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Genetics of salmonid skin pigmentation: clues and prospects for improving the external appearance of farmed salmonids

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Abstract Skin color is an important commercial trait in fish farming, given that this phenotype influences consumer acceptance, thereby determining the commercial value that fish can reach. This character is genetically determined, either by monogenetic or polygenetic control. Over the past few years, progress has been made in studies of quantitative genetic parameters for commercially important traits related to skin pigmentation and, in the molecular field, the mapping and cloning of some genes involved in fish color determination. This study reviews information regarding the genetic determination of salmonid skin color, along with different strategies to improve this character. Data collected in model fish (medaka and zebrafish) are also considered since this information contributes considerably towards improving understanding of the genes that may participate, and of the mechanisms involved in establishing skin coloration in salmonids.

Keywords Fish · Skin color · Chromatophores · Gene pigmentation · Salmon farming

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Introduction

Studies aimed at clarifying the genetic basis of traits related to skin color in fish began at the beginning of the twentieth century in various species considered to be of importance, either in the production field, as ornamental species or for laboratory use (reviewed by Tave 1986; Johnson et al. 1995; Tomita 1992a, b). In salmonids, the inheritance studies for albinism in the brook trout (*Salvelinus fontinalis*) began very early (Pettis 1904). Subsequently, various studies were published on other mutants that appeared, mainly in rainbow trout (Bridges and von Limbach 1972; Wright 1972; Yamasaki 1974; Kincaid 1975; Yamaguchi and Miki 1981; Dobosz et al. 1999; Nakamura et al. 2001; Blanc et al. 2006) and on other species of this group (Hazzard 1943; Leonard and Madden 1963; Yamamoto et al. 1999). Evidence obtained in these studies indicates that, in general, skin color characters in salmonids have simple genetic control, where one locus or very few loci participate, with a dominant, recessive, or co-dominant type inheritance mode. Over the past few decades, new information has become available, suggesting that particular characteristics related to skin color in salmonids can also be subject to polygenetic control, such as the number of black and red spots in brown trout (Blanc et al. 1982, 1994), and the silvered and spotted appearance of skin in rainbow trout (Kause et al. 2003, 2004). Similarly, in recent years, research groups have also focused on the molecular characterization of some of the genes

involved in salmonid skin pigmentation. Included in this research area, are studies on mapping of the dominant albino locus in rainbow trout (Nakamura et al. 2001) and those related to tyrosinase cloning and sequencing in the same species (Boonanuntanasarn et al. 2004). All these studies, many of which are quite basic, provide valuable information about how genetic control of this type of character would occur in salmonids, information that may be pertinent when using this type of character in the applied field. On the other hand, data available on the genetic determination of skin color in salmonids, can be better understood if progress made in studies of some laboratory fish is taken into consideration, given that significant findings have been made for this class of fish, especially on the genetic, cellular and molecular basis of skin pigmentation in the model medaka and zebrafish (reviewed by Tomita 1992a; Johnson et al. 1995; Quigley and Parichy 2002; Parichy 2003; Kelsh 2004). Numerous genes that participate in establishing skin color have been identified in these fish, and molecular characterization of some of them has been carried out. Furthermore, genetic maps and complete genomic sequences are available for these model fish, facilitating genetic analysis and the subsequent comparison with salmonids. In view of the evolutionary proximity of the model fishes and salmonids, and the existence of conserved regions in their genomes, as shown, for example, for numerous EST markers (Rexroad et al. 2005), this molecular information can constitute an important reference point in the search for new genes involved in salmonid skin pigmentation, many of which are, to date, largely unknown.

The aim of the present study is to synthesise and review the genetic, cellular and molecular factors that affect the skin coloration trait in salmonids, information that should serve as source of knowledge for researchers that are interested in managing and improving traits related to skin pigmentation in these fish. Firstly, general aspects on skin coloration in fish will be commented upon, subsequently information available on this topic in the model medaka and zebrafish will be reviewed, and finally consideration will be given to progress made in salmonids in this field. Similarly, a description is provided of the different types of color phenotypes, the skin color pattern in salmonids and the intraspecific differences observed, as well as of the mutants identified for this character within this group. Finally, the commercial significance of the skin color character in some farmed salmonids will be addressed, given that this trait, together with other external traits, is important in fish farming, and consideration will be given to the different strategies that could be applied in an effort to genetically improve these characters, where molecular genetic information can play an important role.

General aspects of skin color determination in fish

Skin color determination in fish is a complex process that involves a series of cellular, genetic and physiological factors that, together, determine the external appearance of a fish at a given developmental stage (Fig. 1). Some of these factors produce a stable color phenotype, while others, because they are influenced by the environment, can produce a changing color phenotype; these changes can, in some cases, be prolonged.

Cellular factors of skin pigmentation in fish

The cellular factors of skin pigmentation in fish, refer to the existence of specialized cells called chromatophores, that can exhibit a characteristic color, given that they can store or synthesize a specific pigment. There are at least five types of pigment cells in fish: melanophores, xanthophores, erythrophores, iridophores and leucophores. These cells can produce, respectively, the colors black or brown (melanin pigment), yellow or orange (pteridine pigment), red (carotenoid pigment), iridescent, blue, silver or gold (guanine platelets) and white (guanine granules; Fujii 1969, 1993). Furthermore, some of these chromatophores can absorb light, as is the case of the melanophores, xanthophores and erythrophores, while others can reflect light, as occurs with the leucophores and iridophores (Fujii 2000). Embryologically, the chromatophores originate from the neural crest, a group of transient cells that derive from the ectoderm shortly after gastrulation (Erickson and Reedy 1998); furthermore, their development begins either during the embryo stage, or in more advanced development stages. This process, known as Dual Origen, is important in establishing the skin coloration pattern in fish,

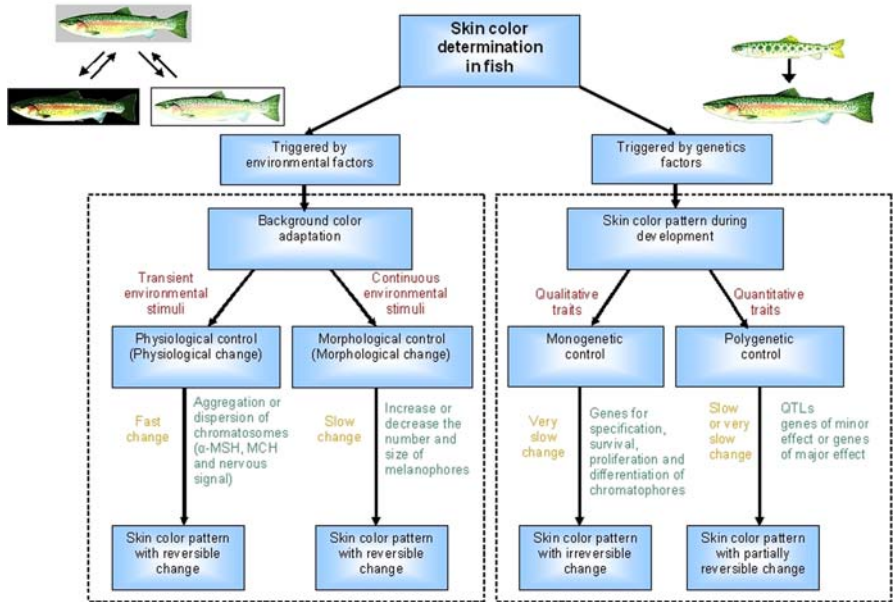

Fig. 1 Factors that determine skin color in fish

which depends on the presence of populations or sub-populations of chromatophores in a given development stage.

Genetic factors of skin pigmentation in fish

The genetic factors refer to the existence of genes that control the expression of skin color phenotypes. This type of control can be monogenetic (Mendelian), if one locus or a few loci control the trait, or polygenetic, if, on the contrary, many minor effect loci or major effect genes are present, that together have an additive effect on the phenotype, producing continuous variation within the population. A lot of evidence has been collected from different species regarding the Mendelian control of skin color (reviewed by Tave 1986). It has been reported that this type of control may be either recessive, completely/incompletely dominant and co-dominant or sex-linked. The genetic basis of monogenetic control has been further clarified over the last few years, thanks to the discovery of various genes involved in skin color production in the model medaka and zebrafish, that have a specific function in establishing this phenotype, either in the differentiation (pigmentation and normal morphology of the chromatophores), or in the recruitment, survival, migration or development of the different types of chromatophores (Quigley and Parichy 2002; Parichy 2003; Kelsh 2004). Studies on the polygenetic basis of skin color in fish are scarce, as opposed to considerable research carried out on other, continuously varying characters, such as growth, sexual maturity, food conversion etc. (Tave 1986; Gjedrem 2000). The few studies available on skin color, indicate that this type of trait exhibits a significant additive genetic variation, given that heritability values are usually medium-high (Houde 1992; Bakker 1993; Blanc et al. 1994; Brooks and Endler 2001; Kause et al. 2003). For example, in rainbow trout the silver and spotty character has heritability values that fluctuate between 0.23 and 0.45 (Kause et al. 2003), while in the guppy (*Poecilia reticulata*) additive genetic variation for the skin color character in males, in relation to phenotypic variation during sexual stress, reaches values between 0.58 and 0.79 (Houde 1992; Brooks and Endler 2001). These heritability values indicate a low environmental influence on this character type, and thus a rapid response to selection efforts, undertaken in the context of a genetic improvement program, would be expected. Important to note is that under monogenetic control, the skin color phenotypes usually remain stable throughout development and also between individuals of the same population, due to the minimum effect of the environment on this type of phenotype. This contrasts with observations on polygenetically controlled characters, where the skin color phenotypes, in

particular those related to color intensity, can change during different developmental stages as a result of various physiological processes such as sexual maturity, or can vary continually within one population, as a consequence of genetic-environmental interaction.

Physiological factors of pigmentation in fish

Physiological factors refer to the presence of hormonal and neural signals that can act on the aggregation or dispersion of chromatosomes (organelles that contain the pigments in the chromatophores), or by increasing or decreasing the number of chromatophores present in the skin, that ultimately produces a change in skin color, and in particular color intensity. The first instance is usually referred to as physiological change (reviewed by Fujii 2000), while the second is termed morphological change (Sugimoto 2002). For example, in the case of physiological change, when a fish is maintained in a dark background, the α-melanophore-stimulating hormone (α-MSH) is secreted by the pars intermedia of the pituitary, provoking dispersion of pigments in the chromatophores, that darken the skin. In contrast, when the fish are on a white background, the melanin-concentrating hormone (MCH) is released by the pars nervosa of the pituitary, causing the opposite effect. These physiological factors can act as a result of various environmental stimuli, especially light factors, that trigger a change in skin color by adapting to the background color—light or dark—where the fish are located, a phenomenon generally known as Background Color Adaptation. Of note, is the fact that background color adaptation is a relatively rapid process that depends on the intensity and duration of the stimulus, and this change is reversible if the fish is returned to its original medium.

Skin pigmentation in the model fishes: how chromatophores paint fish

Comprehension of the genetic basis of skin pigmentation in fish has advanced significantly over recent years, thanks to the study of various mutants of the model medakafish and zebrafish, both natural and induced, that present a wide variety of chromatophore defects. These defects produce a skin color or coloration pattern that differs in various aspects from that of the wild phenotype (Tomita 1992a; Johnson et al. 1995; Odenthal et al. 1996; Quigley and Parichy 2002; Parichy 2003; Kelsh 2004). In the particular case of the zebrafish, these mutant phenotypes are very evident, since the normal coloration pattern in this fish, which comprises longitudinal light and dark stripes, changes radically in the mutants (see review by: Quigley and Parichy 2002; Parichy 2003). The study of these mutants has permitted the identification of 38 genes involved in skin color production in the medaka fish (reviewed by Kelsh et al. 2004) and around 90 in the zebrafish (reviewed by Haffter et al. 1996; Kelsh et al. 1996, Table 1). These genes are involved in different cellular processes, such as specification (determination of the cellular destination), proliferation (increase in the number of chromataphores), survival (maintenance of the number of chromatophores), differentiation (pigmentation and morphology of the chromatophores) and in the production of the coloration pattern (distribution of chromatophores). Molecular characterization of around ten of these genes has been carried out (Lister et al. 1999; Parichy et al. 1999; Kawakami et al. 2000; Kelsh et al. 2000; Parichy et al. 2000 a, b; Camp and Lardelli 2001; Fukamachi et al. 2001; Pelletier et al. 2001; Logan et al. 2003), indicating that they codify membrane receptors and transporters, ligands transcription factors, as well as various enzymes involved in the synthesis pathway of the different pigments (reviewed by Braasch et al. 2007, Table 2). Many of the genes characterized are orthologs with other genes extensively studied in endotherm vertebrates, whose role in skin pigmentation is well defined, such as the case of the *Mift*, *Ednrb* and *Kit* genes, which are involved in the development of the melanophore lineage in the mouse (reviewed by Bennett and Lamoreux 2003).

However, how do these genes participate in the color formation or color patterning of these fish? According to data obtained in the zebrafish, formation of the skin coloration pattern depends on at least three factors: (1) the presence of new chromatophores to populate the bands, (2) local interactions between chromatophores that regulate formation of the bands and (3) the existence of pre-established patterns that orientate and localize the bands. In the first case, evidence was obtained from the study of *sparse* (Parichy et al. 1999; Rawls and Johnson 2001) *rose*

Table 1 Genes involved in different processes of skin pigmentation in fish models, obtained through the study of various skin color mutants or skin color pattern mutants observed in these fish (according to Kelsh et al. 1996, 2004)

Process (i.e., genes)	Mutant class (i.e., mutant)	No. of zebrafish genes	No. of medaka genes
Specification (*Mift*, *Sox10*)	Reduced chromatophore number (no chromatophores)	6	2
Patterning (*mes*, *Da*)	Abnormal chromatophore distribution (Abnormal pigment pattern)	5	1
Proliferation (*Ednrb*, *Kit*)	Reduced chromatophore number (reduced melanophore)	2	4
Survival (*bcl*, *gu*)	Reduced chromatophore pigmentation (melanophore degeneration, pale xantophores, dull iridophores)	52	14
Differentiation (*Tyr*, *Dct*)	Pigment level reduced (pale melanin, delayed melanophore differentiation, pale xantophores with dull iridophores)	24	17
	Abnormal melanophore morphology (spindly melanophores, small melanophores, stella chromatophores, no background adaptation)		
		Total = 89	Total = 38

Table 2 Genes involved in skin pigmentation with molecular characterization in fish models

Species	Gen	Protein class	Function	Mutant phenotype	References
Zebrafish (*Danio rerio*)	*Kita*	Membrane receptor	Early melanophore survival	Sparse	Parichy et al. (1999)
	Ednrb1	Membrane receptor	Late melanophore survival. Late iridophore survival	Rose	Parichy et al. (2000 a)
	Csf1r	Membrane receptor	Differentiation and survival of xantophores. Melanophore stripe pattern organization	Panther	Parichy et al. (2000 b)
	Mc1r	Membrane receptor	Melanin synthesis mediator	–	Logan et al. (2003)
	Fbxw4	Ligand	Iridophore survival. Melanophore and iridophore stripe pattern organization in the anterior part of the trunk	Hagaromo	Kawakami et al. (2000)
	Mitfa	Transcription factor	Melanophore specification and differentiation	Nacre	Lister et al. (1999)
	Tyr	Enzyme	Melanin synthesis	Albino, golden	Camp and Lardelli (2001)
	Dct	Enzyme	Melanin synthesis	Sandy	Kelsh et al. (2000)
	Gch	Enzyme	Pteridine synthesis	Edison, Yobo	Pelletier et al. (2001)
	Xdh	Enzyme	Pteridine synthesis	–	Braasch et al. (2007)
Medaka (*Oryzias latipes*)	*AIM1*	Membrane transporter	Melanin synthesis mediator	Pale orange	Fukamachi et al. (2001)

(Parichy et al. 2000 a) and *puma* (Parichy et al. 2003), mutants. Absence of melanophores recorded in the *sparse* and *rose* mutants during the embryo and adult stages respectively, produced low intensity and irregular dark bands, due to the lack of melanophores necessary to populate the melanophore bands being formed. Furthermore, the study of these mutants indicates that development of the melanophores is temporally regulated, one population being of embryonic origin and another metamorphic, both coexisting in the adult skin coloration pattern. In the case of the *puma* mutant, that has an almost indistinguishable pattern of dark bands, the effect of melanophore absence in the formation of the coloration pattern is greater, given that this mutant experiences a recruitment defect of the stem cells during metamorphosis, cells that are necessary for the development of new pigmentation cells. In the second case, it has been observed that interaction between different types of chromatophores in the skin, especially between

xanthophores and melanophores, is crucial to the development of the banding pattern in zebrafish, since the absence of one type of chromatophore prevents the organization of the other. For example, in the *panther* or *fms* mutant, that has limited xanthophore development (Parichy et al. 2000b; Parichy and Turner 2003), the melanophores present in the skin are not organized in the classic dark bands that normally characterize this fish, but rather remain disorganized. Furthermore, this has been confirmed through cell transplant experiments aimed at creating chimeras, where incorporation of xanthophores in the skin of *panther* mutants, enables recuperation of the dark melanophore bands (Parichy 2003). This type of interaction between xanthophores and melanophores has also been observed in cell transplant studies in the *Nacre* mutant (Maderspacher and Nusslein-Volhard 2003), that only develops xanthophores in the skin (it does not possess melanophores), due to a mutation in the *Mitfa* gene, given that when melanophores obtained from a normal phenotype are transplanted, these become organized in regular bands, as observed in the wild phenotype. Interaction between melanophores of the same class is also important in the formation of the coloration pattern, given that correct aggregation depends on this aspect. This phenomenon has been analysed in studies of *obelix* and *leopard* mutants (Maderspacher and Nusslein-Volhard 2003). Thus, in the *obelix* mutant, melanophore aggregation is affected, resulting in the formation of fish with only two prominent dark bands in the homozygous individuals. In the case of the *leopard* mutant, interaction between chromatophores of similar or different types, also varies, as a result of which the dark bands are irregular or broken in these individuals. This situation would result from a variation in the late development of the melanophores or an error in the early aggregation of the same, as observed in the *obelix* mutant. Thirdly, development of the zebrafish skin coloration pattern would also depend on factors related to orientation and position of the chromatophores, known as *prepatterning mechanism*, given the existence of a residual pattern (Lister et al. 1999). For example, in the *Nacre* mutant of the zebrafish, which only possesses xanthophores in the skin, these continue to be distributed in an orderly fashion in the interband region they normally occupy in the wild phenotype; furthermore, they are absent in the ventral region, where the dark band composed of melanophores should have developed. Some authors have suggested that environmental factors would influence this *prepatterning mechanism*, such as location of the horizontal mioseptum and the posterior lateral nervous line (Maderspacher and Nusslein-Volhard 2003). Is there a model that synthesizes how a color or skin coloration pattern is established in the model fish in particular, and fish in general? Information obtained from the model fish indicates that the most probable guideline would consider the spatial distribution of the chromatophores during development as an essential process in the formation of these phenotypes (Quigley and Parichy 2002; Parichy 2003; Kelsh 2004). According to this model, development of skin pigmentation would depend mainly on regulation of the spatial and temporal distribution of the chromatophores, that would permit their differential positioning in the skin in a given moment; together, these two factors would determine a certain phenotype. Various mechanisms would operate in this model, such as interaction between neighboring chromatophores, the generation de novo of chromatophores and local environmental factors (Kelsh 2004). Within this model, local interaction between different types of chromatophores is a crucial process, given that the absence of any cellular class resulting from some mutation, for example in the specification, produces a significant change in the coloration pattern. This occurs because the organization or aggregation of the other types of chromatophores present in the skin, is affected. Of note, is that this model contrasts with the model proposed to account for skin pigmentation in mammals (reviewed by Barsh 1996), where skin color in certain zones of the body would depend, rather, on the differential synthesis of various types of melanin (eumelanin, black/brown color, or pheomelanin, red/yellow color) by the only pigmentary cells present in these vertebrates that correspond to the melanocytes, through the action of hormones and antagonist proteins, known as the Aguti Signal System. The action of these hormones and antagonistic proteins would explain, among other things, the difference observed in the dorso-ventral intensity of skin coloration in mammals (dark dorsum and light belly; Vrieling et al. 1994). There is a lot of evidence in mammals regarding this physiological-type regulation system (Barsh 1996) and evidence to date indicates that it may also be operating in fish (Cerda-Reverter et al. 2005).

Skin color determination in salmonids

Only very general information is available about the differences in skin color or skin coloration pattern in salmonids, both at an interspecific and intraspecific level (Ade 1989). The different species of this group, in general, show a species-specific coloration pattern, that is fully established in the adult stage (Fig. 2), given that in earlier stages, such as fry and smolt, this phenotype tends to be very similar, comprising mainly of black, vertical spots on the flanks, known as *parr* marks. Skin coloration between different species of salmonids can be differentiated according to the background color (light or dark), the distribution of the spots and dots (dark, light or colored), usually numerous in the dorsum and the dorsal or caudal fins, and in the size, form and intensity of the red band located on the side of the body of the fish. Although each species presents characteristic skin coloration, this can display wide intraspecific variation, as has been observed in the number of black and red spots in the brown trout (Blanc et al. 1982, 1994), the number of black spots in the anterior area below the lateral line (Islam et al. 1973) and in the number black spots and the background color of the dorsum in the rainbow trout (Fig. 3). This coloration pattern can also be significantly modified during the reproductive period, producing marked differences between males and females (Ade 1989). Another important aspect, is that the color of the dorsum in salmonids is always darker than the belly, a characteristic that is common to many fish and to other vertebrates, including mammals. This is probably due to a differential spatial distribution of the various chromatophore types, although, as was mentioned earlier, this may also be due to the action of a system with physiological regulation of skin color (Cerda-Reverter et al. 2005).

Some skin pigmentation color mutants have been described in salmonids, with coloration that differs considerably from the wild type. These mutants include albino (Pettis 1904; Hazzard 1943; Leonard and Madden 1963; Bridges and von Limbach 1972; Nakamura et al. 2001); golden or yellow forms, including the palomino phenotype (brownish yellow skin with black eyes; Wright 1972; Dobosz et al. 1999, 2000; Yamamoto et al. 1999), and the blue varieties that can be either iridescent metallic blue (Kincaid 1975), cobalt blue (Yamasaki 1974) or iridescent blue variant (Blanc et al. 2006). Other rare skin color mutants have also been observed in salmonids, such as the mottled varieties with patches of yellow or wild coloration (Clark 1970; Galbreath and Plemmons 2000; Yamaki et al. 2006). It has been suggested that the albino and yellow mutants would be produced as a result of depigmentation of the melanophores, and the blue varieties would occur due to a structural change in the pigments present in certain types of chromatophores, rather than by the absence of any of these (Yamaguchi and Miki 1981; Blanc et al. 2006), which would produce an optical effect through scattering of the incident light in the tegument, known as Tyndall effect, causing the intense blue color observed in these fish (reviewed by Bagnara et al. 2007). Furthermore, the depigmented mutants should present a defect in the chromatophore differentiation, while the blue mutants, apart from a change in the structure of some pigments, could present some kind of defect in the specification or survival of some chromatophore types, specifically the melanophores and iridophores. This can be concluded on the basis of observations made in other fish, where the production of the color blue depends on the interaction between these two types of cells (Goda and Fujii 1998). To date, all these mutant

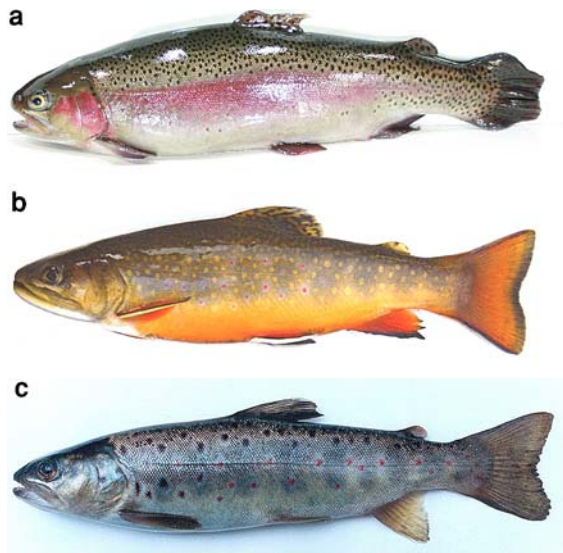

Fig. 2 Examples of interspecific variability in salmonid skin color. Skin color in adult stage of: **a** rainbow trout (*Oncorhynchus mykiss*), **b** brook trout (*Salvelinus fontinalis*) and **c** brown trout (*Salmo trutta*)

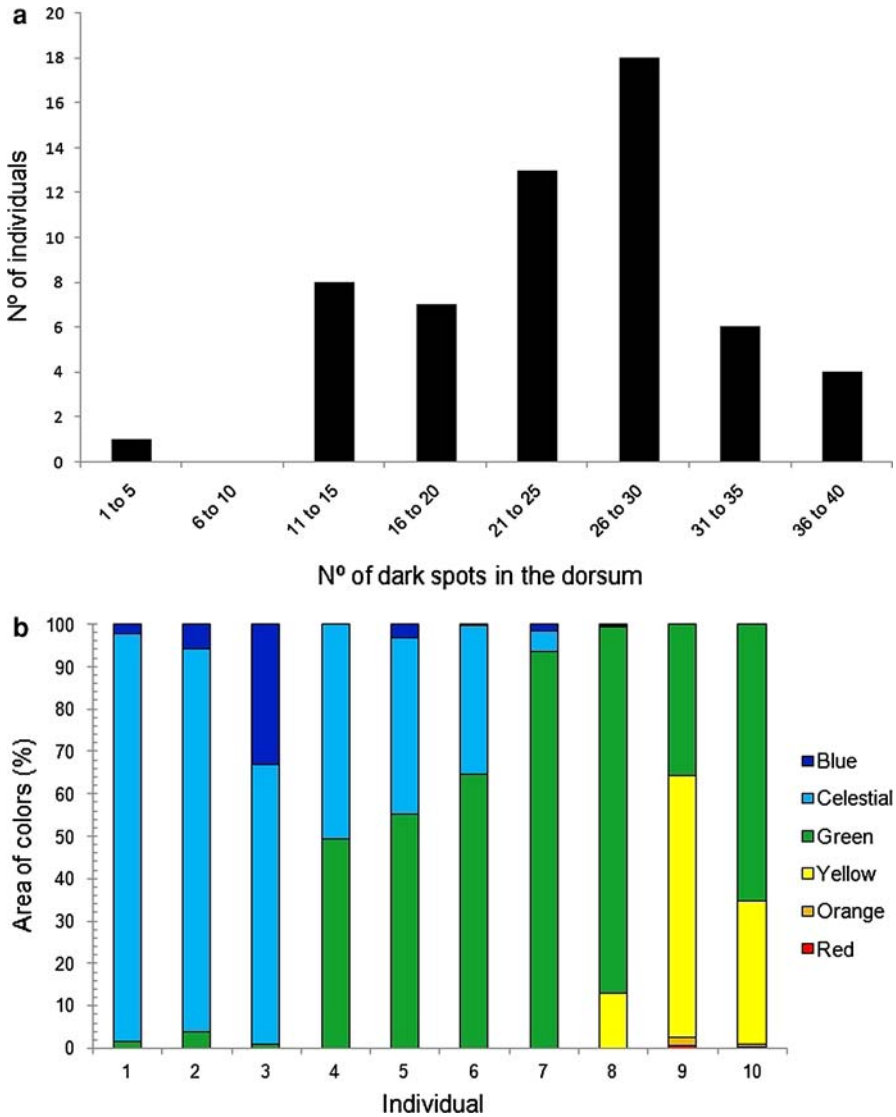

Fig. 3 Examples of intraespecific variability in *skin color* of the rainbow trout dorsum. **a** Variability in number of *black spots* ($n = 30$), and **b** *background color* ($n = 10$). Individuals number one, two and three in (**b**), show an intensive *blue color* in the dorsum (*Blue Back trait*) which is considered an attractive trait for marketing. The analysis considered 9 cm^2 skin patches of the anterodorsal region in 2 year old specimens, obtained with a digital camera. Image analyses were undertaken with ImageJ 1.34s and SigmaScan Pro 5.0 software

classes have been identified in the rainbow trout, while in *Salvelinus fontinalis*, *Salvelinus namaycush*, *Oncorhynchus tshawytscha* and *Oncorhynchus masou ishikawai*, only albino and mottled mutants have been described (Pettis 1904; Hazzard 1943; Leonard and Madden 1963; Yamamoto et al. 1999; Yamaki et al. 2006). Some skin color mutants in the rainbow trout display adverse pleiotropic effects, such as lower survival and growth (yellow mutant: Dobosz et al. 2000) and obesity and sterility (cobalt blue: Oguri 1974). Nevertheless, in spite of this, as will be discussed later in this review, the existence of these mutant cases has helped to clarify the genetic base that underlines skin pigmentation in these species.

There is not much information about the types of chromatophores that exist in the skin of salmonids, and what data is available, refers to Coho salmon (Hawkes 1974), where three chromatophore types were reported: melanophores, xantophores and iridophores. These cells are distributed differentially in various body zones (for example, higher abundance of iridophores in the belly than in the dorsum) and similarly, they are located in defined skin strata, either isolated or in cell groups, interrelated one to the other, forming structures known as Chromatophore Units, comprising melanophores and iridophores. The presence of these chromatopore units, also observed in other lower vertebrates (Bagnara

et al. 1968), would explain the variety of shades of color observed in the different body zones of this salmonid (light and silver appearance, with small, dark spots on the dorsum). With respect to the start of skin pigmentation in salmonids, it has been observed that in the rainbow trout, this began during the final phase of organogenesis, just before the hatching stage (Ballard 1973). In both the rainbow trout and other salmonids, the types of chromatophores pigmented first have not been identified, neither has the body zone where this process begins.

Skin color mutants identified in rainbow trout have aided progress in the genetic and molecular characterization of these phenotypes. This has occurred thanks to the study of the albino mutants (Bridges and von Limbach 1972; Nakamura et al. 2001; Boonanuntanasarn et al. 2004), golden, yellow or palomino mutants (Wright 1972; Dobosz et al. 1999), and the blue variants (Yamasaki 1974; Kincaid 1975; Blanc et al. 2006, Fig. 4). Evidence obtained indicates that these mutant phenotypes are controlled by a Mendelian mechanism, and that their inheritance mode may be recessive (albino: Bridges and von Limbach 1972; iridescent blue and blue variant: Kincaid 1975; Blanc et al. 2006), dominant (albino: Nakamura et al. 2001; Boonanuntanasarn et al. 2004), incomplete dominant (golden or yellow: Wright 1972) or complete dominant (palomino color to yellow color: Dobosz et al. 1999). As in other vertebrates, recessive albinism would be the result of a mutation, in this case of a point mutation, in the tyrosinase gene (Nakamura et al. 2001; Boonanuntanasarn et al. 2004); on the other hand, dominant albinism would be produced by a mutation of this same gene (orange phenotype with black eyes; Boonanuntanasarn et al. 2004), or a mutation in another gene that has yet to be discovered (yellow phenotype, with red eyes), located in a different linkage group to the tyrosinase, affecting synthesis of the black or brown pigment within the eumelanin pathway (Nakamura et al. 2001). Furthermore, the blue (blue variant) and golden phenotypes would be controlled by two different loci, that have still not been mapped or cloned, that would segregate independently (Blanc et al. 2006). Likewise, evidence indicates that the yellow body color in rainbow trout is controlled by two loci (Dobosz et al. 1999), the A locus being epistatically dominant to the B locus, with the wild phenotype expressed in the presence of A allele and the yellow phenotype expressed in the presence of homozygous a allele. The B locus appears to moderate the expression of yellow color, producing the palomino phenotype in the presence of B allele and the albino phenotype in the presence of the homozygous b allele condition. As regards the number of genes that participate in salmonid skin pigmentation, about which some type of molecular information is available, to date, 13 have been identified, including the tyrosinase gene (*tyr*), with four that participate in the melanin synthesis pathway (*tyr, tyrp I, dct* and *silv*), eight in the pteridine synthesis pathway (*gchla, gchfr, pts, spr, clot, pcbd, dhpr* and *pam*; Braasch et al. 2007), and one in the specification of the xanthophores (*csflr*; Parichy et al. 2000b). Most of this information derives from EST analysis and synteny studies (Braasch et al. 2007). One interesting aspect to consider is that more than half of these genes are duplicated in the genome of these fish, as occurs with *tyr, silv, gchla, gchfr, dhpr, pcbd* and *pam*. Phylogenetic and synteny analysis (reviewed by Braasch et al. 2007) suggests that some of these genes would originate from an early genomic duplication event that could have occurred in fish between 250 and 350 million years ago (e.g., *tyr*), while others would have arisen as a result of a later autotetraploidy duplication event, that occurred

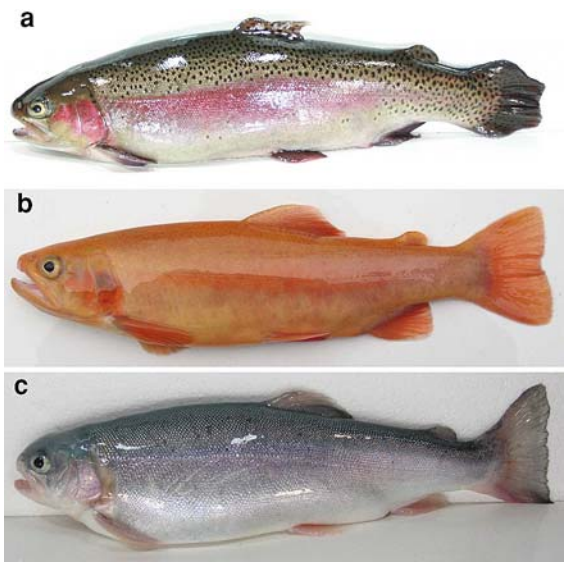

Fig. 4 *Skin color mutants* in rainbow trout. **a** wild type, **b** yellow mutant and **c** blue variant mutant. The *blue variant mutant* exhibits a phenotype with *silvery blue color*, *white belly* and a *diminutive red band* on the side of the body

within the evolutionary line of salmonids (e.g., *gchla*), that is widely documented in these organisms (Allendorf and Thorgaard 1984). It has been stated that these gene duplication events were most important during the evolution of the color genes, that would explain the diversity and complexity of skin coloration in fish in general and in salmonids in particular (Braasch et al. 2007). Nevertheless, to date, only a few studies report a causal relationship between these two factors (Sugie et al. 2004; Braasch et al. 2006).

Discussion

Commercial importance of skin color in salmonids: color of the fish–color of the money

Although skin coloration and body shape are important production traits in farmed fish, given that they affect consumer acceptance, the production of farmed stocks with specific skin coloration that satisfies market demands is still limited. The culture of improved stocks would provide the opportunity to standardize and improve product appearance, contributing considerably to achieving greater stability and expansion of the industry (Knibb 2000). The limited development of this aspect in the salmon farming, contrasts with the use of color applied to other characters, in various species animals. In the latter case, advances made, either due to the addition of pigments to the diet (i.e., carotenoids), or the development of stocks with allele combination that favor the expression of a particular trait of interest, have been commercially applied in a range of situations (reviewed by Hudon 1994). This management of color traits, has enabled requirements to be met with regard to degree and type of coloration in certain products, in accordance with consumer demand, such as meat color (salmon and trout; Steine et al. 2005), skin color (chicken and pork) and egg shell and yolk color (hens). Worldwide, one of the few examples where the skin color character in fish has been developed for production purposes is in tilapia, in response to the demand for red strains which are highly valued on the market (Wohlfarth and Hulata 1989; Garduño-Lugo et al. 2004). At present this constitutes one of the most important types of tilapia farmed in the world (Green 2006). In commercially important salmonids, such as *Salmo salar*, *Oncorhynchus kisuch* and *O. mykiss*, skin coloration is an important aspect, especially those that are sold whole carcass such as *O. mykiss*, given that the market prefers silver fish with a few dark spots or, alternatively, none at all. This aspect is critical to salmon culture given that it has even limited the use of certain species that, otherwise, have intensive culture potential, such as the brown trout (*Salmo trutta*; Krieg et al. 1992), because it has an excessively spotty skin, being less silvery and sometimes yellowish (Chevassus et al. 1992; Blanc et al. 1994). During salmon culture, skin coloration undergoes considerable intrapopulational variation, and a large percentage of fish can be observed with dark skin and large spots, undesirable traits that decrease their market value, as is the case with the rainbow trout (Kause et al. 2003). These undesirable phenotypes are even more evident during sexual maturity, where, furthermore, a very pronounced red band appears along the flanks and opercules of fish (Aknes et al. 1986). In some producer countries, such as Chile, this external aspect is particularly critical in the case of rainbow trout farming, given that this species is commercialized mainly on the Japanese market (Taub and Palacios 2003), where demands is for specimens with few spots and as silvery as possible. The first studies analysing the quantitative genetic parameters related to external appearance in rainbow trout were carried out recently (Kause et al. 2003), among which, skin color (silver shining, dark silver and dark), size of the dark spots (small, moderate and large), and body shape (slender, medium and rotund) were considered, together with condition factor. This study showed that characters for skin color and spots have medium heritability values ($h^2 = 0.29$ and 0.45 respectively), with moderate phenotypic and genetic correlations between both ($r \geq 0.33$), indicating that improvement in both traits would result from the selection of either one. Nevertheless, with respect to other external characters, such as condition factor and body shape, these skin color characters, have low correlations ($r = -0.10$ to 0.21), and are also negatively correlated with weight ($r =$ between -0.28 and -0.07). These results indicate, on the one hand, that a rapid response could be expected to selection efforts aimed at color or spots in rainbow trout skin, and, in turn, a simultaneous selection for growth rate and skin coloration should be successful, given that no

undesirable correlations would exist. In *Salmo trutta*, heritability values with respect to the number of black and red spots are higher and fluctuate between 0.40 and 0.70 (Blanc et al. 1982, 1994), which should produce a rapid response to selection efforts aimed at improving these characters for this species.

Another aspect that requires discussion in the context of genetic improvement of skin color is the profit associated with the use of improved stocks, as compared to normal stocks. In the case of the culture of tilapias with a red body color, their mass production has been developed over the past few years, because these strains are highly valued on the market (Garduño-Lugo et al. 2004; Green 2006). An economic evaluation of the advantage of farming stocks with improved skin color, has still not been undertaken in salmonids. Nevertheless, in the case of the rainbow trout, a harvested fish of this species with an optimum external appearance, that in addition to good skin coloration, also meets other parameters related to caliber and shape of the fish, versus specimens that have a less desirable appearance, the best rated fish (premium class) can reach a market price per kilogram around 15% higher than lower quality fish (grade 1 class). Thus, it is evident that farming stocks with improved external appearance is more profitable for this species.

How can skin color be improved in salmonids?

Improved skin color in salmonids, in particular those species that when harvested present undesirable commercial phenotypes, and therefore require genetic improvement, can be obtained by adopting different strategies, whose selection will depend, basically, on the type of genetic control (monogenetic or polygenetic) of the character of production interest. However, it is necessary to mention that external appearance in salmonids, including skin color, has traditionally been controlled indirectly by using all-female triploid populations (Thorgaard 1992; Hulata 2001), given that because these specimens are sterile, they do not reach sexual maturity and, as a result, do not experience the deterioration of external appearance associated with this physiological process. Nevertheless, by inhibiting sexual maturation, it is not possible to obtain fish with a specific skin color, in accordance with market demands, given that the external appearance is limited to that of specimens that have not reached sexual maturity, with all the variations particular to the population under study, and therefore, selective breeding to improve color in these fish seems appropriate. In the case of characters with monogenetic control, implementation of systematic recovery programs aimed at qualitative traits in aquaculture installations (deliberate recovery of mutants) can be considered (Knibb 2000). Nevertheless, this task may prove difficult, given that this phenotype depends on recessive genes whose frequency is low, or on the combination of rare alleles, that appear very occasionally in the progenies. Methodologies that can be considered in this respect, are those related to increasing inbreeding in the offspring, whether through directed cross-breeding between related individuals or through the artificial production of gynogenetic offspring. It is worth mentioning that once a mutant of this class is selected, its use on a production level will depend on whether it is positively evaluated with respect to various production parameters (growth rate, survival rate, etc.), given that these fish can present adverse pleiotropic effects, with negative outcomes for fitness and commercial performance. This situation, as was previously mentioned, can occur commonly with regard to skin color in some mutants, both in salmonids (Oguri 1974; Dobosz et al. 2000) and in other fish such as the carp (Wolhfarth and Moav 1970). In general, this inconvenience has limited the adoption of this production strategy, although there are some successful examples in farm animals (MacLennan and Phillips 1992; Leroy et al. 1990; Piper et al. 1985; Hanset and Michaux 1985). In the case of continuously varying traits, that depend on the sum of additive genes with either a minor or major effect, the latter accounting in some instances for a considerable amount of phenotype variation, selective breeding should be considered for each case. In effect, individual selection or mass selection would be recommended for characters that are controlled by genes with a minor effect that exhibit medium-high heritabilities. To implement this strategy, certain requirements must be met, such as the need to apply a high differential selection with high effective population sizes, to avoid increased inbreeding, which is not convenient from the production point of view, given that inbreeding depression may occur. In the case of the characters that present medium-low heritabilities, family or intra-family selection should

be adopted. In the former case, it is possible to reduce the phenotypic variance due to the environment, and in the latter, although environmental variations could exist, it is possible to select the individuals with the best breeding values. Other, more efficient selection strategies can also be considered, such as those based on the study of the additive genetic value of each individual, considering the phenotypic record of the breeder fish and its relatives, using Best Linear Unbiased Predictor (BLUP; Neira et al. 2004); or those that incorporate assistance with molecular markers (Marker Assisted Selection) (reviewed by Dekkers and Hospital 2002). Nevertheless, this latter strategy is debatable, given that the use of genetic markers in selection is recommendable when the character has low heritability or when the phenotype is difficult to record. This does not appear to be the case of the phenotypes related to skin color in fish in general and salmonids in particular (Houde 1992; Bakker 1993; Blanc et al. 1994; Brooks and Endler 2001; Kause et al. 2003). Finally, in the skin color characters that can be controlled by genes with major effect, the search for quantitative trait loci (QTLs) that contain these genes, should be considered. To this end, the QTL search strategy using molecular markers that are linked to these chromosome regions, can be implemented, involving a direct search, using association tests for candidate genes in non-structured populations, or through genome scanning in specialized populations, such as back crossing, based on linkage maps. Unfortunately, markers linked to QTLs for color traits in salmonids have still not been reported (Araneda et al. 2008); to date, the only available markers are those linked to genes involved in the skin pigmentation of rainbow trout (Nakamura et al. 2001) and Randomly Amplified Polymorphic DNA (RAPD) markers, associated with the number of red and dark spots in brown trout and with the blue back character in the rainbow trout (Gómez 2005; Lobos 2005; Díaz et al. 2007). If information on molecular markers is available, it can be incorporated into a selection program where it is possible to combine this data with phenotypic information about the trait of interest. This contributes to a more efficient selection process, increasing responses to selection that can vary between 2 and 60% (Neira 2005).

Another important element in the process of improving a skin color trait, is to record and measure this trait during the selection process, given that this parameter is important to increasing the selection response. This procedure is pertinent to skin color traits, which, although they are easy to observe externally, possess a complexity of expression that may make measurement difficult; particularly due to the variations produced as a result of different physiological and environmental factors. To avoid the chromatic changes that can be produced by the effect of type of light used during the recording of a phenotype, standardized artificial light (daylight) should be used, with a high color temperature (7,500 K). Thus, on the one hand, it is possible to control variations in the perception of color that are produced when natural light is used, where quality depends on the time of day and the season of year when the recording is undertaken; and on the other, it is possible to control the range of colors the object displays, since a high color temperature guaranties full chromatic expression. This technical aspect is important, because the selection process is not always undertaken at the same time of day (ideally at mid-day, when color temperature is greater), or at the same time of the year. Similarly, selection of a skin color trait should not be undertaken when physiological processes that can alter color expression are occurring, such as sexual maturity (Aknes et al. 1986; Garduño-Lugo et al. 2004), smolting (Johnston and Eales 1970) and stress (Höglund et al. 2000); and also when other environmental factors, that have a similar effect are present, for example, changes in density (Metusalach et al. 1997), type of food (No and Storebakken 1992), background color (Green et al. 1991; Susuki et al. 1997) and changes in photoperiod (Gines et al. 2004). The recording and measurement of a character subject to selection can be undertaken in two ways: (1) by direct visual analysis of fish or (2) by computer analysis of photographs obtained with a digital camera. The first method requires the prior definition of the phenotypic categories of productive interest, to classify the fish to be used in the successive selection generations. This method has the advantage of being low cost and easy to implement, as it does not require much equipment and has been used successfully in some selection programs (Kause et al. 2003). The second method requires taking digital photographs of each of the fish selected and carrying out computer analysis to generate different phenotypic categories. This

requires specialized software (SigmaScan Pro, ImageJ, etc.) to undertake a spectral analysis of the images for quantification of different aspects of color pattern present in fish (intensity, color, saturation, etc.). Based on this type of analysis, the color of different body zones can be studied, for example the color of the back (Fig. 3a), where its value as a production trait can be determined. The image analysis method is more accurate than the visual method, because it reduces the bias of the observer, although it demands more time and resources, such as the use of digital cameras and specialized human and computer resources. Methods to evaluate salmonid color parameters base on image analysis have been described for fillet color quality in Atlantic salmon (Misimi et al. 2007). The use of these methods for skin color traits in future selection programs, as opposed to the visual method, should be based on a favorable cost benefit rate.

Conclusions

Skin pigmentation in fish depends on environmental and genetic factors. Environmental factors can produce a rapid change in the skin color, especially in the color intensity, that can be controlled physiologically, where hormonal and neural signals participate, regulating the dispersion or aggregation of pigments in the chromatophores; or morphologically, where the number of melanophores in the skin increases or decreases. This type of change in pigmentation enables fish to adapt to their environment, and is known as Background Color Adaptation. Genetic factors are responsible for the color or skin pigmentation pattern of a fish at a given development stage; control is either monogentic, when few loci participate in the regulation of qualitative changes in color, or polygenetic, when many genes with an additive effect participate, or when major effect genes exist, both regulating color change in a continuous manner. The genetic factors are expressed by acting upon the different pigmentary cells present in the skin of these vertebrates, regulating specification, proliferation, survival, differentiation and the production of the coloration pattern. In the model medaka and zebrafish, numerous genes have been discovered that participate in these processes, some of which have already been characterized at a molecular level. There are significant differences in the skin coloration pattern of salmonids, both at the interspecific and intraspecific level, with still only very general information available to account for this variability. Similarly, the cell basis of the underlying skin pigmentation pattern observed in these fish, is still largely unknown. In past years, some mutants for skin color have been discovered, especially in rainbow trout, that can be classified as those produced by depigmentation of the melanophores (albino, golden or yellow phenotypes), or those resulting from a probable change in the structure of the pigments present in the chromatophores (blue phenotypes). Evidence indicates that these mutations are determined by simple Mendelian control, with, at the most, three loci participating, that would appear to be located in different linkage groups. Molecular information is available on the tyrosine gene in salmonids and around a dozen more genes that participate in the different pigment synthesis pathways. Skin color in salmonids, as in other farmed fish, is a commercially important trait because it affects consumer acceptance. Nevertheless, skin color can experience wide intrapopulational variation during culture of these species, resulting in a considerable percentage of fish with dark skin and large spots, traits that decrease their commercial value, especially in the case of the rainbow trout. Studies aimed at determining the quantitative genetic parameters for this trait report a significant additive genetic variance, with medium-high heritability values, which would make it possible to obtain rapid selection responses in a genetic improvement program. Possible strategies aimed at genetically improving skin color in salmonids depend on the type of trait control (monogenetic or polygenetic). Included in the first case (monogenetic control) are strategies aimed at the systematic recovery of skin color mutants in fish culture installations, applying methodologies that increase inbreeding in the offspring; the second case (polygenetic control) involves the application of either mass or family selection, including, in some cases, the use of genetic markers or the search for QTLs.

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References

Ade R (1989) Trout and salmon handbook. Facts on file Inc., New York, 122 pp

Aknes A, Gjerde B, Roald SO (1986) Biological, chemical and organoleptic changes during maturation of farmed Atlantic salmon, *Salmo salar*. Aquaculture 53:7–20

Allendorf F, Thorgaard G (1984) Tetraploidy and the evolution of salmonid fishes. In: Turner B (ed) Evolutionary genetics of fishes. Plenum Press, New York, pp 1–53

Araneda C, Neira R, Lam N, Iturra P (2008) Salmonids. In: Kocher TD, Kole C (eds) Genome mapping and genomics in animals, volume 2. Genome mapping and genomics in fishes and aquatic animal. Springer-Verlag, Berlin, pp 1–43

Bagnara JT, Taylor JD, Hadley ME (1968) The dermal chromatophore unit. J Cell Biol 38:67–79

Bagnara JT, Fernandez PJ, Fujii R (2007) On the blue coloration of vertebrates. Pigment Cell Res 20:14–26

Bakker TCM (1993) Positive genetic correlation between female preference and preferred male ornament in sticklebacks. Nature 363:255–257

Ballard WW (1973) Normal embryonic stages for salmonid fishes, based on *Salmo gairdneri* Richardson and *Salvelinus fontinalis* (Mitchill). J Exp Zool 184:7–26

Barsh GS (1996) The genetics of pigmentation: from fancy genes to complex traits. Trends Genet 12:299–305

Bennett DC, Lamoreux ML (2003) The color loci of mice- a genetic century. Pigment Cell Res 16:333–344

Blanc JM, Poisson H, Vibert R (1982) Variabilité génétique de la ponctuation noire sur la truitelle fario (*Salmo trutta* L.). Ann Genet Sel Anim 14:225–236

Blanc JM, Chevassus B, Krieg F (1994) Inheritance of the number of red spots on the skin of the brown trout. Aquat Living Resour 7:133–136

Blanc JM, Higuette P, Quillet E (2006) A blue variant in the rainbow trout, *Oncorhynchus mykiss* Walbaum. J Hered 97: 89–93

Boonanuntanasarn S, Yoshizaki G, Iwai K et al (2004) Molecular cloning, gene expression in albino mutants and gene knockdown studies of tyrosinase mRNA in rainbow trout. Pigment Cell Res 17:413–421

Braasch I, Salzburger W, Meyer W (2006) Asymetric evolution in two fish specifically duplicated receptor tyrosinase kinase paralogous involved in teleost coloration. Mol Biol Evol 23:1192–1202

Braasch I, Schartl M, Volff J-N (2007) Evolution of pigment synthesis pathways by gene and genome duplication in fish. BMC Evol Biol 7:74

Bridges WR, von Limbach B (1972) Inheritance of albinism in rainbow trout. J Hered 63:152–153

Brooks R, Endler JA (2001) Direct and indirect sexual selection and quantitative genetics of male traits in guppies (*Poecilia reticulata*). Evolution Int J org Evolution 55:1002–1015

Camp E, Lardelli M (2001) Tyrosinase gene expression in zebrafish embryos. Dev Genes Evol 211:150–153

Cerda-Reverter JM, Haitina T, Schoith HB et al (2005) Gene structure of the Goldfish Agouti- Signaling Protein a putative role in the dorsal- ventral pigment pattern of fish. Endocrinology 146:1597–1610

Chevassus B, Krieg F, Guyomard R et al (1992) The genetics of the brown trout: twenty years of French research. Buvisindi Icel Agr Sci 6:109–124

Clark FH (1970) Pleiotropic effects of the gene for golden color in rainbow trout. J Hered 61:8–10

Dekkers C, Hospital F (2002) The use of molecular genetics in the improvement of agricultural population. Nat Rev Genet 3:22–32

Díaz NF, Gómez G, Lobos M et al (2007) RAPD polymorphism associated to skin pigmentation in rainbow (*Oncorhynchus mykiss*) and brown (*Salmo trutta*) trouts. Aquaculture 272S1:S251

Dobosz S, Gorycsko K, Kohlmann K et al (1999) The yellow color inheritance in rainbow trout. J Hered 90:312–315

Dobosz S, Kohlmann K, Goryczko K et al (2000) Growth and vitality in yellow forms of rainbow trout. J Appl Ichthyol 16:117–120

Erickson CA, Reedy MV (1998) Neural crest development: the interplay between morphogenesis and cell differentiation. Curr Top Dev Biol 40:177–209

Fujii R (1969) Chromatophores and pigments. In: Hoar WS, Randall DJ (eds) Fish physiology, vol III. Academic Press, New York-London, pp 307–354

Fujii R (1993) Cytophysiology of fish chromatophores. Int Rev Cytol 143:191–255

Fujii R (2000) The regulation of motile activity in fish chromatophores. Pigment Cell Res 13:300–319

Fukamachi S, Shimada A, Shima A (2001) Mutations in the encoding B a novel transporter protein, reduce melanin content in medaka. Nat Genet 28:381–385

Galbreath PF, Plemmons BP (2000) Mottled color in a rainbow trout is associated with mosaicism for albinism. J Hered 91:405–407

Garduño-Lugo M, Muñoz-Cordova G, Olvera-Novoa MA (2004) Mass selection for red colour in *Oreochromis niloticus* (Linnaeus 1758). Aquac Res 5:340–344

Gines R, Afonso JM, Arguello A et al (2004) The effects on long-day photoperiod on growth, body composition and skin colour in inmature gilthead sea bream (*Sparus aurata* L.). Aquac Res 35:1207–1212

Gjedrem T (2000) Genetic improvement of cold-water fish species. Aquac Res 31:25–33

Goda M, Fujii R (1998) The blue coloration of the common surgeonfish, *Paracanthurus hepatus*-II. Color revelation and color changes. Zool Sci 15:323–333

Gómez G (2005) Identificación de polimorfismos RAPD asociados con la pigmentación de la piel en trucha café (*Salmo trutta*). Tesis de Ing, Agrónomo, Facultad de Ciencias Agronómicas, Universidad de Chile, 52 pp

Green BW (2006) Tilapia fingerling production systems. In: Lim C, Webster C (eds) Tilapia: biology culture, and nutrition. Food Products Press, Binghamton, pp 181–210

Green JA, Baker BI, Kawauchi N (1991) The effect of rearing rainbow trout on black or white backgrounds on their secretion of melanin-concentrating hormones and their sensitivity to stress. J Endocrinol 128:267–274

Haffter P, Odenthal J, Mullins MC et al (1996) Mutations affecting pigmentation and shape of the adult zebrafish. Dev Genes Evol 206:260–276

Hanset R, Michaux C (1985) On the genetic determinism of muscular hipertrophy in Belgian white and blue cattle breed. I. Genet Sel Evol 17:359–368

Hawkes JW (1974) The structure of fish Skin II. The chromatophore unit. Cell Tissue Res 149:159–172

Hazzard AS (1943) Record of an albino lake trout *Christivomer namaycush* (Walbaum). Copeia 4:253

Höglund E, Balm PH, Winberg S (2000) Skin darkening, a potential social signal in subordinate arctic charr (*Salvelinus alpinus*): the regulatory role of brain monoamines and pro-opiomelanocortin-derived peptides. J Exp Biol 203: 1711–1721

Houde AE (1992) Sex-linked heritability of a sexually selected character in a natural population of *Poecilia reticulata* (Pisces: Poeciliidae) (guppies). Heredity 69:229–235

Hudon J (1994) Biotechnological applications of research on animal pigmentation. Biotech Adv 2:49–69

Hulata G (2001) Genetic manipulations in aquaculture: a review of stock improvement by classical and modern technologies. Genetica 111:155–173

Islam A, Nose Y, Yasuda F (1973) Number and distribution pattern of the black spot on body surface of rainbow trout. Bull Jpn Soc Sci Fish 39:727–739

Johnson SL, Africa D, Walter C et al (1995) Genetic control of adult pigment stripe development in zebrafish. Dev Biol 167:27–33

Johnston CE, Eales G (1970) Influence of body size on silvering of Atlantic salmon (*Salmo salar*) during parr-smolt transformation. J Fish Res Board Can 27:1901–1909

Kause A, Ritola O, Paananen T et al (2003) Big and beautiful? Quantitative genetic parameters for appearance of large rainbow trout. J Fish Biol 62:610–622

Kause A, Ritola O, Paananen T (2004) Breeding for improved appearance of large rainbow trout in two production environments. Aqualcult Res 35:924–930

Kawakami K, Amsterdam A, Shimoda N et al (2000) Proviral insertions in the zebrafish *hagoromo* gene, encoding an F-box/WD40-repeat protein, cause stripe pattern anomalies. Curr Biol 10:463–466

Kelsh RN (2004) Genetics and evolution of pigment patterns in fish. Pigment Cell Res 17:326–336

Kelsh RN, Brand M, Jiang Y-J et al (1996) Zebrafish pigmentation mutations and the process of neural crest development. Development 123:369–389

Kelsh RN, Schmid B, Eisen JS (2000) Genetic analysis of melanophore development in zebrafish embryos. Dev Biol 225:277–293

Kelsh RN, Ch Inoue, Momoi A et al (2004) The Tomita collection of medaka pigmentation mutants as a resource for understanding neural crest cell development. Mech Dev 121:841–859

Kincaid HL (1975) Iridiscent metallic blue color variant in rainbow trout. J Hered 66:100–101

Knibb W (2000) Genetic improvement of marine fish–which method for industry? Aquac Res 31:11–23

Krieg F, Quillet E, Chevassus B (1992) Brown trout, *Salmo trutta* L.: a new species for intensive marine aquaculture. Aquacult Fish Manage 23:557–566

Leonard L, Madden E (1963) Possible albino adult Chinook salmon observed. Res Briefs Ore Fish Comm 9:67

Leroy P, Naveau J, Elsen JM et al (1990) Evidence for a new major gene influencing meat quality in pigs. Genet Res 55:33–40

Lister JA, Robertson CP, Lepage T (1999) Nacre encodes a zebrafish microphthalmia-related protein that regulates neural-crest-derived pigment cell fate. Development 126: 3757–3767

Lobos M (2005) Identificación de polimorfismos RAPD asociados al fenotipo dorso azul en trucha arcoiris (*Oncorhynchus mykiss*). Tesis de Ing, Agrónomo, Facultad de Ciencias Agronómicas, Universidad de Chile, 37 pp

Logan DW, Bryson-Richardson RJ, Pagán KE et al (2003) The structure and evolution of the melanocontin and MCH receptors in fish and mammals. Genomics 81:184–191

MacLennan DH, Phillips MS (1992) Malignant hiperthermia. Science 256:789–794

Maderspacher F, Nusslein-Volhard C (2003) Formation of the adult pigment pattern in zebrafish requires leopard and obelix dependent cell interactions. Development 130: 3447–3457

Metusalach B, Brown JA, Shahidi F (1997) Effects of stocking density on colour characteristics and deposition of carotenoids in cultured Arctic charr (*Salvelinus alpinus*). Food Chem 59:107–114

Misimi E, Mathiassen JR, Erikson U (2007) Computer vision-based sorting of Atlantic salmon (*Salmo salar*) fillets according to their color level. J Food Sci 72:S030–S035

Nakamura K, Ozaki A, Akutsu T (2001) Genetic mapping of the dominant albino locus in rainbow trout (*Oncorhynchus mykiss*). Mol Genet Genomics 265:687–693

Neira R (2005) Uso de marcadores en selección asistida. In: Díaz N (ed) El uso de marcadores genético moleculares en el mejoramiento genético de peces. Serie de publicaciones para la acuicultura, número 4, Grupo de Ciencias de la Acuicultura, Universidad de Chile, Santiago de Chile, pp 58–63

Neira R, Diaz NF, Gall GAE et al (2004) Genetic improvement in Coho salmon (*Oncorhynchus kisutch*). I. Selection response and inbreeding depression on harvest weight. Aquaculture 257:9–17

No HK, Storebakken T (1992) Pigmentation of rainbow trout with astaxanthin and canthaxantin in freshwater and saltwater. Aquaculture 1001:123–134

Odenthal J, Rossnagel K, Haffter P et al (1996) Mutations affecting xantophore pigmentation in the zebrafish, *Danio rerio*. Development 123:3191–3398

Oguri M (1974) On the pituitary remnant in "cobalt" variant of rainbow trout. Bull Jap Soc Sci Fish 40:869–875

Parichy DM (2003) Pigment patterns: fish in stripes and spots. Curr Biol 13:947–950

Parichy DM, Turner JM (2003) Temporal and cellular requirements for Fms signaling during zebrafish adult pigment pattern development. Development 130:817–833

Parichy D, Rawis JF, Pratt SJ et al (1999) Zebrafish *sparse* corresponds to an orthologue of *c-kit* and is required for the morphogenesis of a subpopulation of melanocytes, but is not essential for hematopoiesis or primordial germ cell development. Development 125:3425–3436

Parichy DW, Melgren EM, Rawls JF et al (2000a) Mutational analysis of endothelin receptor *bl* (rose) during neuronal crest and pigmentation pattern development in the zebrafish, *Danio rerio*. Dev Biol 227:294–306

Parichy DM, Ransom DG, Paw B et al (2000b) An orthologue of the *kit*-related gene *fms* is required for development of neural crest-derived xantophores and a subpopulation of adult melanocytes in the zebrafish, *Danio rerio*. Development 127:3031–3044

Parichy DM, Turner JM, Parker NB (2003) Essential role for *puma* in development of post-embryonic neural crest-derived cell lineages in zebrafish. Dev Biol 256:221–241

Pelletier I, Bally-Cuif L, Ziegler I (2001) Cloning and developmental expression of zebrafish GTP cyclohydrolase I. Mech Dev 109:99–103

Pettis CR (1904) Albino brook trout. Science 19:867–868

Piper LR, Bindon BM, Davis GH (1985) The single gene inheritance of the high liter size of the Booroola Merino. In: Land RB, Robinson DW (eds) Genetics of reproduction in sheep. Butterworths, London, pp 115–125

Quigley IK, Parichy DM (2002) Pigment pattern formation in zebrafish: a model for developmental genetics and the evolution of form. Micros Res Techniq 58:442–455

Rawls JF, Johnson SL (2001) Requirements for *kit* receptor tyrosine kinase during regeneration of zebrafish fin melanocytes. Development 128:1943–1949

Rexroad CE, Rodriguez M, Coulibaly I et al (2005) Comparative mapping of expressed sequence tags containing microsatellites in rainbow trout (*Oncorhynchus mykiss*). BMC Genomics 6:54. doi:10.1186/1471-2164-6-54

Steine G, Alfnes F, Rora MB (2005) The effect of color on consumer WTP for farmed salmon. Marine Resource Economics 20:211–219

Sugie A, Terai Y, Ota R et al (2004) The evolution of genes for pigmentation in African cichlid fishes. Gene 343:337–346

Sugimoto M (2002) Morphological color changes in fish: regulation of pigment cell density and morphology. Microsc Res Techniq 58:496–503

Susuki M, Bennett P, Levy A et al (1997) Expression of MCH and POMC genes in rainbow trout (*Oncorhynchus mykiss*) during ontogeny and in response to early physiological challenges. Gen Comp Endocrinol 107:341–350

Taub S, Palacios S (2003) La acuicultura en Chile. Technopress, Santiago de Chile, 325 pp

Tave D (1986) Genetics for hatchery managers. AVI Publishing Company Inc., Westport 229

Thorgaard GH (1992) Application of genetic technologies to rainbow trout. Aquaculture 100:85–97

Tomita H (1992a) The lists of the mutants and strains of the medaka, common gambusia, silver crucian carp, goldfish and golden venus fish maintained in the Laboratory of Freshwater Fish Stocks, Nagoya University. Fish Biol J Medaka 4:45–47

Tomita H (1992b) Studies on the mutant of medaka, *lf*. Fish Biol J Medaka 4:37–39

Vrieling H, Duhl DM, Millar SE et al (1994) Differences in dorsal and ventral pigmentation result from regional expression of the mouse agouti gene. Proc Natl Acad Sci USA 1994(91):5667–5671

Wohlfarth GW, Hulata G (1989) Selective breeding of cultivated fish. In: Shilo M, Sarig S (eds) Fish culture in warm water systems: problems and trends. CRC Pres, Boca Ratón, pp 21–63

Wolhfarth GW, Moav R (1970) The effects of variation in spawning time on subsequent relative growth rate and viability in carp. Bamidgeh 22:42–47

Wright JE (1972) The palomino rainbow trout. Penn Angler Mag 41:8–9

Yamaguchi K, Miki W (1981) Comparison of pigments in the integument of cobalt, albino, and normal rainbow trout, *Salmo gairdnerii irideus*. Comp Biochem Physiol 68B:517–520

Yamaki M, Yamaguchi S, Arai K (2006) Mottled color of haploid-diploid and diploid-triploid mosaic amago salmo *Oncorhynchus masou ishikawae*. Fisheries Sci 72: 157–165

Yamamoto A, Nagura J, Omori Y et al (1999) Albinism in the cultured Amago salmon *Oncorhynchus masou ishikawai*. Abstr Suisanzoshoku 47:43–47

Yamasaki F (1974) On the so-called "cobalt" variant of rainbow trout. Bull Jpn Soc Sci Fish 40:17–25