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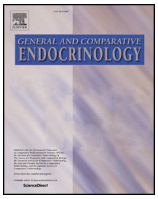

Invited Review

Sex determination in Neotropical fish: Implications ranging from aquaculture technology to ecological assessment

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ABSTRACT

The high biodiversity of fish in the Neotropical region contrasts with scarce or biased studies on the mechanisms involved in the sex determination in members of this fauna. In this review, we attempted to compile the information available on determination, differentiation, and manipulation of sex for Neotropical species, with special focus on silversides and other two speciose groups, known as characins (Characiformes) and catfishes (Siluriformes). Currently, there is plenty of information available on chromosomal sex determination systems, which includes both male and female heterogamety with many variations, and sex chromosomes evolution at the macro chromosomal level. However, there is hitherto a blank in information at micro, gene/molecule levels and in research related to the effects of environmental cues on sex determination; most of reported studies are limited to silversides and guppies. In view of such a high diversity, it is critically necessary to establish key model species for relevant Neotropical fish taxa and also multi-disciplinary research groups in order to uncover the main patterns and trends that dictate the mechanisms of sex determination and gonadal differentiation in this ictyofauna. By increasing our knowledge on sex determination/differentiation with the identification of sex chromosome-linked markers or sex-determining genes, characterization of the onset timing of morphological gonadal differentiation, and determination of the environmental-hormonal labile period of gonadal sex determination in reference species, it will be possible to use those information as guidelines for application in other related groups. Overall, the strategic advance in this research field will be crucial for the development of biotechnological tools for aquaculture industry and for conservation of fish fauna from the Neotropical Region.

1. Introduction

The need to increase our knowledge on how the sex is driven during early development has grown in the last years, especially due to the growing importance of sex control in aquaculture and assessment of the potential effects of climate change on sex ratios of wild populations. Moreover, for species that have reached large-scale production levels, manipulation of reproduction and sex ratios are considered as important hallmarks toward optimization of productivity. Those advances have been conquered by intensive research combining approaches such as genetic mapping, transcription analysis of sex-related genes or environmental/endocrine manipulation of sex. However, those analyses are restricted to a few Neotropical species, which includes several species with promising characteristics for aquaculture and/or that are under the risk of extinction. Therefore, the elucidation of sex differentiation and reproduction mechanisms in fish of this region remains a key area of research.

1.1. Mechanisms of sex determination

In fish, sex determination mechanisms can be grouped into two main categories that act through different switches: genotypic (GSD) and environmental (ESD) sex determination (Devlin and Nagahama, 2002; Volff et al., 2007; Fig. 1). In fish with GSD, the primary sex of an individual is determined at fertilization by heritable genetic elements that differ between sexes and that are usually located in sex chromosomes. Although fish group presents more than 32,500 described species (Nelson et al., 2016), just few sex-determining genes have been identified, whereby most of them are male-specific and are present in the non-pseudo autosomal region of the Y chromosome, such as *dmy* (Y-

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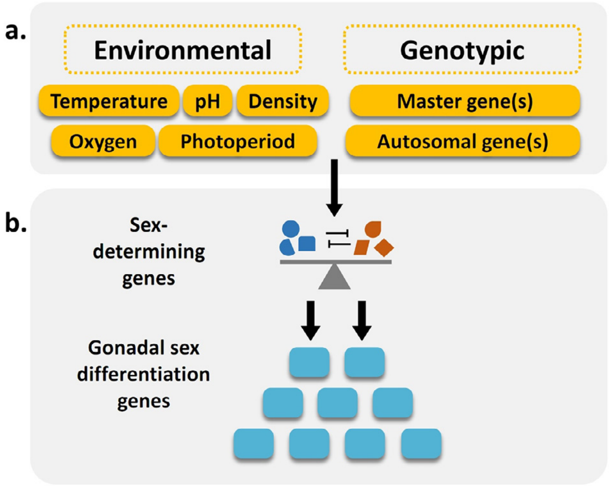

Fig. 1. a. Current model for two mechanisms of sex determination, b. with multiple feedback loops. Adapted from Capel (2017) and Crews and Bull (2009).

specific DM-domain) and *gsdfy* (gonadal soma-derived growth factor on the Y chromosome) genes in medakas (*Oryzias latipes* and *O. luzonensis*) (Matsuda et al., 2002; Myosho et al., 2012), the *sdY* gene (sexually dimorphic on the Y chromosome) in salmonids (*Oncorhynchus mykiss*) (Yano et al., 2013), the *amhy* gene in silversides (*Odontesthes hatcheri*, *O. bonariensis*, and *Hypoatherina tsurugae*; Hattori et al., 2012; Yamamoto et al., 2014; Bej et al., 2017) and in the Nile tilapia (*Oreochromis niloticus*; Li et al., 2015), and the *amhr2* (anti-Müllerian hormone receptor type II) gene in fugu (*Takifugu rubripes*; Kamiya et al., 2012).

Moreover, gonadal sex in ESD species can be environmentally modulated at an early and critical period of gonadogenesis (Devlin and Nagahama, 2002; Penman and Piferrer, 2008; Strüssmann and Nakamura, 2002). Teleosts present a variety of ESD strategies (Fernandino et al., 2013a; Goikoetxea et al., 2017; Liu et al., 2017) and therefore are interesting models to study the effects of environment on the gonadal fate. Those environmental cues are capable of affecting the process of genetic determination, overriding the predetermined genetic sex and shifting the sex differentiation cascade to another direction in an irreversible way (Capel, 2017; Fernandino et al., 2013a; Heule et al., 2014; Volff et al., 2007). These two systems, GSD and ESD, are not mutually exclusive and the limit between both mechanisms is blurred and variable, supporting the notion that both systems are extremes of a continuum (Bachtrog et al., 2014; Mork et al., 2014; Baroiller & D'Cotta, 2016; Yamamoto et al., 2014; Perrin, 2016), whereby one system can prevail over another according to the environmental milieu.

1.2. Gonadal sex differentiation

The differentiation of a bipotential gonad is defined by the interaction between ESD and GSD during a period early in life (Sarre Stephen et al., 2004). This process, named as gonadal sex differentiation, encompasses a period when the gonadal primordium differentiates to form either an ovary or a testis. The characterization of this critical time of gonadal sex differentiation is important for manipulation of sex, because during this period the gonad still possess the plasticity to be reversed regardless of the predetermined sex (as presented later). Thus, the gonadal fate can be manipulated by proper administration of sex steroids or by modulation of environmental stressors during a specific, labile time, ultimately inducing functional sex reversal of the gonads.

To determine the critical time of gonadal differentiation, it is initially recommended to characterize the first evidences of morphological sex differentiation by gonad histology. In teleost fish, the timing of gonadal development and the anatomy of the gonads vary greatly between and within groups; during this process, the initial evidence of sexual dimorphism from a morphologically bipotential gonad is observed first in females in the majority of the gonochoristic teleosts examined to date (see review of Strüssmann and Nakamura, 2002). Only few species, such as some tilapias, present simultaneous differentiation of both sexes (Nakamura and Takahashi, 1973; Nakamura and Nagahama, 1985; 1989), but no case of male precedence has been reported. The first signs of ovarian differentiation can be judged by the onset of intensive germ cell proliferation (mitosis) and differentiation (meiosis), and/or peculiar arrangements of somatic cells (somatic cell outgrowth) that eventually lead to the formation of the ovarian cavity in most teleosts (Strüssmann and Nakamura, 2002). In case of males, the first clear sign of testicular differentiation is the appearance of the anlagen of the efferent duct; also, male germ cells are arrested in mitosis when in females they enter meiosis (Nakamura and Takahashi, 1973; Shimizu and Takahashi, 1980; Strüssmann et al., 1996a). Thus, once the onset time of morphological evidences of gonadal development is characterized, the critical time of gonadal sex differentiation can be estimated.

1.2.1. Sex steroids and gonadal development

Sex steroids have been considered to play critical roles during gonadal sex differentiation in non-mammalian vertebrates. Although they are not considered as initiators of gonadal sex differentiation, their timely appearance and maintenance are fundamental for the subsequent development of ovaries and testes. Fish embryos/larvae are highly sensitive to sex steroids and the administration of estrogens or androgens during the critical period of gonadal sex differentiation often leads to a functional sex inversion (Guiguen et al., 2010). It is currently believed that while estrogens are essential for female sex differentiation, androgens, on the other hand, are the mediator or consequences of male differentiation pathway (Devlin and Nagahama, 2002; Fernandino et al., 2013a; Guiguen et al., 2010). Thus, the conserved downstream cascade of genes during sexual development is under the control of sex steroid hormones.

There are two well-known genes involved in the sex steroid pathway: the gonadal aromatase (*cyp19a1a*) and the 11-beta hydroxysteroid dehydrogenase type 2b (*hsd11b2*), with the first implicated in the estrogen and the later in androgen synthesis pathways. 11β-hydroxylase (Cyp11b) is also involved in androgen pathway, but it seems to act more downstream in testicular differentiation (as discussed later). Gonadal aromatase (*cyp19a1a*): in retrospective, the synthesis of estrogen was the main focus of many studies that aimed to analyze the participation of sex steroids in the gonadal sex differentiation. The gene *cyp19a1a* encodes the cytochrome P450 aromatase enzyme involved in the conversion of androgens into estrogens, thus, determining the balance between these two groups of steroids (Guiguen et al., 2010). The gonadal aromatase is very important for feminization because its high expression and/or activity are tightly associated with the process of ovarian differentiation at early stages of development and, conversely, its inhibition induces testicular differentiation (Guiguen et al., 2010). The mechanism of down-regulation of aromatase was studied during the temperature-induced masculinization (Hattori et al., 2009a; Yamaguchi et al., 2010; Navarro-Martin et al., 2011), whereby *cyp19a1a* suppression was demonstrated by two mechanisms. In the first one, which is based on epigenetic mechanisms, *cyp19a1a* promoter is hyper-methylated, the transcription of *cyp19a1a* is suppressed, and consequently the feminization process is inhibited (Navarro-Martin et al., 2011). In the second mechanism, the elevation of cortisol directly suppresses *cyp19a1a* transcription by binding of cortisol-glucocorticoid receptor onto glucocorticoid responsive element of *cyp19a1a* promoter (Yamaguchi et al., 2010).

In the androgen pathway, the enzymes 11β-hydroxylase (Cyp11b) and the 11β-hydroxysteroid dehydrogenase type 2 (11β-HSD2) are involved in the synthesis of 11-oxygenated androgens and in the metabolism of glucocorticoids (GCs). The first one catalyzes the 11-

hydroxylation of steroids such as the testosterone and androstenedione (D4) to 11-hydroxy-testosterone (11-OH-T) and 11-hydroxy-androstene-dione (11-OH-D4), respectively (Borg, 1994; Lokman et al., 2002). However, the transcript abundance of this gene did not show a dimorphic expression during the sensitive period of sex determination (Blasco et al., 2010; Raghuveer et al., 2011; Socorro et al., 2007). The 11β-HSD2 participates in the final step of the major fish androgen biosynthesis, the 11-ketotestosterone (11-KT; Fernandino et al., 2013a; Goikoetxea et al., 2017), and have been related with the masculinization induced by environmental stressors, such as water temperature, one of the most studied and relevant environmental parameter involved in fish's ESD (Fernandino et al., 2012; Ribas et al., 2017). The regulation of sex-steroidogenesis or the bioavailability of sex steroids are, therefore, being considered as putative linkers between GSD and various forms of ESD (Heule et al., 2014).

1.2.2. Glucocorticoids as the link between ESD and GSD

In the last decade, other non-sex steroid hormonal axis, as the hypothalamus-pituitary-interrenal gland (HPI), has emerged as a new player, particularly in the ESD mechanism. In teleost fish, the production of glucocorticoids by the interrenal gland, equivalent to the mammalian adrenal cortex, is regulated in the central nervous system by the adrenocorticotropic hormone (ACTH), whose release is under the control of the hypothalamic peptide corticotrophin-releasing hormone (CRH; Mommsen et al., 1999; Wendelaar Bonga, 1997). The main glucocorticoid in vertebrates is cortisol, which has an important role on the modulation of the adaptive intermediary metabolism (Vijayan et al., 1994). The role of glucocorticoids on the gonadal fate at masculinizing-temperatures was also evidenced in teleost species, such as the pejerrey (Hattori et al., 2009a), the Japanese flounder (*Paralichthys olivaceus*; Yamaguchi et al., 2010), and the Japanese medaka (*O. latipes*; Hayashi et al., 2010;), suggesting a commonly conserved mechanism among teleosts.

1.3. Importance of hormones and their use in the manipulation of sex/time-window period of sex determination

Steroidogenesis is the biological process by which cholesterol is converted into steroid hormones, including sex steroids, glucocorticoids, and mineralocorticoids, by a battery of oxidative enzymes in several steroidogenic organs like gonads, interrenal gland, and the brain (Blazquez and Somoza, 2010; Wendelaar Bonga, 1997). The importance of sex steroids for gonadal sex differentiation is broadly known based on the effects of exogenous steroids treatment on sex manipulation during a period known as "labile period". At this time, bipotential gonads are susceptible to hormonal or environmental factors, requiring a minimum combination of dose and duration to activate the sex differentiation of gonads. After this "labile period", stronger and/or longer treatments may be necessary to change the direction of the gonad that has been already canalized, which in many cases are impossible to achieve (Baroiller et al., 1999; Piferrer, 2001). Thus, the characterization of this period for each species/group is crucial to effectively manipulate the sex of the offspring.

2. Sex determination/differentiation and sex manipulation in freshwater Neotropical fishes

Studies on sex determination and gonad differentiation in Neotropical fish is fragmentary and limited to a very few species. There have been intensive studies on sex chromosomes characterization and evolution, especially for tropical fish from South America. However, research on molecular, cellular, histological, or endocrine process involved in gonad differentiation, and the effects of environmental factors are largely unknown. In this section, we summarized the main findings that were achieved in silversides (Atheriniformes) and tried to gather related information available for the two most representative fish groups in Neotropical region: the Characiformes and Siluriformes.

2.1. Sex determination in Atheriniformes fish

The most studied environmental factor in fish is temperature and this particular sex-determining system is known as temperature-dependent sex determination (TSD). This mechanism has been well characterized in a group of species known as silversides (Atheriniformes).

2.1.1. Odontesthes bonariensis

In the pejerrey (*O. bonariensis*), the differentiation of phenotypic sex is driven by temperature during a sensitive period early in life, defined as the minimum critical period (also sensitive window) of gonadal formation and commitment to ovary or testis fate. Thus, in pejerrey cold temperatures (17–19 °C) induce 100 % of females in the progeny, whereas warm temperatures produce 100 % of males (Strüssmann et al., 1996a, 1997b). Those pioneering studies with simple thermal manipulations, established the critical thermolabile period of gonadal sex determination in pejerrey. With basis on this critical period, the expression of several genes involved in the sex steroid synthesis, such as *cyp19a1a*, was studied in relation to the gonadal sex differentiation process and the rearing temperature. Gonadal aromatase showed to be over-expressed at female-producing compared to male-producing temperature-reared larvae (Karube et al., 2007). Moreover, the pharmacological inhibition of aromatase activity induced a male skewed sex ratio (Fernandino et al., 2008), evidencing the importance of this gene for ovarian development.

In case of masculinization induced by warm temperatures, a series of experiments were conducted in order to evaluate the role of cortisol in the gonadal differentiation process. Thus, the mode of action of cortisol during environmental masculinization has been firstly elucidated in this species, whereby high cortisol levels were detected in larvae reared at warm, male-induced temperatures (Hattori et al., 2009a). Moreover, the supplementation of cortisol or the cortisol agonist dexamethasone in the food at a mixed-sex-producing temperature (around 24–25 °C) induced male-biased sex-ratio through inhibition of aromatase and induction of gonadal apoptosis (Hattori et al., 2009a; Strüssmann et al., 2008). A third characteristic induced by high levels of cortisol during the critical period of sex determination, that temporarily precedes these two events, was the synthesis of androgens as a by-product of cortisol metabolism (Fernandino et al., 2012, 2013a; Hattori et al., 2009a). This correlation between these two steroid pathways was very important because it is well known that high levels of androgens, especially the 11-oxigenated 11-KT presented a masculinizing effect in several teleosts (Devlin and Nagahama, 2002). So, in this species, it was established for the first time a cross-talk between two endocrine axes, the hypothalamic-pituitary-gonad and the adrenal/interrenal, linking the masculinization with an environmental stressor.

2.1.2. Odontesthes hatcheri and Chirostoma estor

The Patagonian pejerrey *O. hatcheri* has been selected as a model species for the study of genotypic sex determination in *Odontesthes* for being the species showing the weakest sex ratio response to water temperature and for presenting a wider thermal range with stable, balanced sex ratios (Strüssmann et al., 1996a,b). The use of a species or strain that produces stably balanced sex ratios at certain incubation and rearing conditions (temperature, photoperiod, density, salinity, among others) can be determinant for conducting studies on sex determination, as many of those factors are reported to affect sex ratios (Fernandino et al., 2013a) in a way that varies according to the population such as those of the Northern and Southern in the silverside *Menidia menidia* (Duffy et al., 2015), or according to the strain such as in Japanese medaka *O. latipes* (Sato et al., 2005; Hattori et al., 2007; Selim et al., 2009), zebrafish *Danio rerio* (Ribas et al., 2017), and also Nile tilapia *O. niloticus* (Wessels and Hörstgen-Schwark, 2007). The establishment of a strain (Hattori et al., 2009b) of *O. hatcheri* inheriting faithfully a male-linked genetic marker (Koshimizu et al., 2009) was an important hallmark for the advance in the knowledge on both molecular and histological processes of gonadal differentiation in this species, especially during early development. By assessing the genotypic sex (XX/XY system) at early embryonic and larval stages, it became possible to conduct gene expression analysis before and during the onset of histological sex differentiation. Several comparative studies were also conducted, in parallel, with the congeneric species, *O. bonariensis* in order to uncover the molecular particularities that could be implied in differences between the thermosensitivity in the sex determination (Hattori et al., 2007; Fernandino et al., 2008). Another cornerstone for the advance of research in this group of fish was the discovery of the *amhy* in *Odontesthes hatcheri* (Hattori et al., 2012) and also in *O. bonariensis* (Yamamoto et al., 2014), both from Atherinopsidae family. It may also be possible that most, if not all, related groups of atheriniforms possess a Y-linked *amh* sex-determining gene, based on a recent discovery of a Y-linked *amh* in the cobalt cap silverside *Hypoatherina tsurugae* (Bej et al., 2017), from Atherinidae family, the phylogenetically the farthest family in relation to Atherinopsidae. The availability of a sex-determining gene in a group of fish that shows TSD, whereby not only masculinization but also feminization by temperature alone occur, a unique feature of silversides, is considerably interesting to investigate the impacts of environment in the current climate change scenario with colder winters and hotter summers (Peterson et al., 2012). They also represent attractive biological models to understand the evolution process of both TSD and GSD mechanisms in fish and to clarify the molecular, cellular, and hormonal process underlying these mechanisms.

2.2. Characiformes: mechanisms of sex determination

This order represents the most speciose group of Neotropical fish with nearly 2,000 species apportioned in 18 families, whereby members of Characidae represent more than half of described species. Almost 90 % of Characiformes are found in Central and South America and the remaining 10 % in Africa (Oliveira et al., 2011). They inhabit a large variety of freshwater habitats, from headwaters to coastal areas and many of them are ecologically important due to their abundance and for occupying relevant tropic niches. This order includes many farmed species such as Pacu (*Piaractus mesopotamicus*) or Tambaqui (*Colossoma macropomum*, Serrasalmidae) and thus represents important sources of animal protein for human consumption. Besides the large abundance of species, characids are also well-known because this family includes sports fishing species such as dourado (*Salminus brasiliensis*) and brycon (*Brycon* spp.), and ornamental fish, such as the miniature or small-sized characins.

There have been intensive chromosomes studies in this group and, for many of them, morphologically differentiated sex chromosomes and the respective sex chromosome systems have been described, as presented below. Some considerations are also made based on their importance from ecological, economical or phylogenetic points of view.

Triportheus (Triportheidae) species, also known as hatchetfish, are appreciated as ornamental fish worldwide. This is the closest related group to Characidae family with highly conserved sex chromosomes and sex chromosome system (ZZ-ZW) at genus level, whereby the smaller W chromosome can be morphologically distinguished from the larger Z by both morphology and heterochromatin content (Artoni and Bertollo, 2001; de Bello Cioffi et al., 2017; Yano et al., 2016).

Crenuchidae is another characiform family with small-sized fish widely distributed along South America and some in Central America. *Characidium* is the genus with the widest distribution and largest one in terms of species richness (Buckup, 2003). In this genus, sex is genetically determined by a ZW/ZZ chromosome system that was originated along *Characidium* evolution, whereby Z and W chromosomes can be morphologically distinguished (Pazian et al., 2013; Vicari et al., 2008). In a recent study, Utsunomia et al. (2017) identified several female-specific and sex-associated markers in *C. gomesi* W chromosome. Annotation of these markers revealed the presence of single copy genes potentially involved in sex determination of this species.

Erythrinidae family members are commonly known as wolf fishes, tiger fish or trahira, and are distributed along Central and South America. Many of these fish show high growth rates, can be easily bred in captivity, present high tolerance to low oxygen levels (Rantin et al., 1992), and have a highly appreciated flesh, characteristics that are among main preconditions for fish farming (Salaro et al., 2008). However, their aggressive behavior (highly territorial) and cannibalism from early stages are the major constrains for development of their aquaculture (Luz et al., 2000). Differently from the *Triportheus* and *Characidium* species, members of this family are characterized by male heterogamety with some variations from the simple XX/XY system, such as X_1X_2/X_1X_2Y, even within the same species (Bertollo and Mestriner, 1998; de Bello Cioffi et al., 2017).

Anostomidae family includes several medium-sized fish with economic importance, widely distributed in Central and South America. *Leporinus* is a very important group due to the large number of described species and also to economic importance for fisheries and fish farming. The female heterogametic system ZZ/ZW has been reported for many *Leporinus* species (Venere et al., 2004).

Parodontidae family is composed by small-size species found in Central and South America. They are divided into *Parodon*, *Apareiodon*, and *Saccodon* genera. The female heterogametic systems with Z and W chromosomes at different degrees of differentiation have been reported for these three groups (Moreira-Filho et al., 1993; Schemberger et al., 2011).

2.2.1. Sex differentiation studies

Most of characiforms are probably gonochorists because sex chromosomes have been widely described and also due to the absence of reports on hermaphroditism in this group. Juvenile hermaphroditism in *Gynomocorhynbus ternetzi* (Mazzoni et al., 2015) and intersex adult gonads in natural populations of *Astyanax scabripinnis* (Sá et al., 2008; Cornelio et al., 2017) have been reported, but these species are likely gonochorists rather than a case of true hermaphroditism.

The molecular cascade of sex differentiation is not known for any species. Some attempts were made in *Astyanax altiparanae* (Adolfi et al., 2015), whereby the sex-related genes *dmrt1* and *sox9* have been analyzed. However the authors could not clarify their roles during sex differentiation, particularly during testis formation. In this experiment, they recognized ovary and testis differentiation in 58 and 73 days after hatching (dah) larvae, respectively. We can assume that the sensitive period of sex determination would encompass a period between 5 and 58 dah, for the rearing conditions used in this study (Adolfi et al., 2015).

Effects of endocrine factors on sex determination are also poorly explored. In *Astyanax altiparanae* (Characidae), estradiol valerate administered into the diets at concentrations of 20, 40, and 80 mg/kg during 161 days produced female-skewed sex ratios (Cristina de Bem et al., 2012).

2.3. Siluriformes: mechanisms of sex determination

This group is characterized by species without scales and with a cylindrical body. They can inhabit both freshwater and marine environments and are widely distributed in Americas, Africa, and Asia. Together with Characiformes order, catfishes, as they are known, show a high diversity of species in the Neotropical region with more than 2,200 described species (Ota et al., 2015; Fig. 2). The most representative families in terms of biodiversity are Loricariidae and Trichomycteridae with 48 % and 22 % of the total diversity, respectively. Another important group is the Pimelodidae family, which includes giant catfishes such as jau, pintado (shavel nose catfish), cachara,

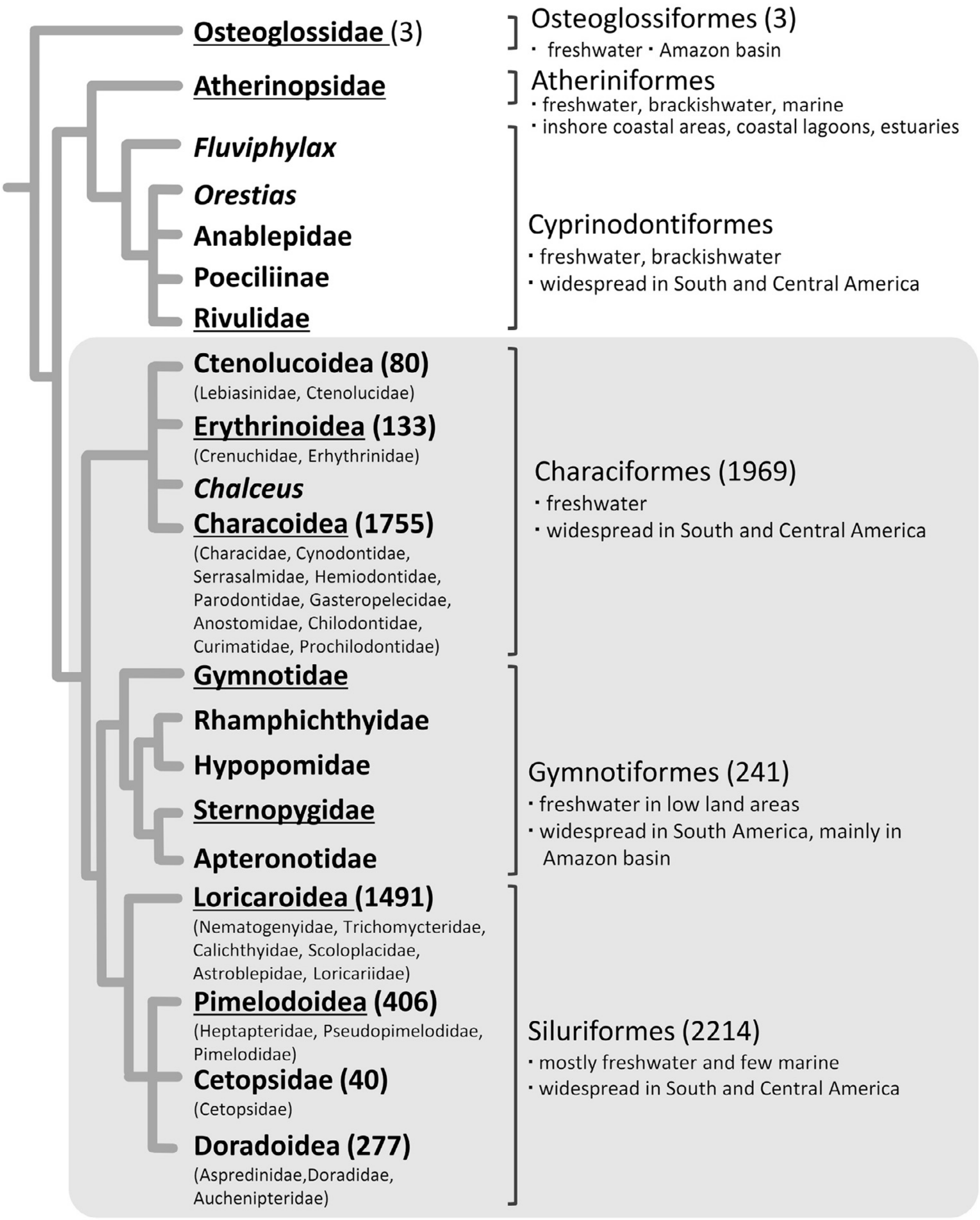

Fig. 2. Phylogenetic relationships between the main clades with potential importance for aquaculture or for ecotoxicological studies (modified from Albert and Reis (2011), Reis et al. (2003). Groups with studies related to sex determination are underlined. Number of species is between round brackets. The main habitats of each order are described. According to Albert and Reis (2011), three order represent 77 % of fish biodiversity in Neotropical region (shaded area).

surubim, piarara or piraiba, some of which can reach more than 200 kg of body weight and three meters of body length. This group includes many members with commercial importance for fisheries but with wild populations in decline due to overexploitation and changes in habitats as a result of anthropogenic activities. Heteromoriphic Z and W sex chromosomes (ZZ/ZW system) are described for a very few *Hypostomus* species (Loricaridae) (Artoni et al., 1998) and in *Imparfinis mirini*, (Heptaridae) (Vissotto et al., 1997), but none of them include species with high importance for aquaculture or fisheries.

2.3.1. Steroids and sex reversal

In the catfish *Rhamdia quelen* (Heptapteridae), larvae fed diets containing 17β-Estradiol (E_2) at 100 mg/kg of food were highly skewed to females, but this dose also produced some sterile gonads (Amaral-Junior et al. 2008). Although E_2 also caused feminization in channel catfish *Ictalurus punctatus*, it has been shown that some sex steroids or sex steroids analogs may have ambiguous effects, such as masculinization by estrogenic (Green and Kelly, 2009) and feminization by androgenic compounds, including non-aromatizable androgens (Goudie et al., 1983; Davis et al., 1990). Paradoxical feminization by these androgens has also been obtained in congeneric *I. furcatus* (Davis et al., 1992). The effects of temperature in channel catfish are also somehow ambiguous in relation to the majority of teleosts, since high temperature (34 °C) yields female-skewed sex ratios in relation to a control temperature (27 °C; Patiño et al., 1996). Whether this pattern is related to ambiguous effects of sex steroids or whether Neotropical catfishes also display a similar pattern represent important research subjects from both evolutionary and endocrinology perspectives.

2.3.2. Sex differentiation studies

The process of ovarian differentiation has been well characterized in shovelnose catfish *Pseudoplatystoma fasciatum* (Pimelodidae), whereby the onset of ovarian differentiation, characterized by the somatic cell outgrowth that later on differentiates to form the ovarian cavity formation, was observed in some larvae with an average size of 44.7 ± 6,4 mm (Valentin et al., 2016), suggesting that the critical period of sex determination likely spans a period before larvae reach this size.

2.4. Other minor fish groups

2.4.1. Sex determination and sex differentiation studies

A species that reach remarkable size and growth rates is the paiche or pirarucu (*Arapaima gigas*; Osteoglossiformes), one of the largest species inhabiting mainly the Amazon River. Pirarucu farming is growing locally and also abroad, and can be considered a very promising species for aquaculture. Due to sex-specific growth rates and the importance of phenotypic sexing for efficient broodstock management, attempts to identify sex-linked genetic markers (Almeida et al., 2013) or sex chromosomes (Marques et al., 2006) have been made, but without success. Currently, sex determination of adults in conducted by the analysis of body phenotype during reproductive season or can be performed by using hormone measurement, such as sex steroid assays (Chu-Koo et al., 2009).

In the viviparous fish *Chapalichthys encaustus* (Cyprinodontiformes), a gonochorist species endemic to Mexico, Guerrero-Estévez and Moreno-Mendoza (2012) have conducted studies on sex differentiation and, interestingly, they have shown that the onset of gonadal sex differentiation starts when larvae are still inside the ovarian lumen; at birth, sex is therefore already determined. Another characteristic of this species is the fusion of paired gonad primordia to form an unpaired single gonad in both sexes.

In another Cyprinodontiformes species known as guppy (Poecilidae), multiple sex chromosome systems have been described (Tripathi et al., 2009). These species are considered as models of sex chromosome evolution, with intensive research on specific sex-linked *loci* aligned to chromosome recombination events. Due to their small size and for being easy to breed, this fish has also been used in studies involving the effects of endocrine-disrupting chemicals (EDCs) on fish reproduction. In adult males of *Cnesterodon decemmaculatus* for instance, long term exposure to ethinylestradiol (EE_2) induced the development of oocyte and caused alteration in duct structure of testis (Young et al., 2017).

3. Conclusions and future perspectives

3.1. High biodiversity versus few studies

With over 32,500 known species, Teleostei group represents more than half of the living vertebrates (Nelson et al., 2016), of which more than 17 % (5,600 described species) are currently represented by Neotropical freshwater fishes (Albert & Reis, 2011; Fig. 2). Although a large part of this high diversity is represented by Neotropical fishes, the variety of sex determination strategies in fish of this region is scarcely known. In a recent revision of Neotropical fish, Barletta and co-authors (2010) presented a common diagnose: the lack of the appropriate information about ecology, biology, and taxonomy (especially in the remote Amazon basins) for each biome and basin within the continent (Barletta et al., 2010). Moreover, most of the information generated about fish species of this region derives from taxonomic and systematic studies, and some of them were focusing in microsatellite DNA or identification of sex chromosomes. For this reason, more studies are necessary to generate a linkage between taxonomy and systematic, ecosystem and management practices, which should be provided by solid sex determination and endocrinological knowledge of each fish species. Considering this particular situation, a good regional strategy in key model species from relevant Neotropical groups would be important in order to unveil conserved patterns and trends within this biodiversity.

3.2. The need to establish key model species for relevant Neotropical groups

Perhaps an interesting example of a key model for ESD established in a Neotropical fish is the pejerrey *O. bonariensis* described above. From initial studies of the reproductive biology (see revision of Somoza et al., 2008), to its establishment as an environmental sex determination model (see revision of Fernandino et al., 2013b), studies in pejerrey have “paved the way” for other atheriniforms (Corona-Herrera et al., 2016; Strüssmann et al., 1996b; Martínez-Palacios et al., 2007; Bej et al., 2017). To this end, it will be necessary firstly to identify key model species that present great interests for aquaculture or for ecological/conservation studies, to then establish studies on life cycle, with special focus in sex determination and reproduction.

For Characiformes, *Triportheus* or other potentially cofamiliar species known as hatchetfish may stand out as key reference group for unravelling the mechanisms of genotypic sex determination and to understand the gonad differentiation process due to intensive research on sex chromosomes, along with their small size, short life cycle, absence of cannibalism, and the possibility of breeding in captivity. Another relevant group is the *Astyanax*, a group with more than 150 valid species with wide distribution (Oliveira et al., 2011) and similar biological characteristics to *Triportheus*. Although morphologically-differentiated sex chromosomes or major sex-determining genes have not been identified so far and the controversy on monophyletic condition of *Astyanax* (Oliveira et al., 2011), the availability of genome sequence for *Astyanax mexicanus* and the possibility of identification of sex-determining genes by promising Next Generation Sequencing Platforms may be instrumental to establish *Astyanax* as reference species for this group.

Regarding Siluriformes, a promising species is the catfish *Rhamdia quelen*. This species is being bred in captivity for fish farming industry and, as described previously, there are reports on sex manipulation for sex control purposes (Amaral-Junior et al., 2008). Sexual maturity is achieved in the first year in males and in the second year in females. The mRNA expression pattern of *vasa* gene has been analyzed during early larval development as germ cell marker (Ricci et al., 2018) and will be useful for studies on reproductive biology of this species. Several studies failed to identify morphologically-differentiated sex chromosomes in *R. quelen*, but the identification of the sex-determining gene as in *Astyanax*, can make of *R. quelen* a potential reference species for Neotropical catfishes.

3.3. Guidelines for the identification of SD genes to improve the efficiency of sex control in non-domesticated species

Although sex-determining genes in Neotropical species are currently described only for two *Odontesthes* species (Hattori et al., 2012; Yamamoto et al., 2014), intensive research using cytogenetic techniques have described the presence of differentiated sex chromosomes and thus, chromosomal sex determination system in many groups such as in *Gymnotus*, *Eigenmannia*, *Characidium*, *Tryportheus*, *Leporinus,* among others (see Table 1). This basic information has critical implications, since the presence of morphologically distinguishable sex chromosomes may evidence the presence of strong genotypic sex determination (GSD) system and possibly weak environmental sex determination (ESD). By employing and allying Next Generation Sequencing techniques such as *DNAseq* and *RNAseq* in these groups, it may be possible to identify sex-linked markers or sex-determining genes in a fastest way.

3.3.1. Hybridization and environment-induced sex reversal

In some Neotropical species with high commercial importance, hybridization has been used to increase growing performances and tolerance to low temperatures, by making use of *hybrid vigour*. This has been employed in catfishes, such as Shovel nose catfish and Surubim, and also in round fishes such as Pacu and Tambaqui. However, there

Table 1

Compilation of the current knowledge on sex determination mechanisms (Genetic and environmental), hormonal manipulation of sex, and the importance for fisheries or aquaculture of Neotropical fish species. ND: not determined; NA: not available; EE_2: ethynilestradiol; E_2: 17beta-Estradiol; EV: estradiol valerate; AI: aromatase inhibitor; GC: glucocorticoid; *Male heterogamety with variations; **Female heterogamety with variations; References: [1]Corona-Herrera et al. (2016), [2]Strüssmann et al. (1997a), [3]Strüssmann et al. (1997b), [4]Fernandino et al. (2008), [5]Pérez et al. (2012), [6]Hattori et al. (2009a), [7]Fernandino et al. (2012), [8]Yamamoto et al. (2014), [9]Hattori et al. (2012), [10]Adolfi et al. (2015), [11]Cristina de Bem et al. (2012), [12]Pazian et al. (2013), [13]Vicari et al., (2008), [14]Utsunomia et al. (2017), [15]Bertollo and Mestriner (1998), [16]de Bello Cioffi et al. (2017), [17]Venere et al. (2004), [18]Moreira-Filho et al. (1993), [19]Schemberger et al. (2011), [20]Carvalho et al. (2002), [21]Feldberg et al. (1987), [22]Artoni and Bertollo (2001), [23]de Bello Cioffi et al. (2017), [24]Yano et al. (2016), [25]Oliveira et al. (2007), [26]Artoni et al. (1998), [27]Vissotto et al. (1997), [28]Andreata et al. (1993), [29]Amaral-Junior et al. (2008), [30]Marques et al. (2006), [31]da Silva et al. (2014), [32]Almeida-Toledo and Foresti (2001).

Order Species (family)	Genotypic sex determination (GSD)	Environmental sex determination (ESD)	Hormone manipulation of sex ratios	Importance for A: Aquaculture/F: Fisheries	Additional information	Reference
Atheriniformes						
Chirostoma estor (Atherinopsidae)	ND	Temperature	NA	A, F	–	1
Odontesthes argentinensis (Atherinopsidae)	ND	Temperature	NA	F	–	2
Odontesthes bonariensis (Atherinopsidae)	XX-XY (*amhy*)	Temperature	EE2, E2, AI, GC	A, F	–	3, 4, 5, 6, 7,
Odontesthes hatcheri (Atherinopsidae)	XX-XY (*amhy*)	Temperature	NA	F		8
						3, 9
Characiformes						
Astyanax altiparanae (Characidae)	ND	NA	EV	A, F	Expression analysis of *dmrt1*, *sox9*	10, 11
Characidium sp. (Crenuchidae)	ZZ-ZW	NA	NA	No	Sex-linked genetic markers available	11, 12, 13
Erytrinus sp. (Erythrinidae)	XX-XY*	NA	NA	A, F	–	14, 15
Leporinus sp. (Anostomidae)	ZZ-ZW	NA	NA	A, F	–	16
Parodon sp. (Parodontidae)	ZZ-ZW	NA	NA	A	Ornamental species	17, 18
Semaprochilodus taeniurus (Prochilodontidae)	ZZ-ZW	NA	NA	A, F	–	19
Thoracocharax cf. *stellatus* (Gasteropelecidae)	ZZ-ZW	NA	NA	No	Ornamental species	20
Triportheus sp. (Triportheidae)	ZZ-ZW	NA	NA	A	Ornamental species	21,22,23,24
Siluriformes						
Ancistrus Kner spp. (Loricariidae)	ZZ-ZW	NA	NA	F	–	25
Hypostomus sp. (Loricariidae)	ZZ-ZW	NA	NA	No	–	26
Imparfinis mirini (Heptapteridae)	ZZ-ZW	NA	NA	No	–	27
Microlepidogaster leucofrenatus (Loricariidae)	ZZ-ZW	NA	NA	No	–	28
Rhamdia quelen (Heptapteridae)	ND	NA	E2	A	–	29
Osteoglossiformes						
Arapaima gigas (Arapaimidae)	ND	NA	NA	A, F	–	30
Gimnotiformes						
Eigenmannia sp. (Sternopygidae)	XX-XY*	NA	NA	No	Ornamental species	31
Gymnotus sp. (Gymnotidae)	XX-XY*	NA	NA	No	Used as fish bait	32

are several cases of full fertility in those hybrids, which are produced by fish farmers without proper broodstock management (Hashimoto et al., 2012), resulting is gradual contamination of pure strains kept in captivity, which are available only by farmers or public institutions with strict management policies. Apart from the consequences of uncontrolled hybridization for fish farming industry (e.g. loss of genetic variability and *hybrid vigour* in post-F1 generations), there are ecological concerns, related to presumable escapees of hybrids from fish farms that have been detected in wild environments Hashimoto et al., 2012). Those hybrids can potentially interbreed with non-introgressed, pure stocks and result in genetic contamination of natural populations.

In terms of sex determination, it has been shown in tilapias (Mair et al., 1991), medakas (Shinomiya et al., 2006; Kato et al., 2010), and also in silversides (Inazawa et al., 2011) that both genetic and environmental sex determination in reciprocal hybrids displays very unusual patterns, due to interaction of primary and secondarily sex-determining factors or to alterations in sex differentiation pathways.

3.4. Sex control and conservation

Most of teleosts show sex-specific growth rates after first sexual maturation, which occurs first in males in the majority of species. Before and during spawning season, the energy used for body growth starts to be also delivered for reproduction, especially gonad maturation and sexual behavior, impairing not only the body mass, but also the flesh quality that decreases considerably because reproduction becomes the physiological priority of the organism (Dunham, 2012). Increased levels of sex steroids can direct nutrients from muscle tissue to gamete production, but in females this process seems to occur in less intensity (Piferrer, 2001; Dunham, 2012). Nevertheless, growth and gain of body weight are highly impaired during reproductive season. A promising alternative is to produce sterile females through fertilization of oocytes by neomales (XX males) (Fig. 3) followed by chromosome manipulation techniques by means of thermal/pressure shock for triploidy induction. Thus, growth rates are maintained even during breeding season in sterile fish.

In the Atheriniform *O. bonariensis*, female show higher growth rates than males after first sexual maturation in captivity (Strüssmann et al., 1996a). In *Astyanax scabripinnis* (Navarro et al., 2006) and other characiforms such as *Piaractus mesopotamicus* or *Leporinus elongatus* similar patterns are observed. Differently from the channel catfish or blue catfish from North America, in which males display higher growth

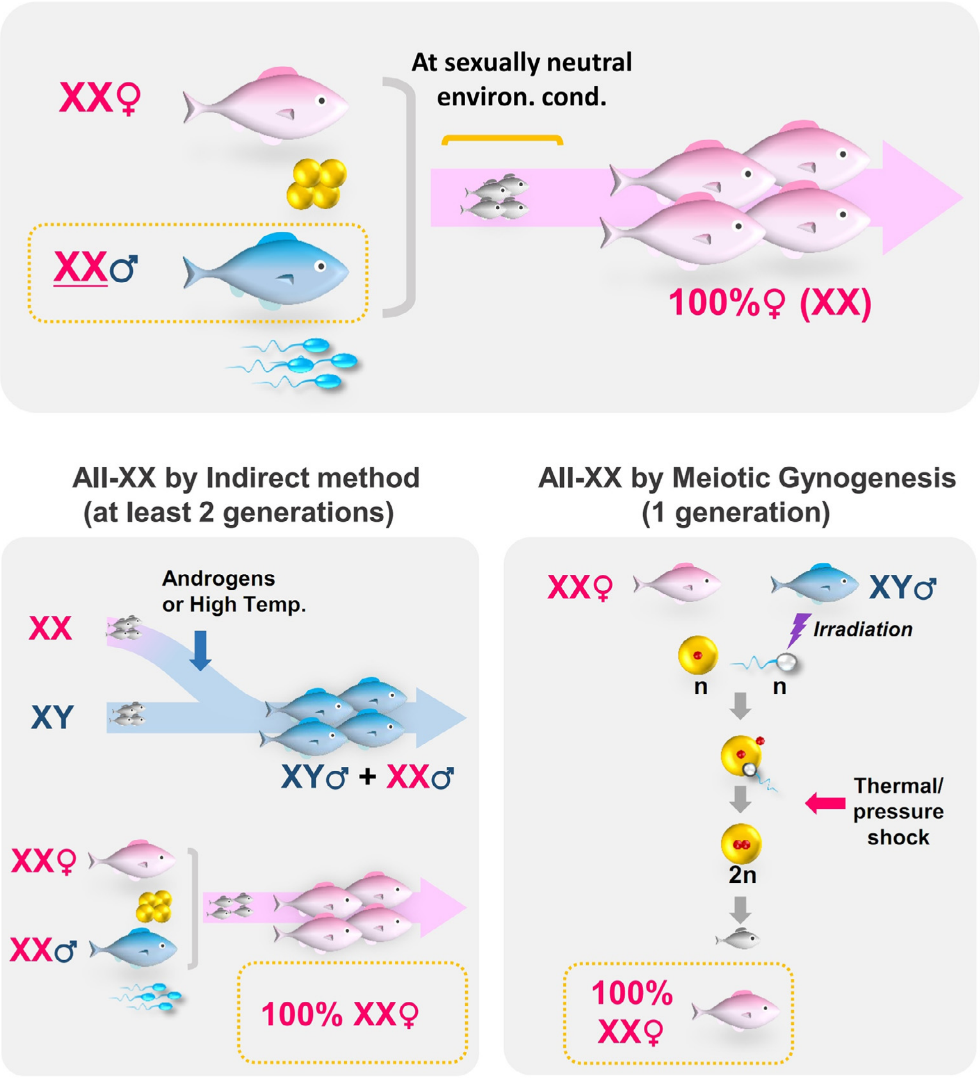

Fig. 3. Schematic representation showing the process for production of all-female progeny by using a sex-reversed XX male (top, left) and by meiotic gynogenesis (right), considering the XX-XY system. For species with strong ESD, incubation/rearing at sexually neutral conditions is essential to ensure non-sex-reversed progenies.

rates, Central and South America's catfishes show an opposite pattern whereby females have higher growth rates than males as in *Rhamdia quelen* (Nunes and Amaral-Junior, 2007) and *Pseudoplatystoma fasciatum* (Valentin et al., 2016).

Production of all-female populations (XX or all ZW/WW) can be achieved by the indirect method, which consists in using hormonally or environmentally-sex-reversed fish, such as XX males or ZW males (Figs. 3 and 4). In the first case, a strategy widely used in salmonids (Dunham, 2012), milt from XX males are used to produce all-XX progenies by inseminating XX oocytes (Fig. 3). In the last case, ZW sex-reversed males are mated with ZW females, producing WW super-females, as it has been obtained in the tilapia *Oreochromis aureus* (Mair et al., 1991) and tongue sole *Cynoglossus semilaevis* (Chen et al., 2012). However, the viability and fertility of this genotype should be evaluated because, analogously to YY supermales, there could be developmental impairments of WW due to the absence of essential genes that are exclusive to the Z chromosome, making the use of WW inviable. By using WW superfemales, all ZW female progenies, can be yielded by mating with ZZ males (Fig. 4), considering the absence of sex reversal by environmental factors (e.g: temperature, pH, density, tank color, and other forms of ESD). By producing WW females and WW males, it is possible to produce and maintain a strain composed solely by this genotype, without Z chromosome. Whether WW fish are less sensitive to environmental factors than ZW is under scrutiny, but if they are less prone to suffer sex reversal, such as YY genotypes in pejerrey in relation to XY (Hattori et al., 2018), an all-WW progeny would be advantageous to ensure seeds with female-skewed sex ratios.

For the production of WW superfemales, an alternative approach for the indirect method is the meiotic gynogenesis, which is based on production of a viable diploid female by fertilizing the oocyte with UV-inactivated sperm and subsequently inhibiting the release of 2nd polar body by thermal or pressure shock (Fig. 4; Quillet & Gaignon, 1990). Mitotic gynogenesis is not encouraged for these cases, because it may reduce the genetic diversity and may allow the expression of deleterious genes. In view of the abundance of species with ZZ-ZW system in Neotropical species analyzed so far (more than 71.4 % of the genera in Fig. 2, considering those with known sex chromosomes), in spite of male heterogamety being considered as the most common system (Mank et al., 2006), and the interest in producing all-female progenies, protocols for the production of gynogenetic fish, much faster than the indirect method, should be adapted for each species in order to foster the production of WW fish, which is essential for obtaining all-ZW populations.

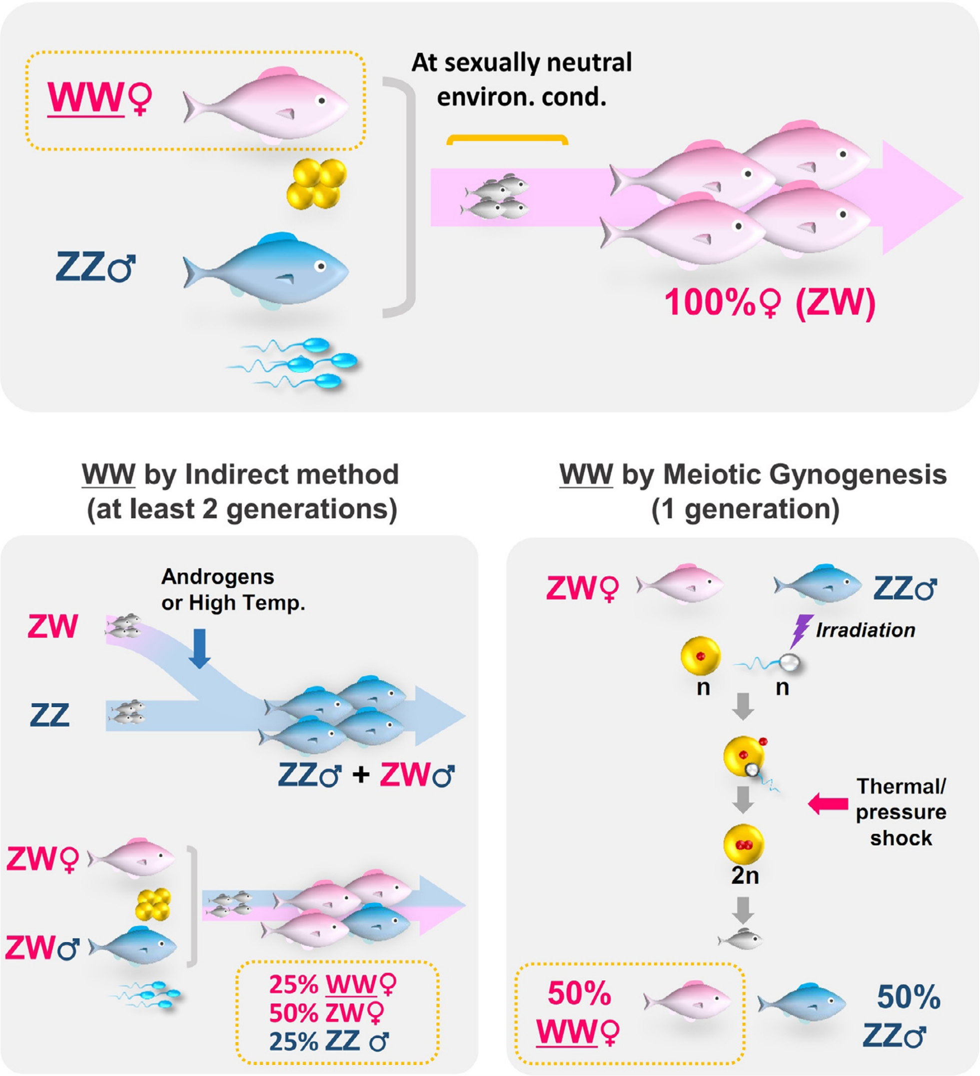

Fig. 4. Schematic representation showing the process for production of all-female progeny by using a superfemale WW (top), generated by mating a ZW female with a ZW sex-reversed male (left), or by meiotic gynogenesis (right), considering the ZZ-ZW system. For species with strong ESD, incubation/rearing at sexually neutral conditions is essential to ensure non-sex-reversed progenies.

3.4.1. Assessment of climate change and other anthropogenic impacts

Unusual environmental conditions in water parameters as a consequence of climate change or endocrine disruptors, which are released by human activity, have the potential to affect fish reproduction. One of those impacts may occur during early life, resulting in sex ratio bias as a result of sex-reversal. Assessment of sex proportions in natural populations can be an informative indicator of environmental and/or endocrine effects, but the bias generated by sampling methods or sex-specific mortalities can eventually result in misevaluations. In this sense, PCR-based methods for discriminating sex-reversed from non-sex-reversed individuals (Yamamoto et al., 2014; Baroiller & D'Cotta, 2016; Hattori et al., 2018), associated with other analytic tools such as otolith microchemistry, methylation analysis, or assays with sex steroid hormones, can be used to propose causal relationships and, therefore, conduct more consistent assessment in the wild.

3.4.2. Mitigation or eradication through restocking considering sex ratios

Although the control of genotypic or phenotypic sex ratio of fingerlings released by restocking programs are not well considered, populations experiencing abnormally high skews in sex ratios, as a consequence of climate change or human activities, may face serious threats due to impacts on its structure and size, as proposed for wild pejerrey in lake Kasumigaura, Japan (Strüssmann et al., 2003). The assessment of sex ratios and genotypic-phenotypic sex mismatches in natural populations prior to fingerlings release activities can be considered in order to mitigate the impacts on population structure. For example, in populations with highly-male skewed sex ratios, individuals with specific genotypic and phenotypic sex ratios (and even sex-reversed fish) could be released in order to counterbalance the proportion of females.

Another use of specific genotypes is for biologic control of invasive species. A program that is being evaluated by simulations and also by field experimentation is based on YY supermales. This idea is based on the release of YY genotypes in order to intentionally skew sex ratios of a population toward males, through a program known as Trojan Y chromosome program (Teem & Gutierrez, 2014; Wang et al., 2016; Schill et al., 2016). This could reduce the proportion of females, which in turn, reduces the amount of offspring in the population, resulting eventually in a significant population decrease or even a complete collapse.

3.5. Development of key biotechnological tools for sustainable fisheries and aquaculture technology

The biannual report of the Food and Agriculture Organization of the United Nations highlights the importance to promote responsible and sustainable fisheries and aquaculture in an economically, socially, and environmentally responsible manner (FAO, 2014). This is crucial because fisheries production, especially in freshwater environments, in South America are showing clear signs of decline due to habitat loss, overfishing, introduction of exotic species, and poor fisheries management (Barletta et al., 2010).

Within this scenario, the control of fish sex is one of the most important and highly targeted areas in aquaculture industry. This is because without the ability to regulate sexual differentiation and reproduction, farmers have little control over breeding processes. In order to manipulate the sex of the offspring, farmers have adopted mainly the direct treatment with exogenous hormones (Budd et al., 2015; Guerrero, 1975; Abo-Al-Ela, 2018).

On this regard, a reasonably strategy could be find sex-determining genes in key species from relevant taxa, whose prospection have been remarkably hastened and optimized by RADseq and RNAseq sequencing platforms. Other biotechnological approach is the use of the indirect method by means of genetic markers for sex in combination with environmental cues, such as temperature (Fernandino et al., 2013a; Tessema et al., 2006), for producing sex-reversed broodstock. These alternative strategies to promote the implementation of more “eco-friendly” approaches should be evaluated to reduce the impacts on wild environments. The combination with the manipulation of chromosome ploidy (triploids) or fertility (sterile fish) should also be explored for the generation of fish lines with better growth performances.

3.6. Conclusion remarks

Despite of the high biodiversity of Neotropical fish species, their potential for both aquaculture and ecological assessment is still underexplored, because suitable biotechnological tools have not been appropriately implemented and also due to absence of improved fish lines (monosex or sterile fish). Governments and farmers from the Neotropical region have the opportunity to develop a sustainable fishery applying the newest aquaculture technologies. On this regards, the first and more important step will be the identification of key reference species from relevant taxa, and so then, find sex-determining genes, and well characterize the labile period of gonadal sex determination to a suitable management of the progeny. The application of these biotechnologies will contribute for the advancement of both basic and applied research on conservation and sustainable aquaculture of Neotropical fish fauna.

4. Disclosure summary

The authors have nothing to disclose.

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