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Research Article

Behavior response, growth, and structure of the eye retinal layer in juvenile Seabass, *Lates calcarifer*: Light-induced changes

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Abstract

Light is a key environmental factor that is strongly related to fish activity and behavior. Exposure to certain wavelengths is known to affect growth performance and survival of teleost larvae and juveniles. Our study aimed to determine the effects of exposure to three light sources [red (710 nm), blue (453 nm) and green (510 nm)] on growth performance, behavioral response, visibility (time to eat, in minutes), and the structure of the retinal layer in juvenile [approx. 4.3 cm in total length (N = 30)] seabass *(Lates calcarifer).* Fish were acclimated to the three light conditions for four weeks prior to data collection. Behavioral responses, including schooling organization, swimming speed, time to consume prey, and feeding response, were all improved in juveniles reared under red light (710 nm). Preliminary histological observations revealed that fish from the red-light environment have the thickest retina layers and the highest density of photoreceptors. Our data suggest that red light is useful in the aquaculture of juvenile *L. calcarifer*.

1. Introduction

Basic behaviors, such as feeding, stress avoidance, and schooling, are essential for the growth and survival of fish (Volpato et al., 2013; Utne-Palm et al., 2018). These behaviors are influenced by several factors, including light (Fielder et al., 2002; Trippel & Neil, 2002; Howell et al., 2003; Imsland et al., 2006; Ballagh et al., 2008; Martínez-Cárdenas & Purser, 2011; Gunnarsson et al., 2012). Therefore, fish have the ability to respond and adapt to different light environments (Parr, 1927; Parr, 1931; Volpato et al., 2013; Utne-Palm et al., 2018) by changing various factors, such as nutrient absorption and digestive enzyme activity (Li et al., 2020). Intensity and wavelength are two

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important factors that determine the response of fish to light (Marchesan et al., 2005). Fish exposed to an insufficient light intensity suffer from stress conditions (Boeuf & Baile, 1999). Light intensity has been documented as an important factor for successful growth and/or reproduction in ponds and/or aquaria (Pillay & Kutty 2005; Kawamura et al., 2015). Light quality (wavelength) also affects the behaviors of fish. For example, Kim et al. (2004) found that green and blue lights have a positive impact on the growth rate of Atlantic salmon *Salmo salar* under artificial conditions, compared to red and yellow lights. The wavelength preference could be changed by culture conditions, because red light was best for improving the weight-specific growth and survival rate of *S. salar*, compared to blue and green light (Naas et al., 1996).

The seabass *Lates calcarifer* is an economically important brackish water fish in Thailand and other Asian countries, as well as in Australia. This species is a good source of nutrients for humans (Department of Fisheries, 2017) and has been widely farmed for more than three decades. Although this species has been intensively studied in various fields related to aquaculture, e.g., nutritional requirements (Glencross 2006; Glencross et al., 2013) and reproductive biology (Guiguen et al., 1994; de Jesus-Ayson et al., 2014), behavioral responses to light and the structure of the retinal layer are still rarely explored. Ulmann et al. (2011) investigated the effect of light exposure on the visual system, color preference, and growth performance of *L. calcarifer*, but behaviors such as schooling organization and swimming speed under different light treatments remain unknown.

Photoreceptor cells in the retina receive light signals and send them to the central nervous system (CNS). This modulates the behavioral response of fish (Blaxter, 1968; Kawamura & Ishida, 1985). Like other vertebrates, the neural retina of seabass contains specialized photoreceptor cells; rod and cone cells (Genten et al., 2009). The rod cells mediate the sensitive response to low-intensity lights, giving low-resolution images. The density of the rod cells increases with the habitat depth, up to a certain depth (Hunt et al., 2015), and a high density is observed, especially in nocturnal and deep-sea fish. In contrast, the mosaic arrangement of cone cells is believed to be important for good visual perception, and fish relying on vision have well-ordered mosaic arrangements. Fish living in shallow habitats have regular square cone mosaic structures (Hunt et al., 2015). The cone cells are active to high-intensity lights (Kawamura & Ishida, 1985). Nocturnal and deep-sea species generally do not have cone mosaics (Hunt et al., 2015). Because of the different features of the two types of photoreceptor cells, change in the number of photoreceptor cell types impact the visual performances of fish (Kobayashi, 1962; Kawamura et al., 1984; Lythgoe & Partridge, 1989).

This study aimed to investigate the effects of various light sources on the growth rate, behavioral patterns, and histological characteristics of the photoreceptor cells in the retinal layer of juvenile *Lates calcarifer*. This stage is considered to be a critical period for aquaculture performance parameters including survival and growth. The results from our study are useful for improving the survival and growth rates of *L. calcarifer* and, thus, may support the aquaculture of this fish species.

2. Materials and methods

2.1 Fish preparation and experimental setup

One hundred and fifty healthy 1-month-old juvenile seabass (*Lates calcarifer*) with an average total length of 4.20 ± 0.93 cm were collected from an aquaculture farm in Bangpakong District, Chachoengsao Province, Thailand. They were distributed in 15 glass aquaria (30×40×60 cm^3) filled with brackish water (25 - 28 ppt) at the density of ten fish per aquarium. The fish were reared for a couple of weeks for acclimation and divided into five experimental groups. Four groups were cultured under polychromatic lights with different wavelengths (full spectrum [control], 435 nm [blue], 510 nm [green], and 710 nm [red]), while the fifth group was reared in darkness. The Kaitai LED Electronic Submerged Lamp T4-400 6 W model was used, and the light was kept on throughout the experimental period. The sides of each experimental tank were blacked out.

After 21 days, all fish were subjected to the behavioral analysis (Cuvier-Péres et al., 2001). The experiment was conducted in three replicates (N = 10 per tank, N = 30 per group). The laboratory temperature was kept at about 25 ºC. Aquaria were filled with artificial seawater; the oxygen level was maintained by aeration of the aquaria. The ambient salinity of water was 0.5 ppt, and the water temperature was checked daily. The experimental procedures were approved by the Animal Care and Use Committee of the Faculty of Science, Chulalongkorn University (Protocol Review No. 19230004).

2.2 Behavioral observation and growth rates

Juvenile *Lates calcarifer* were visually observed and measured for several behavioral patterns, including feeding, schooling, and swimming, at the end of the 21-day culture period. The minimum and maximum observation times were approximately 30 and 60 min, respectively. The on-site observation was performed by three observers, and all observers reported the same data.

The length of time required for fish to consume 50 brine shrimps was recorded from three observations. After 21 days of light exposure, 50 mature brine shrimps were fed to the fish three times, at 8:00 am, 12:00 am, and 16:00 pm. The number of fish that successfully captured prey was also counted for each aquarium. Feeding behaviors were scored from 0 to 5, based on how many fish fed: 0 = no fish fed; 1 = only 1 fish fed; 2 = 2–4 fish fed; 3 = 5–7 fish fed; 4 = 7–9 fish fed; and 5 = all fish fed. Schooling behavior (fish moving together in the same direction) was observed at the feeding times as follows (Heerhartz & Toft, 2015). The scores of schooling behaviors ranged from 0 to 5: 0 = no schooling; 1 = 2–3 fish schooling; 2 = 4–5 fish schooling; 3 = 6–7 fish schooling; 4 = 8–9 fish schooling; and 5 = all fish schooling. The swimming behavior was also observed at the feeding times and scored from 0 to 5: 0 = no fish swimming; 1 = 4–5 fish swimming; 2 = 5–6 fish swimming; 3 = 6–7 fish swimming; 4 = 8–9 fish swimming; and 5 = all fish swimming. Swimming behaviors of 3 and above were considered to be of good quality.

The growth rates (g/week), total weights (Tw, g), and total lengths (TL, cm) of all fish were measured at the end of the 30-day culture experiments (after the behavioral examination). Fish were then killed by a rapid cooling method (Wilson et al., 2009). The morphology of the eye structures was conducted to assess their retinal activity and were photographed with an Olympus Compact Digital Camera STYLUS TG-Tracker (1920×1080 pixels) [OLYMPUS (THAILAND)].

2.3 Histological structures of retinal and photoreceptor cell layers

The eyes of all fish were dissected and intermediately fixed in Davidson's fixative with a mixture of acetic acid, formaldehyde, and alcohol for 48 h before being transferred to 70 % ethanol. Eyes were processed by standard histological protocols (Presnell & Schreibman, 2013; Suvarna & Layton, 2013). Paraffin blocks were cut into serial sections at 4 µm in thickness by a rotary microtome. The sectioned tissues were stained with hematoxylin and eosin (H&E). The histological structures of eyes were observed under a light microscope and were photographed by a digital camera model Canoscope DG–105–W. Histological sections of one right eye from each experimental group were randomly measured at four randomly chosen areas to determine the retina and photoreceptor layer widths (at 10×), following Matsuoka (1999) and Ahmad et al. (2017). These data were represented as averages and respective standard errors (averages ± SE).

2.4 Statistical analysis

Data were analyzed with SPSS Version 23 (IBM Corp, 2015) for Windows 64 at 95%/99% confidence intervals. The growth rates of *Lates calcarifer* juveniles were compared for hypothesis testing between different wavelength groups, behaviors of feeding, schooling, and swimming of each light wavelength group, and retinal and photoreceptor layers by using one-way ANOVA, followed by Tukey test.

3. Results and discussion

3.1 Growth performance of juvenile *L. calcarifer* under different light regimes

No death was observed during our experiments. The fish reared in red light, blue light, and darkness had similar weights and lengths, and were larger than those reared in either full spectrum light or under green illumination. However, both TL and TW of juvenile *L. calcarifer* were significantly different across experimental groups ($p < 0.01$) (**Table 1**). The highest TL (5.61 ± 0.53 cm) and TW (2.35 ± 0.50 g) were recorded in fish exposed to red light (710 nm) (**Figure 1**). These results were consistent with previous findings in tropical damselfish *Acanthochromis polyacanthus* (Begg & Pankhurst 2004) and seabass (*Lates calcarifer* (Ulman et al., 2011), where all fishes had the highest TL after exposure to red light.

3.2 Behavioral patterns and latency of *L. calcarifer* during juvenile stage

The color of light in the aquatic environment affects the larva and juvenile stages of aquatic animals, leading to changes in feeding response, growth, and survival rates (Blaxter, 1968; Kawamura & Ishida, 1985; Ruchin, 2004). All behavioral scores examined in juvenile *L. calcarifer* were statistically different among fish reared in different light wavelengths (F = 32.91, 30.85, 7.86, 196.1; $p < 0.01$, **Table 2** and **Figures 2A - 2C**). The highest score was observed under red light for feeding behavior (4.67 ± 0.94 points), as well as for swimming behavior (4.458 ± 0.60 points) and schooling behavior (4.625 ± 0.61 points). Blue and dark groups tended to have higher scores following the red group, whereas fish exposed to green light had the lowest scores.

The feeding response scores of juvenile *Lates calcarifer* were also significantly different between groups [(F = 196.10; $p < 0.001$) and **Figure 2D**]. The feeding response was determined based on the time to feed on prey (latency), and it is reasonable that we observed an opposite tendency to feeding and swimming scores. Fish under the red light had the shortest time of 1.33 ± 0.22 min. This result is consistent with a previous study, where fast feeding was more frequently observed under red light compared to other light conditions in *Oreochromis niloticus* (Volpato et al., 2013). Naas et al. (1996) reported that the growth and survival of fish larvae in a red aquarium was increased more than those in other colors (blue and green aquariums); this increase was due to the scattering of red light in the water, which made the prey have bright coloration and, hence, be more easily recognized by salmon. However, other reports have shown that blue light has more positive effects on fish behaviors than other colors (Downing & Litvak, 1999; Karakatsouli et al., 2007). The color preference appears to be species-specific, but blue light can help reduce the performance-related condition of stress in general. A similar pattern has also been found in juvenile anemonefish (Job & Bellwood, 2007) and *Danio rerio* (Yoshimatsu et al., 2020) throughout other fish, including *Cyprinus carpio*, *Carassius auratus*, *Ca. carassius*, *Perccottus glenii*, and *Poecilia reticulata* (Ruchin, 2004).

Table 1 One-Way ANOVA results for difference in growth performance of juvenile *L. calcarifer* under different light regimes.

Growth performance	Sum of Squares	Df	Mean Squares	F	Sig.
A. Total length					
Between groups	89.61	4	22.40	89.68	< 0.0001
Within groups	21.23	85	0.2498		
Total	110.8	89			
B. Total weight					
Between groups	55.30	4	13.83	87.70	< 0.0001
Within groups	13.40	85	0.1576		
Total	68.70	89			

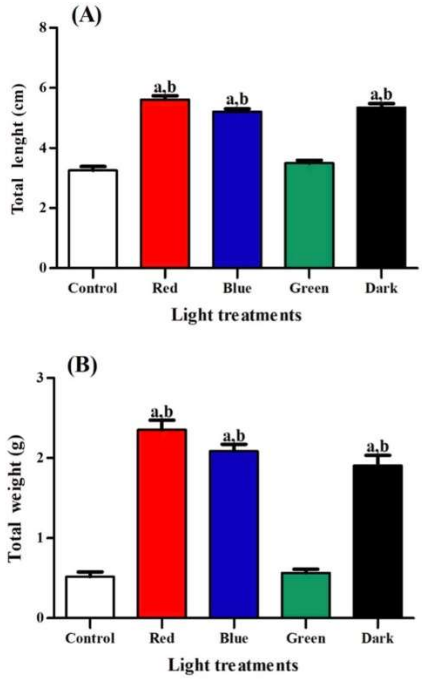

Figure 1 Growth performance measured as total length (A) and total weight (B) of *L. calcarifer* during juvenile stage when reared under five different light treatments. Values are expressed as mean ± SEM, $^{a}p < 0.01$, compared with control, $^{b}p < 0.01$, compared with green.

Table 2 One-Way ANOVA results for difference in the behavior patterns of *L. calcarifer* during juvenile stage when reared under different light treatments.

Behavioral patterns	Sum of Squares	Df	Mean Squares	F	Sig.
A. Feeding behavior					
Between groups	78.16	4	19.54	32.91	< 0.0001
Within groups	20.78	35	0.5937		
Total	98.93	39			
B. Swimming behavior					
Between groups	31.78	4	7.944	7.869	0.0001
Within groups	35.33	35	1.010		
Total	67.11	39			
C. Schooling behavior					
Between groups	59.54	4	14.89	30.85	< 0.0001
Within groups	16.89	35	0.4825		
Total	76.43	39			
D. Visibility behavior					
Between groups	53.11	4	13.28	196.1	< 0.0001
Within groups	2.031	35	0.06769		
Total	55.14	39			

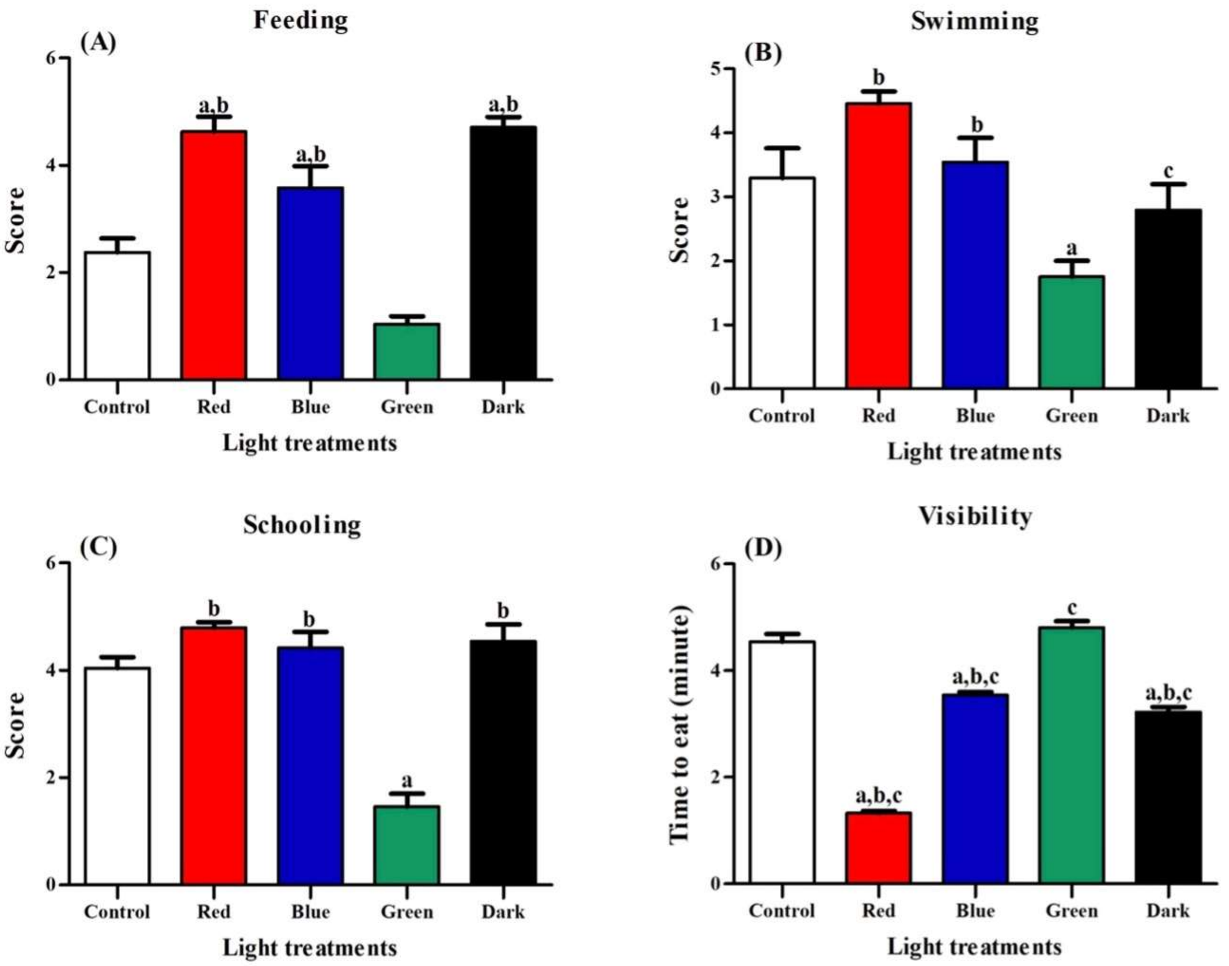

Figure 2 Behavior patterns of *L. calcarifer* during juvenile stage when reared under different light treatments. Vertical whiskers indicate standard error of mean (± SE). A: Feeding behavior; B: Swimming behavior; C: Schooling behavior; D: Visibility (latency) behavior. Values are expressed as mean ± SEM, $^{a}p < 0.05$, compared with control, $^{b}p < 0.05$, compared with green, $^{c}p < 0.05$, compared with red.

3.3 Retinal layer and photoreceptor structures of *Lates calcarifer* during juvenile stage

Histological structures were examined for thickness of the retinal layer and the photoreceptor cell layer in fish grown under the five light treatments (**Figure 3**). There was a significant difference (F = 73.92, 496.40; $p < 0.01$) (**Table 3**) between the thickness of these layers, in which fish under the red light showed the highest values (**Figure 4**). More specifically, the thicknesses of the retinal layer and the photoreceptor cell layer in the red-light treatment were 188.18 ± 38.16 μm and 25.00 ± 3.46 μm, respectively, being significantly higher than those in other groups. Again, the green group showed the lowest values. It is possible that the red light influenced the development of the visual system, as reported in other fish (Kobayashi, 1962; Kawamura et al., 1984; Lythgoe & Partridge, 1989). These results are similar to those reported in *Metynnis roosevelti*, which also acclimated to red light mainly by an expansion of the photoreceptor layer (Donatti & Fanta, 1999).

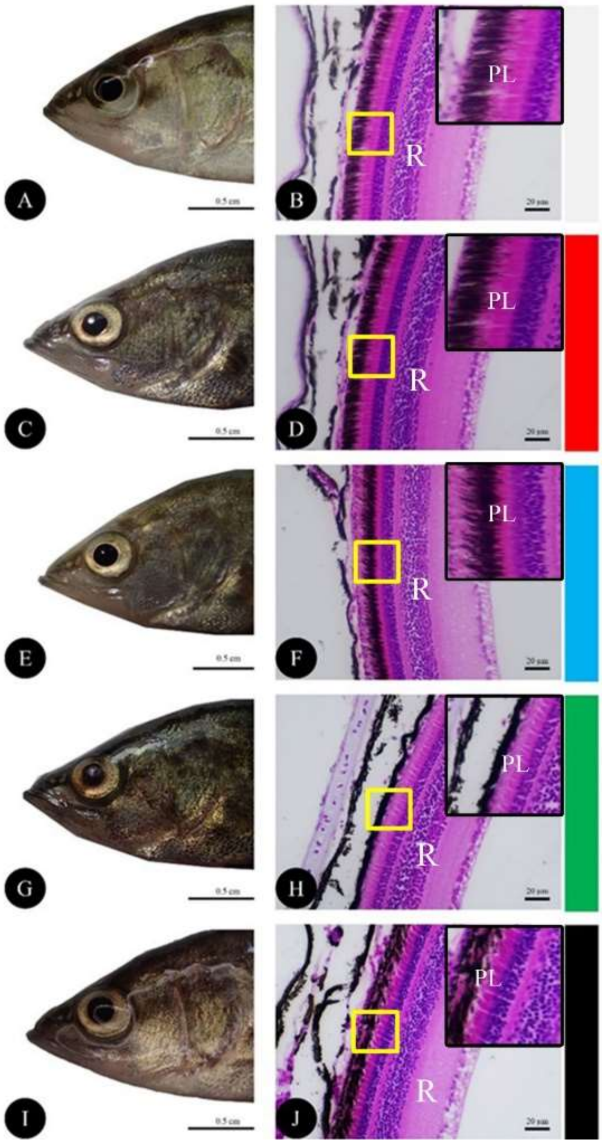

Figure 3 Morphology and transverse section of retinal layer (R) and photoreceptor cell layer (PL) of *L. calcarifer* during juvenile stage when reared under different light treatments. A-B: Control group; C-D: Blue 435 nm; E-F: Green 510 nm; G-H: Red 710 nm; I-J: Dark conditions.

Table 3 One-Way ANOVA results for difference in retinal organization of *L. calcarifer* during juvenile stage when reared under different light treatments.

Retinal organization	Sum of Squares	Df	Mean Squares	F	Sig.
A. Retinal layer					
Between groups	170200	4	42550	73.92	< 0.0001
Within groups	204300	355	575.6		
Total	374500	359			
B. Photoreceptor cell layer					
Between groups	9408	4	2352	446.4	< 0.0001
Within groups	1870	355	5.269		
Total	11280	359			

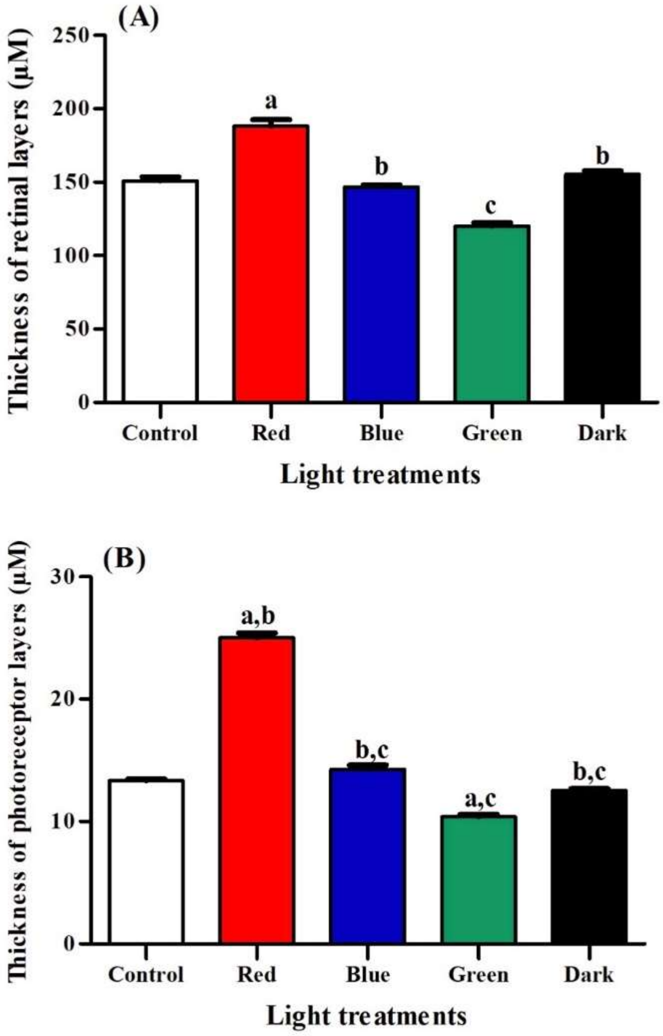

Figure 4 Statistical evaluation of retinal organization of *L. calcarifer* during juvenile stage when reared under different light treatments. A: Retinal layer; B: Photoreceptor layer. Values are expressed as mean ± SEM, $^{a}p < 0.01$, compared with control, $^{b}p < 0.01$, compared with green, $^{c}p < 0.01$, compared with red.

4. Conclusions

Red light treatment positively affected swimming behavior and feeding response of *Lates calcarifer* juvenile compared to other light treatments. The red-light treatment also led to the highest growth performance, measured as average weight and total length. Additionally, our preliminary analysis showed that fish grown under red light had the greatest thicknesses of the retinal layer and photoreceptor cell layer. These results demonstrate that red light is optimum for the cultivation of *L. calcarifer* juveniles, which might stimulate motivation for feeding activity and improvement in growth rate of its aquaculture and farms. A limitation of this study is that we did not measure light intensity. The spectral irradiance of a wavelength spectrum is generally measured in watts per square meter per meter ($W \cdot m^{-3}$) or, more commonly, watts per square meter per nanometer ($W \cdot m^{-2} \cdot nm^{-1}$). While we consider that the results are useful in practical settings, it is possible that the observed differences are attributed not only to wavelength, but also to intensity. Further studies are needed to accurately understand the effect of light on the aquaculture of *L. calcarifer*.

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References

Ahmad, A. M., Shoman, H. M., El-Deeb, R. M., Abdelhafez, H. M., & Samei, E. A. (2017). Comparative studies on the histology of eye retina in some Nile fishes with different dial activities. *Egyptian Journal of Hospital Medicine, 68*, 815-823. https://doi.org/10.12816/0038179

Ballagh, D. A., Pankhurst, P. M., & Fielder, D. S. (2008). Photoperiod and feeding interval requirements of juvenile mulloway, *Argyrosomus japonicus*. *Aquaculture, 277*, 52-57. Https://doi.org/10.1016/j.aquaculture.2008.02.025

Begg, K., & Pankhurst, N. W. (2004). Endocrine and metabolic responses to stress in a laboratory population of the tropical damselfish *Acanthochromis polyacanthus*. *Journal of Fish Biology, 64,* 133-145. https://doi.org/ 10.1111/j.1095-8649.2004.00290.x

Blaxter, J. H. S. (1968). Light intensity, vision and feeding in young plaice. *Journal of Experimental Marine Biology and Ecology, 2*, 293-307. https://doi.org/10.1016/0022-0981(68)90021-X

Boeuf, G., & Bail, P. Y. L. (1999). Does light have an influence on fish growth? *Aquaculture, 177*, 129-152. https://doi.org/10.1016/S0044-8486(99)00074-5

Cuvier-Péres, A., Jourdan, S., Fontaine, P., & Kestemont, P. (2001). Effects of light intensity on animal husbandry and digestive enzyme activities in sea bass *Dicentrachus labrax* post-larvae. *Aquaculture, 202*, 317-328. https://doi.org/ 10.1016/S0044-8486(01)00781-5

Department of Fisheries. (2017). *Statistical analysis of estuarine fish, 2017*. Department of Fisheries Science. Retrieved from https://www.fisheries.go.th/strategy-stat/themeWeb/books/2559/1/yearbook_2559.pdf

De Jesus-Ayson, E. G., & Ayson, F. G. (2014). *Reproductive biology of the Asian seabass, Lates calcarifer* (pp. 67-76). In Jerry, D. R. (Ed.). Biology and Culture of Asian Seabass *Lates calcarifer*. CRC Press, Boca Raton. https://doi.org/10.1201/b15974-6

Donatti, L., & Fanta, E. (1999). Morphology of the retina in the freshwater fish *Metynnis roosevelti Eigenmann* (Characidae, Serrasalminae) and the effects of monochromatic red light. *Revista Brasileira de Zoologia, 16*, 151-173. https://doi.org/10.1590/S0101-81751999000100011

Downing, G., & Litvak, M. K. (1999). The effect of photoperiod, tank colour and light intensity on growth of larval haddock. *Aquaculture International, 7*, 369-382. https://doi.org/10.1023/A:1009204909992

Fielder, D. S., Bardsley, W. J., Allan, G. L., Fielder, D. S., & Pankhurst, P. M. (2002). Effect of photoperiod on growth and survival of snapper *Pagrus auratus* larvae. *Aquaculture, 211*, 135-150. https://doi.org/10.1016/S0044-8486(02)00006-6

Genten, F., Terwinghe, E., & Danguy, A. (2009). *Atlas of fish histology* (pp. 1-138). Science Publishers. https://doi.org/10.1201/9780367803599

Glencross, B., Wade, N., & Morton, M. K. (2013). *Lates calcarifer nutrition and feeding practices* (pp. 1-326). Taylor and Francis, Boca Raton.

Glencross, B. (2006). *Nutritional requirements: Carnivorous fin-fish. Aquaculture nutrition master class* (pp. 1-40). Bangkok, Thailand: Asian Institute of Technology.

Guiguen, Y., Cauty C., Fostier, A., Jacques F., & Jalabert, B. (1994). Reproductive cycle and sex inversion of the Seabass, *Lates calcarifer*, reared in sea cages in French Polynesia: Histological and morphometric description. *Environmental Biology of Fishes, 39*, 231-247. https://doi.org/10.1007/BF00005126

Gunnarsson, S., Imsland, A. K., Siikavuopiom, S. I., Árnason, J., Gústavsson, A., & Thorarensen A. (2012). Enhanced growth of farmed Artic charr (*Salvelinus alpinus*) following a short day photoperiod. *Aquaculture, 350-353*, 75-81. https://doi.org/10.1016/j.aquaculture.2012.04.014

Heerhartz, S. M., & Toft, J. D. (2015). Movement patterns and feeding behavior of juvenile salmon (*Oncorhynchus spp.*) along armored and unarmored estuarine shorelines. *Environmental Biology of Fishes, 98*, 1501-1511. https://doi.org/10.1007/s10641-015-0377-5

Howell, A., Berlinsky, D. L., & Bradley, T. M. (2003). The effect of photoperiod manipulation in the reproduction of black sea bass, *Centropristis striata*. *Aquaculture, 218*, 651-669. https://doi.org/10.1016/S0044-8486(02)00343-5

Hunt, D. E., Rawlinson, N. J. F., Thomas, G. A., & Cobcroft, J. M. (2015). Investigating photoreceptor densities, potential visual acuity, and cone mosaics of shallow water, temperate fish species. *Vision Research, 111*, 13-21. https://doi.org/10.1016/j.visres.2015.03.017

IBM Crop. (2015). *IBM SPSS Statistics for Windows, Version 23.0*. Armonk, NY: IBM Crop.

Imsland, A. K., Foss, A., Stefansson, S. O., Mayer, I., Norberg, B., Roth, B., & Jenssen, M. D. (2006). Growth, feed conversion efficiency and growth heterogeneity in Atlantic halibut (*Hippoglossus hippoglossus*) reared at three different photoperiods. *Aquaculture Research, 37*, 1099-1106. https://doi.org/10.1111/j.1365-2109.2006.01533.x

Job, S. D., & Bellwood, D. R. (2007). Light sensitivity in larval fishes: Implications for vertical zonation in the pelagic zone. *Limnology and Oceanography, 45*, 362-371. https://doi.org/10.4319/lo.2000.45.2.0362

Karakatsouli, N., Papoutsoglou, S. E., Pizzonia, G., Tsatsosa, G., Tsopelakos, A., Chadio, S., Kalogiannis, D., Dalla, C., Polissidis, A., & Papadopoulou-Daifotic, Z. (2007). Effects of light spectrum on growth and physiological status of gilthead seabream *Sparus aurata* and rainbow trout *Onchorhynchus mykiss* reared under recirculating system conditions. *Aquacultural Engineering, 36*, 302-309. https://doi.org/10.1016/j.aquaeng.2007.01.005

Kawamura, G., Bagarinao T. U., & Lim, L. S. (2015). *Fish behaviour and aquaculture* (pp. 68-106). In Mustafa, S., & Shapawi, R. (Eds.). Aquaculture Ecosystems: Adaptability and Sustainability. Wiley-Blackwell, Oxford. https://doi.org/10.1002/9781118778531.ch3

Kawamura, G., & Ishida, K. (1985). Changes in sense organ morphology and behaviour with growth in the flounder *Paralichthys olivaceus*. *Bulletin of the Japanese Society of Scientific Fisheries, 51*, 155-165. https://doi.org/10.2331/suisan.51.155

Kawamura, G., Tsuda, R. Kumai, H., & Ohashi, S. (1984). The visual cell morphology of *Pagrus major* and its adaptive changes with shift from pelagic to benthic habitats. *Bulletin of the Japanese Society of Scientific Fisheries, 50*, 1975-1980. https://doi.org/10.2331/suisan.50.1975

Kim, H. H., Goins, G. D., Wheeler, R. M., & Sager, J. C. (2004). Green-light supplementation for enhanced lettuce growth under red-and blue-light-emitting diodes. *HortScience, 39*, 1617-1622. https://doi.org/10.21273/HORTSCI.39.7.1617

Kobayashi, H. (1962). A comparative study on electroretinogram in fish, with special reference to ecological aspects. *Journal of Shimonoseki University of Fisheries, 11*, 407-538.

Li, N., Zhou, J., Wang, H., Wang, C., Mu, C., Shi, C., & Liu L. (2020). Effects of light intensity on growth performance, biochemical composition, fatty acid composition and energy metabolism of *Scylla paramamosain* during indoor overwintering. *Aquaculture Reports, 18*, 100443. https://doi.org/10.1016/j.aqrep.2020.100443

Lythgoe, J. N., & Partridge, J. C. (1989). Visual pigment and the acquisition of visual information. *Journal of Experimental Biology, 146*, 1-20. https://doi.org/10.1242/jeb.146.1.1

Marchesan, M., Spoto, M., Verginella, L. & Ferrero, E.A. (2005). Behavioural effects of artificial light on fish species of commercial interest. *Fisheries Research, 73*, 171-185. https://doi.org/10.1016/j.fishres.2004.12.009

Martínez-Cárdenas, L., & Purser, G. J. (2011). Effect of stocking density and photoperiod on growth and survival in cultured early juvenile pot-bellied seahorses *Hippocampus abdominalis* Lesson, 1827. *Aquaculture Research, 43*, 1536-1549. https://doi.org/10.1111/j.1365-2109.2011.02958.x

Matsuoka, M. (1999). Histological characteristics and development of the retina in the Japanese sardine *Sardinops melanostictus*. *Fisheries Science, 65*, 224-229. https://doi.org/10.2331/fishsci.65.224

Naas, K., Huse, I., & Iglesias, J. (1996). Illumination in first feeding tanks for marine fish larvae. *Aquacultural Engineering, 15*, 291-300. https://doi.org/10.1016/0144-8609(95)00019-4

Parr, A. E. (1927). A contribution to the theoretical analyses of the schooling behavior of fishes. *Occasional papers of the Bingham Oceanographic Collection*, *1*, 1-32.

Parr, A. E. (1931). Sex dimorphism and schooling behavior among fishes. *The American Naturalist, 65*, 173-180. https://doi.org/10.1086/280359

Pillay, T. V. R., & Kutty, M. N. (2005). *Aquaculture principles and practices* (pp. 1-640). Blackwell, London.

Presnell, J. K., & Schreibman, M. P. (2013). *Humason's Animal Tissue Techniques* (pp. 1-600). 5th eds. Johns Hopkins University Press, Baltimore.

Ruchin, A. B. (2004). Influence of colored light on growth rate of juveniles of fish. *Fish Physiology and Biochemistry, 30*, 175-178. https://doi.org/10.1007/s10695-005-1263-4

Suvarna, K. S., & Layton, J. D. (2013). *Bancroft Bancroft's Theory and Practice of Histological Techniques* (pp. 1-573). 7th ed. Elsevier, Canada.

Trippel, E. A., & Neil, S. R. E. (2002). Effects of photoperiod and light intensity on growth and activity of juvenile haddock (*Melanogrammus aeglefinus*). *Aquaculture, 217*, 633-645. https://doi.org/10.1016/S0044-8486(02)00198-9

Ulmann, J. F. P., Gallagher, T., Hart, N. S., Barnes, A. C., Smullen, R. P., Collin, S. P., & Temple, S. E. (2011). Tank color increase growth and alters color preference and spectral sensitivity in barramundi (*Lates calcarifer*). *Aquaculture, 32*, 235-240. https://doi.org/10.1016/j.aquaculture.2011.10.005

Utne-Palm, A. C., Breen, M., Løkkeborg, S., & Humborstad, O. B. (2018). Behavioral response of krill and cod to artificial light in laboratory experiments. *PLoS One, 13*, e0190918. https://doi.org/10.1371/journal.pone.0190918

Volpato, G. L., Bovi, T. S., Freitas, R. H. A., Silva, D. F., Delicio, H. C., Giaquinto, P. C., & Barreto, R. E. (2013). Red light stimulates feeding motivation in fish but does not improve growth. *PLoS One, 8*(3), e59134. https://doi.org/10.1371/journal.pone.0059134

Wilson, J. M., Bunte, R. M., & Carty, A. J., (2009). Evaluation of rapid cooling and tricaine methanesulfonate (MS222) as methods of euthanasia in zebrafish (*Danio rerio*). *Journal of the American Association for Laboratory Animal Science, 48*, 785-789.

Yoshimatsu, T., Schröder, C., Nevala N. E., Berens P., & Baden T. (2020). Fovea-like photoreceptor specializations underlie single UV cone driven prey-capture behavior in Zebrafish. *Neuron, 107*, 320-337. https://doi.org/10.1016/j.neuron.2020.04.021