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The giant freshwater prawn *Macrobrachium rosenbergii* alters background colour preference after metamorphosis from larvae to postlarvae: In association with nature of phototaxis

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Abstract

The giant freshwater prawn *Macrobrachium rosenbergii* larvae have apposition eyes and are positively phototactic, whereas the postlarvae (PL) have superposition eyes and are negatively phototactic. *M. rosenbergii* has colour vision as early as larval stage. We discovered that *M. rosenbergii* alters background colour preference after metamorphosis from larvae to PL in association with nature of phototaxis. The test circular glass aquaria covered with a pair of two-colour papers contained with a group of 100 larvae or 20 Pl, and the number of individuals in each colour background was recorded five times for each colour pair. The background colours tested were light blue, green, yellow, red, white and black. The numbers of larvae or PL in each colour background of different pairs were analysed by the Thurstone's law of comparative judgment. In the larvae, significant bias towards yellow was evident. In the PL, of the four pairings of black with other colours, all biased to black. The mean *z*-scores were highest for yellow in the larvae, and for black in the PL. To determine the possible background brightness preference of the larvae and PL, six different colour backgrounds were presented in pairs. The larvae significantly preferred light blue over dark blue, white over yellow and white over black. The PL exhibited reversed preference. The relationship between *z*-scores and light reflectance levels of five colour papers was significantly positive in the larvae and negative in the PL. The observed background colour preference was probably due to relative brightness rather than chromaticity difference.

KEYWORDS
brightness, chromaticity, metamorphosis, phototaxis

1 | INTRODUCTION

Animals in farms are able to detect unfavourable stimuli but are unable to avoid unfavourable conditions and move to favourable locations, unlike the wild animal populations at sea with vast area to explore. In hatcheries and grow-out farms, it is crucial that the environmental conditions are kept at optimum of tolerable levels for the animal stocks. Confinement in high-density farms is stressful and often leads to abnormal behaviour and disease and parasites.

The colour of the farm environment has significant effects on the growth and stress response of farmed animals. The effects of background colour have been studied also for decapod crustaceans. Feed intake was significantly affected by tank colours in the giant freshwater prawn *Macrobrachium rosenbergii* (Lin & Omori, 1993; Yasharian, Coyle, Tidwell, & Stilwell, 2005) and Amazon River prawn

M. amazonicum (Maciel & Valenti, 2014). Tank colours affected the survival and development of larval mud crab *Scylla serrata* (Rabbani & Zeng, 2005), blue swimming crab *Portunus pelagicus* (Azra, Wendy, Talpur, Abol-Munafi, & Ikhwanuddin, 2012) and red cherry shrimp *Neocaridina heteropoda* (Laohavisuti & Ruangde, 2014). On the other hand, no effect was detected in *M. rosenbergii* postlarvae reared with black nylon netting shelter or blue one (Harun et al., 2016).

There are three dimensions of colour: hue (chromaticity), saturation and brightness. While colour vision of test animals is uncertain, experiments on the effects of light colour and tank colour are often based on the assumption that the test animals have colour vision. The effect of colour of light or tank varies depending on the spectral sensitivity of the test animals. For example, true demersal marine fish are not sensitive to red light and receive less or no effect of red light or tank even though they have colour vision (Kawamura, Bagarinao, Anraku, & Okamoto, 2017a). In the previous studies on the background colour, a direct comparison of the results was difficult because the reflectance spectra for the background colours and spectral sensitivity of the test animals were not available. The reflectance spectra give information on the three dimensions of colour of tanks, which enable data interpretation dissociating chromaticity from brightness.

Macrobrachium rosenbergii shifts habitat from a pelagic to a benthic habitat undergoing a considerable change of optic environment. The larvae hatch with apposition compound eyes but grow to have reflecting superposition compound eyes by late larval or early postlarval phase (Anger, 2001). In general, reflecting superposition eyes are more light-sensitive and thus, advantageous for species that live under dim light conditions. The postlarvae (PL) may protect their sensitive eyes by avoiding the water surface during daytime (Bialetzki Nakatani, Baumgartner, & Bond-Buckup, 1997; Moreira & Collart, 1993). In the hatchery, the larvae are photopositive but the benthic PL are photonegative (Kawamura, Bagarinao, Yong, Faizal, & Lim, 2017c). Therefore, it is possible that *M. rosenbergii* alters background colour preference associating with phototactic nature.

The objective of this study was to determine background colour preference of *M. rosenbergii* larvae and PL in the laboratory. *M. rosenbergii* has colour vision as early as in larval stage (Kawamura, Bagarinao, Yong, Jeganathan, & Lim, 2016), and its eyes are sensitive to a wide range wavelengths with a peak at 563 nm (Matsuda & Wilder, 2014).

Macrobrachium rosenbergii is now an important aquaculture commodity, and its global production has increased rapidly since the 1990s (New, 2002). Efforts are continuing to improve its growth, survival and production under various conditions. In order to ensure the welfare of farmed animals in the hatchery, it is necessary to understand their behaviour (Mench, 1998).

2 | MATERIALS AND METHODS

2.1 | Ethical approval

All the experimental trials were conducted in accordance with the Researcher's Guidelines On Code Of Practice For The Care And Use Of Animals For Scientific Purposes Universiti Malaysia Sabah.

2.2 | Test animals and holding condition

This study was conducted in the Shrimp Hatchery of Borneo Marine Research Institute, Universiti Malaysia Sabah, Malaysia. A berried female with greyish eggs was selected and reared in a 100-L circular tank filled with 10 mg/L brackish water. Black netting was used to cover the tank and reduce the light intensity in the tank. Hatched larvae were reared in a 360-L grey-walled conical circular tank (diameter 93 cm, depth 53 cm) filled with 10 mg/L brackish water. At stage zoea V, they were fed with *Artemia* nauplii and egg custard (egg yolk 80 g, milk powder 50 g, vitamin premix 2 g, and cod-liver oil 8 ml). Water temperature ranged from 25.7 to 27.4°C; dissolved oxygen, 6.0 to 8.2 mg/L; pH 7.5 to 8.7; and salinity 8 to 12 mg/L (pH/ORD/EC/DO tester, Hanna Instruments, HI 9,828, Washington, USA) during the holding.

Macrobrachium rosenbergii larvae and postlarvae (PL) were obtained from the Shrimp Hatchery ad libitum and used in this study. The PL were acclimated to freshwater over a 10-day period in another 360-L grey-walled conical circular tank (PL rearing tank) and fed a formulated diet (protein content 42%, lipid content 6%) (CP Aquaculture Limited, Thailand) twice daily. Water temperature ranged 25.6–27.6°C; pH 7.18–7.64; and dissolved oxygen 4.6–5.2 mg/L.

2.3 | Background colour materials

Seven different colour papers were used to represent different background colours: light blue, dark blue, green, red, yellow, black and white. For the behavioural tests, five transparent circular glass aquaria (23 cm diameter, 10 cm height, 4 cm water depth) were used. Their outside of half bottom wall and half side wall were covered with a colour paper, and the other parts were covered with a different colour paper.

The luminance at the water surface ranged from 24.8 to 51.7 cd/m^2 (Luminance meter, Konica Minolta LS-150, Tokyo, Japan). The light reflectance spectra of the colour papers were recorded under natural light with a spectroradiometer (HSR-8100, Maki Manufacturing Co., Ltd., Hamamatsu, Japan) in the wavelength range of 400–700 nm (Figure 1).

2.4 | Background colour preference test

Five different colour backgrounds were used: light blue, green, yellow, red and black.

The aquaria were arranged on a table placed in the roofed hatchery, and each aquarium contained with a group 100 larvae (stage VI onward) or 20 Pl transferred from the rearing tanks. Then, the water was stirred gently with a glass rod to homogenize the distribution of larvae or PL in the aquaria. After 30 min acclimation, the larvae or PL were photographed at 5 min intervals (total 25 min) with a digital camera (IXUS 160, Canon, Tokyo, Japan) positioned at 40 cm above the water surface. In each subsequent trial, the assigned aquarium was rotated randomly by 60°–180° relative to the previous trial in order to randomize the colour position. This procedure was repeated five times (five replications) for each colour pair. The pairing of two colours was made at random using a die, and all the 10 possible colour pairs were tested. To avoid a possible effect of the prior colour background on subsequent background colour preference, a group of larvae or PL was replaced with a new group after five repeated trials with each pair.

2.5 | Background brightness preference test

In order to determine the possible background brightness preference of the larvae and PL, six different colour backgrounds were presented in pairs: light blue versus dark blue, yellow versus white and black versus white. The experimental procedure and stages of the animals used were the same as in the background colour preference test.

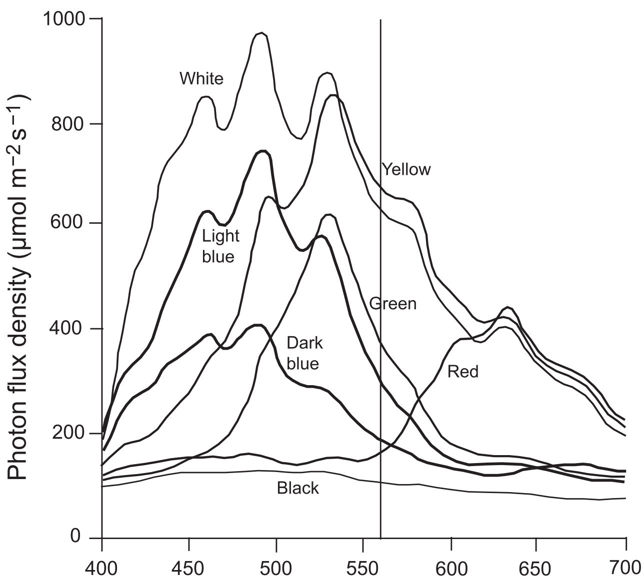

FIGURE 1 Light reflectance spectra of six colour papers of light blue, dark blue, green, yellow, red, grey, black and white recorded under natural light with a spectroradiometer. Height level of spectra shows level of brightness in the order of white, yellow, light blue, green, dark blue, red and black. Vertical bar shows a peak sensitivity wavelength of *Macrobrachium rosenbergii* at 563 nm

2.6 | Data analyses

In the background colour preference test, the numbers of larvae or PL in each colour background of different colour pairs were analysed using the chi-squared test to judge if the distribution of the larvae or PL is homogeneous or biased towards a certain colour. The comparative background colour preference for each colour was judged by the Thurstone's law of comparative judgment (Thurstone, 1927). The numbers of larvae or PL counted in each background colour were summed over the five trials for each colour, and then transformed into proportions, and the *z*-scores were obtained from the table of cumulative probabilities of the standard normal distribution. The relative preference of *M. rosenbergii* for different colours was deduced from the mean *z*-score of each shelter colour. A negative *z*-score is below the mean, a positive *z*-score is above the mean, and a higher *z*-score shows a higher preference for a colour (Kawamura, Kasedou, Maniya, & Watanabe, 2010). Thus, the *z*-scores imply the magnitude of relative preference. For statistical comparison of the mean *z*-sores, 95% confidence interval was calculated for each mean *z*-score.

The relationship between mean *z*-scores and the light reflectance levels (brightness) was determined for five colour papers to detect the contribution of comparative brightness to the background colour preference. For the direct comparison of five reflectance levels, the photon flux densities at wavelength 563 nm were employed (Figure 1), which is the peak visual sensitivity of *M. rosenbergii* (Matsuoka & Wilder, 2014).

In the background brightness test, the summed number of *M. rosenbergii* in each background colour in each combination was analysed using the chi-squared test. Chance probability associated with this is ½. Significant level was set at $\alpha = 0.05$.

3 | RESULTS

The larvae and PL could move freely between two background colours and showed a clear preference to some colours. Results of the

TABLE 1 Summary of number of prawn in each background colour presented as colour pairs to groups of prawn

Prawn (group size)		Number of prawn by colour pair (left colour:top colour)			
		Black	Green	Red	Yellow
Larvae (100)	Light blue	390:110**	397:103**	399:101**	82:418**
	Black		427:73**	74:426**	26:474**
	Green			291:209**	17:483**
	Red				8:492**
Postlarvae (20)	Light blue	17:83**	44:56	25:75**	78:22**
	Black		68:32**	70:30**	82:18**
	Green			61:39*	92:8**
	Red				85:15**

Notes: * and ** denote significances at α = 0.05 and α = 0.005 respectively (χ^2-test).

background colour preference test are summarized in Table 1 for the larvae and PL. Of the 10 pairings, significant difference was evident in all pairings in the larvae, and in nine pairings in the PL, indicating biased distributions.

The mean *z*-scores were highest for yellow (1.315) (significant at α = 0.05) and lowest for black (−0.899) in the larvae, whereas in the PL the mean *z*-scores were highest for black (0.575) and lowest for yellow (−0.826) (significant at α = 0.05) (Figure 2). Figure 3 shows the relationship between the relative light reflectance levels and the mean *z*-cores for five colour papers. The relationship is significantly positive for the larvae (r = 0.9498, p = .0134) and significantly negative for the PL (r = −0.9378, p = .0188).

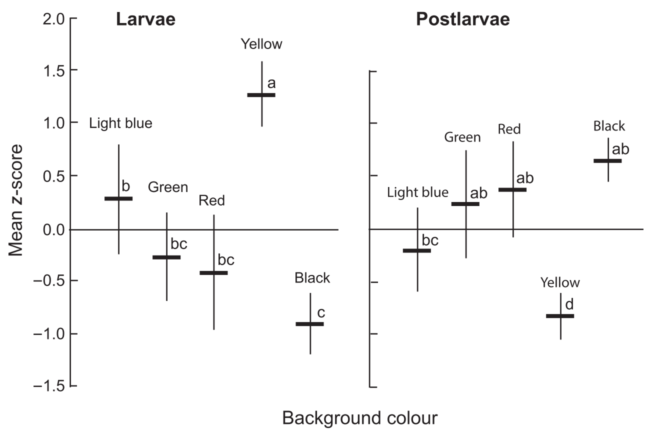

FIGURE 2 Mean *z*-scores for the response of *Macrobrachium rosenbergii* larvae and postlarvae to different colour backgrounds. Means with different letters are significantly different (p < .05). Note: vertical bar, 95% confidence interval

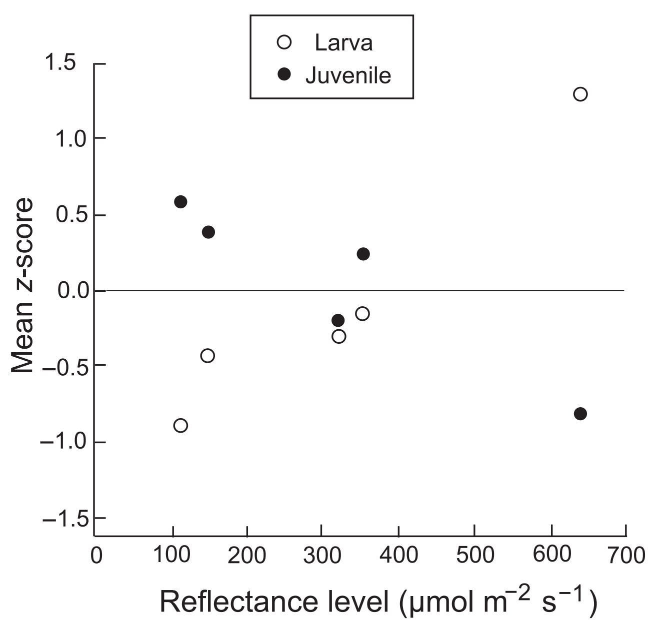

FIGURE 3 Relationship between relative light reflectance levels and mean *z*-cores for five colour papers. The relationship is significantly positive in larvae and negative in PL

Table 2 shows the results of the background brightness test. The larvae preferred light blue over dark blue, white over yellow and white over black (p < .005). The PL preferred dark blue over light blue and black over white (p < .005), but there was no difference between yellow and white (0.5 < p < .75).

4 | DISCUSSION

This study clearly demonstrated that *M. rosenbergii* larvae and PL detected and preferred different colours of the background. In the colour background preference test, the most and least preferred colours were reversed in larvae and PL; while the larvae preferred yellow most and black least followed by red, the PL preferred yellow least and black most followed by red. In the background brightness preference test, the larvae preferred lighter colours while the PL did darker colours in each colour combination. The light reflectance spectra (Figure 1) indicated that the brightness was highest for white paper followed by yellow, light blue, and black was lowest followed by red. Giving that the green sensitive eye of *M. rosenbergii* is less sensitive to red than to blue (Matsuda & Wilder, 2014), red might be seen darker than dark blue to *M. rosenbergii*. In the larvae, the mean *z*-scores were highest for yellow followed by light blue, green, and black was lowest. This order is consistent with that of the level of light reflectance. In the PL, the mean *z*-scores were highest for black followed by red, green, and lowest for yellow, consisting with that of the level of brightness. The correlation coefficient between the reflectance levels and the mean *z*-scores was significantly positive for the larvae and significantly negative for the PL.

All these results imply that the background colour preference is not a consequence of chromaticity response of *M. rosenbergii*, but of background brightness preference. The shift in background colour preference from lighter colours to darker colours, as expected, might be associated with the nature of phototaxis. As mentioned earlier, *M. rosenbergii* shifts the phototaxis from positive to negative at the metamorphosis from larvae to PL, consisting with the shift of the background brightness preference. The apposition compound eyes of larvae of decapods are designed for planktonic life (Nilson, 1983), and the electrophysiological measurements showed that the superposition eye is much more sensitive than the apposition eye (Meyer-Rochow & Gál, 2004; Meyer-Rochow & Horidge, 1975). The change in the eye sensitivity coincides well with the change in behavioural response to ambient light intensity.

Preference test can be usually used as an indicator of an optimal rearing environment (Luchiari & Pirhonen, 2008). The results of this study infer a practical application for the preferable colour of raising tanks; white (or lighter colour) for the larvae and black (or darker colour) for the PL. This inference coincides with the findings of Juarez, Holtschmit, Salmon, and Smith (1987) who reported that the captive *M. rosenbergii* juveniles preferred black bottom to blue or white bottom and showed greater growth rates in aquaria with black bottom. Withyachumnarnkul, Poolsanguan, and Poolsanguan (1990) indicated a positive effect of darkness on growth and survival

TABLE 2 Number of larvae and postlarvae in each colour background in each colour combination

Prawn	Trial	Colour combination					
		Light blue versus dark blue		Yellow versus white		Black versus white	
Larva	1	80	20	21	79	15	85
	2	77	23	16	84	13	87
	3	87	13	32	68	21	79
	4	85	15	25	75	14	86
	5	89	11	28	72	11	89
	Total	418	82	122	378	74	426
	χ^2-test	χ^2 = 225.792, p < .005		χ^2 = 131.072, p < .005		χ^2 = 247.808, p < .005	
Postlarvae	1	4	16	11	9	15	5
	2	7	13	10	10	12	8
	3	6	14	12	8	13	7
	4	8	12	10	10	17	3
	5	6	14	14	6	19	1
	Total	31	69	57	43	76	24
	χ^2-test	χ^2 = 14.440, p < .005		χ^2 = 0.1.960, 0.50 < p < .75		χ^2 = 27.040, p < .005	

of *M. rosenbergii* juveniles. According to Valenti and Daniel (2000), in the larval *M. rosenbergii* rearing tanks (8 tonnes) at Mississippi State University, the bottom wall and the side wall were painted white, which gave a good colour contrast to *Artemia* and allowed the larvae to feed more efficiently. *M. rosenbergii* larvae, PL, and juveniles are primarily visual feeders (Kawamura et al., 2016, 2017) and their prey detection by sight might be affected by background colours. The background colour produces different contrast for food, and it is well documented that more visible prey with high contract against the background is better detected and consumed by predators in open water and tanks (Browman, Flamarique, & Hawryshyn, 1994; Browman & Marcotte, 1987; Dendrinos Dewan & Thorpe, 1984; Hacker & Madin, 1991; Leclerc, Sirois, Planas, & Bérubé, 2011).

However, *M. rosenbergii* larvae have an innate food preference for blue which is discriminated by chromaticity rather than the contrast to the background colour (Kawamura et al., 2016). And Yong, Kawamura, Lim, and Gwee (2018) reported significantly greater growth performance in *M. rosenbergii* larvae fed blue coloured feed than those fed conventional yellow egg custard. The white leg shrimp *Litopenaeus vannamei* also have colour vision and the adults have food colour preference for yellow regardless of background colours (Kawamura et al., 2017). The innate food colour preference was reported also in marine teleost fish; the girella *Girella punctata*, the black porgy *Acanthopagrus schlegeli* and the Japanese silver bream *Acanthopagrus latus*, all these species have colour vision, showed innate food colour preference for yellow over blue, green, red and black in different colour environments: in white and grey tanks, sea cages made of black netting, and an earthen pond (Kawamura et al., 2010). In the juvenile African catfish *Clarias gariepinus*, the food colour preference for red and blue over green, yellow and white was not affected by five different background colours (Kawamura, Bagarinao, Asmad, & Lim, 2017b). Beverté, Betana, Gómez, and Bosch (2016) reported the flower colour choice mediated by the innate colour preference in six insect groups: bees, ants, wasps, coleopterans, dipterans and lepidopterans. Thus, colour per se is important in food choice irrespective of background colour in wide taxa.

Yasharian et al. (2005) reported that colours (blue, green, yellow, red, black and white) of 16.7 L tanks did not impact growth performance of the *M. rosenbergii* larvae but survival was higher in red and green tanks. This result is inconsistent with that of Valenti and Daniel (2000). The growth performance is affected by various factors such as temperature, water quality, stocking density and size of tank, quality and quantity of food, social nature of the test animal. The reason for inconsistency is uncertain but possibly due to the size of tanks used. The growth performance is significantly affected by size of tanks (Juarez et al., 1987).

Animals reared in a preferred background colour perform better food intake and growth (Duray, 1995; Lin & Omori, 1993; Maciel & Valenti, 2014; Strand, Alanärä, Staffan, & Magnhagen, 2007). But, it is noteworthy that behaviourally determined background colour preference did not coincide with the performance of larvae reared in tanks with different colours. Shi et al. (2019) reported that the swimming crab *Portunus trituberculatus* larvae showed a strong behavioural preference for white bottom over blue, green, red, yellow and black, whereas, in the rearing experiment with *Artemia* nauplii as feed, the best larval performance was obtained in red and yellow tanks, while the larvae in white tank had the least survival rate. However, the preference for white background might be a consequence of the adaptation of the larvae in the white resting zone before the larvae were allowed to choose coloured spaces. The prior residence in a certain colour environment affects subsequent colour preference in laboratory experiments (Luchiari & Pirhonen, 2008).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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