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Circadian Rhythm of Freshwater Prawn Genus *Macrobrachium* (*M. pilimanus* and *M. sintangense)* Under Laboratory Conditions

Diky Dwiyanto[1], Nurul Magfirah Sukri[2], Henta Ria Anisa[2], Refda Maulana Trisuji[2], Rika Raffiudin[2*]

[1]Agrotechnology Study Program, Program Studi di Luar Kampus Utama (PSDKU), Universitas Tadulako Tojo Una-Una, Jalan Jompi, Ampana Kota 94683, Central Sulawesi, Indonesia
[2]Animal Bioscience Study Program, Department of Biology, Faculty Mathematics and Natural Science, IPB University, Gedung Biologi, Jalan Agathis Kampus IPB Dramaga, Bogor 16680, West Java, Indonesia

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Abstract
Macrobrachium pilimanus and *M. sintangense* are two indigenous freshwater prawn species in Indonesia with good prospects in freshwater aquaculture. This study aimed to determine the daily activity patterns of circadian rhythm related to differences in periods (night and day phase) and sex (male and female) in passive-active behavior from two species of freshwater prawns, *M. pilimanus* and *M. sintangense*. We observed the behavioral pattern using the scan sampling method on three individuals from each species during night and day periods for 60 minutes. The results showed that *M. pilimanus* and *M. sintangense* have the highest percentage of passive behavior (04.00–07.00 PM), i.e., hiding and partially inactive. The active and passive behavior of *M. pilimanus* was affected only by sex but not by time. In *M. sintangense*, male individuals mostly spend their time in passive behavior during the day, while female in night. Also, in *M. sintangense*, only sex (female higher than male) affects the active behavior. This finding indicates that shelter for hiding is vital for freshwater prawn species as a strategy to increase productivity and animal welfare.

INTRODUCTION

Freshwater shrimp of the genus *Macrobrachium* Bate, 1868, is one of the groups of the subfamily Palaemoninae with the most numerous members, reaching 234 species (De Grave & Fransen, 2011). This genus is easy to recognize by the absence of a branchiostegal spine, the presence of a hepatic spine on the carapace, elongated second chelipeds with fingers not equipped by dense tufts of setae and a simple dactyl can be found in the last three pairs of pereopods (Chace & Bruce, 1993; Short, 2004). Some species of *Macrobrachium* are also well-known as good commodities in aquaculture in various countries (Holthuis, 1980). However, to date, more efforts are still being focused on *M. rosenbergii* or the giant freshwater prawn (New, 2002; Wowor & Ng, 2007). With its diversity of aquatic invertebrate creatures, Indonesia has several species of freshwater prawns that can potentially be developed as an alternative protein source (Said *et al*. 2014). Therefore, to ensure these species are correctly understood, studies in further detail, including their behavioral patterns, are much needed (dos Santos *et al*. 2017).

*Coresponding Author: rika.raffiudin@apps.ipb.ac.id
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Long-term research has been done on the taxonomic of freshwater prawns in Indonesia belonging to the genus *Macrobrachium* Spence Bate, 1868. Large islands like Sulawesi (Celebes) (see Thallwitz, 1891; De Man, 1892; Dwiyanto *et al.* 2017; Laewa *et al.* 2018) including its satellite island, Banggai Archipelago (Annawaty *et al.* 2022), Java (see De Man, 1892; Wowor, 2010; Prodhiana *et al.* 2022), Kalimantan (Borneo) (see De Man, 1898; Wowor & Short, 2007), and Sumatera (see De Man, 1879; 1892) have provided the majority of the new species descriptions. Most of them can be classified into two main types based on their reproductive biology, i.e., prolonged type – larvae need sea or brackish water to develop, and abbreviated type – larvae grow and develop fully in freshwater (Jalihal *et al*. 1993). Two freshwater prawns native to Sundaland (Java, Kalimantan, and Sumatra) (De Man, 1879; 1892) that spend their entire lives in freshwater environments (abbreviated type) are *Macrobrachium pilimanus* (De Man, 1879) and *M. sintangense* (De Man, 1898). It is possible to develop both of these species for freshwater aquaculture (Djajadiredja & Sachlan, 1956; Longhurst, 1970; Said *et al*. 2014).

Behavior connected to the biological clock or circadian rhythm, which is also significantly impacted by photoperiod (Rafinetti, 2000), is one of the fascinating issues to investigate in *Macrobrachium*. Like other crustaceans, freshwater prawns are nocturnal (Nakamura, 1975) and prefer to avoid light (Karplus & Harpaz, 1990). *Macrobrachium* are nocturnal, aggressive, and omnivorous; some species even exhibit cannibalism when starving (Choudhury, 1970). Clock genes, which control circadian rhythms in crustaceans like lobsters (Sbragaglia *et al*. 2015) and prawns (Yang *et al*. 2006), typically continue to express even when they are under laboratory conditions. Research on circadian rhythms involving the day-night phase (24 hours) is crucial because it can provide data on behavior patterns such as eating, moving and agonistic. In decapod groups like freshwater crayfish, movement activity is higher at night than during the day (De Miguel & Aréchiga, 1994). The behavioral patterns of numerous prawn species, including *Penaeus duorarum* (Hughes, 1972), *P. semisulcatus*, and *P. monodon* (Moller & Jones, 1975), which have high economic value in India, Madagascar, New South Wales, Japan, Mexico, and the United States (see Holthuis, 1980), have also been extensively studied using such behavioral research. However, in Indonesia, the cultured prawn *M. rosenbergii* research is only about reproductive and growth aspects (Wijaya *et al*. 2020), and there needs to be data on behavioral patterns.

Behavioral research on freshwater prawns has discussed the activity patterns of *Macrobrachium rosenbergii* both in monosex and mixed populations (dos Santos *et al*. 2015; dos Santos *et al*. 2018). However, there is no research on circadian rhythms in *M. pilimanus and M. sintangense*. This study aims to investigate daily activity patterns based on differences in periods (night-day) and passive-active behavior in males and females of two species, *M. pilimanus,* and *M. sintangense,* under laboratory conditions. It is anticipated that the findings of this study will serve as baseline information for efforts to reveal the potential of Indonesian prawns in aquaculture.

MATERIALS AND METHODS

Samples of *M. pilimanus* and *M. sintangense* were collected from their natural habitat in the Ciapus River (06°32.923' S and 106°43.264' E), Dramaga District, Bogor, West Java, Indonesia. This river is located at an altitude of about 154 m above sea level (a.s.l). The river substrate is composed of large boulders with moderate to fast currents, and the vegetation on the river banks is dominated mainly by shrubs and plantation plants. Human activities slightly pollute this river because piles of garbage along the river banks are also found in freshwater shrimp microhabitats. Sampling was conducted on February 15 and 23, 2020, using a tray net (Ng, 2017). *Macrobrachium pilimanus* was found among the macrophytes near large rocks and strong currents. Meanwhile, *M. sintangense* was mainly collected among the *Pennisetum* sp. and dead branches on the bank with moderate to slow currents. The substrates are gravel and rock, with water depths ranging from 25–30 cm. The samples were kept in a small tank and transported into the laboratory for observation. The carapace length (CL) (Fig. 1A) was measured with digital calipers (0.01 mm) from the postorbital to the posterior median margin (Wowor & Ng, 2007). The sex of each individual was observed using a Nikon SMZ445 stereomicroscope based on the presence and absence of the appendix masculina on the second pleopod (Figure 1B).

The prawn was kept in a glass aquarium measuring 30 × 19 × 20 cm, filled with 11 litres of water with a ratio of 50 : 50 (water from river : tap water or PDAM), and equipped with an aerator to supply oxygen (Figure 2) (dos Santos *et al.* 2017). Once a week, about 70% of the aquarium water was replaced with fresh tap water. Water temperature was measured three times, i.e., morning (0800–1000 h), afternoon (1300–1400 h) and evening (1600–1700 h) using a thermometer. The average temperature (°C) in the morning, afternoon, and evening was 27.8±0.47, 26.2±0.7, and 27.7±0.41, respectively. The bottom of the aquarium was given a layer of thick gravel (± 1 cm) and stones from natural habitats to facilitate shrimp in hiding or sheltering behavior. The genus *Macrobrachium* is a predator and tends to be carnivorous (Jayachandran & Joseph, 1989). The artificial food (pellets) (dos Santos & Almeida, 2018) and shredded fish (fish meal) (Hossain & Paul, 2007) were given twice a day, i.e. at 0800–1000 h and 1500–1700 h through the *ad libitum* method, to avoid feeding during the observation period. Feeding and light simulation continued for seven days from the acclimatization period before the observation began (February 23–28, 2020) (Trevisan *et al.* 2014). The artificial light (photoperiod) was given following after 24 h (12 light and 12 dark) (Trevisan *et al*. 2014). For lighting during the day, we used a 6 W Submersible T4 Led bulb (Armada ACT-SP300A-T4-LED), while at night, two red bulbs were installed near the aquarium (5 W and 200 lm) (modified from Trevisan *et al*. 2014).

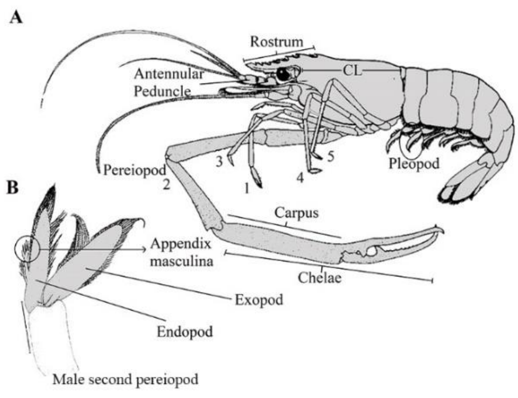

Figure 1. Freshwater prawn of the genus *Macrobrachium.* A. General morphology (modified from Carpenter and Niem, 1998; Wowor *et al.* 2004), B. Appendix masculina on male second pleopod (modified from Mejia-Ortiz *et al.* 2008 with permission).

The observation was performed on February 29 and March 08, 2020. A total of three individuals were observed for each species: one male, one female without eggs (non-ovigerous female), and one egg-bearing female (ovigerous female). Analysis of the percentage of male and female behavior only uses males and females without eggs, while comparing the frequency of behavior uses all individuals. Observation of the circadian rhythm was divided into two periods, i.e., day (light) and night (dark). The observation time was divided into four episodes: i.e., 1000 h, 1300 h, 1600 h, 1900 h (day), and 2200 h, 0100 h, 0400 h, and 0700 h (night) (Trevisan *et al.* 2014). In each episode, observations were made directly through the aquarium glass for 60 minutes using the scan sampling method (Altman, 1974) with intervals of 5 minutes. The distance between the observer and the aquarium was approximately ± 30 cm.

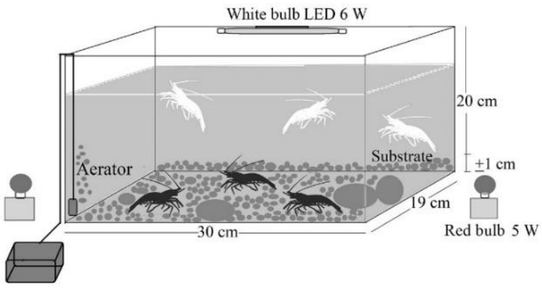

Figure 2. Aquarium design scheme. The colour difference indicates the two freshwater prawn species used in this study.

Table 1. Ethogram of freshwater prawn used in this study (modified from dos Santos & Pontes, 2016)

Behaviour	Description
Passive	
(BR) Burrowing	Digging or moving the substrate using pereiopods (walking legs) and pleopods (swimming legs) causes holes to form, which are then occupied by the prawn.
(HD) Hiding	The prawns enter under rocks or shelters and stay for a long time. The prawns are either completely invisible or only showed their pereiopods or antennae.
(PI) Partially Inactive	The prawns remained stationary, making only slight appendage movements (pereiopods and pleopods), antennae, or separate movements of the cephalothorax, right and left, up or down.
Active	
(MV) Moving	The prawns change places, shifting themselves with the first, second, third, fourth, or fifth pereiopod. Pleopods sometimes help shrimp to move quickly.
(GR) Grooming	The prawns rub or clean their bodies together using the first, second, third, fourth, or fifth pair of pereiopods.
(IN) Ingestion	The prawn holds food with the first pair of pereiopods or pinches the food, turns it over and puts it in their mouth, usually with the help of the second, third, fourth, or fifth pair of pereiopods.
(SC) Social	The prawn approaches or touches another individual. The chelae of the second pereiopod are open and directed or not towards other prawns. The shrimp may attack or threaten. This behaviour includes threatening, fighting or approaching.

Macrobrachium behaviour was divided into two general categories: active and passive. The behavioural ethogram of freshwater prawns was modified based on the daily behaviour of giant prawns (*M.* rosenbergii) (Table 1), which have been widely cultivated in several countries (dos Santos & Pontes, 2016). Much behavioural research has been carried out on *M. rosenbergii*, so the ethogram of this species was used as a reference in research. Observations using video recordings on crustaceans are generally difficult since they cannot show the animal's behaviour when hiding (Trevisan *et al*. 2014).

RESULTS AND DISCUSSION

The measurements of the average carapace length of *Macrobrachium pilimanus* and *M. sintangense* were 11.0 ± 2.16 mm and 13.9 ± 1.35 mm, respectively. The freshwater prawn used in this study had a very different morphological characters. *Macrobrachium pilimanus* has a short rostrum (Figure 3A,a), never reaches the end of the antennular peduncle with small and dense dorsal teeth, and the carpus on the second pereiopod is cup-shaped (Fig. 3A,b) with the chelae covered by pubescence (Fig. 3A,c). In *M. sintangense*, the rostrum is long and generally extends beyond the end of the antennular peduncle with large dorsal teeth (Fig. 3B,a), and the carpus of the pereiopod is sub-cylindrical, slender, and long (Fig. 3B,b) without pubescence (Fig. 3B,c).

Macrobrachium pilimanus was found in river habitats with relatively fast currents affected by human activities. According to Wowor & Choy (2001), the existence of this species is influenced by the physicochemical and vegetation cover, usually, parts of rivers near forests that are not too polluted. This species has a wide distribution from Yunnan (China) and Vietnam to Indonesia (Java and Kalimantan). Unlike the previous species, *M. sintangense* can be found even in disturbed areas with high anthropogenic activities (Johnson, 1964). *Macrobrachium sintangense*, which is also a native species from Southeast Asia, has previously been reported from Thailand, Peninsular Malaysia, Kalimantan (Cai *et al*. 2004) and several streams in Java (Sabar, 1979; Trijoko *et al*. 2015). Although these two species have good prospects in developing their economic value, *M. sintangense* tends to be more popular among the local community (known as Udang Regang). For example, in Java, *M. sintangense* is usually sold by people who live around reservoirs (waduk) or lakes with a price range of IDR 30,000–100,000/kg (Said *et al*. 2014).

Macrobrachium pilimanus showed that the highest percentage of daily behaviour (night and day) was hiding both in males (Figures 4A and 4B) and females (Figures 4C and 4D). In active behaviour, the highest percentage of male *M. pilimanus* was grooming (night and day) (Figures 4A and 4B). Meanwhile, the female *M. pilimanus* showed that the highest active behaviour at night was social (Figure 4C), and the day was grooming (Figure 4D). *Macrobrachium sintangense* male (Figures 5A and 5B) and female (Figures 5C and 5D) in passive behaviour showed the highest percentage in partially inactive (night and day). In active behaviour, the highest percentage of male *M. sintangense* was moving (night and day), while female was grooming both night and day.

Macrobrachium pilimanus shows the highest behavior during the day and night phases, i.e., hiding. This behavior pattern also occurs in their natural habitat, often hiding in the rocks at the bottom (Iwata *et al*. 2003). Hiding or sheltering in freshwater shrimp is generally affected by predators like fish (dos Santos *et al*. 2015) and light (Karplus & Harpaz, 1990). In the amphidromous freshwater shrimp, the sheltering behavior is carried out during the day when the larvae migrate upstream to protect themselves from predators and give time for the larvae to grow (Bauer, 2011). In contrast with the previous species, *M. sintangense* does not show hiding behavior during the day and night but seems more inactive or without activity. The same behavior also occurred during the dark period of *M. rosenbergii* reared in male-male (monosex) and male-female (mixed) populations (dos Santos *et al*. 2018). Passive behavior, which generally occurs in crustaceans, was also observed in cultured *Litopenaeus vannamei*, with a higher frequency during the light than the dark phase (Pontes *et al*. 2006). Increasing inactive behavior in freshwater shrimp can reduce the risk of being detected by predators during the day (Lammers *et al*. 2009). In the case of *M. sintangense* in this study, even though there is no predator, the highly inactive behavior might be caused by their innate behavior in their original habitat due to the limitation in acclimatization time (only a week).

In active behavior, both *M. pilimanus* and *M. sintangense* demonstrated grooming behavior. This behavior is generally carried out using maxillipeds and pereiopods (first to fifth). Like most groups of decapods, grooming has a benefit, including cleaning themselves from microorganisms by using the first to third pair of pereiopods or other limbs with setae or fine hairs (Bauer, 1981). The differentiation in the morphology of the crustacean is also due to adaptations to their grooming activities (see Bauer, 1989). Other active behaviors observed in *M. pilimanus* or *M. sintangensis* were social and moving. Interspecies "social" behavior shown is in the form of feeling threatened or attacking. Based on observations, M. *sintangense* attacks more, whereas *M. pilimanus* shows more threatened. Social dominance is generally found in *Macrobrachium* (e.g., *M. rosenbergii*), with large males (dominant or subordinate) having more access to resources than other individuals (Barki *et al*. 1991). Interspecies social behavior also generally occurs in an area inhabited by two species (sympatric) (Hazlett, 1974). In other groups, such as lobster, attacking behavior tends to be influenced by body size or aggressiveness (Söderbäck, 1991). *Macrobrachium sintangense* in this study was shown to be more aggressive than *M. pilimanus*, supported by its larger body size (CL 13.9 vs. 11.0 mm in *M. pilimanus*). The moving behavior of *M. sintangense* was higher in males than in females. This moving behavior differs from *M. rosenbergii*, where females tend to be more active at night (Peebles, 1979). In another species, *Macrobrachium australiense*, moving behavior is closely related to migration or rheotactic properties caused by water currents (Lee & Fielder, 1979) and avoiding competition (Lee & Fielder, 1982).

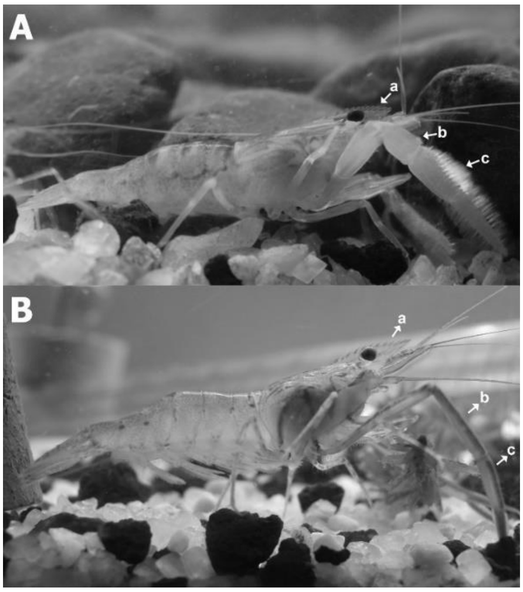

Figure 3. Morphological characteristics the *Macrobrachium* used in this study. A. *M. pilimanus*, B. *M. sintangense*. Description: a. rostrum, b. carpus, c. chelae.

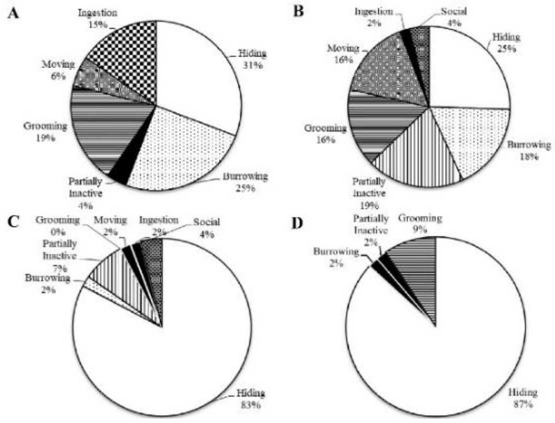

Figure 4. Percentage of the daily behaviour of *Macrobrachium pilimanus*. A. Night period (male), B. Day period (male), C. Night period (female), D. Day period (female).

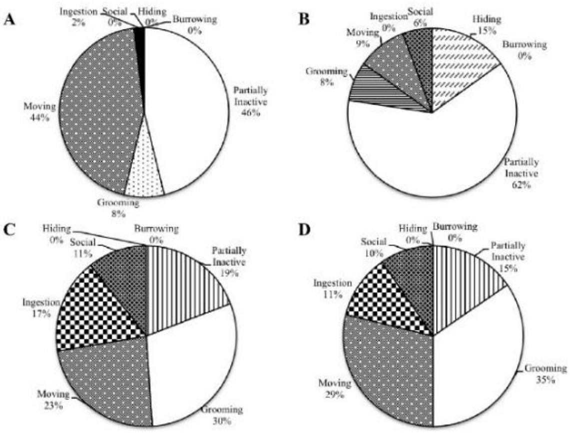

Figure 5. Percentage of the daily behaviour of Macrobrachium sintangense. A. Night period (male), B. Day period (male), C. Night period (female), D. Day period (female)

The three individuals used in this study, i.e., male, non-ovigerous female (female without egg), and ovigerous female (ovi_female or egg-bearing female), showed differences in active and passive behavior. In *M. pilimanus*, the frequency of passive behavior of non-ovigerous and ovigerous females was higher than that of males (Fig. 6A). The active behavior of *M. pilimanus* males was higher than females (non-ovigerous and ovigerous) (Figure 6B). The difference between night and day does not affect the behavior differences in *M. pilimanus*. Moreover, in *M. sintangense*, the behavior differences were more varied between individuals (male, non-ovigerous female, ovigerous female) and time periods (night-day). During the day, the frequency of passive behavior of *M. sintangense* was highest in males, while ovigerous females at night (Figure 6C).

Interestingly, in active behavior, the highest frequency was found in non-ovigerous females both day and night (Figure 6D). Overall in the two species, the frequency of passive behavior was higher than active.

Passive behavior was different in the two species. Female individuals of *M. pilimanus* have a higher percentage of passive behavior than males. Hiding behavior associated with shelter in females is generally associated with an increase in the near spawning period (Figler *et al*. 1995). Although in this study, non-ovigerous female predominated in passive behavior over ovigerous females, indicating no competition for shelter. The same behavior is also shown in *Procambarus clarki* that sex tends not to affect competition in obtaining shelter (Figler *et al*. 1999). In *M. sintangense*, passive behavior is shown more in males (day) and ovigerous females (night). Passive behavior during the day was also observed in *Litopenaeus vannamei* under laboratory conditions (Pontes *et al*. 2006). In active behavior, both *M. pilimanus* and *M. sintangense* showed different dominance between males and females. In *M. pilimanus*, males were more active than females, and inversely proportional to *M. sintangense*. In other crustacean groups, such as crabs, males appear more active than females (Sumpton & Smith, 1990). *Macrobrachium sintangense* is the same as *M. rosenbergii*, with females being more active than males, especially during the day (dos Santos *et al*. 2015). Active and passive behavior that varies in this study may also be caused by stress factors in animals with relatively small aquarium sizes, so they do not provide enough space.

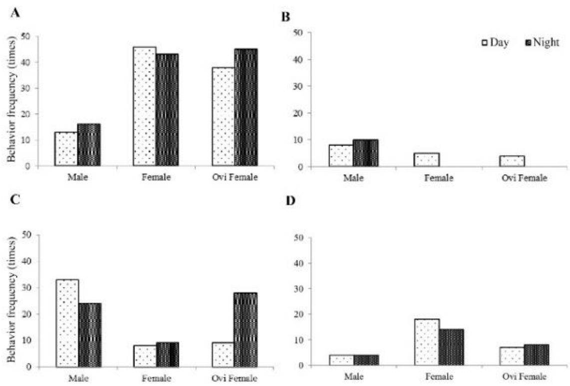

Figure 6. Frequency of active and passive behavior of each individual. A. *Macrobrachium pilimanus* (passive); B. *M. pilimanus* (active); C. *M. sintangense* (passive); D. *M. sintangense* (active).

Determination of the circadian rhythm behavior of *Macrobrachium pilimanus* and *M. sintangense* was based on the dominant behavior of each species, namely hiding and partially inactive behavior for the passive category and grooming behavior for the active category (Figure 7). In passive behavior at night, *M. pilimanus* (black line with full black circle notation) increased throughout the night until early morning (0700 h). In contrast, active behavior increased only in the afternoon until noon (1600 h). In contrast to *M. sintangense*, the passive behavior (dotted line and full black notation) increases in the evening from early evening to midnight (2200 h to 0100 h), whereas during the day, the increase occurs from morning to afternoon (1000 h to 1600 h). In active behavior, *M. pilimanus* activity (black line with empty round notation) increases at midnight (0100 h). In contrast, during the day, the increase occurs only in the late afternoon (1600 h to 1900 h). In *M. sintangense* (dotted line with blank round notation), active nocturnal behavior showed an increase throughout the night (1000 h to 0400 h), whereas during the day, the increase occurred at noon (1300 h).

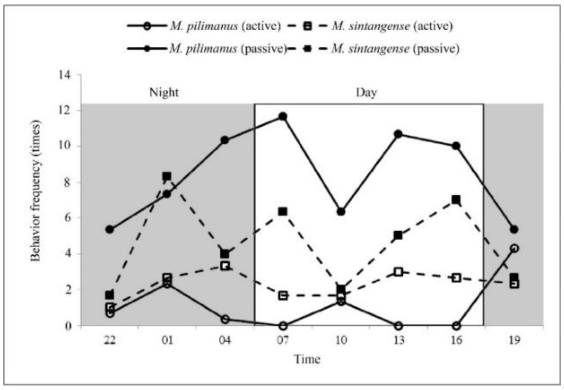

Figure 7. Frequency of using passive-active behavior based on circadian rhythm. Passive behavior was taken from hiding behavior (*M. pilimanus*) and partially inactive (*M. sintangense*), while active behavior was taken from grooming behavior (*M. sintangense* and *M. pilimanus*).

In general, increased passive and active behavior of both species occurred both during the night and the day. Although in some cases, the members of decapod, such as the crab *Aegla schmitti* (Trevisan *et al*. 2004), crayfish (De Miguel & Aréchiga, 1994), and penaeid shrimp, *Litopenaeus vannamei* (Pontes *et al*. 2006) have been reported to be more active at night (nocturnal), several studies have also shown the passive behavior of freshwater prawn which occurs at night (dos Santos *et al*. 2018). These results indicate behavioral variations in freshwater prawns apart from their circadian rhythms, which are generally the result of the expression of specific clock genes (Yang *et al*. 2006). Several factors can affect freshwater prawn's activity, i.e., food availability (Sabar, 1979) and stress. The relatively small size of the aquarium in this study (30 × 19 × 20 cm vs. 50 × 50 × 100 cm in Pontes *et al*. 2018) is likely to be the main factor influencing the prawn. However, nocturnal activity increased between 2200 h and 0100 h, indicating that this is the active time of both species. In the genus *Macrobrachium*, research on active behavior based on circadian rhythms is generally lacking. The results of this study were confirmed in another group of decapod, i.e., *Aegla schmitti*, with the active time occurring at midnight (Trevisan *et al*. 2014).

CONCLUSION

This research on the circadian rhythms of two species of freshwater prawn *M. pilimanus* and *M. sintangense* provides data on freshwater prawn's passive and active behavior based on the night and day (photoperiod) in laboratory conditions. The differences in morphology and habitat preferences of the two freshwater shrimp species show different circadian rhythm behaviors. The results of this study indicate that in the midnight phase, there is an increase in active behavior in both species, thus confirming that the adult individuals of the genus *Macrobrachium* shrimp are nocturnal. There are differences in the behavior patterns of *M. pilimanus* and *M. sintangense*, i.e., the highest behavior in *M. pilimanus* is hiding at night and during the day, and *M. sintangense* shows the highest behavior being partially inactive at night and during the day. Hiding behavior in *M. pilimanus* did not occur in *M. sintangense*. The difference between passive and active behavior in *M. pilimanus* was only influenced by sex. In contrast, in *M. sintangense*, apart from sex, it was also influenced by time (night and day). The results of this study show that the high frequency of passive behavior of both freshwater prawn species was observed, so it is suggested to provide shelter, such as stone, cut bamboo pieces, cut PVC pieces, etc. as an effort to increase productivity for animal welfare.

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