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## **Fish skin pigmentation in aquaculture: the influence of rearing conditions and its neuroendocrine regulation**

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1 **Abstract**

2 Skin pigmentation pattern is a species-specific characteristic that depends on the  
3 number and the spatial combination of several types of chromatophores. This feature  
4 can change during life, for example in the metamorphosis or reproductive cycle, or as a  
5 response to biotic and/or abiotic environmental cues (nutrition, UV incidence,  
6 surrounding luminosity, and social interactions). Fish skin pigmentation is one of the  
7 most important quality criteria dictating the market value of both aquaculture and  
8 ornamental species because it serves as an external signal to infer its welfare and the  
9 culture conditions used. For that reason, several studies have been conducted aiming to  
10 understand the mechanisms underlying fish pigmentation as well as the influence  
11 exerted by rearing conditions. In this context, the present review focuses on the current  
12 knowledge on endocrine regulation of fish pigmentation as well as on the aquaculture  
13 conditions affecting skin coloration. Available information on Iberoamerican fish  
14 species cultured is presented.

15

16 **Keywords:** Fish pigmentation; Chromatophore; Hormones; Aquaculture

17

## 18 **1 Introduction**

19 Aquaculture contributes significantly to global seafood supply, accounting for 46% of  
20 the total production in 2018, and has had the fastest growth rate among major food  
21 production sectors for several decades (FAO, 2020a). Today, aquaculture plays an  
22 important role in income generation and food and nutrition security, particularly in  
23 developing countries (Belton et al., 2018), and promotes local biodiversity and the  
24 preservation of cultural traditions. Fish skin pigmentation is one of the most important  
25 quality criteria dictating the market value of fish for human consumption and  
26 ornamental use (Harpaz and Padowicz, 2007). For instance, colors in food are linked to  
27 anticipated quality and are cues that allow consumers to make judgements about  
28 desirability (Bjerkeng, 2008). However, aquaculture conditions can negatively affect the  
29 natural skin coloration of fish (Lim et al., 2018), thus hampering successful  
30 commercialization. Indeed, skin pigmentation in fish is regulated by both external  
31 (biotic and abiotic) and internal (genetic, cellular, nervous, and hormonal) factors  
32 (Pittman et al., 2013). For that reason, several studies have been conducted aiming to  
33 understand the mechanisms underlying fish pigmentation as well as the influence  
34 exerted by rearing conditions.

35 Aquaculture in Iberoamerica (IA), the Spanish- and Portuguese-speaking nations of the  
36 Americas and Europe, represents 3.05% of the world's global production with nearly  
37 3.5 million tons produced in 2018 (FAO, 2020b), and several studies have addressed  
38 skin pigmentation in fish species cultivated in these countries. Reared flatfish species  
39 (Pleuronectiformes), which are known for their asymmetric pigmentation and their  
40 ability to adapt to background color changes by adjusting their ocular-side pigmentation

41 (Inui and Miwa, 2012), frequently present pigmentation anomalies, such as albinism  
42 and ambicoloration. Research on pigmentation has been conducted on flatfish species  
43 that either are cultivated or have been identified as candidate species for aquaculture  
44 diversification in IA, such as turbot, *Scophthalmus maximus* (also known as *Psetta*  
45 *maxima*; e.g., Reitan et al., 1994; Estévez and Kanazawa, 1995; Estévez et al., 1999),  
46 Senegalese sole, *Solea senegalensis* (e.g., Villalta et al., 2005; Darias et al., 2013a;  
47 Boglino et al., 2014), common sole, *Solea solea* (Lund et al., 2008, 2010), California  
48 halibut, *Paralichthys californicus* (Vizcaíno-Ochoa et al., 2010), *Paralichthys*  
49 *adpersus* (Orihuela et al., 2018), *Paralichthys orbignyanus* (López et al., 2009; Vieira  
50 Rodrigues et al., 2012) or *Paralichthys woolmani* (Benetti, 1997; Bohórquez-Cruz et al.,  
51 2018). Further studies have dealt with other fish species cultivated in IA, such as  
52 salmonids (Colihueque, 2010), red porgy, *Pagrus pagrus* (e.g., Kalinowski et al., 2007;  
53 Tejera et al., 2010), gilthead sea bream, *Sparus aurata* (e.g., Gouveia et al., 2002;  
54 Ribeiro et al., 2017), Nile tilapia, *Oreochromis niloticus* (Ponce-Palafox et al., 2004;  
55 Valente et al., 2016) or ornamental species like *Hyphessobrycon eques* (Berchielli-  
56 Morais et al., 2016), which require dietary carotenoid supplementation in order to  
57 maintain their natural skin coloration (Bjerkeng, 2008). Besides, the influence of rearing  
58 conditions such as tank color, light intensity or social interactions on skin pigmentation  
59 has been studied in other IA fish species, such as *Lophiosilurus alexandri* (Costa et al.,  
60 2017, Santos et al., 2019), *Paralichthys woolmani* (Benetti, 1997; Venizelos and  
61 Benetti, 1999; Han et al., 2005), Neon tetra, *Paracheirodo ninnesi* (Kasai and Oshima,  
62 2006) or *Cichlasoma dimerus* (Alonso et al., 2011; Cánepa et al., 2006, 2012, Delgadin  
63 et al., 2020).

64 In this context, the present review focuses on the current knowledge on endocrine  
65 regulation of fish pigmentation as well as on the aquaculture conditions affecting skin  
66 coloration. Available information on species cultured in IA is presented.

67

## 68 **2 An overview on fish skin pigmentation**

69 Skin pigmentation pattern is a species-specific characteristic that depends on the  
70 number and spatial combination of several types of chromatophores included in the  
71 epidermis and in the dermis (Aspengren et al., 2012; Darias et al., 2013a). Compared to  
72 other vertebrates, it has been suggested that this great variety of pigmentation patterns  
73 in fish is due to the fish-specific genome duplication which gave rise to about 30% more  
74 pigmentation-related genes (Braasch et al. 2008; reviewed in Pittman et al., 2013).  
75 Furthermore, the skin pigmentation pattern can change during life time, for example,  
76 during metamorphosis or the reproductive cycle, or as a response to biotic and/or abiotic  
77 environmental cues (nutrition, UV incidence, surrounding luminosity, and social  
78 interactions) (Price et al., 2008; Leclercq et al., 2010; Darias et al., 2013a, b; Parichy  
79 and Spiewak, 2015). Studies performed in flatfish species have shown that there is a  
80 sensitive period during pre- and pro-metamorphosis, named pigmentation window, in  
81 which different external factors can disrupt the normal development of pigmentation  
82 (Darias et al., 2013a, b; Pittman et al., 2013).

83 In vertebrates, chromatophores cells derive from one of the most fascinating cells of  
84 vertebrate development biology: the neural crest cells (NCC). These cells arise from a  
85 region between the border of the neural plate and the non-neural ectoderm and, after  
86 undergoing an epithelial-to-mesenchymal transition, they migrate throughout the  
87 embryo, colonizing different tissues and organs where they settle and differentiate  
88 (Bronner and LeDouarin, 2012; Theveneau and Mayor, 2012). It has been proposed that

89 all chromatophores are generated from a common chromatoblast (Bagnara et al., 1979)  
90 through progressive fate-restriction processes (Le Douarin and Dupin, 2003; Dupin et  
91 al., 2007; Kimura et al., 2014). Different chromatophores have been described in fish,  
92 classified into light-absorbing chromatophores (melanophores, erythrophores,  
93 xanthophores, and cyanophores) and light-reflecting chromatophores (leucophores and  
94 iridophores) (Fujii, 2000; Sugimoto, 2002). While melanophores, iridophores, and  
95 xanthophores are widely distributed in teleosts (Schartl et al., 2016), leucophores are  
96 less abundant (Menter et al., 1979; Iga and Matsuno, 1992; Nagao et al., 2018). In  
97 addition, two cell types of melanophores and xanthophores, differing in size and  
98 sequentially appearing during development, have been described in Japanese flounder,  
99 *Paralichthys olivaceus*, and Senegalese sole (Seikai et al., 1987; Nakamura et al., 2010;  
100 Darias et al., 2013a). These two different cell types have been identified as larval and  
101 adult melanophores and xanthophores in Japanese flounder (Seikai et al., 1987;  
102 Nakamura et al., 2010), whereas in the case of Senegalese sole melanophores, the two  
103 cell types rather correspond to different morphological stages of newly differentiated  
104 and melanized melanophores at post-metamorphosis (Darias et al., 2013a).

105 Melanophores are the most common and studied chromatophores and are responsible  
106 for the dorsal pigmentation in vertebrates (Aspengren et al., 2012). Melanophores are  
107 dendritic shaped cells that extend their projections, containing the pigmented organelles  
108 (melanosomes), almost parallel to the plane of the skin (Fujii, 2000; Nüsslein-Volhard  
109 and Singh, 2017). In teleosts' skin, melanophores are mostly found in the dermis,  
110 although they can also be observed in the epidermis (Fujii, 2000).

111

112 **3 How does skin color change in fish?**

### 113 **3.1 Cellular mechanisms**

114 Skin color can vary through two different mechanisms. On the one hand, the  
115 physiological color changes, which are rapid and transient, are produced by the motility  
116 of pigment vesicles (chromatosomes) or by the movement of reflective structures within  
117 their cells. On the other hand, the morphological color changes, which occur within  
118 days and/or weeks, involve variations in skin pigment concentration or the density and  
119 distribution of chromatophores in the integument (Leclercq et al., 2010).

120 The translocation of chromatosomes, which are characteristic of physiological color  
121 changes, is coordinated by the microtubule and actin filament architecture of the  
122 cytoskeleton and the associated motor proteins. When light-absorbing chromatophores  
123 receive an input (such as hormones, neurotransmitters or environmental cues) that  
124 produces the aggregation or dispersion of chromatosomes, the specific molecular motor  
125 hauls pigment granules back toward the nucleus or to the cell periphery (Ligon and  
126 McCartney, 2016). In general, decreases in cAMP levels and/or increases in  $\text{Ca}^{2+}$  levels  
127 within chromatophores trigger aggregation responses, while the opposite changes in  
128 cAMP or  $\text{Ca}^{2+}$  levels induce dispersion responses (reviewed in Fujii, 2000). Regarding  
129 iridophores, which contain thin reflecting platelets in their cytoplasm, under certain  
130 inputs they simultaneously change the distance between adjoining platelets, leading to a  
131 shift in the spectral reflectance of the skin (Kasukawa et al., 1986).

132 Chromatophores density variation implies both differentiation and apoptosis processes.  
133 It is believed that the number of melanophores increases through precursor cell  
134 differentiation rather than the division of already differentiated melanophores  
135 (Sugimoto et al., 2002). There is evidence that these precursors are neural crest-derived  
136 stem cells that have been set aside in distinct niches, such as the ganglia of the

137 peripheral nervous system, the base of the fins, or in deep layers of the dermis, which  
138 migrate and differentiate into adult-type pigment cells under specific stimuli (reviewed  
139 in Sugimoto et al., 2002; Yamada et al., 2010; Darias et al., 2013a; Frohnhöfer et al.,  
140 2013). This differentiation implies the molecular action of the chromatophore-  
141 differentiating genes that are also implicated in the regulation of skin pigment  
142 concentration. In particular, microphthalmia-associated transcription factor (*mitf*) is  
143 considered the master regulator of melanophore development and controls expression of  
144 genes required for melanophore development, including dopachrome tautomerase (*dct*),  
145 tyrosinase (*tyr*), tyrosinase related peptides (*trp 1* and *2*) and the receptor tyrosine kinase  
146 (*c-kit*) (Steingrímsson et al., 2004, Darias et al., 2013a, Nagao et al, 2018). Furthermore,  
147 the sodium/potassium/calcium exchanger 5 (*slc24a5*) is crucial for proper melanin  
148 synthesis. The paired box protein 3 (*pax3*) can promote or inhibit melanogenesis  
149 through transcriptional regulation of *mitf* and *cKit*, the latter being necessary for  
150 melanophore differentiation and responsible for the activation of *tyr*. Besides, *pax3* can  
151 also modulate the expression of *trp1* and *trp2* (see model in Darias et al., 2013a).  
152 Although the molecular mechanisms of fish melanophore differentiation have been well  
153 characterized, those of the other chromatophores have remained largely unknown  
154 (Otsuki et al., 2020). It was demonstrated that Sry-box transcription factor 5 (Sox5) acts  
155 antagonistically against Sox10 in the specification of zebrafish chromatophores and in  
156 melanophore and iridophore lineages in medaka. However, in this last species,  
157 xanthophores and leucophores developed from a shared progenitor Pax7a positive. This  
158 progenitor differentiates in xanthophore or leucophore depending on Sox5/Sox10. While  
159 Sox5/10 promotes xanthophore specification, it represses leucophore formation (Kimura  
160 et al., 2014; Nagao et al., 2018).

161 The decrease in chromatophore number occurs by apoptosis stimulated by specific  
162 factors (Sugimoto et al., 2002; Sköld et al., 2016). Interestingly, xanthophores can  
163 eliminate the surrounding melanophores, and vice versa, in zebrafish (Nakamasu et al.,  
164 2009), and similarly, xanthophores in the skin of Senegalese sole pseudo-albinos  
165 seemed to be responsible for the degeneration of melanophores (Darias et al., 2013b).  
166 Besides, variation in melanophore morphology, which mainly implies variation in  
167 dendritic process elongation, has been described as another type of morphological color  
168 change (reviewed in Sugimoto et al., 2002).

169 Since morphological color changes are preceded by physiological color changes, similar  
170 control mechanisms have been proposed to function both in the motile responses and in  
171 the chromatophore densities (reviewed in Sugimoto, 2002).

172

### 173 **3.2 Hormone regulators**

174 Unlike other vertebrate taxa, it is generally accepted that teleost fish present a dual-  
175 hormonal mechanism for skin color regulation (reviewed in Bertolesi et al., 2019). Two  
176 hormones with opposite effects, skin lightening and darkening, have been proposed as  
177 the main morphological and physiological color change regulators: the melanin-  
178 concentrating hormone (Mch) and the melanophore-stimulating hormone (Msh),  
179 derived from precursor Proopiomelanocortin. However, skin color regulation is more  
180 complex, and other regulatory factors have been identified in studies performed on the  
181 regulation over other chromatophores cells. Table 1 summarizes this complex scenario  
182 with the old and new actors involved in skin color regulation in fish. In addition, figure  
183 1 shows the endocrine and nervous effect over the different chromatophores. In this  
184 figure, the lack of studies on the regulation of some pigmentary cells is reflected. More

185 studies will help to improve the understanding of pigment disorders in aquaculture  
186 species.

187

### 188 **3.3 Nervous control**

189 Rapid chromatosome aggregation is mainly controlled by the sympathetic  
190 postganglionic system. Chromatic information is captured by the eyes, processed in the  
191 optic tectum and partly at the level of the motoneurons in the medulla, and sent to  
192 chromatophores via direct nervous connections (Grove, 1994; reviewed in Fujii, 2000).  
193 Since Fujii and Oshima (1994), Fujii (2000) and Sköld et al. (2016) have reviewed this  
194 issue in depth, we will only point out some aspects of this regulation that are relevant  
195 for the following sections. It has been proposed that there is a constant rate of firing of  
196 noradrenaline (NA) from nerve terminals that increases or decreases depending on  
197 different stimuli (Fujii and Oshima, 1994). Other studies have demonstrated that ATP is  
198 released as a co-transmitter together with NA (true-transmitter) and that, in the synaptic  
199 cleft, it is dephosphorylated to adenosine, which survives longer and reverses NA  
200 action, causing re-dispersion of pigment after the cessation of the stimulus (Fujii and  
201 Oshima, 1994).

202 Noradrenaline interacts with  $\alpha$ - and  $\beta$ -adrenoreceptors, with  $\alpha_2$ -adrenoreceptor subtype  
203 being more effective than  $\alpha_1$ -adrenoreceptor in producing pigment aggregation, while  
204  $\beta_2$ -adrenoreceptor subtype induces pigment dispersion. Concerning NA effects over  
205 chromatosomes, its release induces aggregation of these vesicles in melanophores,  
206 xanthophores and erythrophores, but disperses the light-scattering organelles in  
207 leucophores, and also produces a change in the arrangement of reflecting platelets in  
208 iridophores (Fujii and Oshima, 1994; reviewed in Fujii 2000; Sköld et al., 2016).

209 Besides this action, Sugimoto (2000) observed that NA induces melanophore apoptosis  
210 in medaka skin culture, and that denervation decreases melanophore density in this  
211 species (Sugimoto, 1993) (Figure 1).

212

#### 213 **4 Influence of rearing conditions on skin pigmentation**

214 Rearing conditions, such as environment and feeding, which are very different from  
215 those of natural habitats, influence fish physiology and behavior (Eslamloo et al., 2015).  
216 Especially in intensive farming, fish are exposed to grading, handling, transportation,  
217 stocking densities, diseases, vaccination, food withdrawal or aggression, among other,  
218 that affect welfare and can lead to acute or chronic stress (Sneddon et al., 2016). In this  
219 sense, besides nutrition—which is a source of pigments for several species and plays an  
220 essential role in morphogenesis during early development (Bjerkeng, 2008; Rønnestad  
221 et al., 2013)—, stress can trigger skin pigmentation changes. During an acute stress  
222 response, higher amounts of catecholamines (CA), i.e., adrenaline, noradrenaline, and  
223 dopamine, are released from the chromaffin cells of the head kidney and thus, increase  
224 in the bloodstream (reviewed in Wendelaar Bonga, 1997). As chromatophores express  
225 CA receptors, this increase directly impacts fish coloration, generally inducing skin  
226 paling (Figure 1). If the stressful stimulus continues, the chronic stress response begins  
227 with the activation of the hypothalamus-pituitary-interrenal axis. Thus, corticotropin-  
228 releasing hormone (Crh) and thyrotrophin-releasing hormone (Trh) produce an increase  
229 in adrenocorticotrophic hormone (Acth) and  $\alpha$ -Msh secretion, which in turn stimulates  
230 cortisol release causing skin darkening or paling depending on the species. Cortisol can  
231 also exert a negative feedback on  $\alpha$ -Msh and the interrenal cells, in addition to a  
232 downregulation of certain CA receptors, such as adrenergic receptors (Wendelaar

233 Bonga, 1997). Furthermore, stressor-induced cortisol production has been associated  
234 with disruption of the gut microbiome in fish (Uren Webster et al., 2020). Considering  
235 the major role of the gut microbiome in the regulation of the physiology of the  
236 organism, including the modulation of neuronal and endocrine pathways (Lerner et al.,  
237 2017), and the recent association found between the pseudo-albino phenotype and gut  
238 microbiome modification in Senegalese sole (Pinto et al., 2019), deeper research  
239 towards deciphering the molecular mechanisms and cellular processes of skin  
240 pigmentation regulated by the gut microbiome and their link with other biological  
241 processes will undoubtedly shed light into better understanding the intricate and  
242 interlocked processes of physiological regulation in fish.

243 Finally, as more than one stressor can be present at the same time, different effects on  
244 skin pigmentation can be observed depending on the hormonal response to each  
245 stimulus

#### 246 **4.1 Nutrition**

247 The influence of nutrition in fish skin pigmentation has been widely reported; however,  
248 fewer studies have dealt with its endocrine regulation. The association between nutrition  
249 and pigmentation has been mostly studied in flatfish, which can present a high  
250 incidence of pigmentation anomalies under aquaculture conditions, and in fish species  
251 owing their skin coloration to dietary carotenoids.

252 In flatfish, larval nutrition has been proved to be essential for proper physiological and  
253 morphological transformations occurring during the complex process of metamorphosis,  
254 including pigmentation (Hamre et al., 2005; Boglino et al., 2013; Darias et al., 2013b).  
255 Several studies have shown higher survival rates and better pigmentation when fish are  
256 fed copepods than with any other live prey (Seikai, 1985; Shields et al., 1999; Wilcox et

257 al., 2006). Several differences in nutrient composition between copepods and live preys  
258 such as *Artemia* or rotifers have been suggested to account to the dissimilarities in the  
259 pigmentation process of fish, such as the amount of docosahexaenoic (DHA) and  
260 eicosapentaenoic acids (EPA) (and their ratios), polar lipids and amino acids, as well as  
261 vitamin A (VA) and carotenoid composition (Næss and Lie, 1998). Kanazawa (1993)  
262 suggested that albinism in flatfish resulted from the insufficiency of rhodopsin, the  
263 production of which depends on VA, DHA and phospholipids, necessary to the  
264 formation of melanin. According to this author, feeding Japanese flounder larvae fed a  
265 diet deficient in those nutrients during the formation of the retina (at around 10 days  
266 post hatching-dph) hampers the production of rhodopsin in the retina. The absence of  
267 rhodopsin prevents the visual transmission from the retina to the central nervous system,  
268 then the production of Msh is not triggered resulting in the interruption of black  
269 pigment formation (Kanazawa, 1993). Copepods contain 5 times higher DHA content  
270 than *Artemia* (Hamre et al., 2002), thus the involvement of DHA in vision development  
271 and its importance to stimulate melanin synthesis might be the reason behind the  
272 importance of DHA in pigmentation. Copepods also present higher levels of EPA.  
273 Adequate levels of DHA and EPA and their ratios have shown to be necessary for the  
274 correct development of skin pigmentation of turbot (Reitan et al., 1994; Estévez and  
275 Kanazawa, 1995), common sole, *Solea solea* (Heatch and Moore, 1997), Atlantic  
276 halibut, *Hipoglossus hipoglossus* (Hamre et al., 2005), and California halibut,  
277 *Paralichthys californicus* (Vizcaíno-Ochoa et al., 2010). Besides, the lower iodine  
278 content in *Artemia* compared to copepods has been suggested to decrease the level of  
279 thyroid hormone (Th) in fish larvae (Hamre et al., 2005), which could in turn interfere  
280 in the metamorphosis process, including pigmentation (Inui and Miwa, 2012; Wang et  
281 al., 2019). VA also influences the fate of chromatophores in flatfish, high doses of

282 retinoic acid stimulating the development of chromatophores in the blind side of flatfish  
283 (Miwa and Yamano, 1999). It has been suggested that interactions between VA and  
284 fatty acids, as well as between VA and Th at the nuclear receptor level are key in the  
285 stimulation of normal pigmentation (Hamre et al., 2005).

286 Adequate dietary arachidonic acid (ARA) content has also been demonstrated to be  
287 important for proper skin pigmentation of several flatfish species such as Yellowtail  
288 flounder, *Limanda ferruginea* (Copeman and Parrish, 2002), common sole (Lund et al.,  
289 2008), turbot (Estévez et al., 1999), Japanese flounder (Estévez et al., 2001), Atlantic  
290 halibut (Hamre et al., 2007) and Senegalese sole (Villalta et al., 2005; Darias et al.,  
291 2013b; Boglino et al., 2014). Pre- and pro-metamorphosis are the sensitive periods  
292 during which nutrition exerts its greatest influence on pigmentation, coinciding with the  
293 time in which chromatoblast differentiation takes place towards the adult type  
294 chromatophores (Bolker et al., 2005; Darias et al., 2013b). Senegalese sole larvae fed  
295 with high levels of ARA becoming pseudo-albinos at later stages developed  
296 pigmentation in the same way as future normally pigmented specimens, but once  
297 metamorphosed, the future pseudo-albinos began to show different relative proportions,  
298 allocation patterns, shapes and sizes of skin chromatophores that progressively  
299 disappeared during post-metamorphosis (Darias et al., 2013b). This process was mainly  
300 attributed to the down-regulation of *trp1* and *slc24a5*, which prevented melanin  
301 production, and the involvement of *pax3*, *mitf* and *asip1* (agouti signaling protein) in the  
302 developmental disruption of the new post-metamorphic populations of melanophores,  
303 xanthophores and iridophores (Darias et al., 2013b). Melanophores in pseudo-albino  
304 specimens were less abundant and not so aggregated in patches as they were in normally  
305 pigmented ones, whereas their shape differed (round vs. dendrite-like shape) suggesting  
306 their inability to disperse melanin (Darias et al., 2013b). Besides, high amounts of

307 dietary ARA can produce imbalances in the relative content of EPA and DHA (Moren  
308 et al., 2011), which in turn modify the relative concentrations of prostaglandin E of the  
309 2 (ARA-derived) and 3 (EPA-derived) series (Boglino et al., 2014). In fact, EPA and  
310 DHA compete as substrates for cyclo- and lipoxygenases, which are involved in  
311 prostaglandin biosynthesis pathways. Prostaglandin E2 (PEG2) and PEG3 are potent  
312 regulators of metabolism with opposing effects (Bell and Sargent, 2003); thus, the  
313 balance in their synthesis from both series is dependent on a balanced dietary intake of  
314 both ARA and EPA (Hamre et al., 2005). ARA-induced abnormally pigmented  
315 individuals have shown to present higher levels of PGE2 than normally pigmented fish  
316 fed with a control diet in both Senegalese sole (Villalta et al., 2005, Boglino et al.,  
317 2014) and common sole (Lund et al., 2010). Further, pseudo-albino specimens fed a  
318 high ARA content diet displayed higher PGE2 concentrations than normally pigmented  
319 fish fed the same diet (Boglino et al., 2014). In Senegalese sole, high dietary ARA  
320 levels and altered PGE2 concentrations not only affected the pigmentation success, but  
321 also disrupted the process of head remodeling during metamorphosis (Boglino et al.,  
322 2013).

323 Many fish species owe their bright coloration to carotenoids, which are the predominant  
324 pigments in xanthophores and erythrophores. Fish are not able to biosynthesize  
325 carotenoids *de novo*, and thus must obtain them from the diet (Bjerkeng, 2008). In  
326 aquaculture, several cultured fish species require carotenoid supplementation in order to  
327 avoid skin paleness (Bjerkeng, 2008). The effect of carotenoids on the endocrine system  
328 as well as their mechanisms of action remain to be elucidated (De Carvalho and  
329 Caramujo, 2017). However, it is known that carotenoid deposition in the skin is induced  
330 during the breeding season in many fish species, and gonadal hormones such as 17 $\beta$ -

331 estradiol and 11-ketotestosterone have shown to play a role in carotenoid-based nuptial  
332 coloration (reviewed in Leclercq et al., 2010; Lim et al., 2018).

333 Astaxanthin is the main carotenoid used in aquaculture feeds and is either obtained from  
334 chemical synthesis or from natural resources such as algae, fungi, yeast and bacteria,  
335 (Lim et al., 2018). Besides a source of pinkish-red pigments, astaxanthin is known to  
336 improve survival, growth performance, reproductive capacity, stress tolerance, disease  
337 resistance and immune related gene expression (Lim et al., 2018). Several studies have  
338 analyzed the effect of dietary astaxanthin on skin coloration of cultured fish species for  
339 human consumption, such as Atlantic salmon, *Salmo salar*, rainbow trout,  
340 *Oncorhynchus mykiss*, red porgy, gilthead sea bream, red sea bream, *Pagrus major*,  
341 Japanese flounder or Australasian snapper, *Pagrus auratus*, as well as in ornamental  
342 species, such as goldfish, *Carassius auratus*, kissing gourami, *Helostoma temminckii*,  
343 false clownfish, *Amphiprion ocellaris* or koi carp, *Cyprinus carpio*, among others  
344 (reviewed in Lim et al., 2018). Besides, other carotenoid sources have been also  
345 assessed to enhance fish skin coloration, as for example the fucoxanthin-rich microalga  
346 *Phaeodactylum tricornerutum* (gilthead sea bream; Ribeiro et al., 2017), China rose  
347 petals, *Hibiscus rosa-sinensis* (goldfish; Sinha and Asimi, 2007), annatto, *Bixa orellana*  
348 (goldfish; Fries et al., 2014), sea lettuces *Ulva rigida* and *Ulva lactuca* (Nile tilapia;  
349 Valente et al., 2016) or *Spirulina* sp. (yellow tail cichlid, *Pseudotropheus acei*; Guroy et  
350 al., 2012), among others.

351

## 352 **4.2 Tank color**

353 The characteristics of rearing tanks are an important issue to consider in aquaculture,  
354 since it has been demonstrated that they can induce stress (Ishibashi et al., 2013), affect

355 growth and survival (Martinez-Cardenas and Purser, 2015; Wang et al., 2017), induce  
356 skeletal anomalies (Cobcroft and Battaglione, 2009), and alter fish behavior (Höglund et  
357 al., 2002; Cobcroft and Battaglione, 2009) and skin pigmentation (van der Salm et al.,  
358 2005; Doolan et al., 2008b; Eslamloo et al., 2015). Despite all the evidence, tank  
359 characteristics are often under-considered in aquaculture, and, for instance, the color of  
360 the rearing tanks is seldom described in the scientific literature.

361 Background adaptation is widely observed in fish and refers to the ability to modify  
362 body color in response to environmental luminosity, as in the case of dark or bright  
363 backgrounds. This ability is exploited in aquaculture to improve skin pigmentation. For  
364 example, skin darkening in sparids, which negatively affects market value (Matsui et  
365 al., 1992; Kolios et al., 1997; Lin et al., 1998; Rotllant et al., 2003; Booth et al. 2004;  
366 Van der Salm et al., 2004; Doolan et al., 2007), can be reversed by rearing these species  
367 in white tanks (Doolan et al, 2008a, b). However, a white environment has been shown  
368 to induce an increased stress response to overcrowding in *P. pagrus*, which may depend  
369 on the size of the fish (Rotllant et al., 2003; Van der Salm et al., 2004). In tilapia,  
370 *Oreochromis mossambicus*, white and grey backgrounds induce skin lightening,  
371 whereas a black background induces skin darkening and a more stressful response (Van  
372 der Salm et al., 2005). In goldfish, red and blue backgrounds are chronically stressful,  
373 whereas a white background improves fish growth, but generates a skin color loss  
374 (Eslamloo et al., 2015). In *Lophiosilurus alexandri* dark colored tanks promoted an  
375 increase in plasma cortisol levels and a reduction in brightness of the skin, while the use  
376 of light colors resulted in paler skin (Costa et al., 2017).

377 As previously mentioned, tank color not only affects fish pigmentation, but can also  
378 cause other physiological changes. In several fish species, it has been observed that fish

379 adapted to a white background present better growth performance than those adapted to  
380 other background color (Amiya et al. 2005; Karakatsouli et al. 2007; Strand et al. 2007;  
381 Takahashi et al., 2004; Yamanome et al. 2005; Pérez Sirkin et al., 2012; Eslamloo et al.,  
382 2015). In part, this could be due to the high contrast between feed and background color  
383 that improves the visibility of feed in the tanks (Jentoft et al., 2006; Strand et al. 2007;  
384 Eslamloo et al., 2015). Besides, white background induces high levels of Mch and, as  
385 Mch has been proposed to play an orexigenic role in some species (Takahashi et al.,  
386 2014; Volkoff, 2016), the increase in somatic growth could be interpreted as an increase  
387 of food intake. On the other hand, in *C. dimerus*, it was demonstrated that Mch  
388 stimulates Gh release in pituitary cultures, so the increase in fish growth could also be  
389 related to this regulation (Pérez Sirkin et al., 2012).

390 The adaptation to black background results in the dispersion of pigment in  
391 melanophores within a few hours, concomitant with an increase in plasma  $\alpha$ -Msh levels  
392 (Mizusawa et al., 2013). However, the involvement of this hormone in long-term  
393 background adaptation has no consensus in fish (Cal et al., 2017). Despite what would  
394 be expected, gilthead sea bream adapted to a white background for 15 days presented an  
395 increase in plasma  $\alpha$ -Msh levels compared to specimens adapted to grey or black  
396 backgrounds (Arends et al., 2000). Similar results were observed in red porgy adapted  
397 for one month to white or black backgrounds (Rotllant et al., 2003). However, it has  
398 been hypothesized that the regulation of  $\alpha$ -Msh acetylation may be an important  
399 mechanism for background adaptation, more than total amounts of  $\alpha$ -Msh released into  
400 the blood (Arends et al., 2000).

401 The pioneering works of Zhu and Thomas (1996, 1997, 1998) and Zhu et al. (1999)  
402 introduced somatolactin (Sl) as a hormone involved in background color adaptation.

403 They suggested that SI plays a role in background adaptation and possibly regulates  
404 pigment movement in the chromatophores of sciaenid fishes. In *C. dimerus*, the long-  
405 term exposition to a black background produces an increase in the number and area of  
406 SL immunoreactive cells (Cánepa et al., 2006), even from early stages of development  
407 (Delgadin et al., 2020). Moreover, growth hormone receptor 1 (GhR1; probably the SL  
408 receptor) was detected in the epidermis and dermis from fish scales (Cánepa et al.,  
409 2012). This receptor showed changes in its transcript level concomitant with changes in  
410 melanophores, suggesting plausible evidence for the role of SI and its receptor in the  
411 regulation of chromatophores in *C. dimerus* (Cánepa et al., 2012). Furthermore, it was  
412 determined that medaka larvae with biallelic mutations of the GhR1 receptor failed to  
413 adapt to the background, unless at the beginning of development (Delgadin et al., 2020).

414 SL has been shown to be involved in different physiological processes, including  
415 reproduction, stress responses, Ca<sup>2+</sup> homeostasis, acid–base balance, growth,  
416 metabolism, and immune responses (reviewed in Kawauchi et al., 2009); therefore,  
417 changes in tank color can influence the general physiology in different ways, thus  
418 affecting fish welfare.

419

### 420 **4.3 Social interactions**

421 In many social species, skin pigmentation reflects the social hierarchy; for example, in  
422 salmonids, social subordination is associated with skin darkening (Abbott et al., 1985;  
423 O'Connor et al., 1999; Höglund et al., 2000, 2002). Subordinate fish are subjected to  
424 chronic stress induced by aggressive acts from dominant fish (Winberg and Lepage,  
425 1998; Øverli et al., 1999; Höglund et al., 2000, 2002). As it was previously mentioned,  
426 this leads to a chronic activation of the hypothalamic–pituitary–interrenal axis, and to an  
427 increase of  $\alpha$ -Msh that induces interrenal cortisol release and skin darkening (Fujii and

428 Oshima, 1986, Höglund et al., 2000). In *Astatotilapia burtoni* it was demonstrated that  
429 yellow males are more aggressive than blue ones (Korzan and Fernald, 2007; Korzan et  
430 al., 2008). Later on, it was demonstrated that blue males have higher cortisol levels than  
431 yellow ones, indicated by an activation of the melanocortin system in the skin (Dijkstra  
432 et al., 2017).

433 In *C. dimerus*, body color pattern is associated with different social status. A relation  
434 between color and dominance was observed in territorial individuals, which had bright  
435 body color patterns, while non-territorial individuals were opaque grey (Alonso et al.,  
436 2011). Furthermore, a negative correlation was found between plasma cortisol levels  
437 and dominance; fish of lower social hierarchy rank had higher plasma cortisol levels  
438 than those in higher rank (Alonso et al., 2011, 2012).

439 It is important to point out that the color of the tank can increase social agonist  
440 encounters, besides inducing stress. In Nile tilapia, blue and brown tanks increased this  
441 kind of behavior (Merighe et al., 2004), whereas in Arctic char, *Salvelinus alpinus*,  
442 white tanks induced a more aggressive behavior than black ones (Höglund et al., 2002).

443

#### 444 **4.4 Light and other factors**

445 It is known that chromatophores respond directly to incident light. This “primary color  
446 response” can be observed during embryonic and larval stages, when chromatophores  
447 are not innervated or under endocrine control, as well as in adulthood regardless of the  
448 presence of both regulatory systems (reviewed in Fujii, 2000; Oshima, 2001). In this  
449 sense, cone opsin expression has been detected in melanophores (Chen et al., 2013) and  
450 erythrophores (Ban et al., 2005; Chen et al., 2013) in Nile tilapia and in iridophores in

451 Neon tetra (Kasai and Oshima, 2006). Melanophores respond to wavelengths between  
452 380-580 nm by dispersing melanosomes (Chen et al., 2013), and erythrophores  
453 aggregate or disperse pigment depending on exposure to short or middle/long  
454 wavelengths, respectively (Sato et al., 2004; Ban et al., 2005; Chen et al., 2013). The  
455 photo-response of iridophores depends on light intensity, with the wavelength of 500  
456 nm being the most effective one (Kasai and Oshima, 2006). Besides, the photic  
457 environment affects fish pigmentation by modulating nervous and endocrine systems.  
458 Unfortunately, there are few studies conducted on the impact of different wavelengths  
459 on fish pigmentation. For example, adults of red porgy became paler when exposed to  
460 blue light compared to individuals exposed to the full spectrum, with no observed  
461 changes in melanin content or  $\alpha$ -Msh and cortisol levels (Szisch et al., 2002). These  
462 authors proposed that these changes in fish coloration could be due to changes in  
463 melanosome aggregation produced by the control of the nervous system. In addition,  
464 Amano and Takahashi (2009) suggested that, since green light increased somatic  
465 growth in barfin flounder, *Verasper moseri* (Yamanome et al., 2009), *mch* expression  
466 and its secretion could be higher, so the skin color of those animals should be paler.  
467 Unfortunately, the effect of green light on skin color was not analyzed in that study.

468 Light intensity has been shown to affect growth, behavior, physiology, and coloration in  
469 some fish species, such as *Paralichthys woolmani* (Benetti, 1997; Venizelos and  
470 Benetti, 1999; Han et al., 2005). Santos et al. (2019) showed that light influences food  
471 consumption and conversion, behavior, and plasma cortisol levels of *Lophiosilurus*  
472 *alexandri* juveniles; however, no effect on skin pigmentation was observed.

473 Photoperiod can also induce alterations in skin color, given that melatonin not only acts  
474 directly over chromatophores but also modifies other endocrine pathways that affect

475 skin pigmentation. For example, in Neon tetra, the red and brown colors produced by  
476 erythrophores and melanophores were found to be markedly reduced at night,  
477 suggesting the regulation of coloration by an endogenous circadian rhythm (Lythgoe  
478 and Shand, 1983). Differences in skin pigmentation due to photoperiod were also  
479 observed in Japanese flounder after metamorphosis when comparing the effects of  
480 continuous 24 h illumination (LL) to natural light conditions (15 h light: 9 h dark, LD)  
481 during larval development. Itoh et al. (2012) found that larvae reared in LL presented  
482 paler skin color, and a higher ratio of abnormal pigmentation after metamorphosis.  
483 Moreover, LL conditions decreased tyrosine hydroxylase-1 (*th1*) in dopaminergic  
484 neurons, but increased *α-msh* levels in melanotrophs with no changes in *mch*  
485 expression levels in the lateral tuberal nucleus (NLT). Authors concluded that there  
486 could be an accumulation of  $\alpha$ -Msh in the melanotrophs because of the inhibitory  
487 action of Mch over its protein secretion, causing a pale skin color. In another study,  
488 Ginés et al. (2004) found that the skin luminosity of gilthead sea bream was higher  
489 under the longer the photoperiod. Similar results were obtained by Lyon and Baker  
490 (1993) in rainbow trout, who also described that Mch secretion reached a peak during  
491 the light period and then, it gradually declined before night, when the lowest  
492 concentrations were observed. These hormone variations were directly related to animal  
493 skin paleness.

494 Other factors such as handling, crowding, transport, hydrostatic pressure, and variations  
495 in temperature, oxygen, and salinity, can affect either directly or indirectly  
496 chromatophores' physiology and thus modify fish pigment. The direct impact of some of  
497 these stimuli on chromatophores is poorly studied, although, for example, it is accepted  
498 that high temperatures aggregate chromatosomes, while lower temperatures disperse  
499 them (Fujii and Oshima, 1994). In any case, these factors are generally considered as

500 stressors, promoting an acute or chronic stress response depending on the duration of  
501 the stimuli (reviewed in Wendelaar Bonga, 1997).

502

## 503 **5 Conclusions and perspectives**

504 The skin pigmentation pattern in fish is species-specific and is given by the number and  
505 spatial combination of several types of chromatophores. Research efforts have been  
506 made to improve understanding of the underlying endocrine regulation of skin  
507 pigmentation. In particular, recent studies have identified other actors besides the classic  
508 color change regulators Mch and Msh, such as Sl, Asip, and Th, that seem to play an  
509 important role in the regulation of pigmentation. In this sense, more studies are needed  
510 to understand how these factors interact in a coordinated way to regulate skin color.  
511 Furthermore, considering that most studies on the physiology of pigment cells focus on  
512 melanophores and that some studies have demonstrated that cellular communication  
513 between different types of chromatophores is essential in the pigmentation patterning  
514 process, further research on the regulatory factors of all types of chromatophores and  
515 the interactions among them is essential to understand the intricate mechanisms of skin  
516 pigmentation as well as to identify the origin and the causes leading to pigmentation  
517 disorders. Furthermore, as chromatophores derive from NCC, pigmentation anomalies  
518 could be the visible sign of more complex physiological disruptions.

519 Skin pigmentation is one of the most important quality criteria dictating the market  
520 value of fish for both human consumption and ornamental use. Rearing conditions such  
521 as nutrition, tank coloration, UV incidence, surrounding luminosity, or social  
522 interactions can negatively affect the natural skin coloration. In this sense, further  
523 studies are needed to identify pigmentation-related endocrine factors that are being

524 modulated when fish are reared under suboptimal conditions. This knowledge will also  
525 be useful to better understand the impact of rearing conditions on other biological  
526 processes, as many endocrine signals affecting pigmentation are additionally regulating  
527 processes such as growth, reproduction, or nutrition, among others. In this sense, skin  
528 pigmentation could be considered an indicator of fish well-being.

529 New insights on the influence of stress in gut microbiome modulation and on the role of  
530 gut microbiome in the regulation of skin pigmentation reinforces the need for a better  
531 understanding of the influence of environmental conditions. Taken together, research on  
532 the endocrine factors affecting pigmentation, the communication among different types  
533 of chromatophores, the influence of nutrition and abiotic factor in the modulation of  
534 these endocrine signals, and the role of gut microbiome in the regulation of these  
535 physiological processes could contribute to identify the best rearing conditions for  
536 species presenting pigmentation disorders and hence to improve their commercial  
537 production.

538

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548

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- 1153

1154 **Table 1.** Summary of the hormonal skin color regulation in fish. In this table we only  
1155 focus on their role in pigmentation; therefore, some general characteristics of each  
1156 hormone are omitted.

1157 **Mch:** Kawauchi and Baker, 2004<sup>1</sup>; Amano and Takahashi, 2009<sup>2</sup>; Pandolfi et al., 2003<sup>3</sup>;  
1158 Mizusawa et al., 2009<sup>4</sup>; Takahashi et al., 2004<sup>5</sup>; Yamanome et al., 2007<sup>6</sup>; Oshima et al.,  
1159 1986<sup>7</sup>; Mizusawa et al., 2011<sup>8</sup>; Kasukawa et al., 1986<sup>9</sup>; Baker et al., 1986<sup>10</sup>; Yamanome  
1160 et al., 2005<sup>11</sup>. **Msh:** Cal et al., 2017<sup>12</sup>; Takahashi and Kawauchi, 2006<sup>13</sup>; Lamers et al.,  
1161 1991<sup>14</sup>; Arends et al., 2000<sup>15</sup>; Kobayashi et al., 2012<sup>16</sup>; Sánchez et al., 2010<sup>17</sup>;  
1162 Kobayashi et al., 2016<sup>18</sup>; Dijkstra et al., 2017<sup>19</sup>; Fujii and Miyashita, 1982<sup>20</sup>; Kobayashi  
1163 et al., 2011<sup>21</sup>; Ligon and McCartney, 2016<sup>22</sup>; Sugimoto, 2002<sup>23</sup>. **Sl:** Kaneko, 1996<sup>24</sup>;  
1164 Fukada et al., 2005<sup>25</sup>; Chang and Wong, 2009<sup>26</sup>; Cánepa et al., 2012<sup>27</sup>; Fukamachi and  
1165 Meyer, 2007<sup>28</sup>; Zhu et al., 1999<sup>29</sup>; Nguyen et al., 2006<sup>30</sup>; Fukamachi et al., 2004<sup>31</sup>,  
1166 2009<sup>32</sup>. **Asip:** Cerdá-Reverter et al., 2005<sup>33</sup>; Guillot et al., 2012<sup>34</sup>; Ceinos et al., 2015<sup>35</sup>;  
1167 Cal et al., 2019<sup>36</sup>; McNulty et al., 2005<sup>37</sup>. **Cortisol:** Wendelaar Bonga, 1997<sup>38</sup>; Khan et  
1168 al., 2016<sup>39</sup>; Ruane et al., 2005<sup>40</sup>; Yamada et al., 2011<sup>41</sup>; Matsuda et al., 2018<sup>42</sup>. **Prl:**  
1169 Kawauchi et al., 2009<sup>43</sup>; Freeman et al., 2000<sup>44</sup>; Kitta et al., 1993<sup>45</sup>; Oshima and Goto,  
1170 2000<sup>46</sup>; Oshima et al., 1996<sup>47</sup>; Sage, 1970<sup>48</sup>; Sköld et al., 2008<sup>49</sup>. **Mt:** Falcon et al.,  
1171 2011<sup>50</sup>, 2010<sup>51</sup>; Fujii, 2000<sup>52</sup>; Fujii and Oshima, 1994<sup>53</sup>; Nagaishi and Oshima, 1989<sup>54</sup>;  
1172 Oshima et al., 1989<sup>55</sup>. **Th:** Janz, 2000<sup>56</sup> Blanton et al., 2007<sup>57</sup>; Bernier et al., 2009<sup>58</sup>;  
1173 Walpita et al., 2009<sup>59</sup>, 2007<sup>60</sup>; Saunders et al., 2019<sup>61</sup>; Guillot et al., 2016<sup>62</sup>; Yoo et al.,  
1174 2000<sup>63</sup>; McMenamin et al., 2014<sup>64</sup>.

1175

1176 **Figure 1.** Endocrine and nervous factors involved in physiological and morphological  
1177 color changes. This figure summarized the physiological (left) and morphological  
1178 (right) hormone effects over different chromatophores presented in Table 1. Besides,  
1179 local synthesis (as it was described for Asip and Mch) and factors delivered through the  
1180 bloodstream are shown. Note that most studies focus on the regulation of melanophores  
1181 while there is scarce information about other pigmentary cell's regulation. Arrows  
1182 indicate stimulation and T-lines indicate inhibition. Mch: melanin-concentrating  
1183 hormone; Msh; melanophore-stimulating hormone; Sl: somatolactin; Prl: prolactin; Mt:  
1184 melatonin; Th: thyroid hormone; Asip: agouti signaling protein; CA: catecholamines;  
1185 NA: noradrenaline.

Hormone/peptide	Synthesis (place and/or gene)	Mode of action	Receptors	Overall effect	Physiological changes in chromatophores	Morphological changes in chromatophores
Melanin-concentrating hormone (Mch)	-NLT, some neurons project to the hypophysis and bloodstream <sup>1,2</sup>  -Skin neuromast <sup>3</sup>	endocrine  paracrine	Type 1 G-protein coupled receptors.  Two subtypes: Mch-r1 and Mch-r2 <sup>2,4</sup>	Skin paling <sup>5,6</sup>	-Aggregation of melanosomes in several fish species <sup>5,6</sup> erythrosomes in swordtail <sup>7</sup> and xanthosomes in medaka <sup>8</sup> -Dispersion of light-scattering organelles of leucophores in medaka <sup>7</sup> - No effect over iridophores in blue damselfish <sup>7,9</sup>	- Prevents melanin synthesis <sup>10,11</sup> -Prevent melanophore differentiation <sup>11</sup>
Melanophore-stimulating hormone (Msh)	-melanotropes of the <i>pars intermedia</i> <sup>12</sup>  -Skin <sup>16</sup> -In teleost: $\alpha$ -Msh and $\beta$ -Msh isoforms <sup>13</sup>	-endocrine  -paracrine  - $\alpha$ -Msh: des-, mono- (dominant), and di-acetylated <sup>14,15</sup>	Seven transmembrane-domain-G-protein-coupled family/rhodopsin class family A-13.  Subtypes: Mc1R and Mc5R <sup>12,16-18</sup>	Skin darkening <sup>12</sup> and/or promotes yellow coloration <sup>19</sup>	- Dispersion of melanosomes (epidermis and dermis) <sup>20</sup> and xanthosomes in <i>A. burtoni</i> <sup>16,19,21</sup> -Promotes platelet aggregation in motile iridophores <sup>22</sup>	- Stimulate melanin synthesis <sup>23</sup> -Acts as a melanophore differentiation factor <sup>23</sup>
Somatolactin (Sl)	-somatolactotropes of the <i>pars intermedia</i> <sup>24</sup>	-endocrine	Proposed: type I cytokine receptor: growth hormone (Gh) receptor type 1 (GhR1) <sup>25-28</sup>	Skin darkening <sup>27,29-30</sup>	-Dispersion of melanosomes in red drum <sup>29</sup> and zebrafish <sup>30</sup>	-Promotes proliferation of melanophores in <i>C. dimerus</i> <sup>27</sup> , and it is involved in the proliferation and morphogenesis of certain chromatophores in medaka <sup>31-32</sup>
Agouti signaling protein (Asip)	-skin <sup>12,33-36</sup>	-paracrine	Antagonist of Mc1R <sup>33,37</sup>	Determines dorso-ventral pigment pattern <sup>12,33-36</sup> Involved in skin paling?	- Aggregation of melanosomes in medaka <sup>33</sup>	-Inhibits melanogenesis <sup>36</sup> and modulates chromatoblast fate: decreasing melanophores n° in different species of flatfish <sup>33,34</sup> , and also decreasing xanthophores and increasing iridophores n° in zebrafish <sup>36</sup>
Cortisol	- Interrenal cells of the head kidneys <sup>38</sup>	-endocrine	Direct or indirect effect? Proposed to act through <i>asip</i> in	Skin darkening or paling depending on species <sup>39-42</sup>		

Prolactin (Prl)	-lactotropes of the <i>rostral pars distalis</i> <sup>43</sup>	-endocrine	rainbow trout <sup>39</sup> Cytokine/hematopoietin superfamily. Long and Short isoforms of Prlr <sup>44</sup>	Promotes red and yellow skin coloration <sup>45-48</sup>	-Weak aggregating effect on melanophores <sup>45,46</sup> . -Dispersion of xanthosomes in Nile tilapia and the rose bitterling <sup>46</sup> , and of erythrocytes in Nile tilapia, swordtails and paradise gobies <sup>47</sup> . Similar effects in two-spotted gobies and the mudsucker <sup>48,49</sup>
Melatonin (Mt)	-Pineal gland <sup>50</sup>	-endocrine	Seven transmembrane-domain-G-protein-coupled family: Mt1 Mt2 and Mel1c <sup>51</sup>	Skin paling and transparency <sup>49,52</sup>	-Aggregation of melanosomes <sup>52</sup> and erythrocytes <sup>49,53</sup> . -Dispersion of erythrocytes and xanthosomes <sup>49</sup> . -Increase between platelets spacing in iridophores <sup>54,55</sup> .
Thyroid hormones (Th)	-Thyroid follicles, local conversion to T3 <sup>56-58</sup>	-endocrine	transcription factors from the family of type-2 nuclear receptors: $\alpha$ and $\beta$ TR <sup>58</sup>	Skin paling <sup>59-62</sup>	-Prevent melanin synthesis <sup>59,60</sup> -Change the balance of melanophore stem cell proliferation/ differentiation in zebrafish <sup>61,62</sup> and Japanese flounder <sup>63</sup> - Decrease melanophore and increase xanthophore number <i>Danio albolineatus</i> <sup>64</sup>

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