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REVIEWS

Pigmentation enhancement techniques during ornamental fish production

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Abstract The ornamental fish industry has continued to flourish since eighteenth century with increased fascination by enthusiasts in the striking body colours and patterns displayed in the fishes, a beneficial outcome of rigorous selective programmes. The expression of these pigmented colours is the result of the differentiation and orientation of specialised chromatophores located within the dermal layer. The different types of chromatophores found in many ornamental fish species, are the basis of the unique colour hues and patterns. This review discusses the current approaches for enhancing the body pigmentation and pattern of ornamental fishes. Two factors are considered to be the main drivers of body colour regulation: feed additives (pigments) and rearing environment setup, i.e. tank colour and light. Potential candidate pigment genes to manipulate the ornamental fish body pigmentation and pattern have been elucidated through mapping of putative regulatory pathways, buoyed by the rapid development of next generation sequencing technologies. The effects of feed additives, tank background colour and light on various ornamental fish species, and regulatory pathways of involved genes offer valuable insights for enhanced variety production prior to genetic engineering and are herein discussed. It is hoped that the systematic analysis of the current knowledge in this review would be a boon for the ornamental fish community to step up efforts to boost the ornamental fish breeding industry.

Keywords Chromatophore · Light · Tank colour · Decorative · Rearing

Introduction

Ornamental fish petting is one of most popular hobbies of the global community, accelerating the ornamental fish industry since eighteenth century. With an annual worldwide growth rate of 14%, worth US $15 billion, it is an important economic activity in many developing nations (Yanar et al. 2019; Yue 2019). The value of an ornamental fish is determined by its morphological traits and features, in particular its body colours, pattern and shape. For instance, a discus fish

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(*Symphysodon* spp.) (Fig. 1) with unique disc-shaped body and assorted body colours and patterns would cost around USD100–400 locally, while discus varieties with pale and monotonous colour, such as snow white bred (Fig. 1a), receive less attention (personal communication, Aquacity Tropical Shd. Bhd., one of the pioneer discus breeding companies in South East Asia region).

Much efforts have been geared towards enhancing body colour and patterns. In a typical scenario, the original stocks are wild captured and selectively crossbred to produce more attractive domesticated varieties for the ornamental fish trade industry (Ng 2016). Unlike maricultural fish, the selective breeding of ornamental fish emphasizes on beautifying the morphological appearance. Unfortunately, selective breeding is a time and cost-consuming process, which requires the interbreeding over many generations, with the inevitable production of undesirable progenies during the process, before attaining the targeted pure bred (Walster 2008). Several methods have been developed and widely applied for enhancing the morphological appearance of ornamental fishes. These include nutritional supplements such as carotenoid-based diet, varying stocking density and other environmental parameters which could effectively affect the colour hue and brightness (Klann et al. 2021). However, the positive effects may not be permanent, disappearing upon termination of carotenoid supplementation or environmental stimulus fading. Therefore, a multi-pronged strategy is necessary to manipulate the ornamental fish body colours and patterns, in order to expedite the production of new varieties.

Although advances in breeding techniques have positively impacted the ornamental fish industry (Pouil et al. 2020), the majority of marine species remain unsustainably sourced due to the complicated breeding processes involved (King 2019). One strategic approach is to elucidate the molecular mechanisms controlling the various morphological variants which could potentially be engineered for the desired outcomes. Numerous studies (Cerdá-Reverter et al.

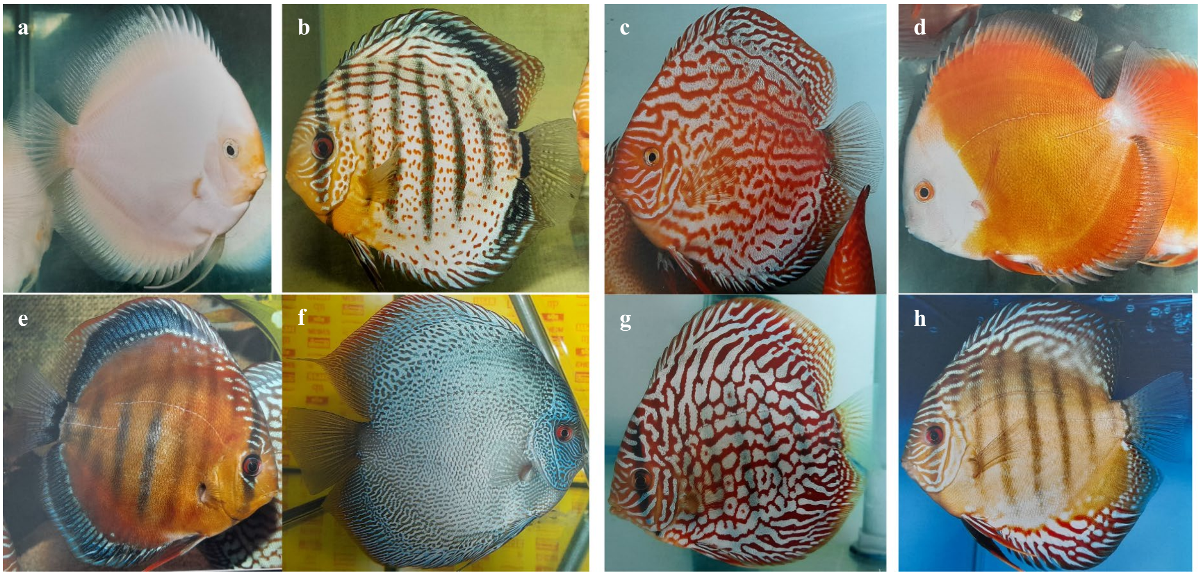

Fig. 1 The varieties of adult discus fish (*Symphysodon* sp.) with various body pigmented patterns. **a** Snow white discus with body entirely covered in white. **b** The spotted green classic discus with melanic vertical bar stripes, orange dotted spots and dorsal wavy stripes with white background. **c** Pigeon blood discus with dorsalvertically wavy orange stripes on top of the white background. **d** Golden tangerine discus with entire trunk covered in golden background colour, head appeared white with transparent fins. **e** Alenquer red discus with melanic vertical bar stripes, blue-white stripes above the lateral line on top of the orange background colour. **f** Blue snakeskin discus with entire body covered in spatial melanic markings with blue iridescent background. **g** Checkerboard discus with body covered in red wavy stripes, melanic vertical bars on top of the white background colour. **h** Wild brown discus with melanic vertical bar stripes and brown background colour, and fins with red wavy stripes. Pictures retrieved from Discus Catalogue (2004) supplied by Aquacity Tropical Sdn. Bhd. Photo credit: Patrik Tan

2011; Cal et al. 2017; Kimura 2021; Luo et al. 2021; Kwon et al. 2022; Liu et al. 2022) on fish pigmentation have permitted a better understanding of the regulatory mechanisms of fish colour and pattern formations. To date, there are at least five types of pigment cells in fish, namely melanophores (black and brown colour), xanthophores (orange and yellow colour), erythophores (orange and red colour), iridophores (iridescence) and leucophores (white colour) (Luo et al. 2021). These pigment cells may share the same neural progenitor cell, which rely on a complicated regulatory network of multiple gene pathways and signalling control of the cell processes of proliferation, specification, migration and orientation (Luo et al. 2021).

Herein, we present a review of the scientific efforts on the effects of selective breeding, feed additives and tank environment, e.g. light and tank colours, on various ornamental fish species. We also discuss candidate genes for potential genetic engineering manipulation of ornamental fish body colours and patterns. This review aims to provide a crucial reference to the scientific community to accelerate future ventures with regional ornamental fish farmers for production of novel ornamental fish varieties.

Breeding of ornamental fish

Fish breeding had long been practised since thousands of years ago in China prior to the initiation of systematic studies and breeding programmes in the 1970s (Gjedrem and Baranski 2009; Zhou and Gui 2018). In the early days of the modern breeding programme, the more systematic documentation of parental lineages over generations gradually led to the development of pedigree breeding models (Gjedrem and Baranski 2009). In freshwater ornamental fish, most breeding approaches for genetic improvement were focused on members of family Cyprinidae particularly the common carp (*Cyprinus carpio*) and goldfish (*Carassius auratus*) (Gui and Zhou 2010; Chen et al. 2020a, b). Genetic trait improvement in common carp through artificial selection involving hybridization, crossbreeding and selective breeding accelerated the production of commercial breeds (Hulata 1995; Vandeputte 2003; Zhou and Gui 2018).

During the early phases of the artificial selection programme, farmers had focused on the breeding of closely related individuals, presumably due to their similarity in expressing the targeted traits. This led to inbreeding, with consequent reduction in productivity even over a span of a few generations. With greater understanding of genetics, crossbreeding techniques was introduced involving mating between distant variaties (Gjedrem and Baranski 2010). This led to the propagation of numerous new breeds of carps, particularly in China (Wu and Zhong 1964; Li and Wang 2001; Zhou and Gui 2018). Numerous novel ornamental red carps have since been produced, frequently with the red common carp contributing as one of the parents including Xingguo red common carp, Purse red common carp and glass red common carp (Li and Wang 2001). Furthermore, other ornamental species such as Swordtail fish variety with red eyes and body have also been propagated through family selection.

However, there have been concerns over the sustainability of the improvement resulting from the artificial selection approach. Genetic improvement through selective breeding is an accumulative and time-consuming process, where only minimal improvement is gained in each cycle; substantial genetic enhancement can only be achieved and maintained through repetitive breeding over many generations (Gjedrem and Baranski 2010). Moreover, the majority of selective breeding programmes were private efforts; unsystematic, with limited scientific basis and documentation, where accurate and detailed records of parental lineages were unavailable for reproducibility or further studies (Ng 2004; Komiyama et al. 2009). The welfare of the cultured fish was frequently of little concern to the aquaculturists, including the rampant practice of culling undesired progenies (Walster 2008; Kirkwood 2012). Furthermore, selection can only target populations with varying phenotypes that are governed by the variation within the genetic pool (Gjedrem and Baranski 2009). However, even with diverse parental lineages, effective population size tends to decrease over generations, thus lowering the likelihood for further improvement (Vandeputte 2003; Lind et al. 2012). One classic example is the case of the selective breeding of *Symphysodon* spp which are currently represented by more than 69 domesticated varieties. However, all are relatively homogeneous with little significant genetic variation among each other (Ng et al. 2021), Therefore, there is a need for proper breeding planning with genetic consideration, while trialling on novel alternatives for pigmentation improvement.

Feed additives

Colour variation in ornamental fishes is exhibited through the expression of dermal chromatophores, particularly xanthophore and erythrophore-based colours originating from the intake of dietary biological pigments. This pigment uptake, modification and deposition in the fish dermal tissue is deemed species-specific (Kop and Durmaz 2008), influenced by multiple factors such as the regulation of several genes (Ahi et al. 2020; Fang et al. 2022) and dietary pigment sources.

Red, yellow and orange enhancers

Carotenoids are the major group of pigments fed to ornamental fish to generate the attractive yellow, red and orange colours on the skin (Table 1) (Das et al. 2016). Besides colouration, carotenoids are essential nutrients for the growth, reproduction and disease resistance in fish (Mente et al. 2011; Sathyaruban et al. 2021). More than 1,100 carotenoids have been identified, which are classified into two groups: carotenes (e.g. beta-carotene and lycopene) and xanthophylls (e.g. astaxanthin, lutein and canthaxanthin). These dietary carotenoids are synthetically produced or naturally extracted from animals (Sathyaruban et al. 2021), microorganisms (Venil et al. 2013), algae (Hu 2019) and plant sources (Singh et al. 2021). As there is no common carotenoid metabolic pathway in fish, its influence on the colouration of various ornamental fish species differs (Table 2). For instance, algae-based carotenoids effectively enhanced the pigmentation in koi carp (Gouveia et al. 2003; Sun et al. 2012) but not in cichlid (Kop and Durmaz 2008).

Table 1 The examples of some common carotenoids and body hue found in fish (Das and Biswas 2016; Kaur and Shah 2017)

Carotenoids	Hue displayed in fish
Astaxanthin	Red
Beta carotene	Orange
Canthaxanthin	Orange red
Doradexanthins	Yellow
Eichinenone	Red
Lutein	Greenish yellow
Lycopene	Red
Taraxanthin	Yellow
Tunaxanthin	Yellow
Zeaxanthin	Yellow orange

Synthetic astaxanthin is the most traded carotenoid, accounting for 25.70% of global carotenoids in the market in 2017 (FIORMARKETS global industry analysis, report id: 376,034). It is also the most widely-used carotenoid in ornamental fish feed such as in cichlid (Kop and Durmaz 2008), dwarf gourami (Baron et al. 2008), koi carp (Sun et al. 2012) and red devil cichlid (Pan and Chien 2009) being most efficient in enhancing body skin carotenoid deposition, thus colouration and intensity, compared to other synthetic and natural sources of carotenoids. However, not all fish are capable of effectively absorbing or utilising astaxanthin directly. Kaur and Shah (2017) classified aquatic organisms into three categories based on their metabolic actions on carotenoids: (i) converts lutein into astaxanthin (e.g. red carp), (ii) accumulates lutein and carotene in the tissue but incapable of converting these carotenoids into other forms (e.g. sea bream), (iii) converts beta-carotene into astaxanthin (e.g. prawn).

Considering the above, the selection of carotenoid supplement should be based on two criteria: (i) the type of carotenoid metabolism and ii) the targeted colour hue to be enhanced (Table 1). For instance, red carp, goldfish and fancy red carp can convert lutein (but not beta-carotene) to astaxanthin and be absorbed into the body (Teruhisa et al. 1972). Therefore, a supply of either astaxanthin or lutein is expected to enhance the redness in these fishes. By constant feeding of the appropriate carotenoids, the production and targeted colour hue and brightness in the ornamental fish is maintained, subsequently increasing its value.

The cost of synthetic carotenoids ranged between USD 250–2,000 kg^{-1}, lower than the cost of natural-derived ones that are priced between USD 350–7,500 kg^{-1} (FIORMARKETS global industry analysis in 2017, report id: 376034). However, natural-derived carotenoids are becoming more popular due to the emerging concerns on the use of synthetic carotenoids in aquaculture, such as inferior quality (Capelli et al. 2013), high market price, limited choice and risk of aquarium pollution from the petrochemical solvents used during the commercial production (Das et al. 2016; Li et al. 2020). Thus, natural-derived

Table 2 The effect of dietary pigments on the skin pigmentations of ornamental fishes

Ornamental fish	References	Supplementary	Amount (mg kg^{-1})	Source	
				Natural	Synthetic
Amphiprion ocellaris Cuvier, 1830 (clownfish)	Ebeneezar et al. (2020)	Paprika oleoresin*	20,000	✓	
		Turmeric oleoresin	20,000	✓	
		Chlorophyll oleoresin	20,000	✓	
		Mixed oleoresin*	20,000	✓	
	Díaz-Jiménez et al. (2021)	Astaxanthin	5000*^	✓	
		Astaxanthin	10000^	✓	
		Astaxanthin	15,000	✓	
		Lutein	5000		✓
		Lutein	10,000		✓
		Lutein	15,000		✓
Astronotus ocellatus (Oscar fish)	Mohammadiazarm et al. (2021)	Spirulina	13,750	✓	
		Spirulina	27,500	✓	
		Spirulina	55,000*	✓	
Carassius auratus (goldfish)	Gouveia et al. (2003)	*C. vulgaris*	80*	✓	
		H. pluvalis	80^	✓	
		A. maxima	80	✓	
		Astaxanthin	80		✓
	Margareta et al. (2021)	Astaxanthin + *spirulina* sp.	0 + 0%	✓	✓
		Astaxanthin + *spirulina* sp.	0.1 + 1%^	✓	✓
		Astaxanthin + *spirulina* sp.	0.1 + 2%	✓	✓
		Astaxanthin + *spirulina* sp.	0.1 + 3%	✓	✓
Cichlasoma citrinellum (red devil)	Pan and Chien (2009)	Astaxanthin	80		✓
		Astaxanthin	160*		✓
		H. pluvialis	80	✓	
		H. pluvialis	160*	✓	
		Beta-carotene	80		✓
		Beta-carotene	160		✓
Cichlasoma severum subsp.,Heckel 1840 (cichlid)	Kop and Durmaz (2008)	Astaxanthin	50*		✓
		Beta-carotene	50		✓
		P. cruentem	50	✓	
Colisa lalia (dwarf gourami)	Baron et al. (2008)	astaxanthin (Lucantin Pink)	100 ppm^		
		Betalain (beetroot juice powder)	100 ppm	✓	
		Anthocyanin (Overseal Carantho powder)	100 ppm	✓	
Cyprinus carpio (Koi carp)	Gouveia et al. (2003)	*C. vulgaris*	80* +	✓	
		H. pluvalis	80	✓	
		A. maxima	80	✓	
		Astaxanthin	80		✓
	Kurnia et al. (2019)	Red dragon peel	50,000	✓	
			100000^	✓	

Table 2 (continued)

Ornamental fish	References	Supplementary	Amount (mg kg^{-1})	Source	
			150,000	✓	
	Maiti et al. (2017)	Beet root powder	1% of total diet*	✓	
		Carrot peel powder	1% of total diet	✓	
		Tomoto peel powder	1% of total diet	✓	
		Mixture of above three peels	1% of total diet^	✓	
	Prabhath et al. (2019)	Carotenoids	10	✓	
		Carotenoids	20	✓	
		Carotenoids	30^	✓	
		Phycocyanin	100	✓	
		Phycocyanin	200	✓	
		Phycocyanin	300	✓	
	Sun et al. (2012)	Carophyll® red	1500*^		✓
		Rhodopseud anonas palustris	200,000	✓	
		Effective microorganisms	200,000	✓	
		Spirulina platensis	75,000*^	✓	
Macropodus chinensis (round tailed paradise fish)	Lee and Lee (2008)	*Parphyra* powder	2% of total diet*	✓	
		Spirulina powder	1% of total diet	✓	
		Astaxanthin	2% of total diet^	✓	
		Paprika extract	1% of total diet^	✓	
Maylandia estherae Konings, 1995 (Red zebra cichlid)	Unver and Hamzaçebi (2020)	*Beta vulgaris* ruba	50	✓	
		Henna	50	✓	
		Astaxanthin	50		✓
Pseudochromis fridmani (Orchid dottyback)	Jiang et al. (2019)	*H. pluvalis*	25 ppm	✓	
		H. pluvalis	50 ppm	✓	
		H. pluvalis	75 ppm^	✓	
		H. pluvalis	100 ppm^	✓	
		Carophyll Pink®	25 ppm		✓
		Carophyll Pink®	50 ppm		✓
		Carophyll Pink®	75 ppm		✓
		Carophyll Pink®	100 ppm^		✓
Symphysodon spp. (discus fish)	Song et al. (2017)	astaxanthin	50		✓
		Astaxanthin	100		✓
		Astaxanthin	200^		✓
		Astaxanthin	300		✓
		Astaxanthin	400		✓
Xiphophorus helleri (orange sword tail fish)	Monica et al. (2019)	Anthocyanin	400^	✓	
	Wagde et al. (2018)	Beta-carotene (Carrot)	200	✓	
		Beta-carotene (Carrot)	250	✓	
		Beta-carotene (Carrot)	300^	✓	
		Beta-carotene (Spinach)	200	✓	
		Beta-carotene (Spinach)	250	✓	

Table 2 (continued)

Ornamental fish	References	Supplementary	Amount (mg kg^{-1})	Source
Zacco platypus (pale chub)	Lee and Lee (2008)	Beta-carotene (Spinach)	300^	✓
		Parphyra powder	2% of total diet	✓
		Spirulina powder	1% of total diet*	✓
		Astaxanthin	2% of total diet^	✓
		Paprika extract	1% of total diet^	✓

*Indicated highest carotenoid deposition in fish body; ^ indicated highest colour intensity displayed in fish body skin

carotenoids from photosynthetic organisms, including microalgae and plants are considered excellent substitutions to synthetic carotenoids in ornamental fish feeds (Hu 2019; Yusoff et al. 2020; Singh et al. 2021). For instance, Wagde et al. (2018) recommended that a supply of raw carrot fruits for as little as 1.33 mg kg^{-1} or 1.82 mg kg^{-1} of raw spinach could efficiently enhance the orange hue in swordtail. However, natural whole foods such as tomato and carrot containing high beta-carotene contents may not be suitable as the sole carotenoid source, as beta-carotene are deemed ineffective for enhancement of body pigmentation in many ornamental fish, such as cichlids (Kop and Durmaz 2008) and betta fish (Thongprajukaew et al. 2014).

Microalgae serve as an excellent pigment source, especially for algae-eating fishes (Rout et al. 2013), as they are capable of accumulating high amounts of various carotenoids (referred to as carotenogenesis), such as astaxanthin, beta-carotene, phytoene, lutein under extreme growth conditions, e.g. nitrogen deficiency (Henríquez et al. 2016; Pérez-Legaspi et al. 2020; Lu et al. 2021). In addition, numerous technological breakthroughs such as industrial bioreactor reformation and strain improvement of microalgae through genetic engineering have led to substantial cost reduction in natural carotenoid pigment production (Lin et al. 2019), a great boost to the ornamental fish industry. Astaxanthin-producing microalgae species, such as *Haematococcus pluvialis*, *Chlorococcum* sp., *C. vulgaris* are commercially cultured in many countries for human and animal consumptions (Pérez-Legaspi et al. 2020). These microalgal carotenoids possess very high bioactivities in numerous physiological functions, playing pivotal roles in the pharmaceutical and cosmetic industries (Patel et al. 2022). Thus, the feeding of microalgal carotenoids not only render comparable or better colouration effects than synthetic carotenoids (Gouveia et al. 2003; Pan and Chien 2009), but also offers health benefits.

Blue and violet enhancers

Phycobiliproteins are light-harvesting compounds that are essential for photosynthetic organisms such as cyanobacteria, red algae and crytophytes (Eriksen 2016). Four main types of phycobiliproteins occur in nature; phycoerythrin, phycocyanin, phycoerythrocyanin and allophycocyanin that are classified based on the absorption peak and chemical structures (Pagels et al. 2019).

Cyanobacteria and plants are recognised as the major sources of phycobiliproteins. Commercial fish feeds such as Artkua® blue color (https://artakua.com/en/portfolio-items/blue-color/) and Dainichi COLOR SUPREME (https://dainichi.com/CichlidFood-ColorSupreme.dmx) developed for blue aquarium fish colour enhancement, consist of phycobiliproteins-producing organisms, such as spirulina. A feeding trial conducted on angelfish (*P. scalare*) demonstrated overall colour enhancement (including blue) with the supplementation of spirulina flour to its commercial basal diet (Lili et al. 2021). Even though commercial production has yet to be reported, scientific efforts are currently focused on optimising the culture parameters and extraction methods, with particular emphasis on phycocyanin from spirulina (Silva et al. 2020; Tan et al. 2021).

Plant pigments, anthocyanins and betalains are commonly found in the Caryophyllales plants (except Caryophyllaceae and Molluginaceae) (Tanaka et al. 2008; Khoo et al. 2017; Rahimi et al. 2019). Anthocyanins are the causative pigments for plant blue, purple, violet, magenta, red and orange colouration (Jackman and Smith 1996). One interesting property of the anthocyanins is its dynamic colour changes based on the pH; it is red in acid condition, change to purple in pH 7 and becomes blue in alkaline condition, all due to its ionic structural modification (Tanaka et al. 2008; Khoo et al. 2017). Betalains occur as two types of pigments; betaxanthins (yellow-orange) and betacyanins (red-violet) (Jackman and Smith 1996). These two plant pigments have long been used as natural colourants in food (Tanaka et al. 2008). Previous studies have shown that 450 mg microencapsulated and 160 mg roselle-extracted anthocyanin could elevate the pigment cell density, growth and feed conversion rates in goldfish (Pérez-Escalante et al. 2012; Vanegas-Espinoza et al. 2019).

Other potential blue enhancers highlighted in the last two decades, include pyocyanin (DeBritto et al. 2020) and marennine (Gastineau et al. 2014). Pyocyanin is a bacterial biologically active phenazine pigment exclusively produced by 95% of the *Pseudomonas aeruginosa* strains (DeBritto et al. 2020; Gonçalves and Vasconcelos 2021). Due to its antibacterial and accessibility properties (Gonçalves and Vasconcelos 2021), the effects of pyocyanin supplement have been examined for growth, cytotoxicity response and carotenoid content in broilers (Ashour et al. 2021), rainbow trout (Priyaja et al. 2016) and cichlid (Ezhil and Narayanan 2013). Another blue enhancer is the marennine or marennine-like blue pigments which were discovered particularly in the diatom, genus *Haslea* and is known to enhance the greening of oysters (Gastineau et al. 2014). Despite the lack of data on the effects of bacterial blue pigment on ornamental fishes, it appears a good blue enhancer candidate for the ornamental fish industry.

Rearing environment

The ornamental fish body colour is known to change dynamically in response to environmental stimuli such as changes in tank background colour and light (Table 3).

Tank colour

The effect of background (environment/tank) colour on cultured fish has been well studied since several decades ago and the evidence show strong correlation between fish colour pigments and tank colour (Eslamloo et al. 2015; Asra Nor Izaty and Norazmi-Lokman 2019; Díaz-Jiménez et al. 2021; McLean 2021). Rearing ornamental fish in colourful tank has been shown to induce temporary or permanent pigmentation, depending on the regulatory mechanisms associated with the skin chromatophores (Eslamloo et al. 2015; Asra Nor Izaty and Norazmi-Lokman 2019).

Most previous studies (Table 3) have demonstrated a decrease in hue brightness in fish reared in white coloured tank with varying growth rate. Skin response towards the tank colour is postulated to be mediated by the background matching mechanism, a neuroendocrine regulated process to control pigment transport, dispersal and aggregation in the chromatophores (McLean 2021). As colour change is energy-consuming (Rodgers et al. 2013), it is postulated that only tank colours that resemble the wild habitat of the species would favour growth. For instance, the natural habitat of yellow gourami fish is from the middle to the top layer of slow flowing rivers or lakes which is highly exposed to sunlight, thus a high affinity for white background. This species has been recorded with increased weight and paler body colour when reared in a white tank (Asra Nor Izaty and Norazmi-Lokman 2019). The body colour intensity of this species increased when reared in a green tank which matches the tank colour, but however, decreased in weight. In contrast, a different scenario was observed in the clownfish, *Amphiprion ocellaris* (Díaz-Jiménez et al. 2021). Clownfish lives in shallow seawater and is protected and sheltered by their sea anemone symbiont from direct sunlight; excessive light could hinder their reproduction (Fobert et al. 2019). The clownfish could still display a yellow body, although with almost invisible bands when grown in a white tank, but the intense red colour with defined black bands is only expressed when reared in the preferred black tank and this is coupled with a high survival rate. These evidences in yellow gourami (Asra Nor Izaty and Norazmi-Lokman 2019) and clownfish (Díaz-Jiménez et al. 2021) imply that background matching mechanism and fish global development are probably interdependently regulated.

Light

Light is indispensable for ornamental fish to function optimally, especially the influences of light intensity and photoperiod in a species that inhabit the top layer of an aquatic environment (Boeuf and Le Bail 1999). Light reflection provides vision and supports fish

Table 3 The environmental stimuli and the changes in ornamental fish body colour or pattern observed in the previous studies

Stimuli	Ornamental fish	Outcome	References
Background/Tank colour	*Carassius auratus* (goldfish)	Skin colour loss and highest growth in white background Golden colour maintained in other colours Red and blue background resulted in immunosuppression	Eslamloo et al. (2015)
	P. reticulate (guppies)	Skin darkens in black background and lighten in white background Colour changed-fish consumed more food pellets	Rodgers et al. (2013)
	Trichopodus trichopterus (Yellow gourami)	Green tank-reared fish increased in colour intensity White tank-reared fish increased in body weight	Asra Nor Izaty and Norazmi-Lokman (2019)
	Amphiprion ocellaris (clownfish)	Black: intense red hue with well-defined black bands White: yellowish hue without visible bands	Díaz-Jiménez et al. (2021)
	Pangasius hypophthalmus (river catfish)	Black: pure black body colouration with lower growth rate White and green: lower black intensity with higher growth rate	Nawang et al. (2019)
	Lophiosilurus alexandri (carnivorous freshwater catfish)	White: highest body brightness and paler Black and blue: lower brightness with more pigmented skin but caused stress	Costa et al. (2016)
	Dawkinsia filamentosa (filament barb)	Black: higher growth and survival rate with improved body pigmentation and carotenoid intake White: poor growth, survival and body colouration	Padhi et al. (2022)
	Melanotaenia australis (western rainbow)	Dark: more dark-pigmented Pale: developed paler body	Rodgers et al. (2010)
Light intensity	Neon tetra fish	Structural colour of lateral stripe changed when light change from blue-green (light-adapted) to indigo (dark-adapted)	Gur et al. (2015)
	Amphiprion ocellaris (clownfish)	Body and fins brightness increased as light intensity decreased Higher orange hue on fins at higher light intensity	Yasir and Qin (2009)
	Oryzias latipes (Medaka)	Xanthophore pigments aggregated at 9000 lx	Oshima et al. (1998)

Table 3 (continued)

Stimuli	Ornamental fish	Outcome	References
	Carassius auratus (goldfish)	0 lx showed poor growth and poor skin pigments development No difference between sunlight and artificial light	Baite et al. (2010)
	Apolemichthys xanthurus (angelfish)	Low light (250–500 lx) recorded with greatest growth and skin colour enhancement	Rajeswari et al. (2017)
Light intensity and wavelength	*Melanotaenia australis* (rainbow fish)	Long wavelength and low light intensity triggered increase in area and red colour brightness of the body colour patterns	Kelley et al. (2012)
Light source	*Amphiprion clarkia* (clownfish)	Artificial light triggered colour changed from light brown with white bars to dark black with milky white bars	Uthayasiva et al. (2014)
	Zebrafish	2 dpf embryos: melanosome dispersed under visible light or UV light 3 dpf and older: melanosome aggregated under visible light and dispersed under UV light	Mueller and Neuhauss (2014)
Photoperiod	Zebrafish	2 dpf larvae: fast dispersion of melanosome regardless of photoperiod 3 dpf and later: continuous illumination led to delayed pigment aggregation	Shiraki et al. (2010)
	Poecilia sphenops (Orange balloon Molly)	Long photoperiod led to brighter skin colour and higher carotenoid content	Zutshi and Singh (2021)
Soil colour (varied by leaf litter)	*Sailfin tetra*	higher colour intensity in dark environment	Pinto et al. (2020)
Temperature	*Carassius auratus* (gold fish)	Maximum pigmentation observed between 26 to 30 °C	Gouveia and Rema (2005)

health (Stevens et al. 2017), where the optimum culture environment is attained when it is aligned to its natural habitat light spectrum. According to Marshall et al. (2019), in the presence of light, vision unlocks several crucial survival processes in fish, including mate choice, feeding, agonistic behaviours and camouflage. Studies have revealed that numerous ornamental fishes, such as goldfish (Baite et al. 2010) and angelfish (Rajeswari et al. 2017) exhibit poor growth and reduced body pigmentation when reared in poor or no lighting condition.

The level of light intensity influences the colour development and the effects may vary among species and is not permanent. For instance, the brightness of body and fins of clownfish increased when exposed to lower light intensity, while a more pronounced orange hue was reported at higher light intensity (Yasir and Qin 2009). In medaka fish, the skin xanthophore pigments aggregate (paler) under high light intensity exposure such as at 9,000 lx but the pigments disperse following a reduction in light intensity (Oshima et al. 1998). Similarly, the red body colour brightness of rainbow fish was also found to increase when exposed to low luminescence (Kelley et al. 2012).

The effects of different light sources on ornamental fish pigmentation reveal varying responses in different species. Artificial white light enhanced light brown and white bars to dark black with milky white bars in the clownfish (Uthayasiva et al. 2014) in contrast to the zebrafish, *Danio rerio* where melanosome aggregated temporarily and resulted in paler colour under the same lighting condition (Mueller and Neuhauss 2014). However, the melanosome aggregation in zebrafish was reversed when shifted to ultra-violet (UV) light, serving its protective function (increased pigmented layer) against UV light. Interestingly, body pattern could also be impacted by different lighting. The structural colour of lateral stripes on the neon tetra fish, *Paracheirodon innesi* changed from blue-green to indigo when moved away from light (Gur et al. 2015). Long wavelength light spectrum coupled with low light intensity was found to induce the spreading of pigmented area (Kelley et al. 2012).

Lighting greatly influences the fish circadian clock, affecting its development especially the melatonin rhythmic secretion which subsequently influences physiological activities, including skin pigmentation (Sánchez-Vázquez et al. 2019). The effects of photoperiod have been reported in several ornamental fishes, such as in the orange balloon molly, *Poecilia latipinna* (Zutshi and Singh 2021) and zebrafish (Shiraki et al. 2010). Both fish exhibited brighter skin colour, higher skin carotenoid content and delayed pigment aggregation under long photoperiod or continuous illumination and good growth development. However, most ornamental fish require a certain duration of dark period for their growth and breeding (Chen et al. 2020a, b).

Optimising rearing conditions: feed supplement, lighting and temperature conditions

In order to enhance pigmentation without compromising the health of the precious ornamental fish, the tank environment must emulate its wild habitat. This would require that the critical parameters such as feed supplement, lighting and temperature be jointly factored into the total environmental conditions and not to be considered in silos.

Sunlight accessibility and the background brightness (i.e. the dark leaf litters or the base soil colour) require full consideration. Rearing ornamental fish that favours darker environment is easier and straightforward, such as angelfish (Rajeswari et al. 2017) and yellow gourami fish (Asra Nor Izaty and Norazmi-Lokman 2019), as they grow well in the dark while pigmentation is enhanced. On the contrary, for fish that favour bright environment, pigment enhancement may be more challenging as they tend to turn paler under such conditions. Unfortunately, it is not ideal to rear these fishes under darker conditions to trigger the pigmentation enhancement, as this digresses from its natural habitat environment and hence require increased energy consumption (Rodgers et al. 2013), retarding its growth and interrupting social signalling (Kelley et al. 2016). Therefore, it would be better to opt for consistent carotenoid feeding to enhance the pigmentation.

Generally, the recommended minimum supplementation of the most common carotenoid, synthetic or natural astaxanthin, for pigmentation enhancement is 50 mg kg^{-1}, a greater amount is likely to result in elevated colouration or deposition in the fish skin, as observed in cichlid (Kop and Durmaz 2008), dwarf gourami (Baron et al. 2008) and paradise fish (Lee and Lee 2008). Diler and Dilek (2002) suggested 35–100 ppm of carotenoid supplement in the breeding of several ornamental species at the juvenile stage, including goldfish and trout. However, beyond a certain limit, the improvement stops, but to date there has been no report of any lethal effect on the ornamental fish due to excess amounts. A certain duration is required for the colour intensity enhancement to occur after the onset of carotenoid feeding. In the orchid dottyback, *Pseudochromis fridmani*, at least 70 days of consistent astaxanthin feeding (vegetative *H. pluvialis*) is required to improve the magenta/raspberry colouration to achieve commercial standard (Jiang et al. 2019). A previous study also showed that inclusion of microbial carotenoid-rich food in *X. helleri* improved colouration and growth after 28-days (Dharmaraj and Dhevendaran 2011). The use of carotenogenic marine yeast, *Rhodotorula paludigena* VA 242 also enhanced the pigmentation and carotenoid content in Koi Carp in a 60-days feeding trial (Rekha et al. 2022).

As described earlier, blue colorants have shown positive results in preliminary blue colour enhancement studies. The current price of phycobiliprotein extract is estimated in the range of USD130 and USD 15,000 per gram, depending on the purity (Pagels et al. 2019). Thus, direct feeding with the blue pigment-rich organisms instead of purified pigments, such as spirulina (Marzorati et al. 2020) and Andean cyanobacteria (Galetović et al. 2020) may be more cost-efficient in improving blue colouration. In fact, spirulina is also an excellent source of other biological pigments (e.g. carotenoids), which may be fed to simultaneously enhance multi spectrum of colours, as observed on the angel fish in 10–40 days trials (Lili et al. 2021). Furthermore, the antibacterial and antioxidant properties of bacterial (pyocyanin and marennine) pigments confers resistance against common aquaculture pathogen such as *Vibrio* and *Staphylococcus aureus* (Ezhil and Narayanan 2013; Prasetiya et al. 2020). Thus, further research is needed to determine the optimum dosage that would offer health benefits without cytotoxicity induced in the ornamental fish.

Light settings including a minimum photoperiod of 12–14 h (Chen et al. 2020a, b) of white light under acceptable level of UV, coupled with light intensity similar to ambient sunlight and bright tank background, are recommended for ornamental fish species that naturally live in the top layer of aquatic environment. On the other hand, the opposite settings, such as darker tank base or background with limited light exposure and photoperiod is suitable for those naturally inhabiting near the underwater with limited sunlight exposure and leaf litters, for example the genus *Betta* (Ng 2016). As previously reported, constant exposure of light/darkness or red light increase the risks of growth abnormalities, while blue light induces better hatching rates and growth (Sánchez-Vázquez et al. 2019). Therefore, the light settings should be carefully designed to target both fish skin pigmentation and health.

Limited studies have been conducted on the effect of temperature on fish colouration although it is an important factor in fish generally, especially of exotic ornamental species. Careful setting and monitoring of temperature are essential to increase the survival rate of the ornamental fish. A study (Yanar et al. 2019) which investigated the thermal tolerance of 13 ornamental fish species showed that, goldfish, koi, doctorfish, sailfin molly and zebrafish could be reared outdoor in subtropical climate, whereas peppered cory, tiger barb and blue dolphin cichlid require shade in tropical and subtropical climates.

Advancing the ornamental fish industry through genetic engineering

Application of transgenic technology for genetic improvement of cultured fishes had been mooted in the early 1990s (Fletcher and Davies 1991), after the successful generation of transgenic goldfish (Zhu et al. 1985). Since the first report on the transgenic zebrafish (Glofish) (Wan et al. 2002), several transgenic lines of ornamental fish have been produced; medaka (Zeng et al. 2005; Cho et al. 2013, 2014) and tetra fish (Pan et al. 2008; Leggatt and Devlin 2020). As in Glofish, the fluorescent genes namely green fluorescent protein (*gfp*) (Wan et al. 2002; Zeng et al. 2005; Leggatt and Devlin 2020), yellow fluorescent protein (*yfp*), cyan fluorescent protein (*cfp*) (Cho et al. 2014) and red fluorescent protein (*rfp*) (Wan et al. 2002; Pan et al. 2008) have been successfully transferred to produce attractive luminous fish. The skeletal muscle gene promoters regulate the fluorescent genes to express various beautifully glowing colours under different light emission (Cho et al. 2014).

However, ethical concerns have been raised on the stability of the targeted traits, the sustainability of the transgenic fish as well as the environmental impacts of escapees, which could easily occur. While Snekser et al. (2006) reiterated that the social activities of Glofish was not affected, Howard et al. (2015) reported that the male Glofish was inferior in mate competition with wild type and the transgenic trait was completely wiped out after 15 generations. Furthermore, Glofish that were reared in natural headwater creeks showed early maturation and produced smaller eggs (Magalhães et al. 2022). Thus, the sustainability of the current transgenic technologies in ornamental fish industries remains in doubt.

Subsequently, technology advancement of next-generation sequencing has led to an explosion of new knowledge with wide applications, including for the improvement of the ornamental fish industry. Transcriptomic analysis has enabled the identification of genes responsible for the expression and regulation of skin colouration and pattern formation in numerous ornamental fish species and groups, such as zebrafish (Iwashita et al. 2006; Huang et al. 2021), Nile tilapia (Lu et al. 2022), Cyprinidae fish (Yu et al. 2021), goldfish (Gan et al. 2021) and red crucian carp (Zhang et al. 2017). In particular, extensive studies on the animal model zebrafish have generated massive output that have unravelled the regulation pathways of skin colouration. The detailed molecular mechanisms of fish pigmentation and the list of pigment genes are well-documented (Baxter et al. 2019; Luo et al. 2021). To date, several genetic tools have been developed to exploit gene editing of the targeted gene, such as zinc finger nucleases and TALENs (Barman et al. 2017). In particular. advanced tool such as CRISPR-Cas9 system (Huang et al. 2021; Yang et al. 2021; Yue et al. 2022), had facilitated the precise manipulation of skin pigmentation and body pattern in zebrafish and betta fish (Lu et al. 2022). Therefore, these pigment genes are excellent candidates in genetic engineering to manipulate fish colouration and patterns.

Quantitative trait locus (QTL) analysis is another potentially powerful tool in ornamental fish morphological enhancement. It has been explored in elucidating the causative pigment genes in ornamental fish species within populations (Irion and Nüsslein-Volhard 2019), such as in tilapia (Li et al. 2019; Liu et al. 2022; Xiong et al. 2022) and cichlid fishes (O'Quin et al. 2013; Albertson et al. 2014; Henning et al. 2014). Moreover, QTL mapping through genome-wide association studies (GWAS) has facilitated the simultaneous identification of multiple coloration and pattern traits that contribute to the diverse variation within a population (Zhang et al. 2022). For instance, the QTL mapping in GWAS of Betta fish identified the causative genes responsible for the various phenotypes produced by Royal Blue crossbred (Zhang et al. 2022). Certainly, this is another approach for moving forward in this area of study.

Manipulation of body colour through genetic engineering

Melanogenesis is the pathway that is responsible for melanin synthesis, which is modulated by several pathways such as MAPK, endothelin and WNT signalling pathways in the upstream. One of the crucial rate-limiting enzymes in this pathway is tyrosinase, encoded by *tyr* gene, which catalyses the oxidation of tyrosine to produce melanin and other pigments. This gene could be targeted to modify the black or brown colour in ornamental fish. For instance, *tyr* gene knockout via CRISPR-Cas9 in *C. auratus* successfully suppressed melanin production and down-regulated the other melanin-producing genes such as *mitf*, *dct* and *sox10*, subsequently resulting in total albinism (Liu et al. 2019). The *tyr* was also mutated in cichlid, *A. burtoni* and inhibited melanophore differentiation (Li et al. 2021). Such approach would be useful to suppress the dominant top-embedded melanic black colour and permit the expression of the other attractive colourful pigments underneath the super-imposed layers of ornamental fish skin.

The microphthalmia-associated transcription factor (*mitf*), is the "master regulator" in the development and differentiation of melanophores (Luo et al. 2021). In ornamental red crucian carp, the decreased expressions of *mitfa* and other melanin synthesis-related genes are responsible for the body colour change from gray to red (Zhang et al. 2017). Moreover, the two variants of *mitf*, *mitfa* and *mitfb*, actively express and modulate the cutaneous and eye melanophores respectively (Luo et al. 2021), excellent candidate genes for the simultaneous manipulation of eye and skin black colour. Another potential gene for colour manipulation is the solute carrier family 24 member 5 (*slc24a5*), which is associated with the regulation of melanophore development and distribution in vertebrates. In particular, the *slc24a5* mutation in ornamental Cyprinids lead to loss of melanophores in both larva and adult fish (Yu et al. 2021).

Aside from the black and brown colours, xanthophore-related genes revealed in transcriptomic studies also allow the manipulation of xanthophore-based colours (i.e. orange, red and yellow colour) in ornamental fish. In order to enhance the xanthophore-based colours, pathways leading to the accumulation of pteridines and carotenoids may be targeted. Transcriptomic studies conducted on red tilapia and Bengal loach, *Botia dario*, showed up-regulation in the genes related to lipid metabolism and carotenoid transport, i.e. *scarb1*, *starb5*, *plin2*, *rdh12* and *stard10* in the yellow and red pigmented regions (Tripathy et al. 2019; Fang et al. 2022). These genes may be considered to regulate carotenoid accumulation in the fish skin, subsequently increasing the carotenoid-based colour hue or intensity in the ornamental fish. On the other hand, genes involved in pteridine metabolism are also useful to engineer body colour change in ornamental fish. Both *pts* gene (yellow colour expression) and *gchl* (differentiation of xanthophore and melanophore) (Braasch et al. 2007) are crucial in pteridine metabolism and potential candidate genes for xanthophore-based colour enhancement.

Iridophore, a pigment cell that contains guanine or purine reflective plates, produces iridescence on the fish body. The iridophore-related genes are often linked to melanophore and xanthophores (Petratou et al. 2018). For instance, Higdon et al. (2013) identified 62 common enriched genes in melanophores and iridophores of zebrafish, implying that the development of melanophores and iridophores was regulated concurrently via cell–cell interaction. These genes are candidate genes that could potentially be altered to target the melanophores and iridophores simultaneously.

Several enzymes are involved in guanine metabolism during the formation of reflective iridescent plates within the iridophores (Higdon et al. 2013). The interactions among their multiple metabolic pathways recycles the phosphorobosyl pyrophosphate, a substrate for purine synthesis, completing the guanine cycle. One of these enzymes, leucocyte tyrosine kinase (*ltk*) acts as the core enzyme in modulation of iridophore establishment, proliferation and survival (Fadeev et al. 2016; Mo et al. 2017). During the modulation, the ligands of both leucocyte tyrosine kinase and anaplastic lymphoma kinase are speculated to induce iridophore differentiation (Mo et al. 2017), whereas *transparent* gene which encodes for the mitochondrial protein Mpv17 is responsible for iridophore survival (Krauss et al. 2013). Hence, the genes encoding these functional proteins could be targeted for iridophore density and survival.

The manipulation of iridophores may also be accomplished by targeting the transcriptional factors (TFs). Several TFs, *sox10*, *tfec, pnp4a* and *mitfa* have been identified as the key players in the complex gene regulatory network of iridophore (Petratou et al. 2018). In the neural crest, iridophore specification from the multiple neural crest progenitors involves a positive feedback loop between *ltk* and *tfec* which is *sox10*-dependent. The *sox10* gene is also actively involved in driving the molecular mechanism in iridophore development and couples with *tfec* in regulating the expression of the key differentiation gene, *pnp4a.* As *pnp4a* mutation led to the total shutdown of guanine metabolism in the medaka iridophores (Kimura et al. 2017), the potential of *pnp4a* gene engineering in producing attractive see-through skin phenotype in ornamental fish could be exploited.

Manipulation of body pattern through genetic engineering

In addition to colours, the exquisite body patterns too are of high value (Fig. 1). Based on zebrafish and anemonefish models, these pigment patterns predominantly arise from the complex cellular interactions and molecular mechanisms underlying the melanophores, xanthophores and iridophores (Patterson and Parichy 2013; Klann et al. 2021). Therefore, establishing the desired pigment pattern through gene editing is deemed more complicated, since a common regulatory gene mutation may trigger undesirable changes in the arrangement of more than one pigment cell types. For instance, when the *transparent* gene in zebrafish was mutated, the melanic stripes turned into spots following the huge reduction in iridophores and melanophores (Krauss et al. 2013).

The melanic horizontal and vertical bar stripes are common pigment patterns observed in many ornamental fish, such as zebrafish, discus, red tilapia, clownfish etc. The stripes are the result of the unique organisation of different pigment cell types (Klann et al. 2021; McCluskey et al. 2021a), where melanophores form black stripes, xanthophores form light interstripes while iridophores exist in both regions (Krauss et al. 2013). A conserved zinc finger gene (*bnc2*) is postulated to be the "switch-gene" that determines the fate of stripe patterning in the zebrafish. It acts as the "master booster" in promoting development and establishment of the three chromatophores; a mutation in the *bnc2* would lead to the loss of stripes and interstripes (Patterson and Parichy 2013). Furthermore, the properties of stripes could be controlled through *asip* and *tspan* genes. The *asip1*-mutant induces changes in the number of different chromatophores in the skin and scales, subsequently increasing the thickness of the melanic horizontal stripes. On the other hand, *tspan* is responsible in maintaining the stripe boundaries, where mutated *tspan* created intermingled stripes in the mutants (Inoue et al. 2014). White bar stripes are modulated through another different set of genes. The spatial white vertical bar stripes (iridophore-based) in clownfish displayed on top of the dark body background are regulated by several requisite genes including *fhl2a, fhl2b, saiyan, gpnmb,* and *apod1a*, through the maintenance and organisation of iridophores (Salis et al. 2019).

Manipulation of the number of horizontal and bar stripes, however, requires different approaches, as the mechanisms for their formation are different. Horizontal stripes are formed when melanophores proliferate along the horizontal myosepta, starting from metamorphosis into adult, whereas the bar number and position dynamically changes as the body length increases (Hendrick et al. 2019). The difference in the formation of the two patterns most probably depends on distinct regulatory pathways, therefore it is strongly recommended to target the genes associated with neural crest progenitor migration, during the metamorphosis stage, to reduce or increase the number of bars.

Fish display dorso-ventral countershading pattern, with dark and light colour, respectively dominant at the dorsal and ventral surfaces. The agouti-signalling protein, encoded by *asip1*, known to be the antagonist of melanisation (Cerdá-Reverter et al. 2005), acts as one of the components in maintaining the countershading pattern in zebrafish and goldfish (Cal et al. 2019). By disrupting the *Asip1*, the melanisation could spread and become established in the ventral region (Cal et al. 2019). Such axial developments (e.g. anterior–posterior, dorsal–ventral) are also under the influences of pattern developmental genes, as observed in the African cichlids (Ahi and Sefc 2017b, 2017a) and wild discus fish (Ng et al. 2023).

There is a scarcity of information on the mechanism of spot formation in ornamental fish. The manifestation of either stripes or spots on two closely-related zebrafish (*D. quagga* and *D. kyathit*) was investigated on early adult stage individuals, which coincides with the establishment and organisation period of the chromatophores (McCluskey et al. 2021b). Although the switching between stripes and spots could be achieved through a single gene change as reported in the widely studied *D. rerio*, complex mechanisms involving multiple genes and gene signallings were detected in these two zebrafish species (McCluskey et al. 2021b). As in red tilapia, wintering black spot was revealed to be regulated by multiple environmental factors under the influences of three potential causative genes, namely *sena-4c*, *uvssa* and *htr2cl1* (Xiong et al. 2022).

Interestingly, growth rate may also be involved in fish pattern formation. Changes in growth rate and sequences of chromatophores could promote further pattern modulation and orientation on various pattern formation, including vertical stripes and maze-like patterns in the zebra fish (Owen et al. 2021). For instance, directional elongation of stripe patterning was driven by the spreading of the chromatophores during growth and subsequently affects the pigment orientation in zebrafish (Míguez and Muñuzuri 2006).

Nonetheless, it is definitely more challenging to manipulate body patterns in ornamental fish, compared to the body colour changes, due to the ambiguous and species-specific coordination among different chromatophores, which is deemed more complicated in some ornamental fish species. The advancement of next generation sequencing and efficient gene editing tool such as CRISPR could facilitate faster target gene discovery for pattern manipulation.

Challenges in pigment gene disruption

The modification of endogenous pigment genes can be hindered by pleiotropic effects of genes regulating the body colouration or patterns in some ornamental fish. For instance, the expression of melanic side-spotting patterns varies among members of family Poeciliidae due to the influences of multiple selective factors and polygenic control (Zerulla and Stoddard 2021). The concerted interaction among multiple genomic regions regulating pigmentation (hypermelanic phenotype), vision and sleep has been documented in the blind cave fish (*Astyanax mexicanus*) (Gross et al. 2016; O'Gorman et al. 2021). Under such pleiotropic effects of pigment genes, imprudent attempt of mutating a candidate pigment gene will rock the boat and likely lead to severe disruption on other survival traits. Although the identification and selection of causative genes for colouration and pattern modifications are highly challenging, it is a highly worthwhile effort in producing novel, attractive domesticated ornamental fish.

Conclusion

Manipulating the colour and patterning in ornamental fish could be achieved through multiple environmental stimuli and genetic factors. Focusing on high dietary supplement of natural carotenoids (versus synthetic) and non-carotenoid pigments has proven to be a more efficient approach to enhance the body colour hue and brightness while also improving the general health of the ornamental fish. Settings of optimum environmental variables, such as tank colour, light intensity, light sources or colour and photoperiod, are important considerations. With the flourishing of genetic engineering techniques, the manipulation of pigment genes would facilitate the production of mutated varieties in ornamental fish species with various body colours and patterns, circumventing time-consuming traditional selective breeding process. However, as many candidate genes are also crucially involved in other developmental and survival processes, careful consideration is warranted in many aspects (e.g. choice of genetic tools) to reduce the risk of severe disruption on the fish growth and survival. The effective collaboration among scientists and ornamental fish industry players is of prime importance to initiate knowledge-sharing, amelioration in fish breeding techniques and establish functional taxonomic classification on new ornamental fish varieties.

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Data availability All data generated or analysed during this study are included in this published article.

Declarations

Conflict of interest All authors certify that they have no conflicts of interest to declare for this project.

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