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Light intensity drives regeneration in fragmented mushroom coral *Lithophyllon repanda* anthocaulus and anthocyathus more than the spectra

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Abstract. *Widiastuti, Diwanti NP, Agnesya, Putri NM, Agustini KMP, Ramadhan A, Prasetia R. 2025. Light intensity drives regeneration in fragmented mushroom coral* Lithophyllon repanda *anthocaulus and anthocyathus more than the spectra. Biodiversitas 26: 5258-5266.* Aquaculture offers a sustainable approach to meeting the high demand in the international ornamental aquarium trade for coral species within the family Fungiidae. Fragmentation, which is the most predominant form of asexual reproduction in the family Fungiidae, helps corals to survive anthropogenic and natural threats. This study aimed to investigate the regeneration phase and time of the artificially fragmented anthocaulus (an attached stalk-like structure) and anthocyathus (a mushroom-like structure) in the mushroom coral *Lithophyllon repanda* under different light spectra (blue and white lights) and intensities. The anthocaulus was horizontally fragmented from its anthocyathus, which was grown under different light spectra and at various intensities (n = 9 per treatment) for 166 days in controlled aquaria. The regenerations were observed and photographed under a stereomicroscope every 2 days. The results demonstrated that, despite differences in light properties, similar regeneration phases were observed in both fragmented anthocaulus and anthocyathus. Moreover, there was no significant difference in the regeneration time to develop primary polyps on the fragmented anthocaulus and recovered anthocyathus under different light spectra; however, they significantly regenerated and recovered faster at intensities of 130-54 µmol m^{-2} s^{-1} for less than 30 days. It implies the vital role of light intensities on the production of new polyps and regeneration of fungiid corals ex situ.

Keywords: Anthocaulus, anthocyathus, coral, fragmentation, *Lithophyllon repanda*

INTRODUCTION

Indonesia is the first live coral exporter to the United States, accounting for approximately 73% of live coral captured from 2003 to 2012 (Petrossian et al. 2020), and is also the leading supplier of 53.3% of live coral stocks in Singapore (Tan et al. 2023). Some members of the mushroom coral family Fungiidae are among the five major export commodities of the international marine biota for the ornamental trade (Wabnitz et al. 2003); however, biological reproduction data remain limited. The species belonging to this family display reproductive plasticity both sexually and asexually, which indicates the sustainability of wild stock (Eyal-Shaham et al. 2019, 2020; Heintz and Laboute 2020; Sayco et al. 2024). The sexual reproduction stages of Fungiidae coral start from the mature anthocyathus (mushroom-like structure), which produces eggs and sperm, which, after fertilization, develop into planktonic larvae (planulae) (Wells 1966; Hoeksema 1989). It is attached to the substrate and then expands into the anthocaulus. During the late anthocaulus stage, coral develops an anthocyathus. The asexual reproduction stages of Fungiidae coral start from the dissolution of calcium carbonate in a zone between the anthocaulus and anthocyathus. It gradually occurs from the columella and septa, then spreads into the corallum wall and the costae (Yamashiro and Yamazato 1987a, 1987b). The mature detached anthocyathus thus starts the sexual life stage, whereas the empty stalk on the substrate may regenerate a new anthocyathus. This new polyp grows on the parent polyps, which are nearly dead, as only a few live tissues remain, such as reported in many fungiid corals, such as *Fungia fralinae* (Nemenzo 1955) (Hoeksema 2004), *F. granulosa* (Klunzinger 1879) (Vizel et al. 2009), and *F. fungites* (Linnaeus 1758) (Gilmour 2002; Hoeksema and Yeemin 2011). This detachment results in damage and injury that mushroom corals can usually repair, allowing recovery and regeneration, as shown in laboratory-grown *F. granulosa* (Vizel et al. 2009) and *Halomitra clavator* in the wild population (Hoeksema and Gittenberger 2010). The asexual regeneration mode in mushroom corals by budding and its regeneration to develop new polyps in Indo-Pacific reefs was reported in the *Cycloseris sinensis* (Milne Edwards and Haime 1851), which inhabited the coral reefs in the Kota Kinabalu, Malaysia (Hoeksema and Waheed 2012), *F. fungites* in the inner gulf of Thailand (Hoeksema and Yeemin 2011) and *F. fralinae* in the Derawan Island, Indonesia (Hoeksema 2004).

In this study, we investigated the asexual reproduction mode (i.e., budding) of *Lithophylon repanda* (Dana 1846), formerly known as *Fungia repanda* (Dana 1846) (Gittenberger et al. 2011), under different light spectra and intensities. This coral has a role as the host of other kinds of organisms,

such as barnacles (Hoeksema et al. 2012), gall crabs (van der Meij et al. 2015), shrimps (Hoeksema et al. 2012), mytilid bivalves (Hoeksema et al. 2012), epitoniid snails (Gittenberger and Hoeksema 2013), and coralliophilid snails (Hoeksema et al. 2012). Thus, its regenerative ability plays a vital role in coral reef ecosystems. Studies on a few coral species have revealed the presence of totipotent cells that enable regeneration from a tiny fragment into a new, complete individual (Levanoni et al. 2024; Talice et al. 2024). Regeneration of fragmented corals may produce more new individuals (Sani et al. 2024), and this process is influenced by specific environmental and biological factors (Bossert et al. 2013; Hall et al. 2015; Sabine et al. 2015). Furthermore, scientific data on how these factors affect anthocaulus and anthocyathus regeneration rates in Fungiidae remains unknown.

Light is one of the primary factors that impact coral growth and survival due to its symbiotic partnership with zooxanthellae (Schutter et al. 2012; Wijgerde et al. 2012), while each coral species has distinct light requirements (Fan et al. 2024; Shi et al. 2024). The differences in light intensity among the reef zones varied the shapes of fungiid coral species, thereby determining their distribution and affecting the mobility of free-living fungiid (Hoeksema and Moka 1989; Hoeksema 1993). Moreover, as the sun penetrates the ocean, only shorter wavelengths of blue light (450-495 nm) are available at greater depths (Godwin 2021). Additionally, seawater has a specific spectrum that can absorb visible light. The regeneration and repair process is critical in coral, so most growth energy is allocated to this process. Sufficient light is therefore necessary during and after the regeneration and repair, particularly for recovery (Rocha et al. 2014). This vital role of light is demonstrated in the artificially wounded *Acropora muricata*, which exhibited faster regeneration *in situ* at lower intensity (81 days) compared to those at higher solar radiation (192 days) (Denis et al. 2013). However, more research has been conducted on the quantity of light (irradiance) in coral culture compared to its quality (light spectrum). Yet, there is disagreement on the effects of light spectra and intensity on corals in a controlled environment (Rocha et al. 2014). Such as the adaptability of corals *Pocillopora damicornis, Acropora millepora*, and *Platygyra sinensis* under prolonged light photoperiods and different light intensities in *ex situ* conditions (Kuanui et al. 2020). To our knowledge, it is the first report on the effect of light spectrum and intensity on the regeneration of anthocaulus and anthocyathus of *L. repanda*. Thus, we hypothesized that (i) blue light accelerates regeneration over white light, and (ii) high light intensities reduce regeneration time.

MATERIALS AND METHODS

Coral collection and husbandry

Eighteen nearly dead specimens of mushroom corals *Lithophylon repanda*, with buddings on top, were collected at 6-12 m depths from Labuan Amuk waters, Karangasem Regency, Bali Island, using SCUBA. The mushroom coral was identified based on the micro-architecture of the samples' corallum, as described by Hoeksema (1989), which is monostomatous and unattached. The shape is discoidal and slightly flat, with a diameter of 15-22 cm. Adult specimens have a perforated wall (Figure 1).

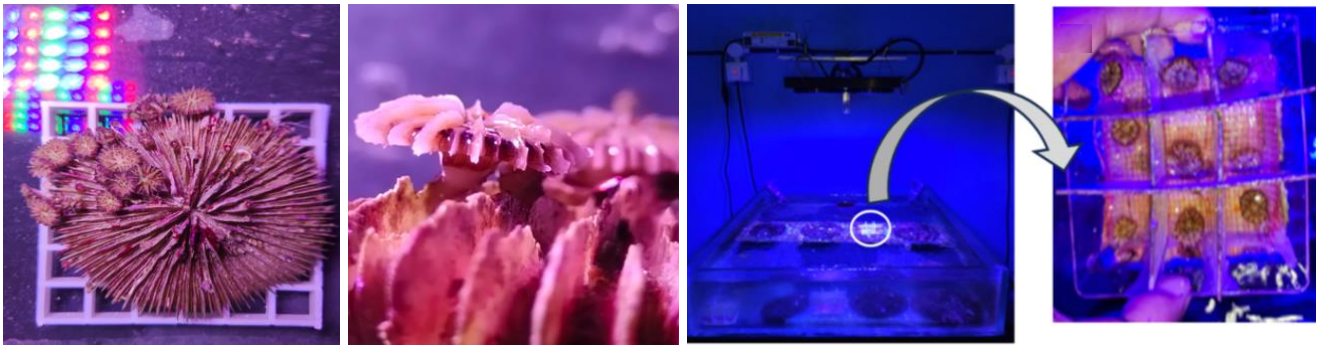
The samples of *L. repanda* were transferred to indoor aquaria (41.4 L, aquarium dimensions: 60 × 60 × 11.5 cm) connected to a protein skimmer (Bubble Magus Curve 3 Extreme, USA), a chiller (Resun Mini 200), and a filter (Resun SP-6000), and acclimatized for 8 weeks. Recirculation was maintained with a submerged pump that provided a flow rate of 1500 L/h. The system operated with collected natural seawater that had settled for 3 days. The corals were illuminated with a blue LED lamp (Illumagic X-4 40 W), placed above the aquaria, delivering Photosynthetic Active Radiation (PAR) of 82-54 μmol m^{-2} s^{-1} at the level of the colonies, with a 12:12 h dark photoperiod. The PAR value was measured with a Quantum Flux meter (Apogee SQ-120, USA) with a submersible sensor.

Coral fragmentation

Three buds from each of eighteen *L. repanda* mother polyps with relatively similar anthocyatus diameters (8-10 mm) were horizontally fragmented using dissecting scissors on the white area of the anthocaulus (Figures 2.A and 2B), producing 54 anthocyathy which were individually placed on a transparent acrylic container with partitioner, whereas the fragmented anthocauli were still attached to their mother polyps (Figures 2.C and 2.D).

A B C D

Figure 1. The skeleton of the mushroom coral *Lithophylon repanda*. A. Upper surface of *L. repanda*. B. The costal ornamentation. C. The perforate corallum wall. D. Upper and lower surfaces of the juvenile of *L. repanda*



A B C D

Figure 2. The fragmentation and experimental design of the mushroom coral *Lithophylon repanda* anthocaulus and anthocyatus. A. The budding on the nearly dead mother polyps of *L. repanda*. B. The fragmentation plane was located in a white area on the anthocaulus (indicated by the black arrow). C. The arrangement of the attached fragmented anthocauli and anthocyathi in the experimental aquaria. The mother polyps were positioned toward the light source. D. The fragmented anthocyathi were placed on the transparent acrylic container with a transparent partitioner with the oral side toward the light source

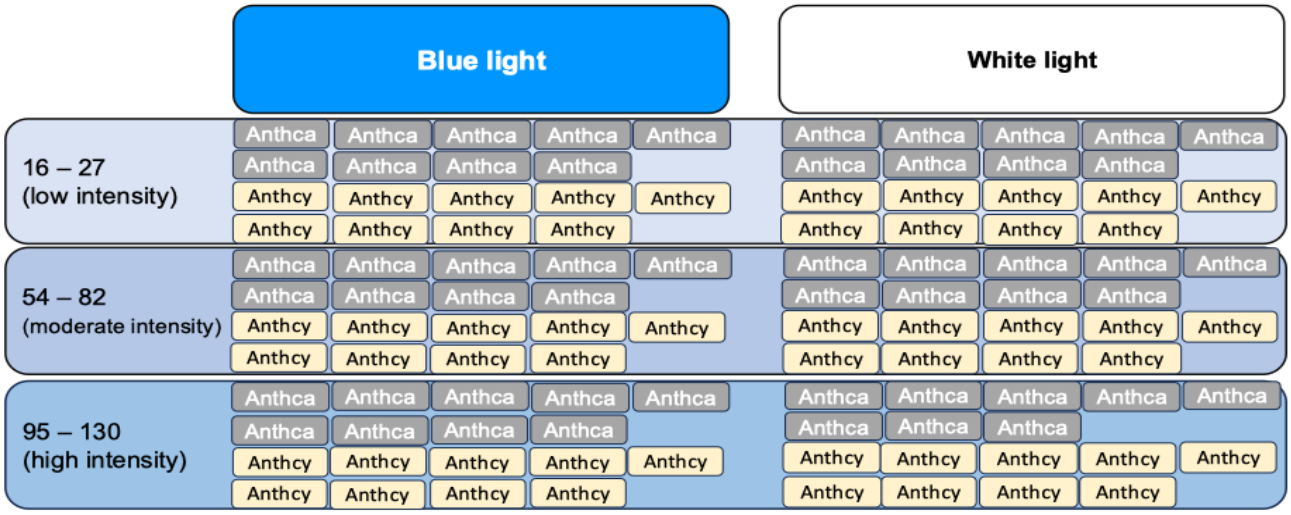


Figure 3. Overview of the experimental setup with six different treatments: blue light at an intensity of 16-27 µmol m^{-2} s^{-1} (low light intensity), 54-82 µmol m^{-2} s^{-1} (moderate light intensity), 95-130 µmol m^{-2} s^{-1} (high light intensity), and white light an intensity 16-27 µmol m^{-2} s^{-1} (low light intensity), 54-82 µmol m^{-2} s^{-1} (moderate light intensity), 95-130 µmol m^{-2} s^{-1} (high light intensity). Fragmented anthocaulus (anthca) (n = 9) and fragmented anthocyathus (anthcy) (n = 9) were used for each treatment

Light treatment

The fragmented anthocauli and their anthocyathi were randomly selected and distributed among the experimental aquaria. Each transparent acrylic container with partitioners contained nine anthocyathy placed on each light spectrum and intensity treatment.

The range of light intensities commonly applied in inland coral culture companies on Bali Island is 82-54 µmol m^{-2} s^{-1} under blue light illumination (personal observation), which we designed as the base for the light properties in this experiment. Thus, to observe the effects of light spectra and intensity, we tested two light spectra (blue or white spectrum), each at three intensities: high (130-95 µmol m^{-2} s^{-1}), moderate (82-54 µmol m^{-2} s^{-1}), and low (27-16 µmol m^{-2} s^{-1}). Therefore, the experiment was set in two aquaria, each with a different light spectrum (blue or white light) and three different light intensities. The corals' position against the light intensities was adjusted based on the depth from the light by placing them on a rack, resulting in nine replicates for each anthocaulus and anthocyathus per treatment. Therefore, each treatment was stocked with three mother polyps, three fragmented anthocauli on the top, and a container containing nine anthocyathi (Figure 3).

The experimental aquaria system consisted of a recirculating system (41.4 L, aquarium dimensions: 60 × 60 × 11.5 cm) connected to a water quality system similar to that of acclimatization aquaria. Two lamp panels above the aquaria provided a blue and white light spectrum, using LED Red, Green, and Blue (Horici, Indonesia), with a 12:12 h dark photoperiod. The light spectrum was measured using a spectral luminance meter (LS330, Linshang, China). The light intensity was measured with a Quantum Flux meter (Apogee SQ-120, USA) with a submergible sensor placed at the surface level of the fragmented anthocaulus and anthocyathus. The fragmented anthocauli and their anthocyathi were fed coral artificial food (100

mL^{-1}) (Polylab Reef Roids) four times a week. Salinity was maintained by adding freshwater and measured with a Refractometer (Atago, Japan). The water temperature was controlled and measured using the chiller. Meanwhile, pH, alkalinity, magnesium, calcium, nitrate, and phosphate levels were determined using Salifert test kits, and all water quality parameters were measured every 2 days. The water parameters were maintained as follows: temperature 25±0.5°C, NO_3^- 3.5±1.5 mg L^{-1}, PO_4^{3-} 0.02±0.01 mg L^{-1}, pH 8.1±0.2, alkalinity 9.9±0.4 mEq L^{-1}, Ca^{2+} 484±15.6 mg L^{-1}, and Mg^{2+} 1434±72 mg L^{-1}.

Regeneration phase and time

The regeneration time for each fragmented anthocaulus and anthocyathus (aboral side) to reach a specific regeneration phase was examined through observation and photography under a stereomicroscope every 2 days for 166 days. The following regeneration phase of the fragmented anthocaulus was observed: i) skeleton development, ii) formation of new tissue, iii) tentacle development, which was suggested by the emergence of tentacle buds, and iv) mouth development, indicated by the emergence of the mouth slit. In contrast, the regeneration phase of the fragmented anthocyathus was determined when: i) the new skeleton developed, ii) the formation of new tissue occurred, and iii) the wound had recovered entirely with soft tissues (Tokuda et al. 2017; Lin et al. 2022).

Statistical analysis

Statistical analyses were performed using SPSS software. Data were checked for normality (Shapiro-Wilk normality test) and homogeneity of variances (Levene's Test) and tested accordingly with ANOVA or Independent Sample T-test. Post hoc tests were done using the Tukey method. P-values of less than 0.05 were considered statistically significant.

RESULTS AND DISCUSSION

The regeneration phase and time of the fragmented anthocaulus polyps at different light spectra and intensities

The regeneration of fragmented anthocaulus under blue and white lights demonstrated relatively similar phases, starting shortly after fragmentation and lasting until its primary polyp features developed on the anthocaulus (Figure 4). Immediately after fragmentation, the fragmented anthocaulus showed a damaged skeleton with unstructured white skeletons (some samples had more brownish spots on the surface of the mesenterial filaments and skeletons), revealing mesenterial filaments without any mouth or tentacles (Day 0). The first regeneration phase observed on Day 2 at all light spectra and intensities was less pronounced, and mesenterial filaments had disappeared due to the development of new skeletons that filled the space in the calice. The newly grown skeletons appeared white. In this stage, the mesentery wall in the calice was well structured. This phase is also involved in the growth of a tissue-like sheet on the surface of the damaged skeleton, starting from certain areas on Day 2 of observation. It becomes thicker before spreading over and covers all the damaged skeletal areas. Its color became more brown than on the day of fragmentation and darker when the regeneration stage was complete, except for the soft tissue around the mouth, which was white or less brown. The third phase is the emergence of tentacle buds with a purple color in the area where the tissue-like sheet became thicker. The tentacle buds emerged particularly between the base of the septa, surrounding the central part of the calice. In this phase, the septa are well structured, and the central part of the calice is slightly depressed. The last regeneration phase observed is the onset of mouth development, as the soft tissue grew thicker and covered all the damaged areas, except in the center of the depression area of the calice, where it left a slit. The skeleton underneath the slit was still visible, and the mesenterial filaments protruded. The soft tissue surrounding the slit then became thicker and developed into the muscles of the mouth. Both the mouth slit and the mouth muscles were able to respond by closing and opening. In this phase, septa are well developed, with teeth on top.

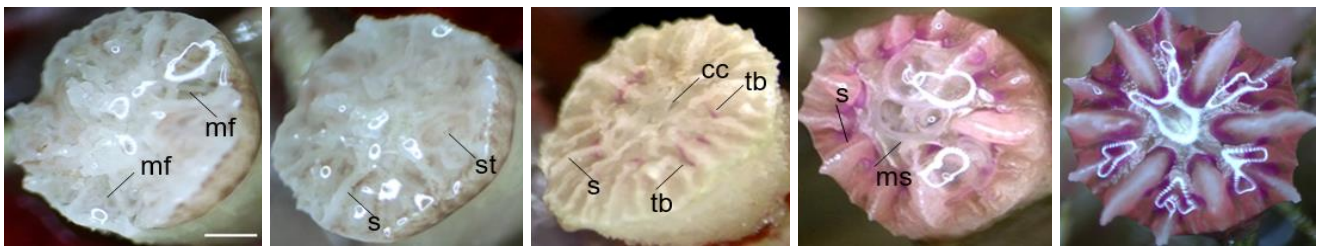
Despite the similarity in the regeneration phase, the time to regenerate to form a primary polyp in the fragmented anthocaulus had no difference under both light spectra ($P = 0.199$); however, it was significantly different at various light intensities, either under blue light ($P<0.05$) or white light ($P<0.05$). The regeneration time of the fragmented anthocaulus significantly differed between 130-54 µmol m^{-2} s^{-1} (high-moderate intensities) and 16-27 µmol m^{-2} s^{-1} (low intensity) ($P<0.05$) under blue and white light. The development of new skeletons that filled the space inside the calice and the well arrangement of mesenteries were observed in all samples starting on Day 2 under different light spectra and intensities ($P = 1.000$). The development of a tissue-like sheet on specific parts of the damaged skeletal surface was also observed in all samples on Day 2 under various light spectra and intensities ($P = 1.000$). The unsynchronized regeneration time among treatments was detected in the development of tentacle buds and the mouth slit. The duration of tentacle bud emergence was mainly observed on Day 12 at different light spectra and intensities, except under white light at low intensity, which showed a delayed emergence of 2 days (Day 14), with no significant difference ($P = 0.126$). The final regeneration phase of anthocaulus is the development of the mouth, which is indicated by the presence of a mouth slit. It started to develop mainly on the samples under blue light at high intensity on Day 12 and was observed on the following two days (Day 14) under white light at the same intensity. This unparalleled regeneration time under different light spectra had no significant difference ($P = 0.054$, Table 1). Aside from high intensity, the presence of a mouth slit was detected 4 days later under blue light at moderate intensity (Day 16). In contrast, it was mainly observed earlier under white light at the same light intensity (Day 14), with no significant difference ($P = 0.293$, Table 1). At low intensity, the presence of the mouth slit was first observed on the samples under blue light on a similar day to the ones at moderate intensity (Day 16); in contrast, it was observed 8 days later under white light (Day 24). This difference in regeneration time was not significant ($P = 0.275$).

Table 1. The time required for each regeneration phase of the *L. repanda* fragmented anthocaulus and anthocyathus under different light spectra

Regeneration phase	Intensity	White light (days)	Blue light (days)	*P*-value
Anthocaulus				
Formation of new skeletons	High	2	2	1.000
	Moderate	2	2	1.000
	Low	2	2	1.000
Development of a tissue-like sheet	High	2	2	1.000
	Moderate	2	2	1.000
	Low	2	2	1.000
Tentacle bud emerges	High	12	12	0.126
	Moderate	12	12	0.244
	Low	14	12	0.215
Development of the mouth	High	14	12	0.054
	Moderate	14	16	0.293
	Low	24	16	0.275
Anthocyathus				
Formation of new skeletons	High	2	2	1.000
	Moderate	2	2	1.000
	Low	2	2	1.000
Development of a tissue-like sheet	High	2	2	1.000
	Moderate	2	2	1.000
	Low	2	2	1.000
Wound covering	High	12	12	1.000
	Moderate	14	14	0.346
	Low	22	18	1.000

Table 2. The time required for each regeneration phase of the *L. repanda* fragmented anthocaulus and anthocyathus under various light intensities

Regeneration phase	Light spectrum	High (days)	Moderate (days)	Low (days)	*P*-value
Anthocaulus					
Formation of new skeletons	Blue	2	2	2	1.000
	White	2	2	2	1.000
Development of a tissue-like sheet	Blue	2	2	2	1.000
	White	2	2	2	1.000
Tentacle bud emerges	Blue	12	12	12	1.000
	White	12	12	14	<0.05
Development of the mouth	Blue	12	16	16	<0.05
	White	14	14	24	<0.05
Anthocyathus					
Formation of new skeletons	Blue	2	2	2	1.000
	White	2	2	2	1.000
Development of a tissue-like sheet	Blue	2	2	2	1.000
	White	2	2	2	1.000
Wound covering	Blue	12	14	18	0.872
	White	12	14	22	0.636



A **B** **C** **D** **E**

Figure 4. Regeneration of the *Lithophylon repanda* fragmented anthocaulus. A. Immediately after fragmentation (Day 0), the unstructured skeleton and the exposed mesenterial filaments are present. B. Regeneration phases 1 and 2 (Day 2): Less protruded mesenterial filaments appeared due to the coverage of newly developed skeletons, and sheet-like tissue septa are more structured. C. Regeneration phase 3: tentacle buds emerge on the base of septa, and the central calice is slightly depressed (Day 12-14). D. Regeneration phase 4 (Day 12-24): mouth development. E. Primary polyp developed on the healed anthocaulus. Note: cc: central calice, mf: mesenterial filaments, mm: mouth muscle, s: septa, ts: tissue, tb: tentacle bud. Scale bar: 5 mm

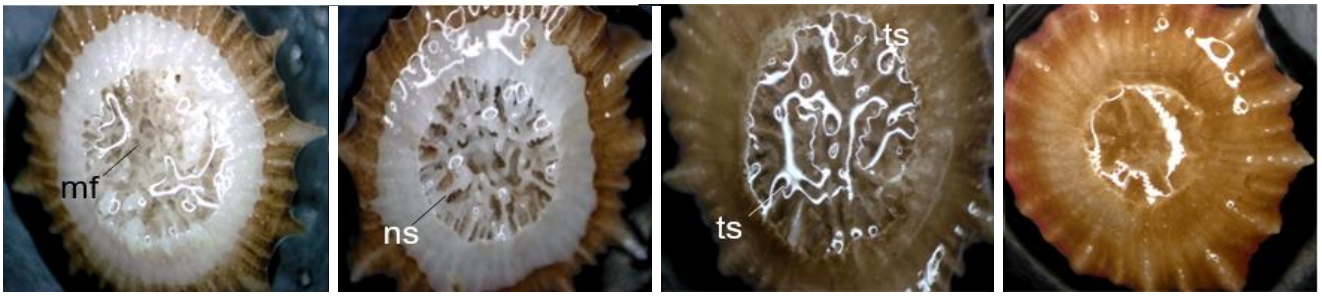


Figure 5. Regeneration of the mushroom coral *Lithophylon repanda* fragmented anthocyathus: A. Immediately after fragmentation (Day 0): Mesenterial filaments can be seen, B. Regeneration phase 1 (Day 2): New white skeletons are developed, C. Regeneration phase 2 (Day 2): A tissue-like sheet spread on the wound's surface and dispersed the nearby skeleton, D. Regeneration phase 3 (Day 12-22): diffused skeletons and thicker tissue covered the wound. Note: mf: Mesenterial filament, ns: New skeleton, ts: tissue-like sheet

Regeneration phase and time of the fragmented anthocyathus

Immediately after fragmentation, the wound on the aboral part of the anthocyathus presented white unstructured skeletons due to fragmentation and mesenterial filaments (Figure 5.A). A significant regeneration was observed on Day 2 (phase 1), with the formation of new skeletons that filled the space in the open wound, thereby making it less noticeable and resulting in no apparent mesenterial filaments (Figure 5B). The grown skeletons appear white and have well-structured mesenteries. The following regeneration phase (phase 2) was the development of a tissue-like sheet observed in the fragmented anthocaulus, which was also observed in all treatment groups on Day 2 (Figure 5.C). This soft tissue contained symbionts and was therefore dark brown in color. This phase spread on the wound's surface and dispersed the nearby skeleton. The last regeneration phase observed in the fragmented anthocyathus was the recovery of the wound, where, gradually, the tissue-like sheet grew thicker inside and near the wounded skeleton, covering it, leaving non-obvious, fragmented, and diffuse skeletons (Figure 5.D). This phase was observed earlier on Day 12 at high intensity under both light spectra. It gradually slowed by 2 days, maintaining a moderate intensity under either white or blue lights. This phase became slower at low light, which was detected on Day 18 under blue light and 4 days behind (Day 22) under white light. Thus, statistically indicated that there was no significant difference in the recovery of fragmented anthocyathus under different light spectra (P = 0.374), however it had significantly difference at various intensities under either blue light (P<0.05) or white light (P<0.05), whereas it specifically differed between 130-54 µmol m^{-2} s^{-1} (high-moderate intensity) and 16-27 µmol m^{-2} s^{-1} (low intensity) under blue light (P<0.05), in contrast, it significantly differed between 130-95 µmol m^{-2} s^{-1} (high intensity) and 16-27 µmol m^{-2} s^{-1} (low intensity) under white light (P<0.05).

Discussion

Compared with that in the *Lithophylon repanda* artificially fragmented anthocyathus, the regeneration phase in its fragmented anthocaulus was more complex. This complexity may be due to more severe damage occurring in anthocaulus than in fragmented anthocyathus, particularly in the absence of mouths and tentacles, thus inhibiting the energy supply. The transversal regeneration phase and repair in the anthocaulus and anthocyathus of Fungiidae remain limited in reports. Yamashiro and Yamazato (1991) was the initial investigation on the regeneration of detached anthocaulus of *F. fungites*. In contrast, Vizel et al. (2009) reported the regeneration of a spontaneously detached anthocyathus of *F. granulosa*, which has a damaged part on the aboral side. They described the appearance of the mouth, tentacles, and septae, as well as the less colorful side of its oral side; however, there was no further explanation of the damaged part of the anthocaulus. These differences in the regeneration phase and repair anthocaulus and anthocyathus when fragmented transversally were also found in the azoxanthellate coral *Truncatoflabellum spheniscus* (Dana 1846) (Family Flabellidae), where the anthocaulus was severely damaged compared to the anthocyathus (Tokuda et al. 2017).

Studies have indicated that the energy for recovery and repair in the absence of the mouth and tentacle is substituted by mesenterial filaments that can project to catch and absorb nutrients and particulate foods in seawater, as they contain proteolytic enzymes in their tissues (Muhlia-Almazán et al. 2008; Raz-Bahat et al. 2017). In adult polyps, coral symbionts inhabit the oral and tentacles rather than the endoderm (Dokkaew et al. 2018; Lin et al. 2022) and are more concentrated in the coenosarc (Lin et al. 2022); therefore, as the anthocyathus is removed, it remains in the thin layer on the skeleton surface inside the calice. Thus, as the anthocaulus and anthocyathus were fragmented, they were exposed to light and surrounded by seawater, enabling them to access the photosynthetic components, as indicated by the changing color of the fragmented anthocaulus and anthocyathus immediately after fragmentation (Day 0), which turned dark brown after Day 2. Along with the mesenterial filaments, the symbiont accelerates the repair and regeneration of damaged anthocaulus and anthocyathus by supplying energy for these processes. Furthermore, after two days of fragmentation, soft tissue initially developed from a particular surface of the damaged area, which was characterized by its thickness and dark brown color, suggesting the symbiont's role in nutrient uptake to support

coral growth. The contribution of coral symbionts to the development of young corals is demonstrated by the infected primary polyps of *Galaxea fascicularis* (Linnaeus 1767) and *Mycedium elephantotus* (Pallas 1766), with the Symbiodinaceae species having significantly developed tentacles (Lin et al. 2022).

In contrast, the tentacles of those without symbionts remained undeveloped in buds (Lin et al. 2022). Studies on the early development of Symbiodiniaceae cell proliferation are proposed to facilitate rapid development in these tissues (Levanoni et al. 2024; Talice et al. 2024). In addition to developing this soft tissue, tentacle buds first emerge. Although the regeneration of *L. repanda* in this study showed a relatively similar phase to that of the azooxanthellate coral *T. spheniscus* (Tokuda et al. 2017), the tentacle buds emerged synchronously with each other, and a mouth slit developed afterward in this coral. Coral *G. fascicularis* also demonstrated a similar phase (Lin et al. 2022); however, the mouth developed earlier than the tentacles in this study. It is assumed that the formation of the mouth prior to the formation of tentacle buds in these corals is related to the even development of soft tissue on the polyp surface. This finding might explain the variation in the regeneration phase of the free-living stage among coral species. As the mouth slit formed, but the tentacle was not yet well developed, the mesenterial filament can still be projected through this opening of the skeleton in the center of the calice to catch particulate food in the seawater (Muhlia-Almazán et al. 2008; Raz-Bahat et al. 2017), playing a role in the energy supply. The latest significant morphological feature to regenerate in the *L. repanda* fragmented anthocaulus is the formation of the mouth, which implies the complex development of the digestive system in corals. Mouth development was also the latest significant morphology development in the coral *T. spheniscus* (Tokuda et al. 2017).

The time for the fragmented anthocaulus to form a primary polyp and anthocyathus to repair under white and blue light was relatively similar. However, it was shorter at moderate and high intensities than at low light intensities. This study demonstrated that white or blue LED lights in an aquaculture system have a similar effect on the regeneration of *L. repanda* anthocaulus and anthocyathus. Most of the detachment of the anthocaulus and anthocyathus of Fungiids is observed in the field or using natural light, which falls within the wavelength range of 400-700 nm (Yamashiro and Yamazato 1991; Gilmour 2004; Vizel et al. 2009), which is within the range of white light (380-780 nm) (Osawa 2025). Studies have indicated that white or blue LED lights do not significantly affect the spat survival and competitor algae growth of the coral *Acropora kenti* (Kreh 2019; Rahnke et al. 2022; Ramsby et al. 2024). Low light intensity is assumed to reduce the photosynthetically active radiation that symbionts require for photosynthesis, resulting in low cell density or growth. Studies have demonstrated that the early development of 8-week-old coral larvae, which had previously established symbiosis after 4 weeks, was significantly faster when the light intensity increased to greater than 120 μmol m^{-2} s^{-1} (Kreh 2019).

Though this study revealed that the regeneration phase are statistically similarly accelerated under either blue or white light, there are disagreements about whether blue, red, or white light speeds up coral growth (Rocha et al. 2014; Mendes et al. 2017) due to the range of light absorption by coral symbionts between blue light (400 and 550 nm) and red light (650 and 700 nm) (Scheufen et al. 2017). The shorter regeneration time of the *L. repanda* anthocaulus and anthocyathus at moderate and high light intensities reflects their natural habitat, that is, shallow reefs, which have high light intensities and are in a full-spectrum area (Hoeksema et al. 2018; Eyal-Shaham et al. 2020). Despite studies on the roles of light properties on the regeneration of budding in fungiid corals remains unreported, studies on the polypolyps coral *Porites lutea* and *P. cylindrical* have demonstrated the effect of the various light intensities of Photosynthetic Active Radiation (PAR) on the duration of the polyp and formation regeneration, and the rate of live tissue extension in the area of damaged fragments (Titlyanov et al. 2005). The more extended period taken to regenerate at low light may threaten coral survival, as they compete with other fouling organisms, such as tube worms, sponges, and green and brown algae, as well as slowly maturing Crustose Coralline Algae (CCA) that flourish more at low light intensities (Mondal and Raghunathan 2017; Ramsby et al. 2024). These fouling organisms appeared 2 weeks after fragmentation and were persistent during the experiment in this study. The low density of zooxanthellae leads to the slow formation of the skeleton and tissue-like sheets, as well as the repair of damaged areas; thus, the fouling organisms will take over it. Over time, the fragmented anthocaulus and anthocyathus may eventually fail to regenerate and die. Moreover, studies demonstrated that the presence of zooxanthellae significantly accelerated the tissue loss repair and regenerated the polyp in the injured coral fragment of the facultatively symbiotic, temperate scleractinian coral *Astrangia poculata* (DeFilippo et al. 2016; Burmester et al. 2017).

In conclusion, the regeneration phases of *L. repanda* fragmented anthocaulus and anthocyathus were similar under white and blue lights at various intensities. On the contrary, the regeneration time of the fragmented anthocaulus and anthocyathus at high and moderate intensities was shorter than at low intensities under either blue or white lights. Given that the light intensity has a greater effect on coral *L. repanda* regeneration than does the spectrum, it is suggested to irradiate the cultured mushroom corals at the intensity range of 54-130 μmol m^{-2} s^{-1} either under blue or white light. These results imply the capability of *L. repanda* to increase its population ex situ by producing the new coral (anthocyathus) and regenerating the fragmented anthocaulus for less than 30 days, which provides the scientific basis of Indonesia's hard coral population dynamics data. Therefore, the duration for the anthocyathus and anthocaulus to regenerate after being detached from their stalks determines their capacity to reproduce new polyp coral, repair the wound, and reduce the mortality from fouling organisms and parasites. Furthermore, it provides the age and size-frequency information on the *L.*

repanda population. However, further studies to investigate the effect of light intensity higher than 130 µmol m^{-2} s^{-1} under both spectra are encouraged, as excessive light intensity leads to photoinhibition in the zooxanthellae, which inhabit the coral due to the increased oxidative stress (Lesser 2019). In addition, this result may not generalize to all fungiid corals, as the susceptibility to the physiology is species-dependent. Such diversity can be determined by the coral's symbiont density in the coral's tissue (Levy et al. 2020), which, in the overabundance of coral symbionts, exaggerated the bleaching potential due to increasing ROS numbers (Cunning and Baker 2013). Therefore, it is necessary to examine the effect of light properties on other fungiid members, such as marine ornamental trade-targeted organisms, such as *Heliofungia actiniformis*.

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