanisms in fish may have a major significance for adaptation of populations and entire species and also confirm the "evolutionary sufficiency principle."

Possibilities for the Practical Use of the Plasticity of Sex-Determination Mechanisms

As is known, individuals of one of the sexes grow faster and reach a larger body size in many fish species. This is due to the fact that the energy costs of the production of reproductive materials in one of the sexes (mostly in males) are lower. Thus, creating single-sex cultures in aquaculture is more profitable. They are obtained in a routine way, which consists in the production of males bearing YY chromosomes, provided that the these fish are viable. These individuals are the result of crossing males that were feminized with hormones or their derivatives (the XY combination of sex chromosomes), with ordinary males (XY). When the obtained YY males are crossed with normal XX females, all the individuals in the offspring will be males [49, 50].

A less costly and safer method to obtain offspring with a shift in the sex ratio towards the prevalence of males involves thermal treatment of embryos at certain stages of development [8, 25]. This treatment causes sex inversion and a significant number of genetic females develop as males.

It should be noted that this newly-found phenomenon is observed not only under man-made conditions but also in natural populations [8]. For this reason, it is important to take this factor into consideration when predictions on natural fish populations are made. Thus, for example, temperature conditions that induce a shift in the sex ratio to one or the other side may occur during the breeding season in some waters. These variations can change the effective population size and cause a mysterious growth or decline of abundance in subsequent generations.

The natural cyclic climate changes on Earth and the trend of anthropogenic impacts that are superposed onto them during the recent decades exert a significant influence on terrestrial and aquatic organisms. Temperature is the most substantial factor; it can have a serious effect on one of the most important parameters of a fish population, the sex ratio, due to the peculiarities of the sex-determination mechanism. Many species experience a sex-ratio shift in progeny as a result of sex inversion when temperature both increases and decreases during early development [8, 17]. A sex-ratio shift towards the prevalence of females would probably influence the population to a lesser degree than a shift towards males. In the latter case, a reduction of the effective population size in year-classes, an increase of inbredness, and, as a result, a decrease in the fitness of the entire population are probable.

The Struggle against Invasive Species

Intentional or accidental introduction of new species into ecosystems has been recorded frequently in the recent decades. In a number of cases, this results in significant alterations of ecosystems and also in the vanishing or quantitative decline of indigenous species. The best-known example among fishes of Russian waters is the Amur sleeper, *Perccottus glehni*, which is a rather dangerous invasive species due to its unique biological properties. A method to extirpate or decrease the abundance of these invaders has been proposed recently. The method consists in the creation of a line with a "Trojan" chromosome [15, 23]. The principle of the proposed method is as follows: females with the YY combination of sex chromosomes are obtained by using estrogens or their derivatives under controlled conditions. If these females are released into a population of the invasive species, crossing under natural conditions gives only males in the offspring. Mathematical modeling predicts that a population numbering a few hundred individuals can be completely extirpated within a relatively short time by introducing an approximately 3% level of females like these [23]. The question of to what extent this approach is feasible in nature remains unresolved.

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