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Reproduction Technology for Sustainable Portunid Crab's Aquaculture: A Review

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ABSTRACT

Portunid crabs, including the genus *Scylla* and genus *Portunus*, are highly commercial due to their tasty flavour and high meat yield. However, until now, crab demand is still heavily dependent on wild-caught crabs, and the domestication of crabs is necessary for the production of viable seed in hatcheries and the grow-out of portunid crabs. To enhance portunid crabs farming, reproductive technologies should be improved, and this information still needs to be compiled and reviewed. As such, the purpose of this paper is to review reproductive technologies for sustainable portunid crab's aquaculture. This manuscript provides a narrative review of reproduction technology, with an emphasis on the portunid crab from two genera, *Scylla* and *Portunus,* covering literature from 2000 up to 2025, which focuses on practical hatchery applications. Three methods, including hormonal injections, dietary feeding, and manipulation of culture conditions, can be implemented in hatcheries to obtain as many spawned crabs as possible. Pregnenolone, 5-HT, GnRH, methyl farnesoate, prostaglandin, thyroxine and estrogen have been proven to support ovarian maturation in portunid crabs. Formulated diet rich in lipids, adding astaxanthin or using natural diet from fish, blood cockle and squid has been shown to stimulate gonad development and increase spawning rates. Manipulating temperature and photoperiod can also lead to improvements in the egg incubation period and hatching success, with higher water temperatures and longer light periods yielding better results. Through this review, knowledge on reproductive technologies has been gathered and could be further implemented during the farming of portunid crabs, making hatchery-based reproduction more reliable.

Keywords: Feeding, hormone, photoperiod, portunid crabs, temperature

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INTRODUCTION

Crab production is ranked second among crustaceans, after shrimp, and high-value commercial crab consists of the portunid crabs such as mud crab, genus *Scylla* (mud crab) and blue swimming crab, genus *Portunus,* due to their high meat yield and delicate flavour, which satisfy consumer demand for premium seafood (Hidir et al. 2022). Mud crabs are notably known for their large size, reaching 1 kg per crab, especially in male mud crabs due to their muscular chelipeds (Hidir et al. 2021). Mud crabs have been classified via morphometric and allozyme electrophoresis, comprising four species*: Scylla serrata, S. tranquebarica, S. olivacea, and S. paramamosain* (Keenan, 1997). Globally, annual mud crab aquaculture production reached around 408,200 tonnes in 2020, with the vast majority of mud crabs still depending on capture-based fisheries (FAO, 2022). The wholesale price of mud crabs is offered at a high price, reaching 30 USD per kg (Sayeed et al. 2021). Among blue swimming crab species, the most commercially exploited crabs are *Portunus pelagicus* and *P. sanguinolentus*, with an annual global production of around 250,000 tons in 2020 (FAO, 2022). The demand for blue swimming crabs surged in 2022, with an average selling price of 18.6 USD (Setioko et al. 2024).

The early juvenile phase of portunid crabs resides in complex substrates, such as seagrass, as nursery areas to increase survival, while adult portunid crabs are found in coastal habitats, estuarine, and mangrove areas (Vay, 2001; Webley et al., 2009). Nowadays, all these areas are being lost for many reasons, primarily due to the expansion of aquaculture farms, leading to a reduction in wild portunid crabs (Xiong et al., 2024). Additionally, global warming may impact the vulnerable life stages of portunid crabs, especially during the recruitment of larvae and juveniles, which are susceptible to temperature changes, leading to high mortality (Hidir et al., 2021). At the same time, significant warming of ecosystems causes atmospheric CO2 absorption in seawater, reducing pH and impacting the calcification rate of portunid crabs. Until now, crab farming has still relied on wild-caught seed, and uncontrolled fishing of these juvenile crabs has led to overfishing, contributing to a decline in future populations (Fujaya et al., 2021). To overcome these problems, domestication of portunid crabs is necessary for the production of viable seed in hatcheries and the grow-out of portunid crabs. Mature females, which have copulated in the wild, are reared in hatcheries to obtain spawning crabs for seed stock, and reproductive technology must be implemented to achieve this. However, knowledge of reproductive technology is still scarce and needs to be collected. Hence, the purpose of this paper is to review reproductive technologies for sustainable portunid crab's aquaculture. This manuscript provides a narrative review of reproduction technology, with an emphasis on portunid crab from two genera, *Scylla* and *Portunus,* covering literature from 2000 up to 2025, which focuses on practical hatchery applications. Developing reproductive technologies will contribute to stock enhancement and may alleviate the pressing issue of reduced wild stock populations of portunid crabs.

REPRODUCTION TECHNOLOGY OF PORTUNID CRABS

Hormonal Induced

The use of exogenous hormones has shown promise as a replacement for eyestalk ablation and has been highly effective in enhancing growth performance in portunid crabs (Table 1). One of the methods used is the administration of serotonin (5-hydroxytryptamine; 5-HT) to portunid crabs, as there is substantial evidence demonstrating the role of this neurotransmitter in promoting ovarian maturation, especially since this hormone has been found in the ovary of portunid crabs (Saetan et al., 2023). Injecting exogenous serotonin induces the mandibular organ to synthesise methyl farnesoate and the Y-organs to synthesise ecdysteroids, which then act on receptors such as the retinoid X receptor (RXR) and the ecdysteroid receptor (EcR), both of which promote ovarian maturation (Girish et al., 2017). Another hormone that could be used is gonadotropin-releasing hormone (GnRH). GnRH injection can activate the crab adipokinetic hormone/corazonin-related peptide (ACP) receptor expression, which plays a role in lipid metabolism and also upregulates phospholipase A and C, COX, and prostaglandin D, E, and F synthases, all of which are involved in ovarian maturation (Saetan et al., 2023). Additionally, GnRH-injected crabs showed upregulation of other genes, such as LHR and FSHR, whose roles in the activation of reproductive steroid hormones have been confirmed (Saetan et al., 2023). Besides 5-HT and GnRH, two other hormones have been recognized as successfully promoting ovarian maturation in portunid crabs: estrogen and prostaglandins. Estrogen plays a vital role in Vg synthesis in the ovary and hepatopancreas of portunid crabs, and Vg is a yolk precursor for the production of vitellin and egg yolk (Lu et al., 2018). At the same time, estrogen indirectly regulates ovarian maturation by inhibiting the secretion of mandibular organ inhibiting hormone (MOIH) from the brain (Lu et al., 2018). Without MOIH, methyl farnesoate can be synthesised by the mandibular organ and play its role in promoting ovarian maturation. Similarly, the administration of prostaglandins via injection resulted in the elevation of methyl farnesoate and ecdysteroids from the mandibular organ and Y-organ, respectively, and both of these hormones mediate the induction of vitellogenesis in portunid crabs (Swetha et al., 2020).

Iromo et al. (2015, 2021) investigated the use of thyroxine, a hormone that has been rarely studied for its effects on ovarian maturation in portunid crabs. Thyroxine is thought to be involved in gonadal maturation, as its concentration has been shown to increase with advancing ovarian stages in crabs (Iromo et al., 2015). Secreted by the thyroid gland, thyroxine regulates metabolism, particularly protein and lipid metabolism, which may indirectly promote ovarian development through these metabolic pathways (Pucci et al., 2000; Tripathi and Verma, 2003). Another rarely used hormone for stimulating ovarian growth is abalone egg-laying hormone (a neuropeptide secreted by the neural ganglia of molluscs), which is known to trigger egg-laying. Interestingly, Saetan et al. (2017)

demonstrated that this hormone could promote the production of estrogen, thereby inducing vitellogenesis in the hepatopancreas and ovary, resulting in ovarian maturation in female *P. pelagicus*.

Overall, most past studies have used hormones such as pregnenolone, 5-HT, GnRH, methyl farnesoate, prostaglandin, and estrogen to stimulate ovarian maturation, and have primarily assessed hormone-related parameters in the haemolymph. Comparing these hormones to determine which hormone is most effective in inducing ovarian maturation is quite challenging since different hormone-related parameters are being used. In terms of fold change (comparing the optimally hormone-treated group to the control group), prostaglandin appears to produce the highest response among the studies. Although the optimal injection concentration used in Swetha et al. (2020) was relatively high (1.0 µg/g, see Table 1), other studies may have used even higher or similar concentrations but did not achieve optimal results. Since fold change alone may not provide a complete picture, future studies should evaluate additional parameters, such as the total number of spawners and the time taken for crabs to spawn, to better determine the most effective hormone. Until now, only the studies by Farouk et al. (2014), Iromo et al. (2015) and Saetan et al (2023) were more advanced, as they also focused on ovarian maturation stages, although no spawning events occurred.

Feeding

One of the main factors for obtaining ovigerous females at a faster rate is manipulating lipid levels to the optimum in portunid crab feeding, and this can be achieved by introducing formulated pellets for portunid crabs (Table 2). In a study by Aaqillah-Amr et al. (2022a) and (2022b), a formulated semi-moist pellet with a high lipid level (120 g/kg) resulted in higher reproductive performance in terms of HSI, GSI, fatty acids, progesterone and estrogen level in the ovary. As the lipid level increases in the hepatopancreas, it shows that this organ absorbs and stores lipid from the formulated pellet, which then provides enough nutrients to produce vitellogenin for egg yolk formation in the ovary. More specifically, the evidence of nutrient transfer from the hepatopancreas was revealed through histological analysis, where the hepatopancreatic cells were observed to reduce in both tubule diameters and R-cell count, while the ovarian cells demonstrated a higher oocyte diameter. A high lipid diet with adequate nourishment of EPA and DHA levels is not only vital for promoting ovarian maturation in portunid crabs but also for the growth performance of crab larvae (Yin & Kian, 2017). For example, both studies by Aaqillah-Amr et al. (2022b) and Ghazali et al. (2017a) highlighted higher levels of DHA and EPA in the ovaries of crabs fed with scadfish, *Decapterus* sp. and blood cockle, *Anadara granulosa*, which resulted in more advanced ovarian maturation stages. Since crustaceans are unable to synthesise these fatty acids de novo, the requirement for these fatty acids is crucial and must be supplemented via their mother's feeding, where they are then stored for later use by hatching larvae

Table 1
Hormonally induced effect on the reproduction of portunid crabs

Portunid Crab's Species	Hormone	Injection Treatment	Optimal Concentration	Result	Reference
Mud Crab, *S. olivacea*	Pregnenolone	Every 10 days for 60 days	0.01 µg/g	Higher ovary stage and GSI (1.5-fold)	Muhd-Farouk et al., 2014
	5-HT + GnRH	Every 14 days for 28 days	1.5 µg/g (5-HT) 0.05 µg/g (GnRH)	Upregulated of genes related to ovarian maturation, such as FAMeT, ESULT (1.2-fold), progesterone-like protein (2.7-fold) and vitellogenin level (2.4-fold)	Saetan et al., 2023
	Methyl Farnesoate	Every day for 20 days	5.0 µg/crab	Higher GSI and oocyte diameter (2.3-fold)	Muhd-Farouk et al., 2019
Mud Crab, *S. serrata*	Prostaglandin	Every 10 days for 28 days	1.0 µg/g	Higher levels of methyl farnesoate, ecdysteroids, GSI, oocyte diameter (5.4-fold), and vitellogenin (7.3-fold)	Swetha et al., 2020
	5-HT	Every 7 days for 28 days	0.0004 µg/g	Higher levels of methyl farnesoate (1.7-fold) and ecdysteroids (2.3-fold)	Girish et al., 2017
	Thyroxine	Every 5 days for 20 days	0.1 µg/g	Higher GSI (3.9-fold)	Iromo et al., 2021
	Thyroxine	Once	0.1 µg/g	Higher GSI (1.9-fold), shorter time for ovarian maturation (3-fold) and egg incubation period	Iromo et al., 2015
Swimming Crab, *P. trituberculatus*	Estrogen	Every 7 days for 35 days	0.01 µg/g	Higher GSI (1.1-fold) and expression of Vg (2.5-fold)	Lu et al., 2018
Blue swimming crab, *P. pelagicus*	Abalone Egg-laying Hormone	Every 7 days for 28 days	0.5 µg/g	Higher GSI (5.3-fold) and ovary vitellin level (6.6-fold)	Saetan et al., 2017

Note. Serotonin, 5-HT; gonadotropin-releasing hormone GnRH; gonadosomatic index, GSI

In the Results section, 'fold' refers to the comparison between the optimally hormone-treated group and the control group

Table 2
Feeding effect on the reproduction of portunid crabs

Portunid Crab's Species	Diet	Optimal Concentration/ Food Type	Result	Reference
Mud Crab, *S. olivacea*	Formulated pellet: Moist pellet from mangrove clams with different lipid levels	120 g/kg lipid	Higher SGR and GSI in crabs, and higher EPA and DHA in the ovary	Aaqillah-Amr et al., 2021
	Formulated pellet: Moist pellet from mangrove clams with different lipid levels	120 g/kg lipid	Higher GSI, HSI, oocyte diameter, and increased progesterone and estradiol in the ovary	Aaqillah-Amr et al., 2022a
	Natural diet: Scadfish and squid	Scadfish	Higher DHA and EPA in the ovary	Aaqillah-Amr et al., 2022b
	Natural diet: Blood cockle and fish	Blood cockle, *Anadara granulosa*	Higher oocyte diameter	Ghazali et al., 2017b
	Natural diet: Blood cockle and fish	Blood cockle, *Anadara granulosa*	Higher EPA in the ovary	Ghazali et al., 2017a
Mud Crab, *S. serrata*	Natural diet: Blood cockle, polychaete and beef liver	Blood cockle, *Anadara granulosa*	Higher GSI and fecundity	Iromo et al., 2025
	Natural diet: Fish, fish + squid + shrimp, pellet	Fish	Reduced both ovarian maturation and berried period, higher ovary egg diameter, larval hatching	Pattiasina et al., 2012
Mud crab, *S. tranquebarica*	Formulated pellets: Dry pellets from fish meal with different additives from astaxanthin and DHA	Astaxanthin: 50 g/kg DHA: 12.5 g/kg	Higher maturation percentage, spawning rate, GSI, and oocyte diameter	Yin and Kian, 2017
Blue swimming crab, *P. pelagicus*	Natural diet: Squid, *Loligo* sp., blood cockle, *Anadara* sp., fish, *Decapterus* sp. and polychaete, *Neries* sp.	Squid, *Loligo* sp.	Higher larval density	Ikhwanuddin et al., 2015
	Formulated pellet: Different levels of vitamin E	400 IU/kg	Higher egg diameter, fertilisation rate, hatching rate, fecundity	Efrizal et al., 2020

Note. Specific growth rate, SGR; gonadosomatic index, GSI; eicosapentaenoic acid, EPA; docosahexaenoic acid, DHA; hepatosomatic index, HSI; IU, international unit

(Aaqillah-Amr et al., 2021). Besides lipids, another nutrient to consider for nourishing the broodstock of portunid crabs via formulated pellet is astaxanthin, as it acts as an antioxidant, thereby preventing the occurrence of lipid peroxidation during the process of ovarian maturation (Yin & Kian, 2017) (Table 2). Meanwhile, another study by Efrizal et al. (2020) modified formulated pellets by supplementing them with vitamin E at an optimal dose of 400 IU/kg, which resulted in a reduced egg incubation period and improved egg quality.

Besides lipids, protein may play a significant role in stimulating ovarian maturation. Iromo et al. (2025) investigated the effects of different natural diets, such as blood cockle, polychaete, and beef liver, and results showed that crabs fed with blood cockle exhibited the highest GSI and fecundity, perhaps because blood cockle had the highest protein content (46%) compared to beef liver (39%). Although beef liver had a lower protein content, it contained a higher lipid content (26%) compared to blood cockle (7%), which may also support ovarian development; however, excessively high lipid levels could potentially have a slight negative effect on the ovarian maturation of *Scylla serrata*. (Iromo et al., 2025). This finding is supported by Hidir et al. (2018), who reported that wild *S. olivacea* crabs consumed more protein-rich sources such as molluscs and crustaceans during ovarian maturation, and this dietary preference corresponded with higher proteolytic enzyme activity (trypsin) secreted in their hepatopancreas. A study by Ghazali et al. (2017a) found that mud crabs fed with blood cockle exhibited improved ovarian development compared to those fed with fish (*Decapterus* sp.), despite the fish having higher overall protein and lipid content. Similarly, Ikhwanuddin et al. (2015) suggested feeding *P. pelagicus* with squid instead of fish to achieve higher larval density after hatching, even though squid contains less protein than fish. These examples indicate that the type of protein, specifically the amino acid composition in the diet, may play a more critical role in ovarian development than the total protein content alone. Therefore, further research is needed to identify the specific amino acids essential for enhancing ovarian maturation. Additionally, combining this knowledge with an analysis of fatty acid composition may provide stronger evidence of the key nutrients required for successful ovarian development in portunid crabs.

Controlled Environment

Portunid crabs in temperate regions typically grow their ovaries rapidly during the breeding season, which appears to be in summer or spring, and this observation suggests that temperature and photoperiod are the prominent environmental factors regulating portunid crabs' reproduction. For example, the mud crab, *S. paramamosain*, in temperate regions develops its gonad and becomes ready to spawn during the warmer months of spring (Zeng et al., 2007). This also occurs in tropical regions, as proven by a study by Babita (2019), which found that gonadal indices increased with temperature (26.5-37 °C) and prolonged photoperiod (12.2-13.9 light hours) from April to August. Hence, from these observations, it can be concluded that higher temperatures with longer photoperiods may induce ovarian

growth. The term “higher temperature” refers to temperatures considered high relative to the species' natural habitat, and vice versa. For example, the optimal temperature in tropical regions ranges from 30-31 °C, while in temperate regions it is lower, around 21 °C, though this is still considered a high temperature relative to the natural conditions of temperate species (Table 3). Table 3 also summarises several previous studies that have manipulated temperature in captivity to examine its effects on the reproduction of portunid crabs.

Hamasaki (2002) showed that the spawning percentage reached 100% under higher temperatures (18 °C - 26 °C). Moreover, higher temperatures shortened the incubation period for egg development in portunid crabs, as Hamasaki (2002) found a reduction of 14 days in the incubation period when the crabs were exposed to 25 °C compared to a 20 °C treatment. Higher temperatures also aided in fertilisation and hatching, as shown in a study by Efrizal et al. (2006), which found that blue swimming crabs incubated at 28 °C - 30 °C demonstrated the highest fertilisation and hatching rates. Premature egg release by crabs is a common issue in hatchery conditions; therefore, maintaining an optimal temperature is essential to ensure the hatching success of broodstock. Hidir et al. (2021) found that at a higher temperature (30 °C), the hatching success rate reached approximately 75%. While at lower (26 °C) or excessively high temperatures (32 °C), hatching often failed, with success rates dropping to only 36% - 37%. The same study reported that higher temperatures at 31°C are necessary to create optimal conditions for larval survival (more than 66%) and growth. However, if an inappropriate temperature is applied to portunid crabs, either too low or too high, abnormal cell division is observed, and egg development is retarded at the gastrula stage (Zeng, 2007), along with a reduction in egg membrane formation (Efrizal et al., 2006).

Incubating portunid crabs under a longer photoperiod (more than 14 hours) has been shown to promote advanced gonadal development. The influence of longer photoperiods on ovarian growth was successfully demonstrated by Babita et al. (2019), Hamasaki et al. (2004), and Kim et al. (2010), where extended photoperiods (13 h, 14 h, and 15 h, respectively) stimulated gonadal development and resulted in higher percentages of ovigerous females (Table 3). The mechanism behind the effect of light remains unclear and therefore requires further investigation, but only one study reported the influence of pigment-dispersing hormone (PDH) in gonad development. Photoperiodic daily rhythmicity was observed to influence the X-organ in the crab's eyestalk to synthesise this PDH hormone (chromatophore-activating neuropeptide) (Huang et al., 2014). This PDH is also related to ovarian maturation in portunid crabs, as the PDH expression level increases in the eyestalk and ovaries during different stages of ovarian development (Huang et al., 2014). Both observations suggest a possible role of this hormone in regulating ovarian growth. Overall, the information regarding temperature and photoperiod from natural wild habitats and previous captivity experiments is pivotal in aquaculture to enhance culture protocols for accelerating portunid crab spawning.

Table 3
Temperature and photoperiod effects on the reproduction of portunid crabs

Portunid Crab's Species	Climate	Optimal Temp (°C)	Optimal Photoperiod (h)	Result	Reference
Mud Crab, *S. paramamosain*	Temperate	N/A	-	PDH expression aligns with both ovarian maturation and photoperiod, revealing a link between photoperiod and ovarian maturation	Huang et al., 2014
	Temperate	18-26	-	Reduced incubation period of eggs	Hamasaki, 2002
	Tropical	30	-	Reduced embryonic stage duration	Zeng et al., 2007
Mud Crab, *S. serrata*	Temperate	29		Reduced egg incubation period, higher zoea, megalopa and crablet survival, reduced larval incubation period	Hamasaki, 2003
Mud Crab, *S. tranquebarica*	Tropical	30-31	-	Higher hatching success, egg diameter, higher survival and growth for zoea and megalopa, higher crablet production	Hidir et al., 2021
Blue Swimming Crab, *P. pelagicus*	Tropical	30	-	Higher fertilisation rate, hatching rate and reduced egg incubation period	Efrizal et al., 2006
Marine Crab, *P. sanguinolentus*	Tropical	22-28	13	Higher gonad index	Babita, 2019
Swimming crab, *P. trituberculatus*	Temperate	21	14	Earlier spawning	Hamasaki et al., 2004
	Temperate	27-29	-	Higher hatching rate, reduced T-AOC, SOD, GSH, CAT, and MDA	He et al., 2022
	Temperate	20 °C	15	Higher GSI, higher ovigerous females	Kim et al., 2010

Note. T-AOC, total antioxidant capacity: SOD, superoxide dismutase, GSH, glutathione, CAT, catalase and MDA, malondialdehyde

CONCLUSION

The demand for portunid crabs has significantly increased, and hence, the domestication of portunid crabs is vital for the production of viable seed in hatcheries and the grow-out of portunid crabs. To support this domestication effort, a better understanding of reproductive technologies is essential; hence, through this review, knowledge on reproductive technologies has been gathered and could be further implemented during the farming of portunid crabs. Reproductive crab performance could be improved through three methods: hormonal injection, feeding, and manipulation of temperature and photoperiod. These methods accelerate ovarian maturation in portunid broodstock, making hatchery-based reproduction more reliable. This enables a continuous supply for farming and consumption while reducing pressure on wild populations.

In the future, several improvements can be made. For hormonal studies, additional parameters such as the total number of spawners and the time taken for crabs to spawn should be included to better determine the most effective hormone, although these parameters may extend the duration of the experiment. For feeding studies, further research is needed to identify specific amino acids that are essential for enhancing ovarian maturation. Regarding culture conditions, there is a lack of studies on the effect of photoperiod on ovarian maturation in crabs. This area should be further explored, and the use of modern technologies could allow not only for manipulation of photoperiods but also the adjustment of light spectra, using different light colours to potentially enhance reproductive development. The mechanism behind the effect of light remains unclear and therefore requires further investigation.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest. The funders had no role in the design of the study, in the collection, analyses, or interpretation of data, in the writing of the manuscript, or in the decision to publish the results.

AUTHOR CONTRIBUTIONS

Ariffin Hidir designed the study, gathered information, analysed data and drafted the paper. Aaqillah-Amr reviewed the paper. Mhd Ikhwanuddin drafted, reviewed the paper and was involved in funding acquisition, project administration, and supervision.

ETHICAL APPROVAL

Ethical approval is not required as no experiments were conducted in the production of this research paper.

DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are included within the paper. No additional data are available.

LIST OF ABBREVIATIONS

5-HT	5-hydroxytryptamine
ACP	adipokinetic hormone/corazonin-related peptide
DHA	docosahexaenoic acid
EcR	ecdysteroid receptor
EPA	Eicosapentaenoic acid
GnRH	gonadotropin-releasing hormone
GSI	gonadosomatic index
HIS	hepatosomatic index
MOIH	mandibular organ-inhibiting hormone
RAS	recirculation aquaculture system
RXR	retinoid X receptor
SGR	specific growth rate

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