

Lability of sex differentiation in fish

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The processes of sex determination and differentiation are labile in teleosts and are amenable for manipulations by ploidy during fertilization, hormone during hatching, temperature during the juvenile stage and other environmental or surgical factors during the adult stage.

IN oviparous teleosts early embryonic events, namely insemination, second polar body extrusion and first mitotic cleavage are manipulable and render 37 different types of ploidy induction possible; such ploidy inductions during early embryonic stages result in the production of all-male, all-female or all-sterile population¹. However, the scope for ploidy alterations to regulate sex determination is restricted to early embryonic stages alone. A large number of previous publications have attempted to precisely delineate the optimum (labile) period, during which it is possible to successfully induce ploidy^{2,3}. The process of sex differentiation in teleosts is also labile⁴, rendering hormonal induction of sex reversal possible in 37 gonochoristic species and 13 hermaphroditic species⁵; hormonal manipulations during the labile period result in the production of monosex population; again, the labile period is restricted mostly to just before and after hatching stages. Thus sex determination and differentiation in fish are labile and can

be reversed by manipulating ploidy, and hormone during fertilization and hatching stages, respectively.

A series of publications by Strussmann *et al.*⁶ and others⁷ have recently documented thermal lability of sex determination in a number of teleosts; for instance, fish exposed to colder or warmer temperature from hatchling to juvenile stage lead to the production of all-female or all-male progenies^{8,9}; hence, thermal induction may serve as a third technique to regulate the sex of teleosts. A number of others, such as social and surgical factors may also induce sex reversal in adults. In many coral fish and in the freshwater Chinese paradise fish *Macropodus opercularis*, hierarchy and aggressive behaviour have led to the formation of a definite social organization and any manipulation to alter the social structure lead to sex reversal¹⁰⁻¹². Besides, it has long been known that gonadectomy induces sex reversal in a few teleosts¹³. For instance, female *Betta splendens* developed testes after ovariectomy and became functional male¹⁴. Therefore, the processes of sex determination and differentiation are labile in teleosts, rendering manipulations of ploidy during fertilization, hormone during hatching, temperature during juvenile, and surgical and social during adult stages. This communication reports the amenability of teleosts to sex regulation almost throughout life by manipulating ploidy, hormone, temperature and other selected environmental factors.

Table 1 lists selected representative species, in which sex reversal has been successfully accomplished by manipulating one or more of the following: ploidy, hormone, temperature and environmental factors. The scope for ploidy manipulation is indeed very strictly restricted to a limited period of few seconds and minutes during fertilization¹; likewise, the duration of the labile period is also very much restricted to a few minutes just before and after hatching, when the immersion technique is chosen for hormonal induction⁵, or a few days immediately following hatching in ornamental fish¹⁵, or a few months in foodfish like carps¹⁶ and salmon¹⁷, when dietary administration is chosen for hormonal induction of sex reversal; rarely, *Poecilia reticulata* has been shown to be amenable for hormonal induction of sex reversal during embryogenesis, just before and after hatching and post-maturity stage^{15,18-20}; yet, the optimum period for hormonal induction of sex reversal is mostly restricted to the hatchling stage. Likewise, the optimum stage for successful sex reversal by manipulating thermal, or any other environmental factor is now shown to be restricted to the juvenile or adult stage. In more than 60% of the selected representatives species, successful sex reversal has been induced by ploidy and/or hormonal manipulation(s) by different authors. In hermaphroditic species like *Monopterus albus*, sex is spontaneously reversed in adults²¹; such spontaneous sex reversal during adult stage is recorded in hermaphrodites characterized by polyandrous or polygynous¹¹ social system; a manipula-

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Table 1. Lability of sex differentiation of selected fish; the lability provides scope for (1) ploidy (during and after fertilization), (2) hormonal (during and after hatching), (3) thermal (during juvenile stage) or (4) environmental (4a: spontaneous; 4b: density dependent or 4c: surgical - during adult stage) manipulations. +* = all ♀ brood ; +** = all ♂ brood

Family	Species	1	2	3	a	b	c	Ref.
Siluridae	<i>Clarias gariepinus</i>	+	+	-	-	-	-	40, 41
	<i>C. lazera</i>	-	+	+	-	-	-	8, 42
	<i>Ictalurus punctatus</i>	-	+	+	-	-	-	7
Anabantidae	<i>Betta splendens</i>	+	+	-	-	+	+	14, 15, 43, 44
	<i>Trichogaster trichopterus</i>	-	-	-	-	-	+	45
	<i>Macropodus opercularis</i>	+	+	-	-	+	-	46, 47
Cichlidae	<i>Oreochromis mossambicus</i>	+	+	+	-	-	-	48, 49
	<i>O. aureus</i>	+	+	+**	-	-	-	49-51
	<i>O. niloticus</i>	+	+	+	-	-	-	52, 53
	<i>Tilapia macrocephalus</i>	-	-	-	-	-	+	13
Salmonidae	<i>Oncorhynchus mykiss</i>	+	+	-	-	-	-	54, 55
	<i>O. masou</i>	+	+	-	-	-	-	56, 57
Poeciliopsis	<i>Poeciliopsis lucida</i>	-	-	+	-	-	-	58
Poeciliidae	<i>Poecilia reticulata</i>	-	+	-	-	-	-	18, 19
Cyprinidae	<i>Cyprinus carpio</i>	+	+	-	-	-	-	16, 59
	<i>Brachydanio rerio</i>	+	-	-	-	-	-	60, 61
	<i>Oryzias latipes</i>	+	+	+	-	-	+	62, 63
	<i>Misgurnus anguillicaudatus</i>	+	-	+	-	-	-	63, 64
Paralichthyidae	<i>Paralichthys olivaceus</i>	+	+	+*/+	-	-	-	3, 65, 66
Atherinidae	<i>Odontesthes bonariensis</i>	+	+	+	-	-	-	6, 22, 63
	<i>Patagonia hatcheri</i>	-	-	+	-	-	-	9

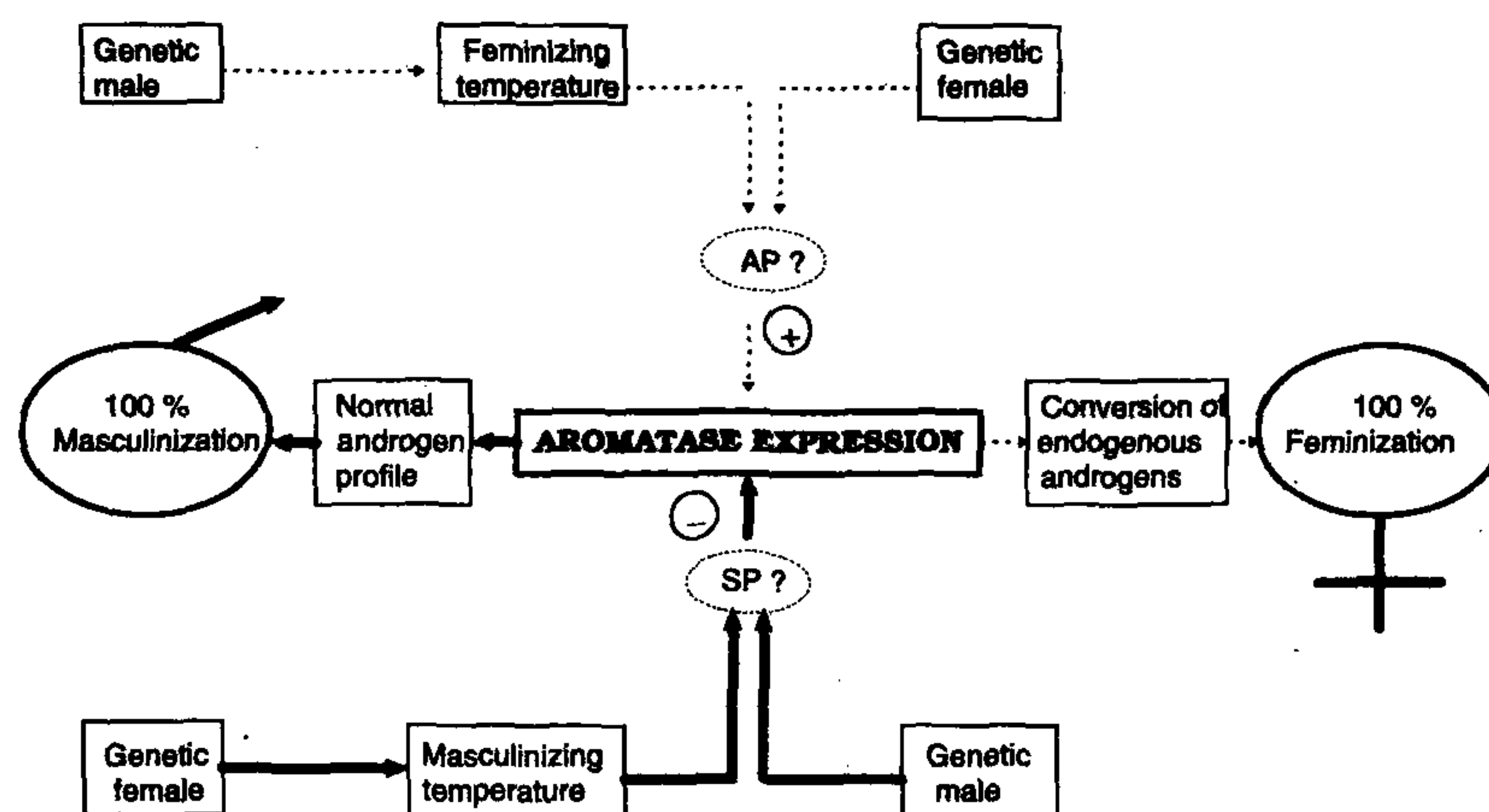


Figure 1. Suggested pathways through which thermal treatment generates all male/female progenies in fish. (AP = Activator proteins; SP = suppressor proteins; ...> Feminizing pathway; → Masculinizing pathway).

tion altering social structure of these hermaphrodites leads to sex reversal in adults of one or more individuals.

Thermal manipulations to induce sex reversal in teleosts have been explored only in recent years; it has thus far been possible to successfully accomplish sex reversal by thermal induction in about 11 species only. While documenting the thermolabile sex determination in the atherinid fish, *Odontesthes bonariensis*, Struss-

mann *et al.*^{6,9,22} who reared the hatchlings at 17°C obtained 100% females and 100% males when the juveniles were reared at 25°C for 48 days. A very similar thermal labile sex determination has also been demonstrated to occur in *Clarias lazera*⁸. It is not yet known how such a thermal treatment can reverse the sex of a genotypic male or female. However, it is known that such thermal treatment induces specific proteins²³, which may modify the expression and hence, the activity

of aromatase, which is a 'turn-key' enzyme in sex differentiation; its full expression may reduce normal androgenic profile in genetic males, resulting in 100% female progeny; alternatively the reduction of its activity maintains normal endogenous androgen profile in genetic females resulting in 100% male progeny²³⁻³⁵ (Figure 1).

Although ploidy and hormonal induction of sex reversal have been widely practised now for over 20 years in many commercially important species, it has increasingly become apparent that these techniques used for sex reversal result in stunted growth (e.g. *Oryzias latipes*¹⁷), sterility (e.g. *Poecilia reticulata*²⁰), intersexuality (e.g. *P. reticulata*²⁰) and/or low fecundity (e.g. *P. reticulata*¹⁵), when the reversed individual is fertile (see also Pandian and Sheela⁵); incidentally, these techniques also require skilled labour, costly chemicals and may involve consumer resistance, when the residual level of the administered hormone is high. Thermal manipulation to reverse the sex may prove to be the cheapest and easiest technique and can easily be practised for mass production by unskilled farmers or by using the equipment for industrial level production of monosex population^{36,37}.

It is known that the primordial germ cells of teleosts are of extra gonadal origin, and retain their bipotentiality to differentiate into male or female germ cells until sexual maturation³⁸. A large number of teleosts are known to retain this bipotentiality, even after sexual maturity³⁹. Thus the ability to retain bipotentiality, a unique characteristic of many teleosts may ultimately be responsible for the observed lability of sex differentiation throughout the life of the teleost species.

It must, however, be mentioned that not a single teleost species has thus far been subjected to all the 4 methods of manipulations to reverse the sex from fertilization to adult stage, although such a possibility is suggested by the present communication.

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