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Blue and Red Light Color Combinations Can Enhance Certain Aspects of Digestive and Anabolic Performance in Juvenile Steelhead Trout *Oncorhynchus mykiss*

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The light spectrum varies with the altitude of the sun and shows different light colors in clear water. In this study, we aimed to investigate the response of juvenile steelhead trout *Oncorhynchus mykiss* (34.67 ± 2.69 g initial weight) under different light color conditions. The effects of different blue and red light combinations on plasma biochemical parameters, digestive enzyme activity, and RNA/DNA ratio were assessed in trout over 16 weeks. Six treatments were randomly assigned to 24 tanks with four replicates per treatment: a constant light intensity of 150 lx: 12 h white light then 12 h dark (12W); 12 h blue light then 12 h dark (12B); 12 h red light then 12 h dark (12R); 1.5 h blue light, 9 h red light, 1.5 h blue light, then 12 h dark (3B9R); 3 h blue light, 6 h red light, 3 h blue light, then 12 h dark (6B6R); and 12 h of both blue and red light then 12 h dark (T12BR). Fish exposed to the 3B9R light environment showed significantly increased plasma levels of total protein (TP), enhanced activities of midgut lipase, trypsin, and gastric lipase; and increased RNA content in the liver and muscle tissue to promote protein synthesis efficiency, thereby improving digestive and anabolic performance compared to fish in the other treatments. This indicates that steelhead trout have adapted well to such variable light conditions during long-term evolution. In contrast, trout exposed to the 6B6R light environment showed significant reductions in plasma glucose, TP, and triglyceride levels, decreased activity of gastrointestinal digestive enzymes, and reduced protein synthesis capacity in the muscle and liver, resulting in weakened digestive and anabolic

performance. Furthermore, despite the high RNA content and RNA/DNA ratio in fish exposed to a 12R light environment, relatively high plasma cholesterol and triglycerides levels were observed, which might indicate oxidative stress. Therefore, this light is not considered suitable for long-term cultivation. In conclusion, the 3B9R treatment was the optimal light condition tested and can be used to improve the digestive and anabolic performance of steelhead trout.

Keywords: anabolism, blue and red light color combination, digestive enzyme, RNA/DNA ratio, plasma biochemistry, steelhead trout

INTRODUCTION

Fish growth is influenced by a combination of exogenous environmental factors and genetic background (Taylor et al., 2006). Light is a vital environmental factor that plays a central role, with light intensity (quantity), photoperiod (duration), and light color (spectrum) affecting the physiological indicators of digestion and metabolism in fish (Villamizar et al., 2011; Zhang et al., 2020a). Light can stimulate the visual organs of fish to produce certain biological information and can influence their physiological and biochemical characteristics by regulating the central nervous and endocrine systems (Ruchin, 2021).

Previous studies have shown that light intensity and photoperiod have significant effects on the digestive and anabolic performance of fish. For example, in groupers (*Epinephelus coioides*), a light intensity of 320–1150 lx significantly increased total protease, amylase, and lipase activities in the liver, stomach, and intestine, and decreased plasma cortisol levels (Wang et al., 2013; Wang et al., 2015). In contrast, Tian et al. (2015) reported that a light intensity above 400 lx could significantly increase plasma cortisol levels in blunt snout bream (*Megalobrama amblycephala*). Shan et al. (2008) found that an 18L:6D photoperiod could enhance the lipase activity of miiuy croaker (*Miichthys miiuy*). Similarly, Wei et al. (2019) showed that long photoperiods (> 16 h/day) could improve lipometabolism as well as increase plasma triglyceride and non-esterified fatty acid content in gibel carp (*Carassius auratus*). However, Li et al. (2021) found that the 24L:0D condition could significantly inhibit digestive enzyme activity in European sea bass (*Dicentrarchus labrax* L.).

Light color also has a significant effect on the digestive and anabolic performance of fish. Under blue and green light environments, accelerated digestive and anabolic performance has been reported for several species, including goldfish (*Carassius auratus*) (Noureldin et al., 2021), turbot (*Scophthalmus maximus*) (Wu et al., 2021), spotted halibut (*Trachinotus blochii*) (Mapunda et al., 2021), and olive flounder (*Paralichthys olivaceus*) (Zou et al., 2022). Conversely, red light environments can enhance the anabolic performance of fish, such as pikeperch (*Sander lucioperca*) (Baekelandt et al., 2019) and yellow perch (*Perca flavescens*) (Head and Malison, 2000). However, most studies have focused on the effect of a single light color on fish physiological and biochemical characteristics, whereas limited information is available regarding the influences of light color combinations on fish digestive and metabolic performance.

Based on our unpublished data, we found that red light color can be beneficial in improving the growth performance of steelhead trout, while blue light color can improve their immune performance. Generally, the growth and immune performance of fish may be cooperative. This phenomenon indicated that single light color may not be suitable for rearing steelhead trout. The altitude of the sun changes throughout the day, and the path length and spectral composition (light color) of light reaching a particular water layer vary with time (Wetzel, 1983; Ruchin, 2021). The light color within a given water layer tends to change from blue to red to blue over time. However, the effects of changes in underwater light color on the physiological and biochemical characteristics of fish remain unclear. Presumably, fish have acclimatized to changing light color environments as a result of long-term evolution. Providing farmed fish with a changing light color environment similar to that experienced in nature may be more conducive to their digestive and anabolic performance. To explore the physiological and ecological responses of juvenile steelhead trout to light color variation, we investigated the influence of various blue and red light combinations on plasma biochemical parameters, digestive enzyme activity, and muscle and liver RNA and DNA content to identify suitable light color environments.

MATERIALS AND METHODS

Source and Acclimation of Fish

Triploid steelhead trout eyed eggs were purchased from Troutlodge, Inc. (Washington, USA). Prior to the experiments, the juvenile trout were acclimatized to a brackish saltwater environment (salinity: 14.2 ± 0.7) for 2 weeks. Fish were fed to apparent satiation twice daily at 08:00 and 18:30 with a commercial trout feed (Greatseven Inc., Qingdao, China) and maintained on 24 h oxygen supply and 12L:12D photoperiod.

Trial Design

For light evaluation, we utilized the mean light intensity values measured at the surface, middle, and bottom water layers as a baseline and established six light color treatments for 150 lx light intensity (12R, 12B, 12W, 3B9R, 6B6R, and T12BR). The light intensity was changed by adjusting the height of the light to the water surface. The light color regimes for the six treatments are listed in **Table 1**. The spectra of white light (full spectrum), blue light (peak at 454.9 nm), red light (peak at 614.8 nm), and mixed blue and red light (peaks at 454.9 nm and 614.8 nm, respectively)

TABLE 1 | Experimental design per time point for six light color conditions.

Treatment	7:30–9:00	9:00–10:30	10:30–16:30	16:30–18:00	18:00–19:30
12W	12 h white light (150 lx)				
12B	12 h blue light (150 lx)				
12R	12 h red light (150 lx)				
3B9R	blue light (150lx)	red light (150 lx)	red light (150 lx)	red light (150 lx)	blue light (150 lx)
6B6R	blue light (150 lx)	blue light (150 lx)	red light (150 lx)	blue light (150 lx)	blue light (150 lx)
T12BR	Total 12 h mixed blue light (75 lx) and red light (75 lx) for 150 lx light intensity				

12W means 12 h white light then 12 h dark; 12B means 12 h blue light then 12 h dark; 12R means 12 h red light then 12 h dark; 3B9R means 1.5 h blue light + 9 h red light + 1.5 h blue light then 12 h dark; 6B6R means 3 h blue light + 6 h red light + 3 h blue light then 12 h dark; T12BR means a total of 12 h of mixed blue light and red light then 12 h dark.

are shown in **Figure 1**. For all treatments, the photoperiod was a 12L:12D cycle (light period: 07:30 to 19:30). The light intensity and spectra were determined using a handheld illuminometer (PLA-300; Everfine Inc., Hangzhou, China). A packaged LED (COB) was used, which was designed and produced by Qingdao Lanchi Technology Company. The 16-week trial was based on a completely randomized block design with four replicates per treatment and with each replicate group comprising 20 fish per tank (380 L volume, 0.72 m height × 0.95 m diameter; white background color). Each tank was covered with a black light-absorbing cloth to prevent light contamination between treatments.

At the beginning and end of the trial, feeding was suspended for 36 h to ensure that the digestive tracts of the fish were empty. Prior to commencing the trial, the fish were anesthetized by immersion in a 30 mg/L tricaine methanesulfonate (MS-222; Sigma-Aldrich, USA) solution, after which they were gently blotted dry with tissue and weighed. During the culture period, all trout (initial weight, 34.67 ± 2.69 g) were fed twice daily (at 08:00 and 18:30) with commercial trout feed. Residual unconsumed feed was collected after feeding for 30 min, and the daily feed intake was calculated by measuring the feed moisture content and correcting the feed intake for leaching. Water was renewed using a single-flow system at a water flow rate of 1.15 L/min. Water temperature, salinity, dissolved oxygen content, and pH were monitored three times daily using a YSI ProPlus handheld multiparameter meter (YSI Inc., Ohio, USA). Water samples were collected at 3-day intervals, and the total ammonia nitrogen (TAN), phosphate, nitrite nitrogen, and nitrate nitrogen concentrations were analyzed using a Cleverchem 380 automatic chemical analyzer (DeChem-Tech Inc., Hamburg, Germany).

During the culture period, values for the water quality parameters (mean ± standard deviation), temperature, salinity, dissolved oxygen, pH, TAN, phosphate, nitrite nitrogen, and nitrate nitrogen were maintained at 16.5 ± 0.2°C, 14.2 ± 0.7, 8.7 ± 0.3 mg/L, 7.3 ± 0.1, at 0.03 ± 0.03 mg N/L, 0.11 ± 0.08 mg P/L, 0.09 ± 0.05 mg N/L, and 3.43 ± 1.9 mg N/L, respectively.

At 4-week intervals, the fish in each tank were treated with 30 mg/L tricaine MS-222, counted, and weighed. At the end of the trial, the final weights of steelhead trout in the 12W, 12R, 12B, 3B9R, 6B6R, and T12BR groups were 277.32 ± 6.23, 278.24 ± 4.89, 294.13 ± 13.20, 295.74 ± 5.61, 264.78 ± 4.86, and 283.10 ±

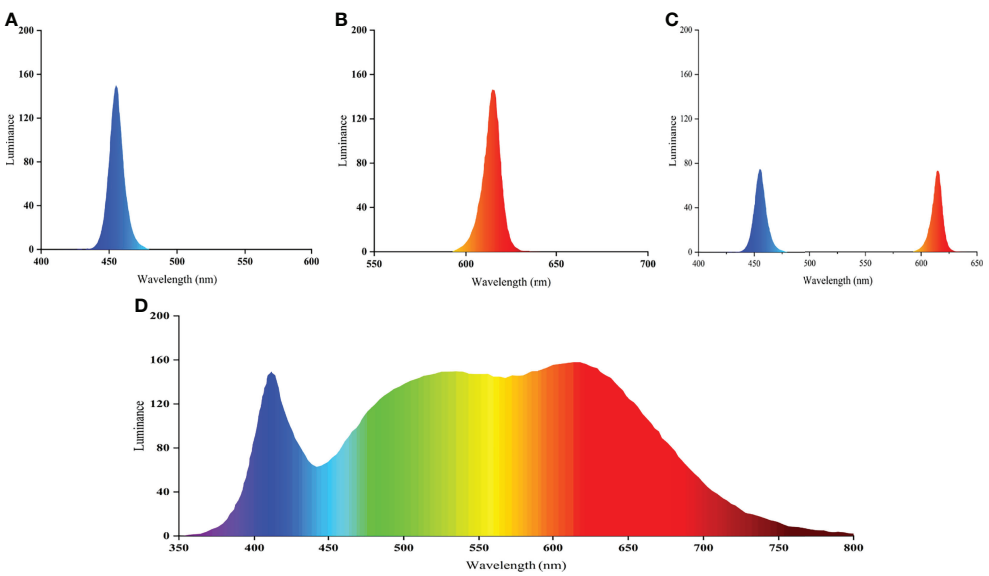

FIGURE 1 | Relative spectral composition of blue light **(A)**, red light **(B)**, mixed blue and red light **(C)**, and white light **(D)**.

16.90 g, respectively. The 3B9R group had the highest final weight, which was significantly higher than that of the 6B6R group. The average daily intake of all groups was 2.26 ± 0.09 g, and no significant differences were found among the groups. At the time of sampling, three fish were randomly selected from each tank and immediately anesthetized with 100 mg/L MS-222. The midgut, stomach, liver, and muscle tissues were immediately collected and frozen in liquid nitrogen. Blood samples were collected in heparin sodium anticoagulant EP tubes, centrifuged at 10,000 r/min (4°C) for 10 min to separate plasma, and immediately placed in liquid nitrogen. All samples were then transferred to a −80°C ultra-low temperature freezer for preservation.

Digestive Enzyme Activity Analyses

After being accurately weighed, midgut and stomach tissues were placed in pre-chilled saline at a weight (g): volume (mL) ratio of 1:9 and homogenized using an automatic freezer mill grinder (Jingxin Industrial Development Inc., Shanghai, China). The tissue homogenate solutions were centrifuged at 3,500 r/min and 4°C for 10 min, and the resulting supernatants were collected for analysis. The commercially available kits (Nanjing Jiancheng Bioengineering Institute, Nanjing, China; A045-4-2, A054-2-1, C016-1-1, A080-2-2, and A080-1-1) were used to determine the total protein content and the activities of lipase, amylase, trypsin, and pepsin in tissues. The total protein content, lipase and amylase activity, and trypsin and pepsin activity were determined as described by Wang et al. (2021b), Lu et al. (2020), and Zhang et al. (2020b), respectively. The determination process was strictly based on the instructions, and absorbance values of total protein content, lipase, amylase, trypsin, and pepsin were measured at 562, 580, 660, 253, and 660 nm, respectively, using a microplate reader (Synergy2; BioTek Inc., USA) and a UV spectrophotometer (UV-5100; Shanghai Metash Instruments Co., Ltd, Shanghai, China). The lipase activity was presented as units per gram of protein; the activities of amylase, trypsin, and pepsin were presented as units per milligram of protein.

Plasma Biochemical Analyses

Plasma levels of glucose (Glu), total protein (TP), triglyceride (TG), and total cholesterol (TC) were determined using a Cobas C-311 automatic biochemical analyzer (Roche/Hitachi Inc., Basel, Switzerland). All commercial kits were obtained from Roche, Inc. (Basel, Switzerland).

RNA and DNA Extractions

Total RNA was extracted from muscle and liver tissue samples using a UNIQ-10 TRIzol Total RNA Extraction kit (Sangon Inc., Shanghai, China), and DNA was extracted using a marine animal tissue genomic DNA extraction kit (Tiangen Inc., Beijing, China). RNA and DNA concentrations were measured at 260 nm using a microspectrophotometer (Nano-300, Allsheng Inc., Hangzhou, China). Purity of the sample was confirmed by determining the $OD_{260/280}$ nm absorption ratio. The $OD_{260/280}$ values for muscle tissue RNA and DNA were 1.96 ± 0.03 and 1.84 ± 0.02, respectively. The $OD_{260/280}$ values for liver tissue RNA and DNA were 1.96 ± 0.03 and 1.83 ± 0.02, respectively. All samples showed $OD_{260/280}$ readings between 1.8 and 2.0 for both RNA and DNA.

Statistical Analysis

All data were analyzed using SAS version 9.4 (SAS Institute Inc., Cary, North Carolina, USA). The normal distribution and homogeneity of variance of the data were initially assessed using the Shapiro–Wilk and Levene tests, respectively. Normally distributed homogeneous data were analyzed using one-way analysis of variance (ANOVA), with mean values compared using Tukey's multiple comparison tests. For analysis of non-normally distributed data, we applied the non-parametric Mann–Whitney rank sum test and Kruskal–Wallis ANOVA of ranks. The results are expressed as the mean ± standard deviation, with differences considered significant at $P < 0.05$.

Ethics Approval Statement

All procedures were performed under the Regulations of the Administration of Affairs Concerning Experimental Animals of China, as well as the Regulations of the Administration of Affairs Concerning Experimental Animals of Shandong Province.

RESULTS

Digestive Enzyme Activity

Digestive enzyme activity data obtained in juvenile steelhead trout are summarized in **Figure 2**. Midgut lipase and trypsin levels were significantly higher in the 3B9R and 12R groups than in the 6B6R group ($P < 0.05$). Furthermore, the midgut and gastric lipase activities showed similar trends. The 3B9R and 12R groups had significantly higher lipase activities than the other groups ($P < 0.05$). However, no significant differences were observed in the amylase (midgut and gastric) or pepsin levels among the groups ($P > 0.05$).

Plasma Biochemistry

Results obtained for the plasma Glu, TP, TG, and TC levels are presented in **Figure 3**. Glu levels in trout in the 6B6R group were significantly lower than those in the other groups ($P < 0.05$). The highest levels of TP were detected in the 3B9R group, which were significantly higher than the levels recorded in the 12W and 6B6R groups ($P < 0.05$). The TG levels in the 12R group were significantly higher than those in the 12W group ($P < 0.05$). The highest levels of TC were detected in the 12R group, which were significantly higher than those in the other groups ($P < 0.05$), whereas the levels of TC in the 12W and 6B6R groups were significantly lower than those in the other groups ($P < 0.05$).

RNA/DNA Content and Ratio

Data relating to the muscle and liver RNA/DNA content and ratios of juvenile steelhead trout are presented in **Table 2**. The muscle RNA content in the 3B9R group was significantly higher than that in the 12W, 12B, and 6B6R groups ($P < 0.05$). Interestingly, the muscle RNA/DNA ratio showed a similar trend to the muscle RNA content, with the 3B9R group having significantly higher values

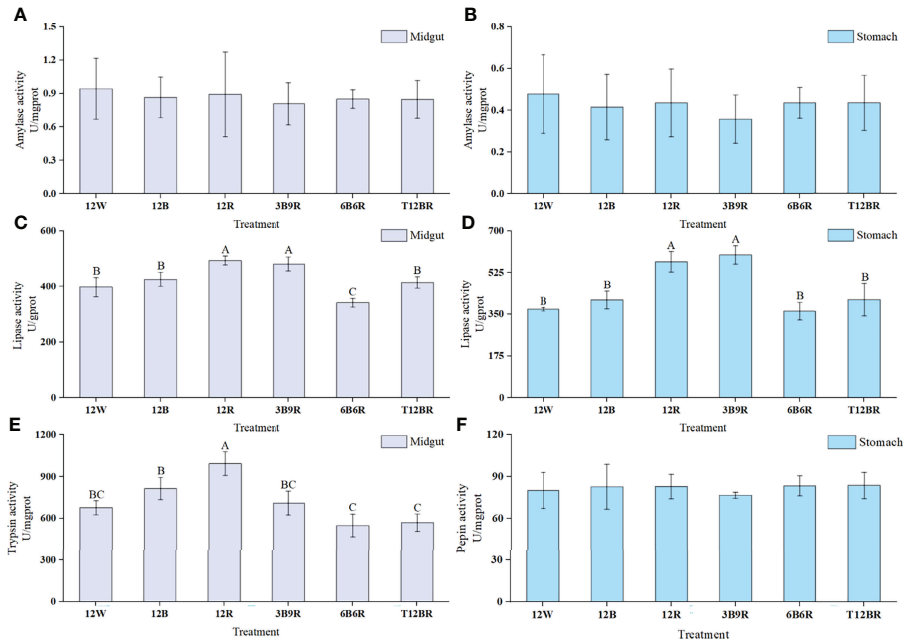

FIGURE 2 | Digestive enzyme activities of the midgut and stomach in juvenile steelhead trout reared under different light color conditions. **(A)** Amylase activity in the midgut; **(B)** amylase activity in the stomach; **(C)** lipase activity in the midgut; **(D)** lipase activity in the stomach; **(E)** trypsin activity in the midgut; **(F)** pepsin activity in the stomach. Different capital letters denote significant differences among the steelhead trout treatments. Results are expressed as mean ± standard deviation (n=12).

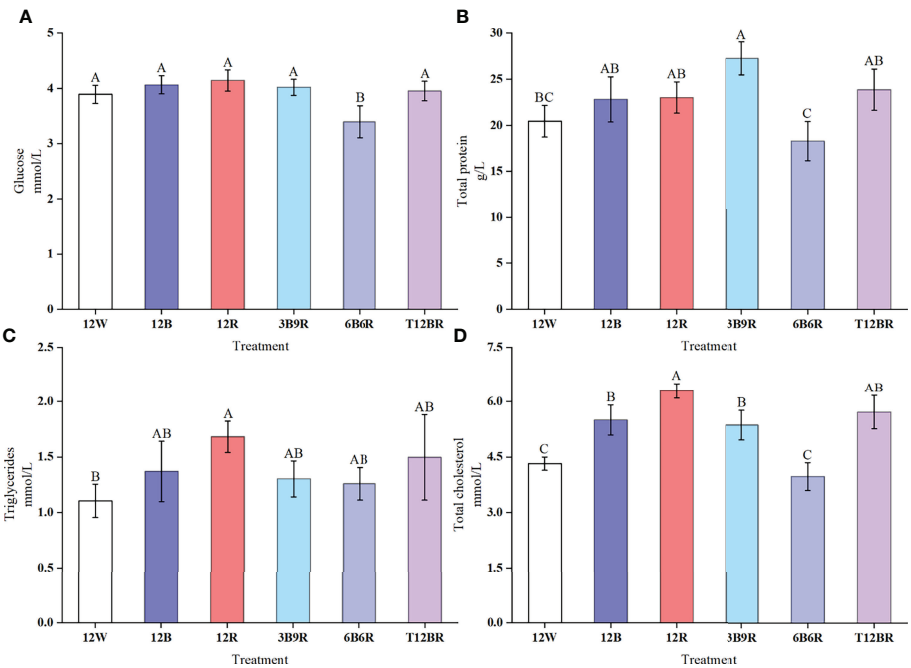

FIGURE 3 | Plasma enzyme levels of Glu (glucose, **A**), TP (total protein, **B**), TG (triglycerides, **C**), and TC (total cholesterol, **D**) in juvenile steelhead trout reared under different light color conditions. Different capital letters denote significant differences among the steelhead trout treatments. Results are expressed as the mean ± standard deviation (n = 12).

TABLE 2 | RNA, DNA, and RNA/DNA ratio in the muscle and liver of steelhead trout reared under different light color conditions.

Treatment	12W	12B	12R	3B9R	6B6R	T12BR	*P value*
Muscle (ug/ml)							
RNA	0.81 ± 0.05^{bc}	0.72 ± 0.06^{cd}	1.00 ± 0.13^{ab}	1.04 ± 0.12^{a}	0.58 ± 0.08^{d}	0.85 ± 0.11^{abc}	<0.0001
DNA	0.21 ± 0.02	0.19 ± 0.02	0.22 ± 0.03	0.21 ± 0.02	0.23 ± 0.04	0.21 ± 0.03	0.4939
RNA/DNA	3.81 ± 0.11^{c}	3.79 ± 0.12^{c}	4.54 ± 0.12^{ab}	4.84 ± 0.18^{a}	2.56 ± 0.40^{d}	4.12 ± 0.43^{bc}	<0.0001
Liver (ug/ml)							
RNA	5.50 ± 0.38^{ab}	5.64 ± 0.18^{a}	6.45 ± 0.41^{a}	6.36 ± 0.65^{a}	4.35 ± 0.94^{b}	5.64 ± 0.30^{a}	0.0004
DNA	0.96 ± 0.05	0.96 ± 0.02	0.95 ± 0.07	0.94 ± 0.08	1.00 ± 0.10	0.94 ± 0.05	0.7967
RNA/DNA	5.76 ± 0.35^{b}	5.84 ± 0.11^{b}	6.81 ± 0.15^{a}	6.80 ± 0.66^{a}	4.3 ± 0.55^{c}	6.02 ± 0.44^{ab}	<0.0001

Values (mean ± standard deviation) are expressed as the means of four replicates. Values on the same line with different superscript letters are significantly different ($P < 0.05$) based on one-way analysis of variance (ANOVA) with Tukey's test.

than the T12BR, 12W, 12B, and 6B6R groups ($P < 0.05$). The lowest liver RNA content was detected in the 6B6R group, which was significantly lower than that recorded for the 12R, 3B9R, T12BR, and 12B groups ($P < 0.05$). In addition, the liver RNA/DNA ratio was significantly higher in the 12R and 3B9R groups than that in the 12B, 12W, and 6B6R groups ($P < 0.05$). However, no significant differences in muscle and liver DNA content were observed among the groups ($P > 0.05$).

DISCUSSION

The altitude of the sun considerably influences the light color composition in the water. In the morning and evening, because of the low altitude of the sun and the long path length of the incident light, red light is quickly absorbed after entering the water, thus increasing the proportion of blue light in the water. At noon, the incident light path is shorter, increasing the proportion of red light in the water. Therefore, the light color tends to exhibit a blue-red-blue variation in the water during the daytime (Wetzel, 1983; Ruchin, 2021). This light color variation in the water is similar to that observed in the 3B9R light environment in the current study. In the 3B9R light environment, TP levels, digestive enzyme activity, muscle/liver RNA content, and RNA/DNA ratio in trout significantly increased compared other light environments, implying that the digestive and anabolic performance was significantly improved under 3B9R light environment. These findings indicate that trout can adapt to variations in the daily rhythm of light conditions during their long-term natural evolution.

Our results showed that the combination of blue and red light was more effective than single light in improving the digestive and anabolic performance in steelhead trout. However, information on the effects of the combination of blue and red light colors in trout is limited. Our findings are similar to those reported by Karakatsouli et al. (2008), who found that red light was beneficial in increasing the anabolic level of rainbow trout (*Oncorhynchus mykiss*), and Guller et al. (2020), who found that blue light can enhance the antioxidant enzyme synthesis of rainbow trout. In contrast, Karakatsouli et al. (2007) documented that blue light can inhibit anabolism and reduce the stress response. Therefore, responses to colored light may vary depending on the species, life stage, and size-class.

Digestive enzyme activity is a vital indicator of the maturity and function of the digestive system in fish (Fang et al., 2019; Pérez-Sirkin et al., 2020). Digestive enzyme activity is closely related to fish feeding habits and is influenced by environmental factors (Castro-Ruiz et al., 2019; Yu et al., 2020; Yan et al., 2021). In the present study, the lipase activity of the 3B9R group was significantly higher than that of the 6B6R group (**Figure 2**), whereas no significant difference in amylase activity was observed. This difference may be explained by the fact that steelhead trout is a carnivorous fish and its lipase activity is susceptible to light color. Furné et al. (2005) reported higher lipase activity in carnivorous fish, whereas higher amylase activity was observed in herbivorous and omnivorous fish. In a recent study on spotted sea bass (*Lateolabrax maculatus*), Hou et al. (2019) found that exposure to blue light could significantly increase digestive enzyme activity. Our results indicate that trout can adapt to variable blue-red-blue light environments during long-term natural evolution. Hence, a suitable light environment can promote the development of the digestive system, as well as the gastrointestinal digestion and absorption capacity of trout, ultimately improving the digestive performance.

Blood functions as a mediator of metabolism and nutrient transport in fish and is widely used to evaluate physiological health, digestion capacity, and anabolic performance (Giri et al., 2018; Chen et al., 2021; Huang et al., 2021). The biochemical characteristics of fish blood can exhibit marked variations in response to environmental changes (Wang et al., 2021a).

In the current study, plasma Glu levels were significantly lower in steelhead trout exposed to the 6B6R light environment than in those exposed to other light environments (**Figure 3**). We suspect that this can represent oxidative stress in the liver of trout caused by the 6B6R light environment, which influences anabolic performance. Glu is mainly synthesized in the liver. When the liver is exposed to oxidative stress, its synthetic capacity is diminished, resulting in decreased Glu levels (Ogueji et al., 2020). Glu is produced by ATP through aerobic oxidation or glycolysis pathways, providing energy resources for tissues such as the liver, muscle, and gastrointestinal tract. Lower levels of Glu can result in a decreased availability of energy resources for the organism, affecting the anabolic efficiency of other tissues in fish (Feng et al., 2022).

Our findings revealed that the TP levels in the plasma of steelhead trout in the 3B9R group were significantly higher than those in the 6B6R group (**Figure 3**). This may be because the 6B6R light environment caused oxidative stress in the liver, leading to lower plasma TP levels. TP is synthesized in the liver and plasma cells of the reticuloendothelial system and its protein synthesis capacity decreases when the liver is exposed to oxidative stress (Afshari et al., 2021). Similarly, Refaey and Li (2018) observed a reduced TP synthesis capacity in the liver of channel catfish (*Ictalurus punctatus*) when subjected to oxidative stress. TP can supply energy to the body *via* gluconeogenesis (Yang et al., 2020) and can indirectly reflect the anabolic performance of the body (Afshari et al., 2021). Our findings showed that the anabolic performance of the 6B6R group was weakened because of a decrease in the efficiency of nutrient transport and metabolism caused by a reduction in TP levels.

Our results showed that TG and TC levels were significantly higher in the 12R group of steelhead trout than in other groups (**Figure 3**), possibly because of the long-term participation in high-intensity anabolism of the liver, leading to overload or oxidative stress caused by this light environment. TG and TC are important components of blood lipids and are mainly synthesized in the liver (Su et al., 2022). Variations in blood lipid levels are closely related to the metabolic and physiological status of fish, and changes in their content can reflect the level of lipid metabolism (Qiang et al., 2018; Jia et al., 2021). As an important biomarker, TC levels reflect liver health (Farag et al., 2022). During oxidative stress, the digestive performance and cell membrane function are inhibited (Narra et al., 2017). Owing to the reduced efficiency of TG reabsorption, a large amount of TG accumulates in the blood, causing increased plasma TG levels. TC is transported by high-density lipoproteins to the liver and synthesized by bile acids. When the liver is under high load or oxidative stress, its capacity to synthesize bile acids by TC is reduced, which leads to elevated levels (Mertens et al., 2017; Xu et al., 2020). Our data showed that the plasma TG and TC levels were significantly lower in the 6B6R group than in the other groups. This difference in the response indicates that the liver and intestine of the 6B6R group were affected by light color, and the liver synthesis of lipids and intestinal absorption of lipids were inhibited, resulting in lower levels of TG and TC. TC is a carrier of nutrients for the body; when its levels decrease, the metabolic capacity of steelhead trout decreases. Thus, nutrients cannot be efficiently transformed and utilized, which affects anabolic performance.

RNA directly participates in protein synthesis, and the metabolic rate of the body is positively correlated with the efficiency of RNA synthesis (Kumar et al., 2018). Conversely, the DNA content of genetic information carrier molecules remains stable (Zehra and Khan, 2017). Consequently, the RNA/DNA ratio, a physiological indicator of the body's protein synthesis capacity, can accurately reflect cell metabolism (Sterzelecki et al., 2021). Our data showed that the DNA content in the muscle and liver of steelhead trout was not significantly different among treatment groups, whereas the RNA content and the RNA/DNA ratio were significantly higher in the 3B9R group than those in the 6B6R group (**Table 2**). The RNA content and RNA/DNA ratio of different tissues in each group revealed similar trends—which may reflect differences in anabolic performance of steelhead trout under different light color conditions—and were positively correlated with the growth trend of trout in our laboratory (Chen et al., unpublished data). Similarly, a positive correlation was found between the RNA/DNA ratio and growth trend in pearl oysters (*Pinctada fucata*) (Chang et al., 2021). Studies have revealed that factors such as feeding, temperature, and light can influence the RNA/DNA ratio in the body (Grimm et al., 2015; Angelo et al., 2021; Quintanilla-Ahumada et al., 2021). Kawamura et al. (2017) reported that exposure to red light could significantly increase the muscle RNA/DNA ratio in red sea bream (*Pagrus major*). Similarly, we found that the 3B9R light environment could enhance anabolic performance by improving the rate of RNA synthesis in steelhead trout.

Light is a vital factor in regulating the physiological characteristics of fish, and an optimal light environment can contribute positively to fish welfare (Owen et al., 2009; Stien et al., 2013; Ruchin, 2021). Our findings on digestive and anabolic performance of trout can partially reflect fish welfare status; however, investigating different aspects of stress response (e.g. oxidative stress process) is important as the welfare index has some limitations (Stien et al., 2013; Parma et al., 2020). Our unpublished data (Chen et al.) showed that blue-red light variation can affect trout growth. This is consistent with the findings of previous studies, which demonstrated that fish growth can be improved by altering the background color of the culture tank and the light color to yield interesting results (Papoutsoglou et al., 2000; Rotllant et al., 2003; Sotoudeh et al., 2019; Kasagi et al., 2020; McLean, 2021; Ninwichian et al., 2022). Overall, our study failed to comprehensively explain fish welfare, which will need to be explored further using an overall model for welfare indicators such as oxidative stress process, behavior, and other aspects.

CONCLUSION

In the present study, the 3B9R light environment was beneficial for increasing plasma TP levels and enhancing gastrointestinal digestive enzyme activity in steelhead trout. This environment also improved the liver and muscle protein synthesis capacity. We conclude that 3B9R is the most favorable light environment for improving the digestive and anabolic performance of trout. Our results indicate that steelhead trout acclimated to variable light conditions during long-term natural evolution. The 3B9R group of steelhead trout had enhanced secretory synthesis capacity through an increase in TP levels. This also improved RNA synthesis, protein capacity, and digestive capacity. This is the primary reason for the relatively high digestive and anabolic performance of fish exposed to the 3B9R light environment compared to that of fish in other light environments. In contrast, the 6B6R light environment significantly reduced plasma Glu, TP, and TC levels. Additionally, the

gastrointestinal digestive enzyme activity was inhibited, and the ability of the muscle and liver to synthesize protein using RNA was reduced, resulting in decreased digestive and anabolic performance. Despite the higher RNA content and RNA/DNA ratio, exposure to the 12R light environment caused relatively high levels of TG and TC in plasma, which indicates the occurrence of oxidative stress. In summary, the 12R light environment is considered unsuitable for long-term cultivation, and the 3B9R light environment may be more appropriate for rearing steelhead trout.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

ETHICS STATEMENT

All procedures were performed under the Regulations of the Administration of Affairs Concerning Experimental Animals of China, as well as the Regulations of the Administration of Affairs Concerning Experimental Animals of Shandong Province.

AUTHOR CONTRIBUTIONS

XC performed the trial and data analysis, wrote the original draft, and proposed the research methods and ideas; YZ and SD supervised research progress, proposed research methods and research ideas, and edited the manuscript. JH performed the data analysis and wrote the original draft; DA, LL, YD, and QG reviewed and edited the original draft. All authors contributed to the article and approved the submitted version.

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