

ABIOTIC LIGHT FACTOR TOWARDS FUTURE CRUSTACEAN AQUAFARMING TECHNOLOGY IN PREPARING FOR GLOBAL CLIMATE CHANGE

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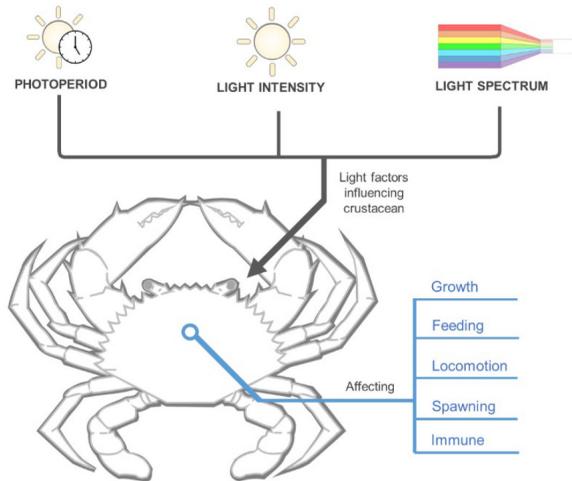
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HIGHLIGHTS

- The review explores the multifaceted impact of light on crustacean circadian rhythm.
- Crustacean larvae exhibit a preference for longer photoperiods (> 18 hours), shifting to shorter ones during the juvenile stage.
- Higher light intensity is crucial for enhancing larval growth and promoting ovarian progression in adult females.
- White light has been shown to enhance survival, growth and stress reduction, whereas individual green, blue and cyan spectra also hold potential for aquafarming applications.
- Optimising light intensity and spectrum is essential for advancing crustacean aquafarming technologies in preparation for global climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

The ramifications of light on crustacean circadian rhythm are complex and multifaceted since light has three core elements, namely photoperiod, spectrum and intensity. Most marine crustaceans have a planktonic larval phase in their life cycle before metamorphosing into benthic juveniles; this ontogenetic shift from planktonic to benthic life requires different levels of the three light core elements. Hence, this review is planned on the basis of referring to a large number of accumulated scientific findings that emphasise the impact of light on different life stages (larva, juvenile, and adult) of crustaceans, with myriad approaches in growth, feeding, locomotion, spawning, and immunity. In terms of photoperiod, there is a high tendency

of larval crustaceans to favour longer photoperiods (more than 18 L) during the early stage. Later, up to a certain extent, perhaps amid the juvenile stage, the photoperiod preference shifts towards shorter time as such stage demonstrated a pressing need for darkness, which is the common nocturnal behaviour in crustaceans. In terms of light intensity, previous studies have shown that more intense light is required as to enhance larval growth, as well as emphasising the positive impact of light intensity on ovarian development in adult female crustaceans. In the context of light spectrum, former evidence deciphered the benefit of utilising white light in terms of survival, growth and stress reduction, as well as rising antioxidant capacity in crustaceans. However, instead of using white spectrum, the green, blue and cyan spectra may also have high potential to be incorporated into aquafarming. Future studies may explore the prioritisation of light intensity and spectrum to better understand the effects on crustacean farming. This review advocates the use of an enclosed system set-up to optimise the effects of photoperiod, light intensity and spectrum in crustacean farming, as such system may promote sustainability and alleviate the catastrophic effects of climate change. Light optimisation in crustacean culture may be a pivotal component to enhanced farming productivity and food security.

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Introduction

Various species of crustaceans are inextricably affected by light as a pivotal abiotic factor. The ramifications of light on crustacean circadian rhythm are complex and multifaceted since it has three core elements, namely photoperiod, spectrum, and intensity (Chen *et al.*, 2022). Many studies have tried to understand the effects of all three core elements on the growth, survival, feeding, locomotion, gonad maturation, and immunity of crustaceans (Jaski *et al.*, 2014). In terms of locomotion and feeding behaviour, the effects of a varied light regime has been shown to play a vital role in influencing growth and survival (Santos-Romero, 2017). In terms of gonad maturation, light is a dominant factor in determining the seasonal reproduction event (Fitzgibbon & Battaglene, 2012). In the immunity context, certain photoperiods have been observed to enhance the immune response of crustaceans, hence, protecting their body against infections.

Most marine crustaceans begin life at a planktonic larval phase before metamorphosing into benthic juveniles. This ontogenetic shift from planktonic to benthic life requires different levels of photoperiod, spectrum and light intensity (Matsuda & Tanaka, 2012). As crustaceans approach adulthood, many would have adopted a nocturnal behaviour, which requires very little light to maintain their survival (Scudder *et al.*, 1981). In short, light is an important environmental cue that implicates the growth, survival, feeding, locomotion, gonad maturation, and immunity of crustaceans at different stages of their life cycle. As a result, their circadian rhythm is very complex. Hence, this review highlights the benefits of optimising light as the most prominent abiotic factor on the different life stages (larva, juvenile, and adult) of crustaceans in growth, feeding, locomotion, spawning, and immunity.

Photoperiod Effect on Crustacean Larvae

Growth Performance

Growth performance in crustaceans is governed by environmental light and researchers have tried to manipulate its effects on crab larvae in the zoeal (Zoea 1 to Zoea 4) and megalopal stage. One study reported that the early life of crabs (Zoea stages) required an extended photoperiod for high survival (Table 1). The root causes for the high survival and growth of zoea crabs kept under prolonged photoperiod may be highly attributed to light, which aids their mobility and capturing of prey for food. For instance, Andres *et al.* (2010) reared the blue swimming crab (*Portunus pelagicus*) larvae under five photoperiods (0 L, 6 L, 12 L, 18 L, and 24 L). They reported that the 0 L group showed the lowest survival rate (19.2%), whereas the 18 L (51.2%) group achieved the highest. Similarly, Ravi and Manisseri (2013) attempted different photoperiod tests (6 L, 12 L, and 18 L) on the larvae of *P. pelagicus* and found that those in Zoea 3 (85%) and Zoea 4 (55%) thrived best in the 18 L photoperiod. Other works by Ikhwanuddin *et al.* (2019) also adopted different photoperiods (0 L, 12 L, and 24 L) on *P. pelagicus* larvae, with 24 L achieving the highest growth rate in early larval stages such as Zoea 1 (4.72), Zoea 2 (5.55), and Zoea 3 (4.05). On the other hand, as the crab larvae entered advanced stages of their life cycle, their preference turned to shorter photoperiods as reported by Ravi and Manisseri (2013). The most ideal photoperiod for *P. pelagicus* megalopa was reported at 12 L, in which the highest survival rate (39%) was noted. A similar trend was observed by Ikhwanuddin *et al.* (2019), where prolonged darkness (0 L) could increase survival rate as the larvae advanced from Zoea 1 (10%) to Zoea 2 (25%), followed by Zoea 3 (78%) and Zoea 4 (58%).

Several researchers have expressed their critical appraisal over the ramifications of different photoperiods on lobster larvae, commonly known as phyllosoma. Certainly, the growth performance of phyllosoma is influenced

by optimal photoperiod requirements and past experiments have demonstrated encouraging results with a favourable tendency for longer photoperiods. For example, Matsuda *et al.* (2012) examined the implications of photoperiods 10 L, 12 L, and 14 L on Japanese spiny lobster phyllosomata (*Panulirus japonicus*) and reported that the rate of metamorphosis increased with photoperiod increments (10 L: 44%, 12 L: 56%, and 14 L: 78%). In phyllosomata of the southern rock lobster *Jasus edwardsii*, Bermudes and Ritar (2008) studied the influence of photoperiod 0 L, 6 L, 12 L, 18 L, and 24 L and found that at Stages 1 and 2, phyllosomata tended to grow faster under increasing light conditions (moult increment from 0.95 mm under 0 L to 1.01 mm under 24 L), whereas at Stage 3, phyllosomata required some light/dark phase (6 L, 12 L, and 18 L with average 1.0 mm moult increment) to optimise their growth than groups under 0 L (0.95 mm) and 24 L (0.85 mm).

In other research on lobsters, Fitzgibbon and Battaglione (2012) investigated the effects of photoperiods (0 L, 6 L, 12 L, 18 L, and 24 L) on the phyllosomata of the Packhorse rock lobster (*Sagmariasus verreauxi*). They reported that more phyllosomata (instar 15-17) had attempted metamorphosis (84.9-93.3%) in photoperiods of 18 L and 24 L, with greatest survival at 79.5%, as well as biggest size (102-103 mm) and weight (63-65 mg). All these results collectively suggest that a longer photoperiod exposure in phyllosomata can promote an ecdysial rhythm, which increases seed production and is essential for improving culture efficiency. It is worth noting that photoperiod likelihood has become the best possible solution to address the common issue of slow phyllosoma-rearing phase in lobster farming.

To get the optimum photoperiod impact on crustacean larvae, the breakthroughs in prawn larval studies may also be extended to crab and lobster larvae. For instance, Wei *et al.* (2021) conducted an experiment to analyse the photoperiod implications (0 L, 6 L, 12 L, 18 L, and 24 L) on giant freshwater prawn larvae (*Macrobrachium rosenbergii*), which

demonstrated that continuous light (24 L) could significantly promote survival (73.9%), metamorphosis (72.0%) and growth (5.49 mg) compared with larvae in other photoperiods (growth: 2.62-4.37 mg). Likewise, Jaski *et al.* (2014) determined that photoperiod (0 L and 12 L) could influence the growth performance of white-leg shrimp (*Litopenaeus vannamei*) larvae. The survival and weight of shrimp larvae cultured under 12 L photoperiod (survival: 48%, weight: 4.66 mg) was higher compared with those subjected to 0 L photoperiod (survival: 37%, weight: 4.38 mg).

The disclosure of the former document pertaining to the photoperiod implications on crab, lobster, and prawn larvae has verified that the early life stage of crustaceans requires a longer photoperiod (more than 18 L) to rev up the larval growth, notably in the phyllosoma-rearing stage that requires a very long period. Larval growth at the fastest pace is crucial in strengthening seed productivity in aquafarming to satisfy the growing global demand for crustacean stocks.

Table 1: Survival rate of crustacean larvae subjected to different photoperiods. Highlighted number indicates the highest survival rate obtained in various studies. Most high readings are reported in longer photoperiods such as 18 L and 24 L

Species	Photoperiod							Citation
	0 L	6 L	10 L	12 L	14 L	18 L	24 L	
Crab survival (%)								
<i>P. pelagicus</i>								
Zoea 1	48	60	-	50	-	70	66	Andres <i>et al.</i> (2010)
Zoea 2	36	56		46		68	52	
Zoea 3	26	48		40		66	52	
Zoea 4	18	30		38		50	37	
Zoea 1	10	-	-	46	-	-	38	Ikhwanuddin <i>et al.</i> (2019)
Zoea 2	28	-	-	48	-	-	56	
Zoea 3	80	-	-	50	-	-	48	
Zoea 4	56	-	-	64	-	-	10	
Lobster survival (%)								
<i>P. japonicus</i> (phyllosomata)			89	67	94.5			Matsuda <i>et al.</i> (2012)

<i>S. verreauxi</i>								
Instar 1	-	82.5	-	87.5	-	85.0	80.0	Fitzgibbon and Battaglione (2012)
Instar 2	82	76		82		84	82	
Instar 3	72	64		72		68	75	
Instar 4	70	62		70		68	75	
Instar 5	62	44		68		62	70	
Shrimp survival (%)								
<i>P. vannamei</i> (Zoea - post larval stage)	37.0	-	-	48.0	-	-	-	Jaski <i>et al.</i> (2014)

Feeding

Researchers have cautiously observed the prominent factors that lead to high survival rate of crustacean larvae in prolonged photoperiods and there is no dispute that the larvae utilise light effectively for feeding. The early larval stage effort is reduced as the light aids their likelihood of capturing prey before their eyes fully develop in the later stage. In a study on crabs, Andres *et al.* (2010) observed that the zoea of *P. pelagicus* did not rely on visual cues only in capturing prey (since the larvae could survive to the megalopal stage under constant darkness). However, the survival and growth under 0 L photoperiod were significantly reduced, which suggested that light was imperative in promoting feeding behaviour by inducing zoeal swimming activity and increasing the probability of prey encounters. Ikhwanuddin *et al.* (2019) reported similar observations while conducting a photoperiod experiment on *P. pelagicus* and crab larvae still relied on light for efficient feeding, particularly newly hatched zoea that was observed to feed frequently (three to four times) during daytime than at night.

In lobsters, research has been conducted meticulously to quantitatively unveil the far-reaching consequences of light on their phyllosomata. For instance, Bermudes and Riter (2008) determined the influence of photoperiod 0 L, 6 L, 12 L, 18 L, and 24 L on feeding activity of early-stage *J. edwardsii* phyllosomata and the results indicated that those in Stages 1 and 2 had a higher tendency to eat more *Artemia*

brine shrimps under increased light conditions (11, 13, 14, 18, and 20 *Artemia* per day, respectively) (Table 2). Another research by Fitzgibbon and Battaglione (2012) showed that early-stage *S. verreauxi* phyllosomata (instar 1-5) fed on more *Artemia* under 24 L condition (0.012 mg *Artemia* phyllosoma-1h-1) than others (> 0.009 mg *Artemia* phyllosoma-1h-1). In the same study, late-stage phyllosomata (instar 15-17) also ingested more *Artemia* at 24 L (110 mg *Artemia* phyllosoma-1h-1) than other light conditions (> 25 mg *Artemia* phyllosoma-1h-1), suggesting increased feeding at 24 L photoperiod might be a result of greater prey encounter due to increased swimming activity (Fitzgibbon & Battaglione, 2012).

Regarding the peak feeding activity in longer photoperiods, Sanudin *et al.* (2014), which were involved in prawn experiments, indicated overlapping views with other research. They examined the ingestion rate of shrimps of different sizes (0.5, 1.0, and 1.5 cm) under light and dark conditions (0 L, 12 L, and 24 L), and the 0.5 cm shrimp had higher ingestion rates of *Artemia* under light condition (62.0%) compared with darkness (39.3%). Meanwhile, the 1.0 cm (0 L: 89.7%, 24 L: 88.1%) and 1.5 cm (0 L: 71.3%, 24 L: 67.3%) shrimps consumed *Artemia* equally under both dark and light conditions. This study proposed that the feeding activity of the smallest shrimp (0.5 cm) was influenced by light condition, in contrast to the feeding activity of bigger-sized shrimps

(1.0 cm and 1.5 cm), which highly relied on their completely grown eye structures that were well adapted to dark conditions to capture prey (Sanudin *et al.*, 2014).

Overall, throughout the accumulation of previous works on crab, lobster, and shrimp, they provide solid evidence that a longer photoperiod is necessary for capturing prey during the early

larval stage, which may be due to the incomplete eye structure development. This is in tandem with stimulated swimming behaviour of both larvae and prey, hence, driving the inevitable encounter between them which will increase ingestion rate to boost the growth and survival of crustacean larvae (Figure 1).

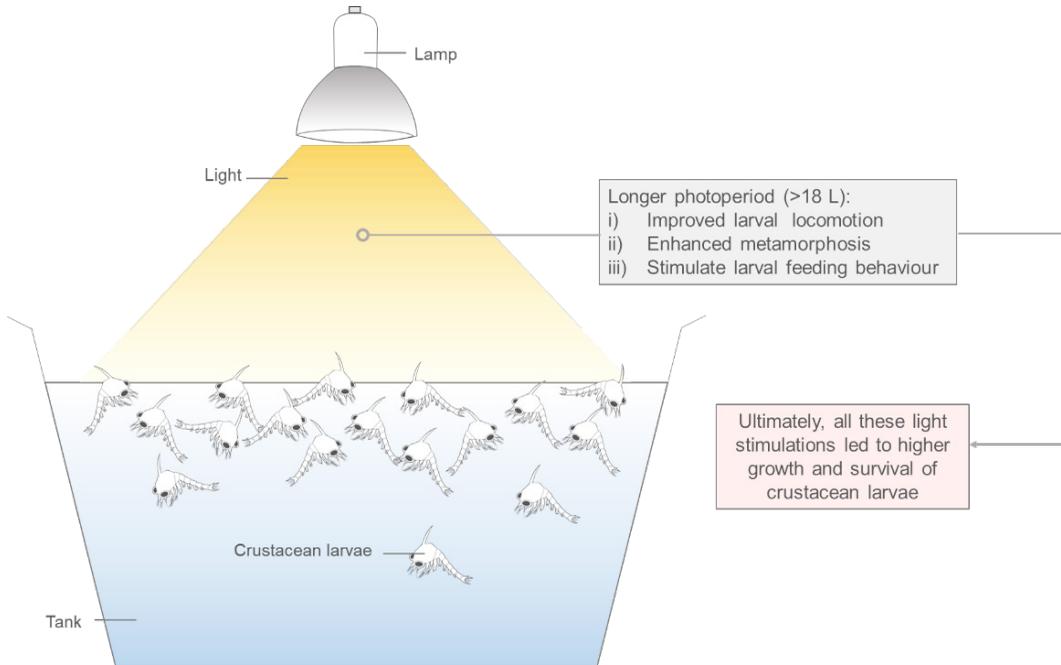


Figure 1: The implications of longer photoperiod on growth and survival of crustacean larvae. This figure summarises the photoperiod impacts reported in Bermudes and Ritar (2008), Andres *et al.* (2010), Matsuda *et al.* (2012), Fitzgibbon and Battaglene (2012), Ravi and Manisseri (2013), Jaski *et al.* (2014), Sanudin *et al.* (2014), Ikhwanuddin *et al.* (2019), and Wei *et al.* (2021)

Table 2: Feeding performance of crustacean larvae subjected to different photoperiods. Highlighted number indicates the highest feeding performance obtained in various studies

Species	Parameter (unit)	Photoperiod					Citation
		0 L	6 L	12 L	18 L	24 L	
<i>J. edwardsii</i>						Bermudes and Ritar (2008)	
Phyllosomata Stages 1-2	Feeding intake (<i>Artemia</i> larva ⁻¹ day ⁻¹)	11	13	15	18	20	
Phyllosomata Stages 2-3		22	29	28	29	30	
Phyllosomata Stages 3-4		29	35	35	31	29	
<i>S. verreauxi</i>						Fitzgibbon and Battaglene (2012)	
Phyllosoma Instar 2	Feeding intake (mg <i>Artemia</i> larva ⁻¹ hour ⁻¹)	0.018	0.016	0.015	0.016	0.019	
Phyllosoma Instar 4		0.009	0.007	0.010	0.008	0.013	
<i>P. vannamei</i>						Sanudin <i>et al.</i> (2014)	
Post-larvae	Feed conversion ratio	0.89	-	0.90	-	0.87	

Locomotion

Aside from growth and feeding, photoperiod effects on the movement of crustacean larvae have also been highlighted, with an upbeat in locomotion momentum in crustacean larvae. However, there are few quantitative evidence being documented on the relationship. For example, in crabs (*P. pelagicus*), Andres *et al.* (2010) observed that the larval crabs' swimming activity increased with light (0 L to 18 L) until a certain point (24 L). However, exposure to daylight was observed to reduce larvae survival, perhaps due to an energy imbalance caused by the excessive swimming, which was no longer compensated by increased food consumption.

Bermudes and Ritar (2008) also reported reduced swimming activity for *J. edwardsii* phyllosomata in dark photoperiod. Besides light directly stimulating the swimming activity of crustacean larvae, at the same time, it also enhances the effectiveness of larval locomotion by indirectly aiding in metamorphosis through

ascertaining fully complete metamorphosis of the later stage, which is imperative for the larval movement. For instance, Matsuda *et al.* (2012) found that phyllosomata of *P. japonicus* subjected to 14 L had fully complete metamorphosis with well-developed setae for active forward swimming. Whereas phyllosomata subjected to shorter photoperiods (10 L and 12 L) tended to result in suppressed metamorphosis with a lack of setae at the pleopods, which impeded the movement of phyllosomata to forage for *Artemia*. As a whole, longer photoperiod may drive the locomotion of crustacean larvae qualitatively. However, future research may focus on the internal physiology that can frame out the mechanisms between photoperiod and larval locomotion. It was a good effort by previous works in describing the development of larval morphology under the influence of various photoperiods.

Photoperiod Effects on Juvenile and Adult Crustaceans

Growth Performance

Well-drafted results from many previous works have consolidated two paramount opinions. First, researchers realised that early juvenile crustaceans require a longer photoperiod as a basic need to grow and develop morphologically and up to a certain point, perhaps amid the juvenile stage, the preference will shift towards a shorter photoperiod as the adult crustaceans adopt a nocturnal behaviour.

In the early juvenile stage, Chittleborough (1975) measured the impact of photoperiod on the Western rock lobster *Panulirus longipes* (weight: 0.5 g) and noticed that their growth was depressed in continuous darkness (12.4%) compared with other photoperiods such as 6 L, 12 L, and 24 L, with respective growth rates of 15.5%, 14.1%, and 15.2%. Santos-Romero et al. (2017) evaluated the implications of two photoperiods (10 L and 14 L) on early juvenile Longarm river shrimps (*Macrobrachium tenellum*) (weight 0.2 g), stating that the longer photoperiod (14 L) (specific growth rate: 2.55) yielded a higher growth rate compared with the shorter one (specific growth rate 1.97). Likewise, Tidwell et al. (2001) worked on early juveniles of *M. rosenbergii* (weight 0.025 g) and revealed that prawn survival was significantly greater in a group raised under continual light conditions (72%) than those raised under 12 L (59%) and 0 L (58%).

For the later juvenile and adult stage, contrast breakthrough was reported in which these crustacean stages appeared to reshift their preferences towards a shorter photoperiod. This phenomenon was confirmed in a study by Morales and Barba (2015), which conducted an experiment to determine the growth of the adult giant mud crab *Scylla serrata* (carapace width: 8.5 cm, weight: 200 g). After exposure to different photoperiods, crabs kept in the dark had significantly higher weight than those kept in normal photoperiod (70% vs. 14.7%). Another study by Withyachumnarnkul et al.

(1990) divided juvenile prawns (*M. rosenbergii*) (weight: 50 g) into four photoperiod groups (0 L, 12 L, 16 L, and 20 L) and prawns reared under 0 L were significantly longer (29 mm) and heavier (160 mg) than those reared under other light-dark conditions (length: > 23 mm, weight: < 100 mg). This showed a positive impact of continuous darkness on growth of *M. rosenbergii* juveniles. Wang et al. (2021) reared the Pacific white shrimp *L. vannamei* under five photoperiods (0 L, 2 L, 4 L, 8 L, and 12 L) and their results showed enhanced growth of shrimps under 2 L (19.3 g) and 4 L (19.7 g) compared with 8 L (16.1 g) and 12 L (14.7 g). Mortality in the 2 L (18.9%) and 4 L (17.8%) groups were significantly lower than those in 8 L (35.5%) and 12 L (43.3%), indicating that excessive photoperiods could inhibit growth and result in high mortality rate.

Feeding

Complementary observations have been expressed on the feeding activity of early juvenile larvae and those in the later stage, in which the early juvenile stage displayed improved feeding activity in longer photoperiods. Adult crustaceans have a higher tendency to feed more in dark conditions. Tidwell et al. (2001) evaluated the feeding performance of early juvenile *M. rosenbergii* (0.025 g) and found a higher feed conversion ratio for prawns subjected to 24 L (1.2) compared with those subjected to 12 L (1.4) and 0 L (1.6).

In contrast, Morales and Barba (2015) conducted an experiment on *S. serrata* (carapace width: 8.5 cm, weight: 200 g) under 0 L photoperiod and the mud crabs exhibited less agitated movement with continuous feeding activity (feeding efficiency: 2.0-4.3) compared with normal photoperiod (12 L) (feeding efficiency: 5.0-9.3), demonstrating the nocturnal feeding habit of this species. Likewise, Scudder et al. (1981) observed the crawling activity of *M. rosenbergii* as a diurnal behaviour compared with vertical migration in the night, which was perhaps a demonstration of the high feeding activity of prawns at night.

Locomotion

A comparison of early juvenile locomotion and later juvenile stage cannot be appraised due to scarce information on the early juvenile crustacean stage. However, a similar event may be anticipated, in which the early crustacean juvenile appears to be active with longer photoperiod, whereas the higher juvenile stage, as well as adult stage are the opposite. Hence, several studies revealing the relationship between photoperiod and crustacean locomotion mentioned here refer to the higher growth stage of crustaceans.

Morales and Barba (2015) observed that the adult mud crabs kept in zero photoperiods (0 L) appeared to be minimal and less agitated than crabs subjected to normal photoperiod (12 L), showing that the effects of darkness likelihood provided favourable conditions as the mud crab tended to burrow into the mangrove mud. Hall and Ham (1998) stated that penaeid prawns such as pink shrimp (*Penaeus duorarum*), eastern school shrimp (*Metapenaeus macleaya*), eastern king prawn (*Penaeus plebejus*), and deepwater rose shrimp (*Penaeus longirostris*) were less active during the full moon. Complementary findings were demonstrated by Scudder *et al.* (1981), which did an experiment related locomotory behaviour of juvenile *M. rosenbergii* in a laboratory by subjecting the prawns to 16 hours of daylight and eight hours of darkness per day. They found that the prawns displayed more swimming activity in the dark phase (activity score: 77.5) than in the light phase (activity score: 47.4). On the other hand, there was more crawling activity in the light phase (activity score: 49.8) than in the dark phase (activity score: 37.9). Collectively, all breakthroughs representing the nocturnal behaviour of crustaceans were possibly to exploit food resources or avoid any encounter with higher trophic predators.

Spawning

The photoperiod is a core abiotic factor in female crustacean gonad maturation. Thorough monitoring on the field had been undertaken

and researchers have noticed that crustaceans easily spawned at a certain point throughout the year. And photoperiod has a high likelihood as the abiotic factor that played an imperative role. For example, Hamasaki *et al.* (2004) demonstrated that ovarian maturation in *P. trituberculatus* could be easily induced with increasing photoperiod from 12 L in early February to 14 L in late April, which resulted in higher ovigerous female percentage (60% to 80%) from April onwards. Babita (2019) studied seasonal variations in the reproduction of three-spot swimming crab (*P. sanguinolentus*). They found the maximum light hours in 2002 was in July (13.10-13.90 L) and in the following year, it was in June (13.10-13.12 L). The gonadal indices (4.17-4.28) of female crabs were observed to be bigger during these periods compared with other months (1.08-2.65), indicating that the photoperiod was crucial in either initiating or terminating the annual reproductive cycle of the crabs (Babita, 2019).

To wind up the debate on whether photoperiod influences the spawning season of crustaceans in the wild and further strengthen such opinion, laboratory studies have been conducted to see the effects of manipulating light exposure in a controlled environment (Table 3). Sachlikidis *et al.* (2005) adopted two photoperiods in the laboratory imitating winter (13 L) and summer (14.5 L) and spawning was significantly greater when lobster was exposed to the “summer” photoperiod (73%) than “winter” photoperiod (28%). Similarly, Lipcius and Hernkind (1987) investigated the photoperiod effect of spiny lobster (*P. argus*) females under long day length (14 L), which developed significantly larger ovaries (gonad index: 333.5) and more of the females also spawned (50%) than those under short daylength (9 L) (gonad index: 177.3, female spawn: 33%). Likewise, Matsuda *et al.* (2001) cultured the spent Japanese spiny lobster (*P. japonicus*) in different photoperiods, and ovarian development was suppressed under shorter photoperiods (10 L, 11 L, and 12.5 L) with 0% female spawning. But in the 14 L photoperiod, most of the spent females spawned again (80%). In short, all these evidence from

the laboratory further verified that photoperiod significantly influenced reproduction in female crustaceans.

In commercial crustacean hatcheries, unilateral eyestalk ablation is commonly used to stimulate spawning in the female broodstock. In the eyestalks, there is an X-organ sinus gland complex that inhibits ovarian maturation and by removing one of the stalks, it will reduce the inhibition of the individual female's reproductive hormone level, thus, stimulating gonad development at the quickest pace. However, the use of this method has come under scrutiny as it is considered cruel and unethical. In 2010, Kim *et al.* (2010) investigated the effects of eyestalk ablation in female crabs cultured under two photoperiods (9 L and 15 L). They found that ablated and unablated females

in 15 L photoperiod had the most profound effect of ovarian maturation, with 84.6% and 83.3% ovigerous female produced, respectively, whereas, both ablated and unablated females exposed to the 9 L photoperiod indicated reduced number of ovigerous females at 44.4% and 8.0%, respectively. These results suggested that gonad maturation in crustaceans could be induced under longer photoperiod to induce off-season spawning without utilising eyestalk ablation. This breakthrough highlighted the importance of prolonged light exposure in boosting spawning maturation to resolve poor quality broodstock concerns. It also proved that there was no necessity to implement eyestalk ablation as prolonged photoperiod exposure alone on unablated female crabs could produce better spawning results than those that had been ablated (Figure 2).

Table 3: Gonad maturation performance of crustacean larvae subjected to different photoperiods. Highlighted numbers indicate the highest gonad maturation performance obtained in various experiments. Most of the highest parameters were noted for the 14 L photoperiod

Species	Parameter (unit)	Photoperiod						Citation
		0 L	9 L	10 L	12 L	14 L	24 L	
<i>S. paramamosain</i>	Expression of Beta-pigment-dispersing hormone	0.4	-	-	0.8	-	0.7	Huang <i>et al.</i> (2014)
<i>P. argus</i>	Gonad index	-	177.3	-	-	333.5	-	Lipcius and Hernkind (1987)
<i>P. trituberculatus</i>	Gonadosomatic index	-	9.59	-	-	12.73	-	Kim <i>et al.</i> (2010)
<i>P. trituberculatus</i>	RNA content in ovary ($\mu\text{g}/\text{mg}$)	-	8	-	-	13	-	Kim <i>et al.</i> (2010)
<i>P. japonicus</i>	Percentage spawners (%)	-	-	0	-	100	-	Matsuda <i>et al.</i> (2002)
<i>P. ornatus</i>	Percentage of matured stage of ovary (%)	-	-	20	-	70	-	Sachlikids <i>et al.</i> (2005)
<i>M. rosenbergii</i>	Gonadosomatic index	-	-	1.978	-	2.469	5.483	Pervaiz <i>et al.</i> (2015)

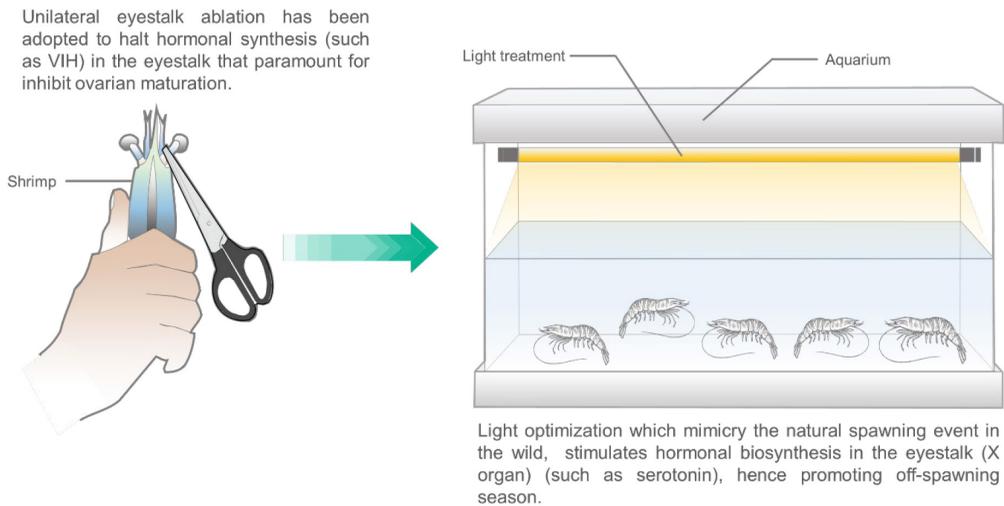


Figure 2: The potential of light manipulation negates the necessity to perform eyestalk ablation in aquaculture. Kim *et al.* (2010) observed that an extended photoperiod (15 L) can induce better off-season spawning results in unablated females compared with ablated ones

Immune Response

In the context of crustacean immunity, selecting specific photoperiod is beneficial to the growth and immunological function of crustaceans. However, more research is needed to unveil the role of light in crustacean immune response. Wang *et al.* (2021) investigated the implications of photoperiod on immune response in *L. vannamei* (body weight: 9.56 g). Shrimps exposed to shorter photoperiod (2 L and 4 L) displayed significantly higher levels of catalase (9 U/mg), superoxide dismutase (25 U/mg), acid phosphatase (155 U/g), phenol oxidase (23 U/mg), and lysozyme (16 U/mg) compared with the longer 8 L and 12 L groups (catalase: < 6.5 U/mg, superoxide dismutase: < 20 U/mg, acid phosphatase: > 130 U/g, phenol oxidase: < 12 U/mg, and lysozyme: < 10 U/mg). Concurrently, the mRNA expression of immune-related genes of the 2 L and 4 L treatments such as crustin (110-120), penaeidin 3a (37-43), Lc1 (200-230), and LGBP (1.7-1.8) had significantly risen more than the control (12 L) (crustin: 20, penaeidin 3a: 5-10, Lc1: > 40, and LGBP: 0.9). Conclusively, reduce photoperiods (2 L and 4 L) could improve the innate immunity and antioxidant

response, subsequently reducing the mortality rate in adult shrimps. These findings rendered the exact mechanism of physiological response in crustacean as well as the first initiatives to better understand of light repercussion in terms of crustacean immunity.

Light Intensity

Light intensity means the brightness or amount of light being observed and its exposure is influenced by many factors. Light intensity decreases as the sea depth increases and is also influenced by the weather in the atmosphere, besides the angle of the sun's ray strike (morning, noon and evening) (Heiden *et al.*, 2016). The crustacean susceptibility to seawater depth layer, global climate and daily light rhythm are then imperative in determining the amount of daily irradiance for larval growth and spawning events.

For instance, Ikhwanuddin *et al.* (2019) adopted three light intensities on larvae of *P. pelagicus*. The highest intensity (1302 lux) resulted in a high growth rate for Zoea 1 (4.90), Zoea 2 (5.93), and Zoea 3 (4.02) larvae compared with Zoea 4 (2.42). The Zoea 4 larvae

had a high preference for medium light intensity (326 lux), in which the highest growth rate (4.3) was observed. In terms of survival, high intensity (1302 lux) resulted in high survival rate in Zoea 1 and Zoea 2 (38-55%) compared with the lower light intensity (1.2 lux, 10-28%). In contrast, medium light intensity (326 lux) resulted in higher survival in Zoea 3 and Zoea 4, with survival rates of 78% and 53%, respectively (Ikhwanuddin *et al.*, 2019). It was concluded that higher light intensity was required during early larval stages (Zoeas 1 and 2) whilst medium light intensity was necessary during the later stage (Zoeas 3 and 4) of culture.

Aside from light intensity aiding in crustacean larval growth and survival, light intensity also exerts prominent implications on the crustacean spawning perspective. Such a phenomenon could be observed in a study by

Huang *et al.* (2014), in which they explored the circadian rhythm of PDH (neuropeptide pigment dispersing factor, specifically for regulating ovarian maturation) under different light intensities. The expression level of PDH remained high (relative expression: 0.9-1.1) under the darkness or dim light (6 p.m. to 6 a.m.) while it significantly declined (relative expression: 0.3-0.7) under bright light (9 a.m. to 3 p.m.), indicating that the exposure of crustaceans to bright light for longer periods could cause the decline of PDH, thus, allowing ovarian maturation. As a whole, former studies have shown that up to a certain point, light intensity is required as a fundamental need to enhance larval growth, as well as ovarian maturation response in crustaceans (Figure 3).

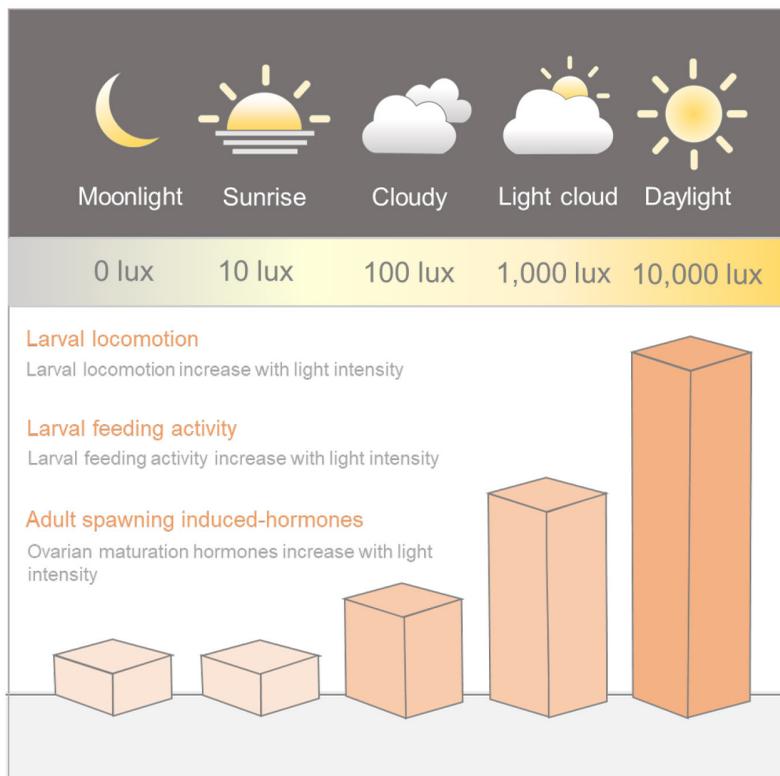


Figure 3: Relationship between light intensity, larva locomotion, and feeding (Ikhwanuddin *et al.*, 2019), as well as light intensity and adult spawning mechanism (Huang *et al.*, 2014)

Light Spectrum

The light spectrum consists of short-wavelengths (violet, 380-440 nm and blue, 440-485 nm), middle-wavelengths (green, 500-565 nm and yellow, 565-590 nm) and long-wavelengths (orange, 590-625 nm and red, 625-740 nm) (Chen *et al.*, 2022). Owing to aquatic crustaceans living in seawater, which contains many chromatic filters such as plankton, suspended particles, dissolved organic substances, and water itself, therefore, understanding the effects of the light spectrum on crustaceans is pivotal to upend its physiological mechanisms. Chen *et al.* (2022) exposed various light spectra (white, violet, blue, cyan, green, yellow, and red) on the green mud crab, *Scylla paramamosain* and juvenile crabs exposed to blue light displayed a high survival rate (94.9%), weight gain (67.6%), and moulting frequency (4.2), besides lower melatonin (> 390 pg/mL) and cortisol levels (> 275 ng/mL). In the context of stress, expression of the hsp90 protein was significantly down-regulated in crabs exposed to the full-spectrum light group with 1.0 relative expression while other groups exposed to violet, blue, cyan, yellow, green, and red showed upregulated expression of more than 2.0 (Chen *et al.*, 2022).

In apoptosis-related genes, bcl-2 expression (1.5) in crabs under cyan is upregulated compared to other groups (> 1.3), suggesting that cyan light may inhibit apoptosis (Chen *et al.*, 2022). Taken together, these results suggested that blue or cyan light could promote growth performance while full-spectrum light could reduce stress response in *S. paramamosain* (Chen *et al.*, 2022). In another study, Wei *et al.* (2021) conducted a light spectrum experiment

(red, yellow, white, green, and blue) on *M. rosenbergii*, with the best results observed under green (survival: 62.5%, metamorphosis rate: 6.36%, body length: 6.4 mm) or white light (survival: 66.6%, metamorphosis rate: 6.36%, body length: 6.4 mm). Red light was found to exert a disadvantage on larval development of prawns with the lowest survival (29.2%), metamorphosis (0.00%), and body length (4.4 mm) (Wei *et al.*, 2021). Also, the antioxidant activities of superoxide dismutase, catalase, alkaline phosphatase, and lysozyme in giant freshwater prawns cultured under red (SOD: 145 U/mg, CAT: 1.4 U/mg, AKP: 80 U/mg, and LZM: 50 U/mg) and yellow light (SOD: 160 U/mg, CAT: 1.4 U/mg, AKP: 80 U/mg, and LZM: 60 U/mg) were significantly higher than those grown under blue, green, and white lights (SOD: > 140 U/mg, CAT: > 1.1 U/mg, AKP: > 75 U/mg, and LZM: > 35 U/mg) (Wei *et al.*, 2021).

Based on these results, exposure to red light should be avoided and the adoption of green and white lights could be utilised in commercial hatcheries to maximise productivity (Wei *et al.*, 2021). Overall, both pieces of evidence here demonstrated the benefit of using white light in terms of survival, growth, and reduced stress, as well as increased antioxidant capacity in the crustacean. At the same time, utilising green, blue, and cyan light spectrum likelihood had a high potential to be implemented in crustacean farming and providing alternative light for the white spectrum as positive progressive results revealed from previous disclosure made by the researchers (Figure 4).

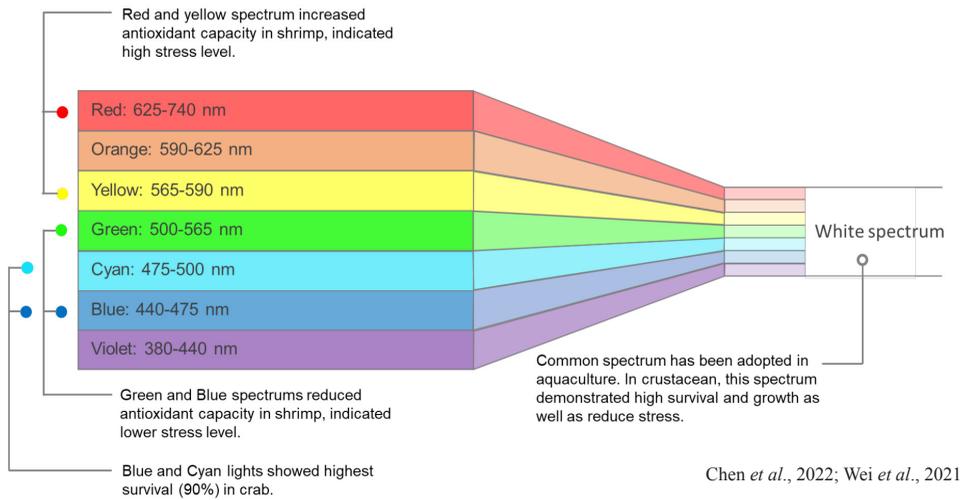


Figure 4: Light spectrum impact on stress level, growth, and survival. Lower spectra such as cyan and blue may reduce the stress level of crustacean likelihood due to their ability to penetrate deeper in seawater compared with other spectrums

Summary, Gap Studies and Future Applications

Based on previous research, crustacean larvae such as zoeas and phyllosomata display common traits in their high tendency to favour longer photoperiods (more than 18 L) and such disclosure is important to rev up the larval growth and development in aquaculture. The root causes for peaked survival and growth of the larval crustaceans kept under extended photoperiods are likely caused by the presence of light, which stimulated swimming behaviour of both larvae and prey, hence, driving the encounter between them, which results in increased ingestion rate and boosting the growth and survival of crustacean larvae. In juvenile and adult context, many studies showed that in early juvenile crustaceans needed longer photoperiods for better growth and locomotion. However, up to a certain extent, perhaps amid the late juvenile stage, photoperiod preference will shift towards shorter times as such stage demonstrated a pressing need for dark photoperiod as reflected in the nocturnal behaviour of adult crustaceans (Figure 5). More specifically, the photoperiod requirement

gradually reduces with the advancing growth stage of crustaceans. Interestingly, in terms of gonad maturation, the photoperiod is depicted as a core abiotic factor that highly influences ovarian growth via thorough monitoring of wild crustaceans and is further confirmed through laboratory evidence. This important finding gives an assurance that there is no need to adopt unethical eyestalk ablation to stimulate off-season spawning.

Studies have shown that more light intensity may be a requisite to enhance larval growth (Figure 5) and ovarian development in crustaceans. For the light spectrum, former evidence has deciphered the benefit of utilising white light in terms of survival, growth, and reduced stress, as well as rising antioxidant capacity in crustaceans. Simultaneously, research has unveiled that instead of using white light alone, an optimised exposure to green, blue, and cyan spectra might also have high potential to promote larva development in aquaculture (Figure 5).

In the context of gap studies, the issues that should be highlighted is that many previous works were carried out on crustaceans focusing merely on photoperiod. The ramification of this crucial issue, going forward, many experts need to take the initiative to engage in upgrading further existing research by prioritising light intensity and spectrum to better understand the effects on crustaceans as a whole. Likewise, in the modern world with advanced research technology, researchers are encouraged to interpret the mechanism behind the internal physiology, besides exploring the implications of light on crustacean growth and health at a genetic level.

In future, the role of aquaculture is expected to grow as the most viable option in ensuring food security, despite its rising challenges such as water pollution, consumption of vast resources, and use of chemicals. For instance, the high economic value of crustaceans (crab, lobster, prawn, and shrimp), coupled with overharvesting of wild fisheries have made commercial production of crustaceans an extremely paramount focus in many countries (Fitzgibbon & Battaglene, 2012). Stock depletion, including difficulty in obtaining seeds from the wild has prompted researchers to use light to frame out a foolproof technology in producing crustacean seeds. Crustacean seed-rearing has been attempted in many hatcheries on

a commercial basis. However, the low survival of larvae, perhaps caused by light-responsive behaviour had hindered commercialisation.

Therefore, to ensure successful seed production, the efforts should be channelled to a fully enclosed system that implements an artificial lighting system to manipulate the early growth stage of crustacean larvae. Additionally, light manipulation has also been proven effective to induce off-season spawning, which is required to start large-scale commercial rearing. And perhaps, the best possible protocol to induce spawning through light regime treatment is the best solution to resolve the ethic issues caused by eyestalk ablation.

A fully enclosed system is also a foolproof solution against weather changes, which is becoming a challenge for open-air farms. As such, the breakthrough from this review fosters as well as advocates farmers and researchers to shift to an enclosed system set-up in terms of optimising light approach, including photoperiod, light intensity, and spectrum (Figure 6). Such light optimisation in crustacean culture is a pivotal avenue to enhanced farming productivity, particularly in spawning and larval production, which assists in increasing cycle harvest annually, hence, stepping up profits for farmers in tandem with providing an assurance of food security for the sake of our next generation.

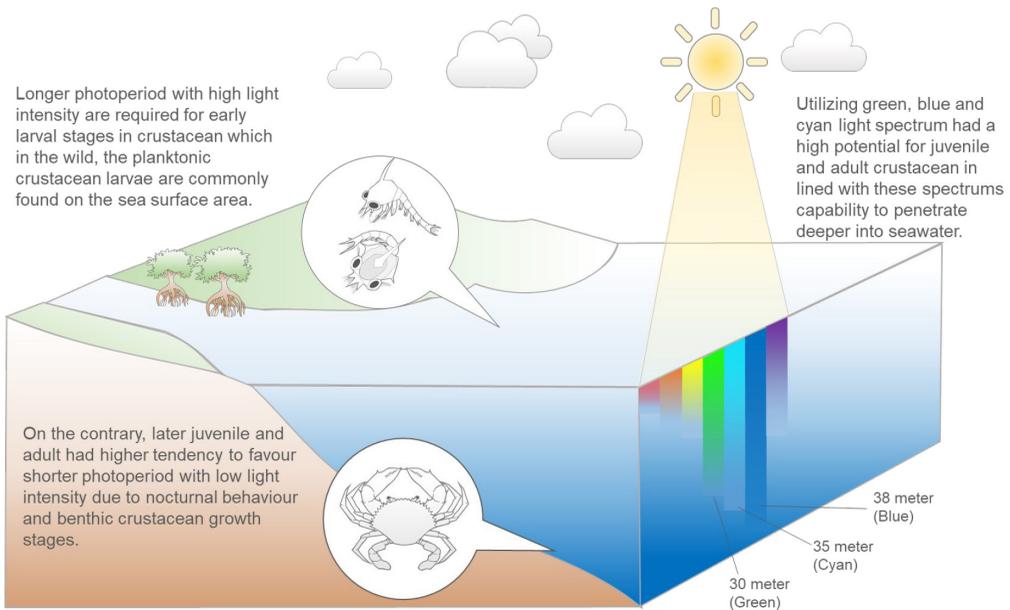


Figure 5: Relation of light requirement with crustacean growth stages. The crustacean ontogenetic shift influences the light requirement needed for larvae, juvenile, and adult. Most marine crustacean has a planktonic larval phase in their life cycle before metamorphosing into benthic juvenile, this ontogenetic shift from a planktonic to a benthic life requires a different level of light photoperiod, spectrum, and intensity

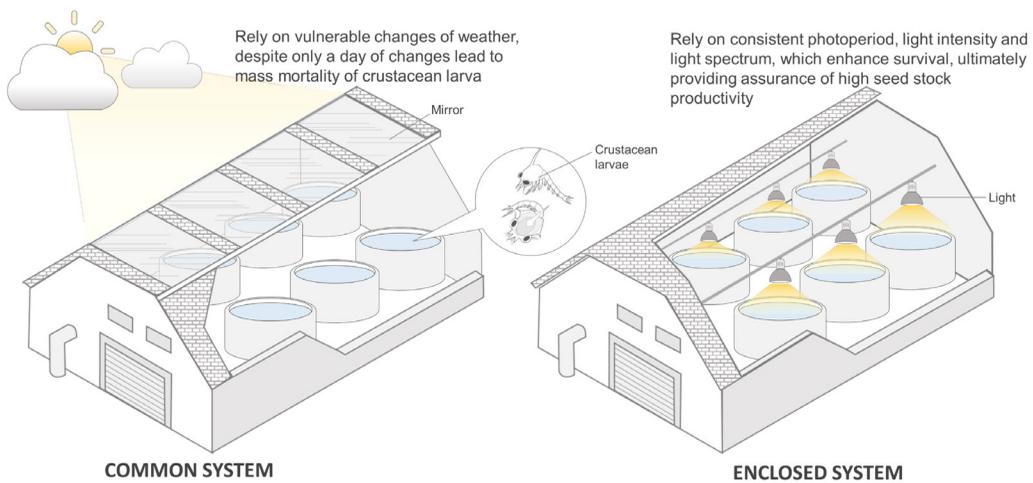


Figure 6: Fully enclosed system by optimising light in terms of photoperiod, light intensity, and light spectrum for future application particularly for seed stock enhancement and boosting spawning performance in crustacean

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Conflict of Interest Statement

The authors declare that they have no conflict of interest.

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