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Review

Larval rearing of mud crab (*Scylla*): What lies ahead

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ABSTRACT

The increasing global demand for mud crabs (genus *Scylla*) and threats to the wild populations highlight the urgency of fully rearing them in captivity. Despite considerable progress in mud crab production, most crab farms still rely heavily on wild-caught crablets and juveniles while the low and inconsistent success rates of larviculture remain as the main bottleneck impeding the development of mud crab aquaculture. Over the years, numerous studies have been conducted to determine the optimum larval rearing parameters, the ontogenic changes in digestive function and feeding behaviour, and the diets for different larval stages. These data, however, are dispersed and not summarised to inform culture practices. This review provides an update on the current progresses and to pinpoint the gaps in knowledge regarding mud crab larval rearing. We include all four mud crab species under the genus *Scylla*, i.e. *Scylla serrata*, *Scylla olivacea*, *Scylla tranquebarica* and *Scylla paramamosain*. Knowledge compiled in this review serves as an important guideline for prospective mud crab larviculture. Future research should gear towards filling in the gaps in our knowledge to advance mud crab larval rearing, thus fully incorporating mud crab into the aquaculture sector.

1. Introduction

Mud crab genus *Scylla* De Haan, 1833 (Brachyura: Portunidae) is an economically important crustacean species that is widely distributed throughout the Indo-West-Pacific region (Keenan et al. 1998). Its taxonomy has been controversial. Mud crabs were previously recognised as a single species, i.e. *Scylla serrata* (Forskål, 1775). Estampador (1949) was the first to report three different species (*S. serrata*, *S. oceanica* (Herbst, 1796) and *S. tranquebarica* (Fabricius, 1798)) and one variation (*S. serrata* var. *paramamosain*) based on their variation in size, colour and shape. However, due to the unclear differentiation between species and variation, different authors had different taxonomic classifications of the genus *Scylla* (Serene 1952; Stephenson & Campbell 1959; Perrine 1978; Quinn & Kojis 1987) until Keenan et al. (1998) revised this genus into four distinctive species based on their morphological, morphometric and molecular differences, namely *S. serrata*, *S. tranquebarica*, *S. olivacea* (Herbst, 1796) and *S. paramamosain* Estampador, 1949. The geographical distribution of *S. serrata* is the widest, covering the tropics and subtropical coastal area of Indo-West-Pacific region whereas the other three species are more concentrated around the equator (Keenan et al. 1998; Ikhwanuddin et al. 2011; Alberts-Hubatsch et al. 2016; Fazhan et al. 2017a).

They inhabit intertidal mangrove forests with fluctuating salinity and support the livelihood of local fishery communities (Keenan et al. 1998; Ikhwanuddin et al. 2011; Alberts-Hubatsch et al. 2016). Global capture production of *Scylla* was above 20,000 t in the last decade (FAO 2018) but the global aquaculture production of mud crabs however, was below 15,000 t since 1980 until 2003, after which it increased exponentially to above 100,000 t with the inclusion of data from China (Fishery Bureau of Ministry of Agriculture of China 2012) and has been increasing steadily ever since (FAO 2018). It is expected that the growth in aquaculture sector will rise due to increasing demand from the global market (Goldburg & Naylor 2005). However, sustainable aquaculture has yet to be achieved for *Scylla* species since crab farms still rely heavily on wild-caught crabs for seed stock, fattening, and soft-shelled crab production (Ewel 2008; Alberts-Hubatsch et al. 2016; Waiho et al. 2016, 2017; Fazhan et al. 2017b). Large scale aquaculture of mud crabs is currently limited due to very low success rate in the hatchery production of juveniles (Quinitio & Parado-Estepa 2008; Holme et al. 2009a; Waiho et al. 2015). For the past years, attempts for mass rearing

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Table 1
General developmental descriptions and the average body length (ABL) of *Scylla* larvae to crab instar (Ong 1964; Jantrarotai et al. 2006; Lumasag et al. 2007; Yi et al. 2009; Thirunavukkarasu et al. 2014).

Crab stage	Description
Zoea (Z) 1	Sessile eyes; abdomen segment = 5; lateral spines present on abdomen segments = 2 & 3 (*S. olivacea*), 3–5 (*S. serrata*); ABL = 1.33 mm (*S. serrata*), 1.12–1.25 mm (*S. olivacea*)
Z2	Stalked eyes; abdomen segment = 5; lateral spines more distinct; ABL = 1.63 mm (*S. serrata*), 1.47–1.65 mm (*S. olivacea*)
Z3	Abdomen segment = 6 (plus telson); observable pereopod buds; ABL = 2.09 mm (*S. serrata*), 1.90–2.17 mm (*S. olivacea*)
Z4	Elongated lateral spines; distinct pleopod buds at the ventral posterior end on segments = 2–6; ABL = 3.05 mm (*S. serrata*), 2.35–2.80 mm (*S. olivacea*)
Z5	Pleopod buds increase in size, with setae and are biramous; ABL = 4.05 mm (*S. serrata*), 3.35–3.80 mm (*S. olivacea*)
M	First pereopod developed into cheliped; increase in carapace width and size; ABL = 1.79 mm (*S. serrata*)
CI	Crab-like appearance; carapace margin serrated; ABL = 3.06 mm (*S. serrata*)

Note: Z1 = zoea stage 1; Z2 = zoea stage 2; Z3 = zoea stage 3; Z4 = zoea stage 4; Z5 = zoea stage 5; M = megalopa; CI = crab instar.

of juvenile seeds in the hatchery had been carried out in countries such as Vietnam (Nghia et al. 2007a), Japan (Hamasaki et al. 2011), and the Philippines (Quinitio et al. 1999, 2001; Quinitio & Parado-Estepa 2008).

Crustacean larvae are highly vulnerable to diseases during the initial developmental stages and require specific biotic and abiotic conditions for normal growth and development (Azra & Ikhwanuddin 2015). Commercial hatchery production of crustacean larvae relies on the optimisation of three interrelated factors: rearing conditions, disease and nutrition (Sorgeloos & Léger 1992; Nghia et al. 2007a). The sub-optimal condition of any one of these factors significantly affects the health and growth of larvae, and if left unattended, results in mass mortality of larvae. Works on various aspects of mud crab larviculture and larval rearing technology were reported throughout the years. However, the production of mud crab larvae remained unsatisfactory and most hatcheries encounter inconsistent survival rates of *Scylla* zoea to crablet stage, primarily due to bacterial and fungal infections (Bian & Egusa 1980; Nakamura et al. 1995; Roza & Hatai 1999; Lavilla-Pitogo & de la Peña 2004; Quinitio & Parado-Estepa 2008; Dan & Hamasaki 2015), and molt death syndrome during the transition from zoea 5 (Z5) to megalopa stage (Williams et al. 1999; Hamasaki et al. 2002; Holme et al. 2007; Quinitio et al. 2015; Pates et al. 2017). Another main obstacle in *Scylla* larviculture is the lack of suitable larvae diets (Quinitio et al. 2001; Baylon et al. 2004; Ruscoe et al. 2004; Holme et al. 2006; Baylon 2009; Holme et al. 2009b; Quinitio et al. 2015). Most hatcheries currently rely heavily on live foods (e.g. *Artemia* and rotifers) that have inconsistent nutritional values (Tucker 1992; Quinitio et al. 1999, 2001; Quinitio & Parado-Estepa 2008; Baylon 2010) and could also potentially introduce harmful pathogens into the culture (Bentzon-Tilia et al. 2016). This review presents and analyses the current knowledge, research trends and efforts of hatchery practices used in mud crab larviculture, with a general emphasis on the larvae of all *Scylla* species, if available. The advantages and differences of each aspect were discussed, and recommendations for the optimal hatchery production of mud crab larvae were suggested. The gaps and bottlenecks that need to be overcome in the future were also identified to drive the *Scylla* larviculture forward.

2. Embryonic and larval development

The ten-stage embryonic development of three *Scylla* species, i.e. *S. serrata*, *S. tranquebarica* and *S. olivacea* has been described in detail by Ates et al. (2012). In general, precleavage and cleavage occur right after egg extrusion, and the embryo enters multicell stage within 1 day. It will then enter the intermediate multicell-gastrula stage where the formation of one or two yolk-free spaces occur. In the following gastrula stage, the yolk-free space increases in size and forms a U-shaped band (germinal disc). Appendage buds are apparent as translucent globular structures in yolk-free space during this stage. A significant decrease in yolk volume (15–20% reduction from 95% in intermediate multicell-gastrula stage) and opacity is expected in the subsequent naupliar stage. In the eye formation stage, a pair of red eyes as short thin strip can be observed. Then, the embryo undergoes differentiation of the thorax and abdominal regions. Heartbeat is detectable at a rate of < 200 beats per min once it reaches stage 9. The differentiation of the telson at the abdomen and the appearance of chromatophores on the thorax also occur during this stage. During the final prehatch stage, the heartbeat rate is > 200 beats per min and the overall zoeal body are more defined. The ratio of embryo:yolk is about 4:1 of the total egg volume. The colour of the egg mass changes from light yellow to dark orange, then becomes light greyish orange and dark grey before turning to black prior to hatching. With a mean rearing temperature of 28–29 °C, the incubation period of *S. serrata* (10.3 ± 0.3 days) was significantly longer compared to that of *S. tranquebarica* (8.7 ± 0.6 days) and *S. olivacea* (8.6 ± 0.2 days) (Ates et al. 2012). When examined in vitro, the duration of embryonic stages of *S. paramamosain* increases with the decrease in water temperature, with eggs incubated at 30 °C hatched within 9 days whereas those incubated at 20 °C took almost a month to hatch (Zeng 2007). Similar results were also reported when eggs of *S. serrata* were maintained in vivo at a range of incubation temperature (20 to 30 °C) (Hamasaki 2003). It is therefore recommended that the incubation temperature of ovigerous females is maintained at 29–30 °C to promote embryonic development and hasten larvae hatching.

The detailed description of larval stages has been reported for the two *Scylla* species, *S. serrata* (Ong 1964) and *S. olivacea* (Jantrarotai et al. 2006). Identification of each larval stage was based on the differences of their appendages, i.e. mandible, maxillule, maxilla including antennule, antenna, maxilliped and telson (Ong 1964; Jantrarotai et al. 2006). In general, a mud crab larva goes through five distinct stages: Zoea 1 (Z1) to Zoea 5 (Z5) (Table 1), each lasts approximately 3–5 days, and megalopa stage which lasts for 7–10 days prior to molting to first crab stage (C1) (Ong 1964) (Table 2). Each zoea stage can be distinguished from each other based on the differences in the number of setation of their maxilla (comparison of *S. serrata* and *S. olivacea* larvae in Jantrarotai et al. 2006). Body length during zoeal stage increases by approximately 30% between each molt (Yi et al. 2009). The larval stages of mud crabs are pelagic and dispersive. It was postulated by Webley and Connolly (2007) that they start to return to the nearshore coastal shelf zone once they reach megalopa stage. The pelagic megalopae then metamorphose into benthic crablets and with the assistance of shore currents and changing tides, these crablets return to intertidal zones and grow into adulthood.

In addition to the five zoeal stages, a sixth zoeal stage (Z6) was observed in *S. paramamosain* when feeding conditions are unfavourable, i.e. unsuitable live food (fed solely on rotifers at later larval stages), insufficient feeding and prolonged starvation (Zeng et al. 2004). The main differences between larvae of Z5 and Z6 were the increase in body length and number of setae at all body parts (Zeng et al. 2004). A similar additional zoeal stage was also reported in the larvae of other brachyurans such as the red frog crab *Ranina ranina* (Linnaeus, 1758) (Minagawa & Murano 1993), grapsid crab *Chasmagnathus granulata* Dana, 1851 (Pestana & Ostrensky 1995) and mud crab *Rhithropanopeus*

Table 2
The duration to molting (days) of each zoea stage of *Scylla*.

Larval developmental stage	Duration to molting						
	S. tranquebarica (Days)	*S. tranquebarica* (Days ± s.d.)	*S. olivacea* (Days)	*S. olivacea* (Days)	*S. serrata* (Days)	*S. serrata* (Days)	*S. serrata* (Days)
Z1 to Z2	4	3.6 ± 0.9	–	–	4–5	3–5	2
Z2 to Z3	3	3.4 ± 0.5	–	–	3–4	3–4	2
Z3 to Z4	3	3.2 ± 0.4	–	–	3	3–4	3
Z4 to Z5	3	2.4 ± 0.5	–	–	3	3–4	3
Z5 to M	3	7.0 ± 0.7	–	–	4–6	3–5	3
M to CI	6	3.4 ± 0.5	–	–	8–10	–	7
TOTAL	22	27–28	18–19 (Z1-Z5)	20–29 (Z1-Z5)	25–31	18–20	20
Reference	Thirunavukkarasu et al. 2014	Zohri 2011	Jantrarotai et al. 2006	Jantrarotai et al. 2004	Motoh et al. 1977	Heasman & Fielder 1983.	Yi et al. 2009

Note: Z1 = zoea stage 1; Z2 = zoea stage 2; Z3 = zoea stage 3; Z4 = zoea stage 4; Z5 = zoea stage 5; M = megalopa; CI = crab instar; s.d. = standard deviation; "-" = no data.

harrisii (Gould, 1841) (McConaugha 1982) when reared in suboptimal dietary conditions. It was postulated that the variability in developmental pathways is a coping mechanism of the larvae by prioritising survival over growth when faced with external stress (Pestana & Ostrensky 1995; Giménez & Anger 2003; Zeng et al. 2004). In the nursery, the occurrence of the sixth zoeal stage strongly suggests that the rearing conditions in the hatchery are not optimal.

3. Collection of zoea and rearing conditions

On average, a female can spawn [illegible] to 5 million eggs per batch and about 80% of the eggs will hatch (Quinitio et al. 2001; Davis et al. 2004). Females in captivity were found to be less fecund compared to wild ovigerous females, with their mean zoeae rate of 7767 ± 4169 zoeae/g. weight and 9307 ± 1200 zoeae/g. weight, respectively (Maheswarudu et al. 2007). The number of offspring produced by broodstocks varied greatly even if they were reared in the same pond (Quinitio et al. 2001), indicating that possible internal factors such as age, genetics and health might play an important role in the reproductive performance of females. Significant decrease in essential fatty acids (e.g. histidine, lysine, isoleucine, leucine and phenylalanine) was reported in successively spawned *Scylla* larvae (second and/or third spawning) (Islam & Yahya 2016). In addition, successive third spawning also showed lower fertilization rates, decreased fecundity, lower production of healthy phototactic larvae, and higher proportion of aborted eggs (Islam & Yahya 2016). This highlights the better quality of larvae hatched from first-spawned eggs, which should be a factor to consider when using larvae for culture. To assess the quality of the newly-hatched Z1, formalin stress test (3 h exposure to 40 mg/L of formalin) is recommended (Quinitio et al. 2018). A low mortality rate of 0%–18% indicates that the batch of larvae is healthy and larval rearing is highly recommended. However, a mortality rate of > 38% indicates that the larvae are of poor quality and further rearing may be discontinued.

Newly-hatched zoeae are recommended to be transferred to suitable clean rearing tanks immediately after hatching to reduce chances of bacterial infection in the spawning tank (Quinitio & Parado-Estepa 2008). Owing to the phototactic nature of the newly spawned zoeae, they may be collected by siphoning or direct scooping under a light source at the water surface. The estimation of zoeae may be carried out during this stage prior to allocating them to different rearing tanks. Acclimatization should be carried out by placing the zoeae in a basin and float the basins in the larval rearing tanks for approximately 20–30 min if there is a temperature difference between the spawning tank and the larvae rearing tanks (Nghia et al. 2007a; Shelley & Lovatelli 2011). Various external factors such as temperature, water salinity, larval stocking density, the use of antibiotic or formalin, and tank colour should be optimized to allow for maximum larval survival.

3.1. Temperature and salinity

Temperature and salinity are considered to be the important factors in mud crab larviculture and changes in either of these factors would influence the internal physiological processes of larvae, ultimately affecting their growth performance and survival (Hamasaki 2003; Nurdiani & Zeng 2007; Baylon 2010; Azra & Ikhwanuddin 2016).

Hill (1974) tested 61 combinations of salinity (0–35 ppt) and temperature (5–36.5 °C) on the first zoeal stage of *S. serrata* (50–200 zoeae per treatment), with an exposure time of 24 h. He found that Z1 of *S. serrata* were not tolerant to low salinity levels (almost 100% mortality when salinity of < 14 ppt at all temperatures except 10 °C). Active zoeae with survival rates of > 90% were recorded when subjected to salinity of > 17.5 ppt at 10–25 °C (except for those combinations that fell out of the > 90% survival curve) (Hill 1974). Hamasaki (2003), however, noticed that Z1 were unable to molt to Z2 at 17 °C whereas normal development until Z5 was found at 20–35 °C (Table 3).

Although tolerant to the fluctuations in temperature and salinity, mud crab larvae showed better survival and faster growth at an optimum range of 25–30 °C and 20–35 ppt (Table 3) (Jantrarotai et al. 2002; Hamasaki 2003; Nurdiani & Zeng 2007; Baylon 2010, 2011, 2013). In addition, faster development was observed at higher temperature for the larvae of both *S. serrata* (Hamasaki 2003; Nurdiani & Zeng 2007; Baylon 2011) and *S. olivacea* (Baylon 2010). A shorter developmental time is preferred as this may reduce the exposure time of larvae to other potentially adverse factors such as predation, physical stress, cannibalism of megalopae on zoea and food availability (Morgan 1995; Quinitio et al. 2001; Baylon 2010). Delayed development was observed at salinities beyond the optimum range (i.e. 15, 40 and 45 ppt) and low temperatures (23 °C and below) (Table 3). Baylon (2011) reared *S. serrata* and *S. olivacea* larvae at different salinity and temperature levels, and the larvae of these two species seem to have similar responses. Parado-Estepa and Quinitio (2011) conducted a study to compare salinity requirements of three *Scylla* species and found out that survival rates of *S. olivacea* and *S. serrata* zoeae to megalopa were not affected by salinity (8, 12, 16, 20, 24 and 32 ppt). That of *S. tranquebarica*, however, were significantly lower in higher salinity (24 and 32 ppt). Interestingly, all three species showed lesser growth (in terms of body weight and internal carapace width) when reared in 32 ppt for 75 days continuously. Parado-Estepa and Quinitio (2011) also indicated that *S. serrata* crab instars could tolerate a wider salinity ranges compared to the other two species.

The tolerance of mud crab zoeae to low temperature and wider salinity range increased with growth (Baylon 2010, 2011). Approximately 95% of C1 juveniles survived at low temperature of 20 °C and their salinity tolerance increased to 15–45 ppt and 5–45 ppt at megalopa stage and C1 stage, respectively (Baylon 2010). The enhanced tolerance is probably due to the internal growth of the mud crab. The

Table 3
Cumulative duration (days) and survival rate (%) of larval development from hatching to first crab stage (C1) of *Scylla* spp. reared under different temperature and/or salinity combinations.

Species	Temp. (°C)	Salinity (ppt)	Cumulative days (survival rate, %) to each stage						Reference
			Z2	Z3	Z4	Z5	M	C1	
S. serrata	17	34	- (0^{a})	- (0^{a})	- (0^{a})	- (0^{a})	- (0^{a})	- (0^{a})	Hamasaki 2003
	20	34	7.95 (91.7^{b})	14.15 (91.7^{b})	21.6 (85.0^{b})	28.85 (71.7^{b})	38.45 (50.0^{b})	- (0^{a})	
	23	34	4.45 (95.0^{b})	8.45 (95.0^{b})	12.85 (95.0^{b})	18.35 (93.4^{b})	25.4 (41.7^{b})	41.8 (23.4^{b})	
	26	34	3.55 (98.4^{b})	6.4 (95.0^{b})	9.45 (91.7^{b})	12.85 (88.4^{b})	17.75 (81.7^{c})	35.35 (40.0^{b})	
	29	34	3.0 (98.4^{b})	5.0 (96.7^{b})	7.05 (95.0^{b})	10.05 (88.4^{b})	13.0 (83.3^{c})	56.2 (68.4^{c})	
	32	34	2.4 (95.0^{b})	4.4 (91.7^{b})	6.7 (85.0^{b})	8.8 (76.7^{b})	11.65 (61.7^{bc})	22.0 (36.7^{b})	
	35	34	2.7 (96.7^{b})	4.8 (88.3^{b})	7.35 (75.0^{b})	10.35 (66.7^{b})	18.0 (1.8^{a})	- (0^{a})	
S. serrata	25	15	5.7	12.6	17.3	–	- (0^{f})	–	Nurdiani & Zeng 2007
	25	20	4.6	7.8	12.3	16.8	22.6^{a} (37.3^{abcd})	31.9	
	25	25	4.5	7.9	11.5	15.6	20.7^{abc} (49.3^{ab})	33.0	
	25	30	4.9	7.8	11.8	15.9	20.6^{abcd} (52.0^{ab})	36.0	
	25	35	5.1	8.5	12.5	16.8	21.4^{ab} (54.7^{a})	35.7	
	28	15	3.3	6.7	10.6	14.2	23.0 (2.7^{ef})	–	
	28	20	3.4	5.8	8.9	12.0	15.8^{e} (50.7^{ab})	23.0	
	28	25	3.2	5.5	8.3	11.2	15.3^{e} (42.7^{abc})	22.7	
	28	30	3.2	5.9	8.9	11.7	15.5^{e} (30.1^{abcd})	24.0	
	28	35	3.3	6.5	9.3	12.1	16.2^{cde} (28.2^{abcde})	25.3	
	31	15	3.8	6.9	9.4	–	- (0^{f})	–	
	31	20	3.3	6.3	9.3	12.5	16.9^{bcd} (33.3^{abcd})	22.8	
	31	25	3.8	6.6	9.6	11.8	16.0^{e} (37.3^{abcd})	23.2	
	31	30	4.0	7.2	9.7	12.5	16.7^{cde} (28.0^{bcde})	24.2	
	31	35	5.0	7.5	10.0	13.1	16.9^{bcde} (20.0^{cde})	26.2	
	34	15	3.0	–	–	–	- (0^{f})	–	
	34	20	3.1	4.9	–	–	- (0^{f})	–	
	34	25	2.8	4.8	7.8	10.9	13.5^{e} (13.3^{def})	20.0	
	34	30	3.1	5.4	8.5	11.6	16.1^{de} (13.7^{def})	–	
	34	35	3.2	5.8	9.1	12.1	18.5^{e} (2.8^{ef})	24.5	
S. serrata	20	0	–	–	–	–	–	–	Baylon 2010
	20	5	–	–	–	–	–	–	
	20	15	–	–	–	–	–	22 (10^{c})	
	20	25	8 (70^{bc})	15 (53^{bc})	22.5 (18^{c})	32 (13^{d})	39 (26^{c})	55.5 (60^{ab})	
	20	35	8 (73^{ab})	14.5 (71^{b})	22 (32^{c})	31.5 (12^{d})	44.5 (49^{b})	62.5 (53^{ab})	
	20	45	–	–	–	–	–	21.5 (13^{cd})	
	26	0	–	–	–	–	–	–	
	26	5	–	–	–	–	–	–	
	26	15	–	–	–	–	–	10 (20^{cd})	
	26	25	3.5 (79^{ab})	7 (94^{a})	10 (88^{ab})	13 (57^{bc})	17.5 (89^{a})	26.5 (70^{ab})	
	26	35	3.5 (87^{a})	7 (96^{a})	10 (90^{ab})	13 (73^{ab})	17.5 (85^{a})	26.5 (57^{ab})	
	26	45	–	5.5 (71^{b})	9.5 (87^{ab})	14 (52^{c})	–	26.5 (17^{cd})	
	32	0	–	–	–	–	–	–	
	32	5	–	–	–	–	–	–	
	32	15	–	–	–	–	–	7 (40^{bc})	
	32	25	2.5 (63^{bc})	5 (92^{a})	7.5 (89^{ab})	10 (82^{a})	13 (83^{a})	19.5 (83^{a})	
	32	35	2.5 (71^{bc})	5 (95^{a})	7.5 (93^{a})	10 (83^{a})	13 (82^{a})	20 (52^{ab})	
	32	45	4 (52^{c})	8 (40^{c})	11.5 (77^{b})	14.5 (49^{c})	17.5 (17^{c})	9 (43^{bc})	
S. olivacea	20	0	–	–	–	–	–	–	Baylon 2011
	20	5	–	–	–	–	–	–	
	20	15	–	–	–	10.5 (53^{c})	24 (26^{e})	35 (5^{d})	
	20	25	9.5 (36^{c})	16.5 (29^{b})	24.5 (35^{bc})	33 (80^{b})	44 (80^{bcd})	57 (58^{bc})	
	20	35	9.5 (35^{c})	16.5 (33^{b})	24.5 (35^{bc})	34 (71^{b})	45 (68^{cd})	57.5 (53^{bc})	
	20	45	–	–	–	–	–	–	
	26	0	–	–	–	–	–	–	
	26	5	–	–	–	–	–	–	
	26	15	–	–	–	5 (69^{b})	10 (84^{abcd})	17.5 (82^{ab})	
	26	25	4 (66^{ab})	8 (79^{a})	12 (50^{a})	16 (91^{a})	21 (97^{ab})	27 (71^{abc})	
	26	35	4 (54^{b})	8 (70^{a})	12 (46^{ab})	16 (71^{b})	21 (56de)	28 (69^{bc})	
	26	45	–	–	–	–	–	9 (5^{d})	
	32	0	–	–	–	–	–	–	
	32	5	–	–	–	–	–	–	
	32	15	5 (27^{c})	8 (27^{b})	12 (29^{c})	16 (76^{b})	19.5 (96^{ab})	25.5 (71^{abc})	
	32	25	4 (69^{a})	6.5 (86^{a})	9.5 (54^{a})	12.5 (92^{a})	16 (99^{a})	5 (93^{a})	
	32	35	4 (66^{ab})	6.5 (75^{a})	9.5 (50^{a})	12.5 (80^{b})	16 (88^{abc})	21.5 (82^{ab})	
	32	45	5 (26^{c})	7.5 (39^{b})	11.5 (31^{c})	15.5 (22^{d})	–	26.5 (47^{c})	
S. tranquebarica	20	0	–	–	–	–	–	–	Baylon 2013
	20	5	–	–	–	–	–	–	
	20	15	–	–	–	–	–	–	
	20	25	9.5 (35)^{c}	21 (10)^{c}	32.5 (9)^{c}	43 (13)^{e}	–	11.5 (20) ed	
	20	35	8.5 (55)^{d}	20 (2)^{d}	31.5 (14.7)^{c}	42 (30)^{d}	–	11.5 (13) d	

(continued on next page)

Table 3 (*continued*)

Species	Temp. (°C)	Salinity (ppt)	Cumulative days (survival rate, %) to each stage						Reference
			Z2	Z3	Z4	Z5	M	C1	
	20	45	13.5 (0)*	–	–	–	–	–	
	26	0	–	–	–	–	–	–	
	26	5	–	–	–	–	–	–	
	26	15	–	–	–	–	–	12 (13) d§	
	26	25	4 (90)^{a}	9 (76)^{a}	13.5 (81)^{a}	18.5 (71)^{b}	26.5 (48)^{a}	37 (67)^{ab}	
	26	35	4 (91)^{a}	9 (79)^{a}	13.5 (71)^{ab}	18.5 (76)^{b}	27 (22)^{b}	37.5 (60)^{b}	
	26	45	6 (20)^{c}	13 (42)^{b}	19 (21)^{c}	26 (45)^{c}	–	–	
	32	0	–	–	–	–	–	–	
	32	5	–	–	–	–	–	–	
	32	15	–	–	–	–	–	10 (27)^{c‡}	
	32	25	2.5 (93)^{a}	6 (70)^{a}	8.5 (62)^{b}	11.5 (87)^{a}	17.5 (51)^{a}	27.5 (78)^{a}	
	32	35	2.5 (91)^{a}	6 (80)^{a}	8.5 (84)^{a}	11.5 (91)^{a}	17.5 (48)^{a}	27.5 (67)^{ab}	
	32	45	4 (82)^{a}	10 (50)^{b}	14.5 (19)^{c}	19.5 (40)^{cd}	–	10.5 (13)^{d‡}	
S. olivacea	–	12	–	–	–	–	–	9.8 (57.1 ^{bB})	Jantrarotai et al. 2002
	–	16	–	–	–	–	–	9.7 (95.2 ^{aA})	
	–	20	–	–	–	–	–	10.3 (95.2 ^{aAB})	
	–	28	– (37.6 ^{bB})	– (18.5 ^{bC})	– (15.8 ^{bC})	– (14.5 ^{bC})	23.6 (13.2 ^{bC})	–	
	–	30	– (51.8 ^{aB})	– (31.8 ^{aC})	– (35.6 ^{aCD})	– (30.1 ^{aD})	24.2 (22.9 ^{aE})	–	
	–	32	– (30.1 ^{bB})	– (14.2 ^{bC})	– (11.0 ^{bC})	– (9.8 ^{bC})	23.8 (8.3 ^{bC})	11.3 (95.2 ^{aA})	
	–	34	– (31.7 ^{bB})	– (13.3 ^{bC})	– (9.6 ^{bD})	– (8.9 ^{bD})	24.0 (7.1 ^{bD})	–	
	–	36	–	–	–	–	–	13.5 (52.4 ^{bB})	
	–	40	–	–	–	–	–	20 (9.5 ^{cB})	

Note: Data of duration and survival rate are expressed as mean; different superscript letters within the same row (uppercase) or column (lowercase) indicate significant difference ($P < .05$) within the same experiment; "–" = no data.

† The same set of larvae were monitored in the entire experiment and survival was taken at every zoeal stage up to crablet 1.

‡ The same set of larvae were monitored in the entire experiment but survival was taken only at crablet 1.

§ From the same batch, new larvae in every stage were used where development & survival was taken up to crablet 1.

* Larvae survived for 13.5 but died without molting to next stage.

thickening and mineralization of the integument as the zoea grow (Freeman 1993) protects them from sudden temperature changes (Baylon 2010) while the formation of functional gills when they reach Megalopa stage (Felder et al. 1986) enables them to withstand extreme salinities.

3.2. Stocking density

Stocking density during the fragile larval rearing stages of *Scylla* has immediate influence on the survival, growth, behaviour, water quality and food intake (Chambel et al. 2015). Setting the stocking density too low (10 and 25 Z1/L) or too high (above 200 Z1/L) was reported to cause adverse effects for *Scylla* larvae in terms of larval survival and metamorphosis (Baylon & Failaman 1999; Nghia et al. 2007a). A low stocking density might result in excess food, thus polluting the rearing medium, promoting bacteria growth and eventually causing mortality. On the contrary, setting the stocking density too high increases food competition among zoeae, introduces stress and impedes their overall development (Nghia et al. 2007a; Chambel et al. 2015). In addition, from an economic point of view, the highest stocking density achievable, without compromising crab's health and normal growth is preferred as this would maximize the usage of space during mass production. Based on previous researches (Tables 4 & 5), stocking density of zoeae at 100–150 Z1/L is recommended for *Scylla* spp.

3.3. Prophylaxis

The larval stages of *Scylla* are highly susceptible to bacterial and fungal infections, and protozoan infestation. If left untreated, often resulted in mass mortality (Armstrong et al. 1976; Quinitio et al. 2001; Quinitio & Parado-Estepa 2008). This is the case for most aquatic cultured species as they are constantly surrounded by an environment that gives equal opportunity for the growth of pathogens (Moriarty 1998). The higher chances of exposure via contact and while drinking or eating, coupled with the low immune system of newly hatched larvae makes them highly vulnerable (Verschuere et al. 2000). The use of antibiotics is still prevalent in most crustacean hatcheries (e.g. mud crabs and shrimps) due to their proven efficacy against *Vibrio* and other infectious microorganisms (Diggles et al. 2000), which improves larval survival (Gardner & Northam 1997; Azam & Narayan 2013). Without prophylaxis, luminescent bacteria (*Vibrio* spp.) were present and detectable in *S. serrata* larvae rearing tanks with an increasing trend from day two onwards and subsequent onset of larval mortality was postulated to be related to the high bacterial load (Quinitio et al. 2001). Due to the small size of the larvae, prophylaxis treatments during larval stages of *Scylla* are often incorporated directly into the rearing water (de Pedro et al. 2007; Pates et al. 2017). Survival rates of larvae treated with antibiotics (oxytetracycline, penicillin G or polymyxin B sulphate) were found to be significantly higher than that of controls (Table 6). The application of antibiotics, however, should be used with caution because bacteria becoming increasingly resistant towards the administered antibiotics (Schmidt et al. 2000) could adversely impact the cultured organisms, the environment and humans (see review by Cabello 2006). In addition, residual antibiotics in aquaculture species due to excessive use are proven to be transmittable to consumers, thus potentially affecting their normal microbe flora and render them susceptible to infection (Angulo et al. 2004). Although the usage of antibiotics (i.e. oxytetracycline and furazolidone) resulted in higher survival and faster growth, morphological deformities were found in both larval (bent dorsal, rostral and furcal spines) and subsequent juvenile stages (fused lateral spines, asymmetrical abdomen, fused frontal spines, depressed abdomen tip and gap between sternites) (Pates et al. 2017). Similar occurrence of deformities was reported in the megalopae of temperate crab *Pseudocarcinus gigas* (Lamarck, 1818) due to the prolonged use of antibiotics (oxytetracycline of ≥25 ppm) since larval stage I (Gardner & Northam 1997).

Apart from antibiotics, other chemicals such as formalin or trifluralin are also commonly used as prophylactic agents in shrimp and

Table 4
Stocking density (Z1/L) and survival rate (%) of *Scylla* spp. Zoea (Z) 1.

Species	Stocking density (Z1/L)	Final survival rate (%)	Reference
S. paramamosain	50	27 (up to Z5)	Djunaidah et al. 2001
	75	39 (up to Z5)	
	100	63 (up to Z5)	Nghia et al. 2007a
	5	4 ± 6 (up to 22 d)	
	100	5 ± 4 (up to 22 d)	
	150	5 ± 1 (up to 22 d)	
	200	5 ± 1 (up to 22 d)	
S. tranquebarica	75	51.8–55 (up to Z2)	Maheswarudu et al. 2007
		50.0–54.3 (up to Z2)	
	100		
S. serrata	30–50	2.7 ± 0.8 (up to three- to five-day old megalopa)	Quinitio et al. 2001

Table 5
The recommended stocking density for zoea (Z) 1.

Species	Stocking density (Z1/L)	Reference
S. paramamosain	100–150	Nghia et al. 2007a
S. paramamosain	100	Djunaidah et al. 2001
Scylla spp.	30–200	Shelley & Lovatelli 2011
S. serrata	50	Baylon & Failaman 1999
S. serrata	80–100	Quinitio & Parado-Estepa 2008

Table 6
The survival percentage (%) of *Scylla* zoeae (Z) treated with prophylactic chemicals.

Species	Test duration	Chemicals used	Survival (%)	Reference
S. serrata	Up to Z4	Control	5 ± 6.2	Azam & Narayan 2013
		Control	7 ± 2.2	
		OTC (10 ppm)	25 ± 2.4	
		OTC (25 ppm)	53 ± 4.1	
S. paramamosain	Up to 22d	Control	9 ± 5.0^{a}	Nghia et al. 2007a
		Formalin (20 μL/L)	11 ± 8.0^{ab}	
		OTC (10 ppm)	21 ± 5.0^{b}	
S. serrata	Up to Z5	Control	0	Brick 1974
		p.B. (10 ppm) + US	60	
		p.G. (40 ppm) + US	50	

Note: OTC = oxytetracycline; p.B. = polymyxin B sulphate; p.G. = penicillin G; US = unfiltered seawater; different superscript letters indicate significant difference ($P < .05$) within the same experiment.

crab cultures (Williams et al. 1986; Gardner & Northam 1997). The latter however, was banned by the European Union due to its toxicity to aquatic organisms and bioaccumulation (European Union 2012). When tested on *Scylla* larvae up to 96 h in each stage (Z1 to Z5), formalin (5 or 10 μg/L) promote better larval survival and higher number of megalopae compared to control (de Pedro et al. 2007). However, prolonged use of formalin as prophylactic treatment however, have been reported to cause deformities and significantly increased molting mortality in other crab species (Gardner & Northam 1997). Thus, periodical exposure to formalin bath (5 or 10 μg/L) is recommended if prophylaxis treatment is needed (Kaji et al. 1991; Hamasaki & Hatai 1993).

Another promising approach in the prophylaxis in *Scylla* larval rearing is the application of probiotics. These are live microorganisms that are advantageous to the host animal (Fuller 1989; Irianto & Austin 2002; Kesarcodi-Watson et al. 2008; Dan & Hamasaki 2015) and added to inhibit the growth of pathogenic bacteria in aquaculture environments (Verschuere et al. 2000; Dan & Hamasaki 2015). Dan and Hamasaki (2015) screened and isolated a strain of probiotic bacteria that work against necrosis-causing bacteria, thus overcome larval necrosis symptoms and mass mortality in *S. serrata*. The inhibiting effect of the probiotic bacteria against pathogenic bacteria was evident up to Z5. Another commercially available probiotics (PondPlus®^{A}, Novozymes®^{A})[1] containing multispecies *Bacillus* was tried on *S. paramamosain* larvae with great success (at concentrations of 0.5 and 1.0 g/50 L) in terms of higher larval survival, faster larval growth and development, and the absence of pathogenic green *Vibrio* at the end of larval culture (Talib et al. 2017). However, these study on probiotics were conducted in small containers using an average of 12,808 (Dan & Hamasaki 2015) and 5000 (Talib et al. 2017) individuals per tank and in controlled conditions. The beneficial effects of probiotics might not be as apparent in commercial-scale seed production as various conditions are complex and hard to control. For example, during seed production in a large scale, culture of larvae and live foods (e.g. rotifer, *Artemia* and phytoplankton) are done in the same rearing vessel and added subsequently with various regiments as the larvae develop (Wang et al. 2005; Baylon 2009). The live foods act as potential pathogen carriers and studies have shown that the structural composition of the microflora in rearing medium is constantly changing (Verdonck et al. 1997). One possible solution to this problem is to administer probiotic via oral admission, i.e. enrichment of live food. A study on the effect of *Bacillus* probiotic (*Bacillus licheniformis* and *B. subtilis*, ratio = 1:1) on the growth and survival of Pacific white shrimp, *Litopenaeus vannamei* (Boone, 1931) revealed that larvae fed with probiotic-enriched live food (*Artemia* nauplii and rotifers) were significantly larger, heavier and had lower mortality rate (Jamali et al. 2015). Garrido-Pereira et al. (2014) also demonstrated that by administering probiotic directly into the rearing water and via live feed, the larvae of marine finfish, *Rachycentron canadum* (Linnaeus, 1766) exhibited higher tolerance towards salinity stress.

3.4. Tank colour

The background colour of the rearing tanks plays an important role in maintaining the general wellbeing of larvae and facilitate predation in vision-oriented larvae by influencing the amount and spectrum of light that penetrates the rearing water column (Maciel & Valenti 2014). Although it might be beneficial for hatcheries to use tanks of lighter background to contrast the dark coloured *Scylla* zoeae for ease in larval monitoring, Rabbani and Zeng (2005) reported that *S. serrata* larvae preferred rearing tanks with dark coloured background, especially black, as evidenced by their significantly higher survival rate, shorter developmental duration and more synchronized molting. In contrast, larvae reared in white tanks had the lowest survival rate and longer developmental time. Similar results were observed in other crustacean species, including the blue swimming crab, *Portunus pelagicus* (Linnaeus, 1758) (Azra et al. 2012) and Amazon River prawn, *Macrobrachium amazonicum* (Heller, 1862) (Maciel & Valenti 2014), with a higher survival and maximum productivity in tanks with black

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[1] The mention of brands does not indicate endorsement of the products.

background in both studies.

Although crustaceans are non-obligated visual feeders – able to feed in total darkness based on random encounter or chemosensors (Minagawa & Murano 1993; Gardner & Maguire 1998), they do rely on their visual cues when available (Gardner & Maguire 1998). Apart from increasing prey visibility, light is also positively associated with cannibalism – minimal cannibalism was found in dark coloured tanks (Rabbani & Zeng 2005). It is also important to note that due to the phototactic behaviour of most larvae, including that of *Scylla* spp., larvae in white tanks tend to aggregate and remain at the tank's bottom whereas those in black tanks were uniformly distributed throughout the water column due to the greater light reflection in lighter-coloured tanks at the bottom of the tank (Rabbani & Zeng 2005; Maciel & Valenti 2014). The reflection and immediate light source from above might cause disorientation and eventually negatively affect their feeding (Rabbani & Zeng 2005). Additionally, the bottom-aggregation behaviour in light-coloured tanks will also increase the exposure of larvae to potential infectious pathogens as most dead natural feed, uneaten food and dead larvae accumulate at the bottom.

3.5. *Rearing system*

Owing to its simplicity, most mud crab hatcheries reared larvae in either clear water or microalgae-enriched systems with manual water exchange (Quinitio & Parado-Estepa 2008; Shelley & Lovatelli 2011; Thirunavukkarasu et al. 2014). Nghia et al. (2007a) reported that clear recirculating systems with biofilters and a water exchange rate of 100% tank volume per 3–4 h were more conducive for *Scylla* larval rearing – higher survival rates at 15 and 18 days after hatch and lower ammonia and nitrite levels, compared to clear water system with manual water exchange (30–50% daily). The advantages of recirculating systems were also reported in the larviculture of other aquaculture animals (Blancheton 2000; Garrido-Pereira et al. 2014; Holan et al. 2014; Joaquim et al. 2014; Ballester et al. 2017). Further, less labour and seawater are needed owing to the automated and water-recycling features of the recirculating systems. Based on the positive results obtained by Nghia et al. (2007a) using rearing systems of 30 and 100 L, large-scale application of recirculating system in *Scylla* larviculture is promising. However, Nghia et al. (2007a) recommended that the rearing of early stages (Z1 and Z2) larvae are more suitable in microalgae-enriched non-recirculating system. Recirculating system could be applied at a later stage once the larvae are stronger (Z3 and above). This is to mitigate the stress imposed by the water current of the recirculating system onto the fragile early crab larvae and also to prevent them from getting caught on the mesh net of the recirculating system, damaging the long spines on their carapaces.

The importance of incorporating microalgae in the rearing system was also highlighted in the study of Nghia et al. (2007a), with larvae reared in clear recirculating systems manifested significantly lower survival rate compared to those reared in algae-enriched recirculating and manual water exchange systems (*Chlorella* for Z1-Z3 stages, *Chaetoceros* for Z4 stage onwards). The lower amount of ammonia and nitrite in recirculating systems (both with and without microalgae) than in manual water exchange systems highlights the positive effect of biofilter in maintaining water quality. Larvae reared in clear recirculating systems also showed significantly lower larval stage index compared to those reared in recirculating systems with microalgae (Nghia et al. 2007a). The benefits of introducing microalgae into rearing systems are numerous. Aside from serving as food for live feed (zooplankton such as *Artemia* and rotifer), microalgae are also known to aid in the stabilization and quality improvement of the introduced rearing medium, including higher dissolved oxygen and pH stabilization (Tendencia et al. 2015), improve gut filling at the initiation of exogenous feeding (van der Meeren et al. 2007), provide probiotic effects (Bergh et al. 1994; Haché et al. 2017), regulate bacterial growth (Krishnani et al. 2010; Cadiz et al. 2016) and enhance growth (Nghia et al. 2007a) and immunity of cultured organisms (Yaakob et al. 2014). Therefore, the conventional clear-water rearing method is now being substituted by the incorporation of microalgae into rearing medium, especially in the aquaculture sector (van der Meeren et al. 2007; Neori 2011; Tendencia et al. 2015). With the aforementioned advantages of microalgae, it is therefore recommended to incorporate them into *Scylla* larval rearing.

4. Nutrition

4.1. *Nutritional requirement*

Nutritional requirements may be viewed as the needed nutrient for optimal growth and/or survival, or the minimum nutrient required to maintain an organism alive or to fulfil a physiological role (Hamre et al. 2013). The nutritional requirement of larvae must be high and differ qualitatively and quantitatively from that of juveniles and adults as they undergo rapid growth, and dramatic morphological and physiological changes during these early life stages (Hamre et al. 2013). Limited research has been conducted to investigate the nutritional requirements of *Scylla* larvae and with the availability of a previous review regarding this topic by Holme et al. (2009b), this section of the current review focuses primarily on studies conducted on *Scylla* larvae to facilitate easier knowledge-transfer and to bring forward the latest discoveries on this topic.

Proteins are made up of amino acids and are an essential ingredient of growth for all animals (Holme et al. 2009b). Although research on the protein requirements of *Scylla* larvae has not been conducted, studies done on juveniles were promising. Those fed with diets containing 50% lipid-free casein (Sheen & Wu 1999; Sheen 2000), 32–40% protein (Catacutan 2002) or 45% crude protein (Unnikrishnan & Paulraj 2010) showed improved growth and survival. The high protein requirement reported in juveniles highlights the importance of protein for the growth and development of *Scylla* species, and it may be postulated that *Scylla* larvae, being carnivorous and showing high protease activity since Z1 stage (Hong et al. 1995), may have a protein requirement similar or higher than in juvenile stages. Research in this area is warranted to determine the protein requirement and suitable protein source of dietary protein for different stages of mud crab larvae.

Essential amino acids are an integral part of the dietary requirement of crustaceans (Holme et al. 2009b). The essential amino acids and non-essential amino acids of day-old *Scylla* zoea was described by Peñaflorida (2004) by comparing with the essential amino acid profiles of rotifers, *Artemia* and *Acartia*. Enrichment of rotifers with histidine, *Artemia* with leucine and tryptophan, and *Acartia* with arginine, leucine and valine are recommended to enhance larvae production.

The importance of essential and non-essential fatty acids such as highly unsaturated fatty acids (HUFA), docosahexaenoic acid (DHA), eicosapentaenoic acid (EPA) and arachidonic acid (ARA) in live feed are shown to influence the survival, development and metamorphosis of mud crab larvae (Suprayudi et al. 2004a; Nghia et al. 2007b). By enriching rotifers and *Artemia* with varying ratios and percentages of DHA/EPA and HUFA respectively, Nghia et al. (2007b) found that no HUFA content or high (50%) HUFA content but low DHA/EPA ratio (0.6) led to delayed development and failure to metamorphose. In contrast, *Scylla* larvae performed best in HUFA content of 30% and DHA/EPA ratio of 4. Dietary ARA improved only the first metamorphosis rate (from Z1 to Z2) but not the survival or development at zoeal stages of *Scylla* (Nghia et al. 2007b).

Crustaceans need cholesterol as a precursor for various important physiological compounds including the production of sex hormones and molting hormones (Sheen 2000). Sterols are considered as essential nutrients for crustaceans as they lack the ability to convert acetate to sterol and have to secure it via dietary route (Kanazawa & Teshima 1971; Sheen 2000). When fed with *Artemia* enriched with cholesterol at levels of 0 ul/l (free sterols = 0.61%), 5 ul/l (free sterols = 0.67%), and 10 ul/l (free sterols = 0.75%), *S. serrata* larvae showed better survival, intermolt duration and body size at C1 stage compared to those fed with 20 ul/l (free sterols = 1.37% of cholesterol (Suprayudi et al. 2012a). Thus, a minimum of 0.61% cholesterol is needed for the normal growth and development of *Scylla* larvae and if *Artemia* is used as live feed, no additional enrichment is necessary as the cholesterol in the *Artemia* nauplii alone is already sufficient (Suprayudi et al. 2012a). It is worthy to note that too much dietary cholesterol during larval (≥1.37%) (Suprayudi et al. 2012a) and juvenile stages (> 1.12%) (Sheen 2000) may exert adverse effects on mud crab growth such as low survival, low weight gain, prolonged intermolt period and smaller carapace width. The exact mechanism resulting in adverse effects due to high level of dietary cholesterol, however, is still unknown but is postulated to be a nutrient-response characteristic which is toxicity-related (Mercer 1982).

Phospholipids play an important role in the structural composition of cell walls and are involved in the absorption of sterol by acting as surfactants for the emulsification of ingested lipid (Teshima 1997; Holme et al. 2009b). They are also the key component during molting by transporting cholesterol to different parts of the target tissue (Conklin et al. 1983). Although crustaceans are being postulated to be able to synthesize phospholipids de novo (Sheih 1969), the synthesis rate was slow and additional dietary phospholipid are needed for maintaining normal growth and development, especially in the early larval stages (Teshima et al. 1986). Among the proven positive effects of dietary phospholipids on crustacean culture include enhanced growth and survival, improved molting rates and reduced molt death syndrome (Conklin et al. 1980; Paibulkichakul et al. 1998; Gong et al. 2001). The most commonly used phospholipid in the aquaculture industry is in the form of soybean lecithin (Holme et al. 2009a). *S. serrata* larvae exhibited improved survival rate, intermolt period and larger carapace width (measured at the first crab stage) when fed with *Artemia* enriched with DHA (25 ul) and soybean lecithin (0–40 ul), and *Artemia* enriched with cuttlefish phospholipids (40 ul) (Suprayudi et al. 2012b). Higher molting synchronicity index was also observed in treatments fed with *Artemia* enriched with DHA and soybean lecithin at 20 ul and 40 ul respectively, and *Artemia* enriched with cuttlefish phospholipids (Suprayudi et al. 2b). Thus, a minimal amount of phospholipid, in combination with essential fatty acids are required for the synchronized growth and development of mud crab larvae. As proven by Suprayudi et al. (2012b), no additional DHA is required if cuttlefish phospholipids were used as they are high in saturated fatty acids and essential fatty acids such as DHA, EPA and ARA (Reis et al. 2016).

Although carbohydrates are thought to be non-essential in the diet of crustaceans and that aquatic species are comparably less efficient in utilizing dietary carbohydrates (Shiau & Peng 1992). However, carbohydrates and lipids are still being incorporated into the feed of most aquaculture animals including crustaceans since these are utilised first to produce energy, then proteins (Stuck et al. 1996; Johnston 2003). From a feed developer's perspective, carbohydrate is preferred as it is the most economical dietary energy source (cost/kcal) (Shiau & Peng 1992). Data on the suitable dietary carbohydrate levels of *Scylla* larvae, however, is still unavailable and the limited studies on other crustacean larvae (*Penaeus* Fabricius, 1798 and *Homarus* Weber, 1795) showed wide variation in their required dietary carbohydrate levels (Kurmaly et al. 1989; Immanuel et al. 2003; Moe et al. 2; Pedroza-Islas et al. 2004; Fiore & Tlusty 2005). It was observed that *S. serrata* juveniles were able to digest and fully utilize (91.6–95.8%) a wide range of carbohydrates, especially from plant feedstuffs such as copra meal, wheat flour, rice bran, corn meal and soybean meal (Catacutan et al. 2003). Digestive enzyme profiles of *S. serrata* (Rutledge 1999) and the spiny lobster *Jasus edwardsii* (Hutton, 1875) (Johnston 2003) suggest that carbohydrates are essential in the diet of small juveniles as indicated by the higher cellulase (in *S. serrata*), amylase and laminarinase (in *J. edwardsii*) specific activity in smaller individuals. This shows that the requirement for dietary carbohydrate varies between development stages and future research on the carbohydrate nutritional requirement of different zoea stages of *Scylla* larvae is needed for a better understanding of their nutritional needs and optimization of their diets.

4.2. Ontogeny of feeding apparatus and feeding behaviour

Although knowing the nutritional requirement of *Scylla* larvae would contribute to the optimization of diet and feeding regimes, it would be useless if the given diets were not ingested by the larvae due to physical and/or behavioural constraints. Understanding of the feeding behaviour, food acquisition process and morphology of the feeding apparatus of *Scylla* larvae are essential for the formulation of feed that would promote ingestion, digestion, and absorption.

Feeding behaviour of *Scylla* Z1 suggests that telson is used to push water, along with any prey or food particles from underneath its abdomen towards its mouth (Maheswarudu et al. 2007). Non-food particles that are stuck onto the maxillules' setae are quickly removed with the aid of two long denticulate setae. Abdomen and telson occasionally exert gentle pressure on maxillules and maxillae, resulting in the temporary bending away (about 45 degrees) of furcal spines and setae and assist in the passing on of food into the foregut (Maheswarudu et al. 2007). Additional flaps by the abdomen direct food towards the mouth. It takes approximately three minutes for food particles (50–55 µm) to be digested as indicated by the gut movement of *S. serrata* Z1. This feeding behaviour of *Scylla* larvae is consistent irrespective of the types of diet (Maheswarudu et al. 2007).

Generally, the feeding apparatus of brachyuran larvae involves the mouthparts and the gastric mill. The mouthparts are further divided into six paired appendages, in which three anterior pairs (mandibles, maxillules and maxillae) are cephalic appendages and another three posterior pairs (first, second and third maxillipeds) are thoracic appendages (Ng 1998; Lumasag et al. 2007). Located posteriorly at the anterior chamber of the foregut, the gastric mill serves as a chewing and grinding apparatus. The most notable difference in the morphology of mouthparts as larvae develop is the presence of teeth and denticles in the mandibles only during zoeal stages but not in megalopa. In addition, the simple and continuous foregut of early zoeae (Z1-Z3) develop and form two distinctive compartments when they reach Z4 or Z5 stages (Lumasag et al. 2007). As the width of mouth opening increases from 61 µm in Z1 to 95 µm, 129 µm, 179 µm and 209 µm in Z2, Z3, Z4 and Z5, respectively (Lumasag et al. 2007), appropriate screening of suitable feed particle size could be conducted, ensuring that only food that could be ingested by larvae are given at a specific stage.

The gut evacuation time of *S. serrata* larvae at different developmental stages was determined by Serrano (2012b) to understand their feeding and digestive strategies. In general, the gut evacuation time was shorter in early zoeal stages (approximately 80 min) than in megalopa and first crab instar stage (120–135 min). A faster gut evacuation time was also recorded when Z3 larvae to first crab instar were fed with live feed compared to those fed with artificial feed (Serrano 2012b). The slower gut evacuation time in larvae fed with artificial diet is postulated to be a result of insufficient enzyme (endopeptidase and exopeptidase) activities (Serrano & Traifalgar 2012) and carnivorous crustacean larvae are known to be unable to regulate their own enzyme levels in response to artificial diets (Jones et al. 1997). In addition, the change in feeding behaviour of *Scylla* larvae is obvious – from feeding on suspended particles in the water column during zoeal stages to looking for food near the bottom during megalopa stage, which is closely related to their metamorphosis from planktonic larvae to clawed megalopae with a more benthic nature (Genodepa 2003; Holme et al. 2006).

4.3. Prey/particle size

It is important to consider the size of prey or food particles presented to any hatchery-reared organisms to maximize ingestion (Knauer & Southgate 1999). *Scylla* larvae are postulated to employ raptorial feeding method as in most caridean and homarid larvae (Jones et al.

1997; Genodepa et al. 2004a). This indicates that they are able to consume food particles with larger size ranges (Genodepa et al. 2004a). The full digestion of feed, however, is still related to the mandibular size of larvae. For example, with the mandibular size of about 61 μm (Lumasag et al. 2007), approximately 80% of the *S. serrata* Z1 successfully digested veliger larvae (*Pinctada fucata* (Gould, 1850)) of size 50–55 μm (positive digestion indicated by the passing through the gut) whereas none could consume pelagic copepods (*Pseudodiaptomus* spp. Herrick, 1884 and *Labidocera* spp. Lubbock, 1853) due to their large size (500–1000 μm) (Maheswarudu et al. 2007). There was preference for bigger food particle size with increasing developmental stage of *Scylla* larvae. Genodepa et al. (2004a) demonstrated that *S. serrata* Z1 ingested more microbound diets of < 150 μm compared to those of 150–250 μm, whereas Z3 were able to ingest microbound diets up to 400 μm (highest ingestion in those of size 150–250 μm) although no statistical significant difference was observed in different feed particle sizes. The Z5 showed significant preference to microbound diets with feed particle size of 250–600 μm compared to those of 150–250 μm while megalopae significantly ingested more feed with particle size of 400–800 μm (Genodepa et al. 2004a). This increase in preferred feed particle size is in positive correlation with the increase in width and development of the mandibles (Lumasag et al. 2007), enabling larvae to feed on larger prey more efficiently. Thus, the suitable particle size range for Z1, Z3, Z5 and megalopae recommended are < 150 μm, 150–250 μm, 250–600 μm and 400–600 μm respectively (Genodepa et al. 2004a). It is also worth mentioning that *Scylla* larvae were observed to only partially ingest their prey or food particle (Baylon et al. 2004).

4.4. *Digestive enzymes*

The larvae of *Scylla* spp. do not possess the anterior midgut diverticulae unlike some crustaceans (Serrano 2012a). Unable to rely on the anterior midgut diverticulae to produce digestive enzymes as in penaeid larvae and their hepatopancreas are still not fully developed until megalopa stage (Serrano 2012b), *Scylla* larvae have to resort to other methods such as increasing the gut passage time in order to digest and absorb more nutrients and energy from their diet (Jones et al. 1993; Serrano 2012b). A recent study by Serrano (2013) confirmed that amylase and leucine aminopeptidase (LAP) levels were low at mud crab Z1-Z3 while trypsin level was minimal at Z1-Z2 and megalopa stages. In the treatments with live feed (rotifers and *Artemia*), however, considerable amount of exogenous LAP (64–80%) and trypsin activities (37–43% at Z2 t[illegible]1) were recorded. These findings highlight the contribution and importance of live feed as an integral source of exogenous enzymes for the development of mud crab larvae.

4.5. *Diets used*

4.5.1. *Live feed*

The current larviculture of mud crab relies heavily on live feed due to beneficial factors including the ease of mass culture, slow swimming characteristics, free dispersal in water and availability in various sizes (Hill 1979; Verischele 1989).

4.5.1.1. Rotifers and Artemia. Their small size (approximately 0.5 μg and 45–200 μm) (Harvey & Epifanio 1997; Davis et al. 2005a; Nghia et al. 2007a) and slow swimming movement make the rotifers, ***Brachionus plicatilis*** (Müller, 1786) ideal first feed for mud crab larvae (Baylon et al. 2004; Baylon 2009). *Artemia* nauplii, with their slightly larger size (2.7 μg and 428–5[illegible]m) (Davis et al. 2005a) compared to rotifers, are commonly used in the larviculture of mud crab as well (Baylon et al. 2004; Ruscoe et al. 2004; Davis et al. 20[illegible]). Although unsuitable as food to early zoeal stages, they are proven to increase the growth and survival of larvae when fed at later larval stages (Baylon et al. 2004; Ruscoe et al. 2004).

Table 7

Common enrichment methods of rotifers and *Artemia* used in aquaculture.

Live feed candidate	Enrichment method	Fed larvae	Reference
Rotifers			
	Tetraselmis spp.	*S. serrata*	Davis et al.
- *Brachionus plicatilis*	*Nannochloropsis* spp.	*S. serrata*	2005a, 2005b
		S. tranquebarica	Suprayudi et al 2002
		S. serrata	Baylon 2009
	Dry Selco®		
- *Colurella adriatica*			Ruscoe et al. 2004
Artemia franciscana nauplii			
	Super Selco®	*S. serrata*	Davis et al. 2005b
- EG® type	Frippak™ CD2 Ultra	*S. serrata*	
- AF grade	larval shrimp food		Ruscoe et al. 2004
Artemia nauplii	Oleic acid, EPA28G, DHA70G	*S. serrata*	Suprayudi et al. 2004b

Note: The mention of brands does not indicate endorsement of the products.

Enrichment of rotifers and *Artemia* are recommended and often carried out to ensure that they provide sufficient nutritional values to promote growth and maintain the general health of the larvae (Quinitio et al. 1999; Davis et al. 2005a, 2005b). Various methods were used to enrich either rotifers or *Artemia* and have been tested to be suitable for mud crab larviculture (Table 7). Unenriched rotifers have minimal nutritional value where the survival of the larvae was not significantly better than that of starved larvae in a feeding experiment conducted on the giant freshwater prawn, ***Macrobrachium rosenbergii*** (de Man, 1879) (Lovett & Felder 1988).

Based on the current findings, a combination of rotifers at 10–40 individuals/ml (Quinitio et al. 2001; Baylon et al. 2004; Ruscoe et al. 2004; Suprayudi et al. 2004b; Baylon 2009) and newly-hatched *Artemia* nauplii at 0.5 individuals/ml (Ruscoe et al. 2004) are to be given once a day at Z1-Z3 and only *Artemia* nauplii at 1.5 individuals/ml or increasing density of 0.5 to 2 individuals/ml (Suprayudi et al. 2002)) when mud crab larvae reach Z3 or Z4 onwards (Suprayudi et al. 2002; Davis et al. 2005a, 2005b; Quinitio & Parado-Estepa 2008; Baylon 2009). The availability of rotifers during the early larval stages, especially within the first hour of hatching to Z1 significantly improved the survival of larvae (Mann et al. 1999). The inclusion of *Artemia* nauplii during the early larval stages are proven to improve metamorphosis rate and increase larvae size ([illegible] length, carapace length and setae bearing pleopods) (Suprayudi et al. 2002; Davis et al. 2005b). It is important to note that the added *Artemia* nauplii density should be kept below 5 ind/mL to reduce unnecessary competition with the crab larvae for space and dissolved oxygen, and to minimize potential water fouling from the contributed metabolites, which in turn could cause stress and even mortality to the crab larvae (Baylon et al. 2004). Due to their lower nutritional values, rotifers may be removed from the mud crab larvae's diet after Z3 as no significant adverse effect on growth and survival was reported (Ruscoe et al. 2004; Baylon 2009). Baylon et al. (2004) reported that there is a reduction in rotifer intake and an increasing consumption of *Artemia* as the mud crab larvae grow. After Z3, the presence of rotifers no longer affects the *Artemia* intake. Shift of preference from rotifers to *Artemia* as food for Z3 larvae was also reported in the Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853 (Sui et al. 2008).

4.5.1.2. Copepods. Essentially the natural diet of various marine fish and crustacean larvae (Okazaki et al. 2008; Takahashi & Uchiyama 2008), copepods are starting to gain attention as alternative first live feed for the larviculture of many aquaculture species due to their known benefits of improving the overall survival, growth and development of larvae (Imsland et al. 2006; Liu & Xu 2009; Barroso et al. 2013; Karlsen et al. 2015). They are more superior in terms of nutritional values (higher protein, essential fatty acids, phospholipids and other micronutrients e.g. taurine, astaxanthin and zinc) (Karlsen et al. 2015) and digestibility compared to other commonly used live feeds such as rotifers and *Artemia* (Pederson 1984; Hamre et al. 2013). Coupled with the broad spectrum of sizes in different life stages (i.e. nauplii and copepodites) (Takahashi & [illegible]yama 2008; Waiho et al. 2013), copepods are excellent candidates to be used as live feed for first feeding of larvae.

Research on the use of copepods in crustacean larviculture, however, are limited. It is still unconfirmed if copepods form the natural diet of mud crab larvae, although the carnivorous nature of *Scylla* larvae and the appropriate size of copepods makes them suitable predator-prey candidates. Using various combinations of rotifer, *Artemia*, microencapsulated feed and frozen copepod, Jantrarotai et al. (2004) found that *S. olivacea* larvae fed with a combination of either rotifer and *Artemia* or rotifer and frozen copepod gave the highest survival rates and fastest growth with development from Z1 to Z5 in 20.7 days and 21.7 days, respectively. Faster growth rate, greater length [illegible] weight gain, and higher astaxanthin content were observed when black tiger shrimp, *Penaeus monodon* Fabricius, 1798 larvae were fed with three types of copepods (*Macrosetella gracilis* (Dana, 1847), *Pseudodiaptomus* sp. and *Oithona rigida* Giesbrecht, 1896) compared to feeding with *Artemia* nauplii alone (Santhanam et al. 2011). The enhanced growth observed in copepod-fed crustacean larvae was also evident in marine fish species (Busch et al. 2010; Koedijk et al. 2010; Cassiano et al. 2011; Leu et al. 2012; Karlsen et al. 2015; de Melo-Costa et al. 20[illegible]). Thus, future research on screening and selecting suitable copepods to be used as live feed for *Scylla* larvae could contribute significantly towards the feed development of mud crab larviculture.

One major hurdle of the potential usage of copepods as live feed in mud crab larviculture, however, is the high costs involved in their mass production and in obtaining sufficient copepods of a particular life stage at a specific time (Genodepa et al. 2004a; Conceição et al. 2010; van der Meeren et al. 2014). Most studies had only produced copepods at a pilot scale (Santhanam et al. 2011; Puello-Cruz et al. 2015). It is therefore recommended to first develop a baseline performance curve using selected species of copepods as live feed for mud crab larvae (Conceição et al. 2010). Once the appropriate species of copepods are identified, they may be incorporated into the daily larvae feed, or partly together with rotifers or *Artemia* while their mass production protocols are being developed (Conceição et al. 1997).

4.5.2. Microbound diet

A main drawback of using live feed is their nutritional inconsistency which varies based on species, strain, age and culture techniques (Tizol-Correa et al. 2006; Amarouayache et al. 2017; Broach et al. 2017). In addition, live feeds are laborious and expensive to culture, and potentially act as vectors for the introduction of pathogenic microbes (Genodepa et al. 2004a; Tizol-Correa et al. 2006; Hamre et al. 2013). Thus, the development of formulated feeds that are applicable in the early larval stages could reduce the current dependency on live feed and could lead to a more consistent hatchery production.

Microbound diets are feeds produced by binding different components together with a binder, which are then dried, crushed and sieved to the required particle size (Holme et al. 2009b; Hamre et al. 2013). Compared to live feed, microbound diets are storable, more convenient in terms of required size and availability, and involve cheaper production costs (Southgate & Partridge 1998; Holme et al. 2009b). Using a formulated microbound diet formula (Table 8), Genodepa et al. (2004b) showed that a 1:4 ratio of microbound diet to *Artemia* resulted in the highest *S. serrata* megalopae survival. Furthermore, molting rate at both treatments (larvae were fed either 100% microbound diet, or purely *Artemia*) was high (90%) but those fed with microbound diet molted earlier (Genodepa et al. 2004b). This suggests that in addition to having sufficient nutrients to support the growth and development up to megalopae, the formulated microbound diet may be nutritionally superior over *Artemia*, especially in enhancing the molting process. Larvae fed with *Artemia* showed shorter development time and higher survival compared to those fed with microbound diet (Holme et al. 2006). In combination, however, a ratio of 1:1 microbound diet:*Artemia* resulted in the highest survival and development rate from Z3 to Z5 whereas larvae fed with 100% microbound diet showed poor survival (Holme et al. 2006). This highlights the potential of incorporating microbound diet into the dietary component of mud crab larviculture. Similar positive results of feeding larvae with a mixed diet of zooplankton and formulated diets have also been reported in other crustacean species, including penaeid prawn (Jones et al. 1993) and lobster (Johnston et al. 2008).

Table 8
Microbound diet composition used for *S. serrata* larvae and megalopae (Genodepa et al. 2004a, 2004b, 2006, 2007; Holme et al. 2006).

Ingredient	Dry weight (%)
Squid meal	39.7
Rotifer	39.7
Fish oil	5.0
Corn oil	1.0
Lecithin	3.0
Cholesterol	1.0
Dibasic calcium phosphate (DCP)	0.6
Mineral mix	4.0
Vitamin mix	3.0
Zein (binder)	3.0
Total	100

When tested on *S. serrata* larvae of each stage (fed with microbound diet twice the equivalent dry weight of live feed), Genodepa et al. (2004a) reported that microbound diet size preference of larvae increases as larvae develop. Further experimentation showed that the ration for larvae was excessive as there was no significant difference ration was reduced by 50%. By studying the radioactive contents hourly after *S. serrata* larvae was fed with ^{14}C-labelled microbound diet, Genodepa et al. (2006) suggest that the formulated microbound diet was readily ingested by all larval stages, with an increase of > 90 folds in ingestion between Z1 and megalopae. The obvious increases in ingestion were in Z3, Z5 and megalopa stages, indicating that the replacement of live feed with microbound diets at the later larval stages was feasible (Genodepa et al. 2006). The suitability of zein as binder was also validated when Genodepa et al. (2007) compared with the leaching rates of the same microbound diets bound with agar, alginate, carrageenan, gelatin or zein. The lowest leaching rate in zein-bound microbound diet is recommended as early and higher leaching rates of microbound diets bounded with other binders decrease their nutritional values and could adversely influences the water quality (Genodepa et al. 2007).

5. Conclusions and recommendations

Mud crab is regarded as a promising aquaculture species with its [illegible] growth rate and high market demand (Fazhan et al. 2017a; Waiho et al. 2017). Significant progress has been made in the last decades to provide the optimum rearing parameters, to better understand the feeding mechanisms and nutritional requirements, and to develop suitable diets for *Scylla* larvae. Collection of newly hatched larvae should be done within an hour after hatching through siphoning or scooping with the aid of light. Acclimatization is recommended if there is a water temperature difference between the spawning tank and larval rearing tanks. The optimum temperature and salinity range combination for larval rearing are 25–30 °C and 20–35 ppt respectively. An initial stocking density of 100–150 Z1/L, use of probiotics as prophylaxis and rearing in dark coloured tanks are proven to enhance the survival, growth and development of *Scylla* zoeae. Non-recirculating system should be used during early stage (Z1-Z2) larvae before switching to recirculating system with biofilters. The incorporation of microalgae throughout larval rearing is important as they serve as food, stabilize the water physical parameters (e.g. pH, dissolved oxygen), regulate bacterial growth and improve overall water quality. The food acquisition process, the development of the larvae feeding apparatus and experiments on prey/particle sizes revealed that the planktonic *Scylla* larvae feed on free-floating particles in the water column, and the preferred particle size increase with development stages, with the recommended suitable particle size range for Z1-Z2, Z3-Z4, Z5 larvae and megalopae are < 150 μm, 150–250 μm, 250–600 μm and 400–600 μm respectively. For diet, a combination of live feed and microbound diet is recommended, with rotifers as live feed during early larval stages and *Artemia* for later stages.

Despite years of research and progress, the low larval survival rate remains a major bottleneck for its commercialization. The reporting of more detailed data on the methods and parameters used for larval rearing as well as both negative and positive results will benefit those engaged in research and development, and hatchery operators to avoid reinventing the wheel and repeating the same mistakes.

The effects of elevated temperature is now a great concern for both broodstock and larvae. Attention should also be given to other equally important parameters most notably, photoperiod and light intensity for both broodstock and larvae. Published literatures on these parameters and their effects on the reproductive performance of broodstock, and survival and growth of larvae are scarce. Future studies on the effects of these physical parameters, as well as their possible synergistic effects with temperature and salinity could hasten the establishment of an optimal mud crab larval rearing protocol.

Another essential element of mud crab larval rearing is the nutrient requirements and feeding strategies, which still require further improvements. Commercially available shrimp larval diets are usually use for the crab larval rearing in the absence of efficient crab larval diet. Although some essential nutrients were studied and the quantitative requirements determined, studies on other nutrients and their requirements in the survival and growth of *Scylla* larvae are largely lacking. Nutritional studies on how to address the issue on the Molt Death Syndrome should be also be given focus.

Trials on the use of antimicrobial and probiotic extracts, and other substitutes for antibiotics to prevent the occurrence of bacterial and fungal infections in eggs and larvae in the hatchery should be given attention.

These highlighted research gaps could serve as guidelines for future studies and spearhead the optimization of *Scylla* larviculture, reducing the dependence on wild seeds and support propagation and restoration efforts throughout most mud crab-available countries, where wild *Scylla* stocks are critically depleted.

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