Environment and sex determination in farmed fish

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Abstract

A plasticity of gonadal sex differentiation was reported in the 1930s following exogenous steroid treatments in fish, but demonstration that environmental factors (temperature, pH, density and social interactions) could influence the sex ratio in gonochoristic species has been relatively recent. In fish, as in reptiles and amphibians displaying environmental sex determination, the main environmental factor influencing sex seems to be temperature (TSD = Temperature Sex Determination). In most thermosensitive species (some Atherinids, Poecilids, Cichlids: tilapias, goldfish, a Siluriform, a flatfish . . .) male to female ratio increases with temperature and/or ovarian differentiation is induced by low temperatures. Conversely, in some rare species (Dicentrarchus labrax, Ictalurus punctatus), high temperatures may produce female-biased sex ratios and/or low temperatures promote male-biased sex ratios. In the hirame Paralichthys olivaceus, both high and low temperatures induce mono-sex male populations while intermediate temperatures yield a 1:1 sex ratio (U-shape curve). Fish show particularities in their TSD patterns since mono-sex populations are generally not produced at extreme temperatures, suggesting the existence of strong temperature/genotype interactions. In reptiles, amphibians and fish displaying TSD, temperature treatments must be applied at a critical sensitive period, relatively similar to the hormone sensitive period. In gonochoristic fish, steroid hormones with estrogens in females and 11-oxygenated androgens in males, are probably key physiological steps in the regulation of gonadal sex differentiation. Cytochrome P450-aromatase, enzyme catalysing conversion of androgens to estrogens, seems to be a critical enzyme for ovarian differentiation. Molecular mechanisms of thermosensitivity have been addressed in two species tilapia Oreochromis niloticus and the hirame, where aromatase gene expression is down-regulated by masculinizing temperature treatments. Furthermore, in tilapia the gene expression of 11β-hydroxylase (a key enzyme involved in the synthesis of 11-oxygenated androgens) does not appear to be affected by temperature treatments. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Environmental factors; Fish; Sex differentiation; Gene expression

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1. Introduction

An array of sex determining mechanisms have been reported in fish. In the majority of fish, sex chromosomes are not sufficiently divergent morphologically to be identified by classical karyotype. Indirect approaches have demonstrated that under normal conditions sex is considered to be strongly determined by genotype. Nevertheless, influence of environmental factors on sex differentiation in fish has long been suggested due to intersexual features detected in the gonads of some gonochoristic individuals and by the presence of skewed sex ratios in wild populations. In these early descriptive studies, evidence was not conclusive as to the possible involvement or the respective role of various environmental factors. The first experimental demonstration that some exogenous factors could influence the sex ratio in gonochoristic species was through the manipulation of gonadal sex differentiation by steroid treatments (reviewed by Yamamoto, 1969). The definitive evidence that an environmental factor affected sex differentiation in a gonochoristic fish has been very recent (Conover and Kynard, 1981), and concerned only one species Menidia menidia. The last few years have clearly established that sensitivity of gonadal sex differentiation to environmental factors (Environmental Sex Determination: ESD) is more widespread than previously expected (reviewed by Baroiller et al., 1999). Until the first evidence that temperature had effects on sex differentiation in M. menidia by Conover and Kynard (1981), most of the studies had been focused on reptile and amphibian models. In these species, the term ESD was used to characterise the global effect, concerning the cascade from sex determination to gonadal sex differentiation. Hayes (1998) described sex determination as ‘the mechanisms directing sex differentiation whereas sex differentiation is the development of testis or ovaries from the undifferentiated gonad’. In vertebrates displaying an environmental sensitivity, the genetic sex determination takes place during fertilisation by the combination of genetic factors brought by the male and female breeders. However, are the environmental effects only acting on the ‘directing genes’ and/or on the sex differentiating genes? The term ESD has also been applied in fish (even by Conover and Kynard, 1981), without knowing exactly if temperature was affecting the sex determination or the process of sex differentiation. Recent data on both reptiles and fish suggest that temperature could be mainly affecting sex differentiation rather than sex determination. Nevertheless, an interesting aspect to consider is the important interactions which have been demonstrated between temperature and genotype (Baroiller and Clota, 1998). Are these interactions related to sex determinism (linked to the sex chromosomes) or to the sex differentiation? This point is still unclear and therefore, in the present review, we will also use the terms ESD and TSD as initially applied in fish. In addition, the terms masculinization or feminization refer to the functional gonadal sex inversions, of at least part of the individuals of a progeny.

Studies focused on two families, the Atherinidae (Menidia menidia, M. peninsulae, Odontesthes bonariensis, Odontesthes argentinensis and Patagonina hatcheri) and the Cichlidae (Apistogramma sp., Oreochromis sp.,...), as well as a marine flatfish, Paralichthys olivaceus, have provided a better knowledge on: (1) the main environmental determinants of sex; (2) the critical period of gonadal sensitivity to these factors; (3) the interactions between genotype and the environmental effects; and (4) the molecular mechanisms involved in the modulation of sex differentiation by external factors. This review will cover these four aspects of the environmental sex determination (ESD) in gonochoristic fish.

2. The main environmental determinants of sex

Among the main demonstrative studies (Table 1), very few environmental factors have been analysed and therefore, it is probably premature to generalise. However, among the factors studied up till now, temperature appears to be the main environmental determinant of sex in most sensitive species. Interestingly, in these species sensitive to temperature and/or pH, there appears to be no effect of other factors such as photoperiod, density, or salinity, and thus suggests a certain specificity for the type of sensitivity to external factors. For instance in the genus Apistogramma, temperature is the major environmental determinant of sex. However, progenies of A. caetei are not sensitive to temperature but their sex ratios are strongly influenced by pH. Similarly, tilapias are sensitive to temperature variations but salin-
Table 1
Main factors and their influence on the sex ratio in fish

<table>
<thead>
<tr>
<th>Species</th>
<th>Environmental determinant</th>
<th>Inefficient factors</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Apistogramma</em> sp. (33 sp)</td>
<td>T, pH</td>
<td></td>
<td>Römer and Beisenherz, 1996</td>
</tr>
<tr>
<td><em>Carassius auratus</em></td>
<td>T</td>
<td>P, d</td>
<td>Goto et al., 2000</td>
</tr>
<tr>
<td><em>Cichlasoma citrinellum</em></td>
<td>d, sf</td>
<td></td>
<td>Francis and Barlow, 1993</td>
</tr>
<tr>
<td><em>Dicentrarchus labrax</em></td>
<td>T</td>
<td>P</td>
<td>Blazquez et al., 1998</td>
</tr>
<tr>
<td><em>Hoplosternum litorale</em></td>
<td>T</td>
<td></td>
<td>Pavlidis et al., 2000</td>
</tr>
<tr>
<td><em>Ictalurus punctatus</em></td>
<td>T</td>
<td></td>
<td>Hostache et al., 1995</td>
</tr>
<tr>
<td><em>Macropodus opercularis</em></td>
<td>sf, d</td>
<td></td>
<td>Patino et al., 1996</td>
</tr>
<tr>
<td><em>Menidia menidia</em></td>
<td>T</td>
<td>S, P</td>
<td>Conover and Kynard, 1981</td>
</tr>
<tr>
<td><em>Menidia pensinsulae</em></td>
<td>T</td>
<td></td>
<td>Conover, 1984</td>
</tr>
<tr>
<td><em>Misgurnu anguillicaudatus</em></td>
<td>T</td>
<td></td>
<td>Conover and Fleisher, 1986</td>
</tr>
<tr>
<td><em>Odontesthes argentinitensis</em></td>
<td>T</td>
<td></td>
<td>Conover and Heins, 1987a</td>
</tr>
<tr>
<td><em>Odontesthes bonariensis</em></td>
<td>T</td>
<td></td>
<td>Conover and Heins, 1987b</td>
</tr>
<tr>
<td><em>Oreochromis aureus</em></td>
<td>T</td>
<td></td>
<td>Conover and De Mond, 1991</td>
</tr>
<tr>
<td><em>Oreochromis niloticus</em></td>
<td>T</td>
<td>d, FR, S</td>
<td>Abucay et al., 1999</td>
</tr>
<tr>
<td><em>Paralichthys olivaceus</em></td>
<td>T</td>
<td></td>
<td>Baroiller et al., 1995a</td>
</tr>
<tr>
<td><em>Patagonina hatcheri</em></td>
<td>T</td>
<td></td>
<td>Baroiller et al., 1995b</td>
</tr>
<tr>
<td><em>Pelvicachromis sp.</em></td>
<td>pH</td>
<td></td>
<td>Baroiller et al., 1996a</td>
</tr>
<tr>
<td><em>Poecilia melanogaster</em></td>
<td>T, pH</td>
<td></td>
<td>Baroiller et al., 1999b</td>
</tr>
<tr>
<td><em>Poeciliopsis lucida</em></td>
<td>T</td>
<td></td>
<td>Baroiller and D'Cotta, 2000</td>
</tr>
<tr>
<td><em>Red tilapia (4-ways hybrid, red Florida)</em></td>
<td>T</td>
<td></td>
<td>Baroiller and Clota, 1998</td>
</tr>
<tr>
<td><em>Verasper moseri</em></td>
<td>T</td>
<td></td>
<td>D'Cotta et al., 2001a</td>
</tr>
<tr>
<td><em>Xiphophorus helleri</em></td>
<td>pH</td>
<td></td>
<td>D'Cotta et al., 2001b</td>
</tr>
</tbody>
</table>

Inefficient factors were those tested but shown to have no effect in thermosensitive species. d: density; FR: feeding rate; P: photoperiod; pH: pH; S: salinity; sf: social factors; T: temperature.
ity (Abucay et al., 1999), density, or confinement (Baroiller, unpublished data) do not seem to influence their sex ratios.

3. Critical sensitive period

As already demonstrated in reptiles (Picau et al., 1999) and amphibians (Chardard et al., 1995), fry or eggs have to be exposed to environmental treatments before and during the onset of the histological gonadal sex differentiation, for temperature to affect sex ratios. In the tilapia, *O. niloticus*, it has been demonstrated that the increase of male proportions in the high temperature-treated groups corresponded to the functional masculinization of genetic females (Baroiller et al., 1995a). In this study XX males (which sire all female populations) have been only detected in the temperature treated group. In order for hormonal treatments of sex inversion to be efficient in fish, they also have to be applied at these very similar critical stages, as has been demonstrated in: tilapia (Baroiller and Toguyeni, 1996); pejerrey, *Odontesthes bonariensis* (Strüssmann et al., 1997); channel catfish (Patino et al., 1996); or Japanese flounder (Kitano et al., 1999). Even though a short temperature treatment (10 days) (Baroiller et al., 1995a) can be just as efficient as a longer (21 days) hormonal treatment (Baroiller and Toguyeni, 1996), both of them cover the same initial critical period comprising the 14–24 days after fertilisation.

Nevertheless, recent results in both tilapia and European sea bass *Dicentrarchus labrax* suggest that different thermosensitive windows may exist. In two tilapia species, *O. niloticus* and *O. aureus*, and in a four-way hybrid of tilapia (red Florida strain), low temperatures had no effect on sex ratios even when applied during the classical period of sensitivity to hormonal treatment (Baroiller et al., 1995b; Despréz et al., 1997; Despréz and Méillard, 1998; Abucay et al., 1999). Similar results have been recently reported in *O. mossambicus*: when treatments were applied from 10 days post-hatching, high proportions of males were induced by elevated temperatures, but low temperatures did not affect the sex ratios. However, Wang and Tsai (2000) exposed the same species to low temperatures (20°C) at earlier stages (from hatching or 5 days post-hatching) and could induce high proportions of females. In the European sea bass, similar results have been found since in one case, low temperature treatments (15°C) applied during the sensitive period to hormonal treatments (57–137 days post-fertilisation) could induce a high proportion of males (Blazquez et al., 1998). On the other hand, high proportions (70–73%) of females could be induced when sea bass were exposed to low temperature (13–15°C) at very early stages (stage of half-epiboly = 30 h post-fertilisation), lasting until the middle of metamorphosis with the following on-growing phase performed under ambient temperature condition (Pavlidis et al., 2000).

3.1. Different patterns of ESD

3.1.1. Influence of temperature

Similarly to what has been encountered in reptiles and amphibians, three main types of response to temperature have been reported in fish (Baroiller et al., 1999). In most of the thermosensitive species, the male to female ratio increases with temperature, and/or ovarian differentiation is induced by low temperatures. This type of response concerns species from various freshwater or marine families such as: the Atherinids (*Menidia menidia, Odontesthes bonariensis, O. argentinensis, Patagonina hatcheri*); Poeciliids (*Poeciliopsis lucida, Poecilia melanogaster*); Cichlids (various *Apistogama* sp. and tilapias); Cyprinids (*Misgurnus anguillicaudatus, Carassius auratus*); Callichthyidae (*Hoplosternum littorale*), Pleuronectidae (*Verasper moseri*)...(reviewed by Baroiller et al., 1999). Conversely, in some rare species (i.e. the channel catfish *Ictalurus punctatus*); high temperatures may produce female-biased sex ratios and/or low temperatures promote male-biased sex ratios (Patino et al., 1996). In the case of the Japanese hirame, *Paralichthys olivaceus*, both high and low temperatures induce monosexual male populations (Yamamoto, 1999) while intermediate temperatures yield a 1:1 sex ratio (U-shape curve).

This classification is probably premature because the same range of temperatures can either masculinize or feminize progenies belonging to a same species depending, on the period when treatment is applied (i.e. the European sea bass or *O. niloticus*) or depending on the sexual genotype in *O. niloticus* (see Section 4).
3.1.2. Influence of pH

In all the pH sensitive *Apistogramma* species (Römer and Beisenherz, 1996), the proportion of males is higher at an acid pH (4.5) than at a more neutral value (6.5).

3.1.3. Influence of density

In the paradise fish, *Macropodus opercularis*, the proportion of females could be directly proportional to the density (Francis, 1984).

3.2. Validity of the experimental results with regard to the natural conditions and adaptive role of ESD?

With the exception of the study by Conover and Kynard (1981) on *M. menidia*, demonstrating an adaptive role of TSD, conclusive studies concerning ESD have been addressed either under controlled or semi-controlled conditions. Hence, in most of these studies extreme conditions of temperature, pH, density… have been often chosen in order to maximise a putative effect on sex ratio. Even if physiological temperatures or pH have been also chosen in some cases, constant regimes were mainly applied. These conditions do not truly mimic the natural regimes, and the demonstration that ESD exists in the wild can be a very difficult issue for some species (sex/age-specific migration, mixing of different progenies in a same shoal…). It has been shown to exist in the case of *M. menidia*, where skewed sex ratios were both obtained in the wild during early or late breeding seasons resulting in high proportion of females and males, respectively, but also under constant laboratory conditions. In another recent case, in the blue tilapia, *O. aureus*, fluctuating temperatures have been demonstrated to have less masculinizing potentials than constant high temperatures but can still produce significant deviations of sex ratios (Baroiller et al., 2000).

Female tilapias after fertilisation collect in their mouth first their eggs and then the vesiculated fry for mouth brooding, fry which will swim into shallow terrace waters or flooded eulitoral grassland (Keenleyside, 1991). A first release of the progeny occurs at approximately day 10–12 post-fertilisation and consist mainly of fry occupying shoals, present in shallow waters during the day, but that take refuge into the mother’s mouth in times of danger and during the night (guarding period). The critical period for gonadal sex differentiation occurs during this guarding sequence; temperatures in the shallow waters occupied by the shoals can reach more than 34–35°C. Under controlled conditions, these high temperatures can strongly masculinize a progeny (Baroiller et al., 1995a).

Likewise, *Apistogramma* species in the wild live in habitats where a temperature gradient exists with respect to the temperature depth which ranges from approximately 23 to 30°C. Under laboratory conditions strong masculinization is induced by 29°C treatments (Römer and Beisenherz, 1996). Therefore putative masculinizing situations can be encountered by tilapias and *Apistogramma* species in the wild.

4. Interactions between temperature and genotype

In tilapia, as in *M. menidia*, a high variability in thermosensitivity has been reported depending on the progenies from a same strain stock (Baroiller et al., 1995b, 1996a; Conover and Heins, 1987b), suggesting strong interactions between temperature and genotype. In the tilapia, *O. niloticus*, parental effects have been first demonstrated at basal temperatures (Fig. 1). Within a defined temperature, sex ratios of successive progenies generated by a given couple of breeders are very similar. Moreover, the masculinizing effect of a same high temperature treatment on these successive progenies is also very stable (Fig. 2). Therefore, both sex ratios and thermosensitivity are very stable for a given couple of breeders (Baroiller et al., 1995b). Finally, parental effects on thermosensitivity have been also reported: a same male or female breeder can generate both sensitive and insensitive progenies. However, only male breeders can sire either all sensitive or all insensitive progenies (Fig. 3).

In the same tilapia species, similar high temperature treatments have been applied on all male, all female, or mixed populations (Fig. 4). All female populations XX, all male populations XY and mixed populations (XX + XY) were obtained by mating a classic female breeder, respectively, with a XX, XY, or a YY male (Abucay et al., 1999; Baroiller and D'Cotta, 2000; Kwon et
Fig. 1. Parental Effects on *Oreochromis niloticus* sex ratios, male proportion % of individual progenies obtained through a diallel mating table between four males (ME, MA, MD, MC) crossed with four females (FA, FB, FC, FD). A minimum of 100 fry per group were sexed by microscopic analysis of gonadal squash (from Baroiller and Clota, 1998).

All male populations YY were obtained by mating a YY male with a YY female (Abucay et al., 1999). In all these experiments, all female and mixed populations were masculinized by high temperature (35–36°C) treatments (Abucay et al., 1999; Baroiller and D’Cotta, 2000; Kwon et al., 2000a). Conversely, YY all male populations were feminized by a similar high temperature treatment (Abucay et al., 1999; Kwon et al., 2000a). The occurrence of a similar feminizing effect on XY genotypes remains controversial (Abucay et al., 1999; Baroiller and D’Cotta, 2000; Kwon et al., 2000a). Therefore, depending on the genotype and more particularly on the sexual genotype, a same high temperature treatment may either masculinize or feminize a same species.

Fig. 2. Stability of sex ratios and thermosensitivity in three successive progenies, obtained from the same couple of *Oreochromis niloticus* breeders reared at the basal temperature of 27°C and the masculinizing temperature of 36°C (from Baroiller et al., 1995b).

5. Molecular mechanisms involved in the modulation of sex differentiation by external factors

Vertebrates have different mechanisms of sex determination but they all seem to undergo a histological neutral stage during embryonic develop-
opment where the gonad is bipotential, and subsequently follow a sex differentiating pathway oriented towards either ovary or testes development. Biochemical and molecular approaches have been used to analyse the cascading events and the genes involved in the sex determination and differentiation of lower vertebrates. To date no testis sex determinant, an SRY (Sinclair et al., 1990) equivalent has been identified in non-mammalian vertebrates. In these vertebrates the DMRT1 gene has been recently suggested to have an important role in maleness due to the evolutionary conservation, being testis-specific and because it has been found during testis sex differentiation of fish (Marchand et al., 2000 and chickens, as well as in mammals (Raymond et al., 1999; Smith et al., 1999). Fish have a certain plasticity during sex differentiation since several functional sex phenotypes can be generated by diverse mechanisms. Most of our knowledge in fish has been initially due to the sex inversion effects of steroid hormone treatments in natural (genetic) sex differentiating species. It is possible that at some point, similar sex differentiating steps may exist between the pathway followed by the temperature-induced sex phenotypes to that of genetic or default sex differentiating fish. We consider that both hypotheses by Yamamoto (1969) and Bogart (1987) are being slowly confirmed in fish, since it appears that gonadal sex differentiation is oriented towards one of the sexes largely dependent on the levels of endogenous sex steroids, but a change in this steroid balance can shift the differentiating pathway.

Administration of androgens to fish larvae at a stage when gonads are still undifferentiated, can generate partial or complete masculinization in a number of fish species (Hunter and Donaldson, 1983). Likewise, functional female phenotypes can also be induced at this same period with estrogens. Steroid assays performed in the gonads of natural differentiating tilapia larvae revealed high levels of 17β-estradiol in genetically (XX) all female individuals and low levels found in genetically (XY) all male fish (Fig. 5). In these fish, low levels of 11-ketotestosterone were found in both genotypes with slightly higher amounts in females than in males at this same period (D’Cotta et al., 2001b). Gonads in these differentiating tilapia males were in a period of semi-quiescent state but yet levels of both hormones could be found. In the case of rainbow trout, elevated levels were found of androstenedione and testosterone in whole body mono-sex individuals (Fitzpatrick et al., 1993). Steroid in vitro metabolism evidenced a specificity of 11-oxygenated androgens during tilapia (Baroiller, 1988), carp (Komen et al., 1995) and catfish Clarias gariepinus testis differentiation (Van den Hurk et al., 1989). Because estrogens are converted from androgens, several studies have been focussed on the cytochrome P450 aromatase enzyme which catalyses this reaction. Aromatase activity has been shown to be elevated in the natural sex differentiation of tilapia (Guiguen et al., 1999). The blocking of estrogen biosynthesis using aromatase inhibitors, results in partial or complete masculinization associated with a functional testis development in tilapia (Guiguen et al., 1999; Kwon et al., 2000b) as well as in salmonids (Piferrer et al., 1994). Furthermore, strong aromatase gene expression was revealed during sex differentiation in genetic female trout (Guiguen et al., 1999) and in female tilapia (D’Cotta et al., 2001a).

Few studies have been dedicated to the molecular mechanisms of fish sex differentiation and even less have dealt with ESD. The type of ESD system involved in these studies is exclusively the influence of temperature on sex differentiation and basically concerns two species: the tilapia O. niloticus; and the Japanese hirame flounder P. olivaceus. Certain temperatures can induce sex
inversions with the development of either testes or ovaries, in a similar manner to hormone treatments. The pathway involved in the natural ovarian differentiation seems to be the activation of estrogen synthesis. The role of estrogen and whether this pathway is also implicated in temperature sex differentiation, similar to what has been demonstrated in TSD reptiles (Pieau et al., 1999), has been addressed in the two thermosensitive fish species mentioned.

In tilapia, functional phenotypic males can be induced by rearing larvae at 35°C during sex differentiation. In these masculinized XX females, a repression of aromatase gene expression has been observed (Fig. 6), and interestingly a repression was also seen when genetic males were treated at 35°C (D’Cotta et al., 2001a). In the Japanese flounder genetic females are obtained at normal temperatures (18°C) while elevated temperatures (27°C) generate male phenotypes. A suppression of aromatase was also shown in male groups, whereas females presented a strong aromatase expression (Kitano et al., 1999). The authors detected only a significant amount of estradiol in females at a late period of differentiation. Both these studies indicate that temperature acts either directly repressing the aromatase gene or indirectly through one or more transcription factors. A putative upstream repressor gene could be, for instance, SOX9. Treatment of 17α-methyltestosterone and the use of fadrozole an inhibitor of the aromatase enzyme, both caused masculinization of genetic female flounders (Kitano et al., 2000). In both these sex-inversed cases a suppression of aromatase gene expression was observed. However, it is unclear if the regulation of the aromatase gene in these two sex-inversed phenotypes of flounder, is similar to that shown in the temperature–male phenotype previously described. Nevertheless, in all these cases it appears that low levels of aromatase gene expression can redirect sex differentiation towards testis development.

Another important aspect is whether in temperature-induced masculinization there is an increase in the expression of 11β-hydroxylase gene, which is a key enzyme for the production of 11-oxygenated androgens. In tilapia, no marked differences were noticed for 11β-hydroxylase in phenotypic males, although unexpectedly temperature appeared to up-regulate the expression when genetic males were treated to high temperatures (D’Cotta et al., 2001b). In these temperature masculinized females, an increase in expression was also revealed for a differentially expressed gene still unidentified called MM20C (D’Cotta et al., 2001b).

An important aspect to consider is the role of the central nervous system in ESD fish. Recent data have evidenced that sex differences already exist in the tilapia brain when the gonads are still undifferentiated (D’Cotta et al., 2001a). The key question remains to be answered: are these brain/pituitary differences a cause or a consequence of gonadal sex differentiation in the thermosensitive species?

6. Conclusion

It is now clearly shown that sex ratios and sex differentiation of various freshwater or marine species, from temperate or tropical habitats can be influenced by some environmental factors. Among them, temperature seems to be the main environmental determinant of sex. The characteristics of thermosensitivity in fish strongly differ from those observed in reptiles, in particular, because very few true monosex populations are induced by the modification of an environmental factor even at extreme values. This seems to be mainly associated with strong temperature–genotype interactions. Therefore, at least in sensitive fish species, sex is probably determined by genetic factors (both major and minor factors) by
environmental factors and their interactions. In temperature sex differentiation of fish (1) there are both up- and down-regulated genes and (2) there is a similarity in the mechanisms or pathways to that of natural fish sex differentiation regarding ovarian development, where estrogen synthesis appears a pre-requisite.

References


