



Mud Crab Genus *Scylla* Broodstock Culture: Current Challenges and the Potential of a Hybrid Specific Pathogen Free Approach

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HIGHLIGHTS

- Mud crab (genus *Scylla*) farming forms an integral part of coastal aquaculture in Asia region. Instability in the production chain promoted the continued reliance on wild-caught broodstock.
- Nutritional strategies employ high-protein feeds to enhance ovarian maturation, but untreated wild-caught feeds heighten pathogen transmission risks.



Mud Crab Genus *Scylla* Broodstock Culture: Current Challenges and the Potential of a Hybrid Specific Pathogen Free Approach

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Abstract: Mud crab (genus *Scylla*) farming forms an integral part of coastal aquaculture in Asia region, with their cultivation supporting coastal livelihoods, driving economic growth through their high market demand and promoting mangrove forest conservation and environmental sustainability via mangrove ecosystem integration. However, instability in the production chain, especially the early stages from broodstock cultivation to larval rearing and crablet, promoted the continued reliance on wild-caught broodstock. Such reliance on wild-caught broodstock introduces significant biosecurity risks, particularly through pathogen transmission and inconsistent reproductive performance. Current management selects mature females based on size and ovarian development, followed by acclimation and prophylactic formalin baths to mitigate bacterial and fungal infections. This review examines the biosecurity risks of relying on wild broodstock and proposes a practical “hybrid” approach that combines the innate immune resilience of wild populations with Specific Pathogen Free (SPF)-like conditions to enhance disease resistance, reproductive success and overall production sustainability. Nutritional strategies employ high-protein feeds, such as fish and bivalves, to enhance ovarian maturation, but untreated wild-caught feeds heighten pathogen transmission risks. By quarantine, disinfection and microbiome management protocol, pathogen load can be reduced while innate immunity can be improved.

Keywords: *Scylla paramamosain*, Specific Pathogen Free, Prophylactic, Broodstock Management, Hatchery

Abstrak: Kaedah penternakan secara ekstensif amat penting dalam akuakultur tropika, kerana ia menyokong mata pencarian penduduk pesisir, memacu pertumbuhan ekonomi melalui permintaan pasaran, dan menggalakkan pemuliharaan hutan bakau serta kelestarian alam sekitar melalui integrasi ekosistem bakau. Namun, ketidakstabilan dalam rantai pengeluaran, terutamanya pada peringkat awal seperti pemeliharaan induk, penetasan larva dan pembesaran anak ketam telah mengurangkan kecekapan dalam penghasilan ketam dewasa bersaiz pasaran. Kebergantungan terhadap induk tangkapan liar membawa risiko biosekuriti yang ketara, terutamanya melalui transmisi

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patogen dan prestasi reproduktif yang tidak konsisten. Pengurusan semasa memilih induk betina matang berdasarkan saiz dan kematangan ovari, diikuti dengan proses aklimatisasi dan rendaman formalin secara profilaktik untuk mengurangkan jangkitan bakteria dan kulat. Strategi pemakanan menggunakan makanan berprotein tinggi seperti ikan dan moluska bercangkerang bagi merangsang pematangan ovari, namun penggunaan makanan tangkapan liar yang tidak dirawat meningkatkan risiko transmisi patogen. Melalui protokol kuarantin, pembasmian kuman, pengurusan mikrobiom dan beban patogen dapat dikurangkan, manakala imuniti semula jadi dapat dipertingkatkan.

Kata Kunci: *Scylla paramamosain*, Specific Pathogen Free, Profilaktik, Pengurusan Induk, Hatcheri

INTRODUCTION

Mud crabs of the genus *Scylla* are predominantly found in association with mangrove ecosystems, where their habitats encompass intertidal and subtidal muddy and sandy-muds area (Le Vay et al. 2007; Holme et al. 2009). Mud crab possess significant market value and commercially important for fishermen and coastal communities throughout their habitats (Petersen et al. 2013; Bhuiyan et al. 2021). Over the past few decades, mud crab has become established as a pivotal species in the aquaculture sector, particularly in Southeast Asia where interest in the aquaculture of *Scylla* species has been documented in tropical Asia since the 1970s (Bir 2016; Syafaat et al. 2021). However, instability in the production chain, from broodstock cultivation to larval rearing and the growth of market-sized adult crabs, remains a significant challenge in mud crab farming due to disease outbreaks and the biosecurity risks associated with relying on wild-caught broodstock (Pattiasina et al. 2016; Waiho et al. 2018 Liew et al. 2023). The objective of this review is to examine the biosecurity risks associated with relying on wild-caught broodstock and to outline a practical ‘hybrid’ approach that combines natural immune resilience with SPF-like conditions to improve disease resistance and production sustainability.

CORE MANAGEMENT PRACTICES IN MUD CRAB AQUACULTURE

Broodstock Selection

Most of the mud crab broodstock is sourced from wild-caught individuals (Table 1), which poses a high risk of pathogen transmission and requires rigorous disease control measures (Shelley 2008; Lovatelli et al. 2025). Broodstock management is crucial for enhancing reproduction and genetic improvements, allowing the entire production chain to achieve sustained efficiency and optimal productivity (Duncan et al. 2013). The implementation of broodstock management protocols and nutritional

strategies significantly influences reproductive parameters, including fecundity, hatching rate, larvae survival rate and growth to maturity (Bromage 1998). The cultivation of optimal broodstock yields high-quality eggs, generally characterised by high fertilisation rates, eye stage development and hatchability.

Mud crab are collected from their natural habitat using methods such as, baited traps, gill nets and handpicking, often sourced directly from fishermen (Butcher *et al.* 2012; Funde *et al.* 2013; Broadhurst *et al.* 2014; Azra & Ikhwanuddin 2016; Fitri *et al.* 2017). After acquiring mud crabs from local fishermen, mature females weighing more than 200 g with all limbs intact and exhibiting fourth-stage ovarian maturation, identified by deep orange-red ovaries that fully occupy the body cavity and are clearly visible when a torchlight is shone through the carapace in a darkened room (Azra & Ikhwanuddin 2016; Hajisamae *et al.* 2025; Lovatelli *et al.* 2025). The broodstocks then undergo a two-day acclimation period before being placed in individual holding system (Lovatelli *et al.* 2025).

TABLE 1. Common mud crab species used in hatcheries in different countries.

Country	Mud crab species used in hatcheries	Reference
China	<i>Scylla paramamosain</i>	(Han <i>et al.</i> 2024)
Vietnam	<i>S. paramamosain</i>	(Ngoc 2002)
Thailand	<i>S. paramamosain</i> ; <i>S. olivacea</i> ,	(Overton & Macintosh 2002; Oniam <i>et al.</i> 2025)
Malaysia	<i>S. paramamosain</i> , <i>S. olivacea</i> , <i>S. tranquebarica</i>	(Islam 2015; Asmat-Ullah <i>et al.</i> 2020; Shaiful Kahar <i>et al.</i> 2022)
Philippines	<i>S. serrata</i> , <i>S. tranquebarica</i> and <i>S. olivacea</i>	(Quinitio 2015)
Bangladesh	<i>S. serrata</i> , <i>S. olivacea</i>	(Hoq <i>et al.</i> 2014; Rouf <i>et al.</i> 2016)

Prophylactics Treatment

Formalin is commonly used as a prophylactic agent to eliminate the indigenous bacterial flora of mud crab broodstock. Prophylactic treatment of 150 ppm formalin solution for 30 min is usually practiced (Hamasaki & Hatai 1993; Azra & Ikhwanuddin 2016; Leal *et al.* 2018a; Lovatelli *et al.* 2025). Post-prophylactic treatment, the broodstock are transferred to individual holding tanks with a substrate of fine sand at the bottom, equipped with flowing water and aeration for berried cultivation (Lovatelli *et al.* 2025).

During spawning stage, recent research indicate that mud crab broodstock exhibits a strong preference for fine sand (< 70 micron) over coarse sand or bare tank bottom, therefore the presence of treated sand is critical not only facilitates the spawning, but also significantly reduce potential external pathogen infection (Fazhan et al. 2022). Once berried broodstock hatched, prophylactic formalin treatments applied to active zoea 1 for approximately 10 sec to mitigate fungal infection and reduce bacterial load (Hamasaki & Hatai 1993). This is a standard protocol in the management of mud crab broodstock for controlling infectious diseases that impact reproduction performance.

Nutritional Management

The nutritional and feeding strategies for mud crab broodstock rely on wide variety of feeds, including trash fish, squid, mussel meat and blood cockle (Millamena & Qunitio 2000; Keenan & Blackshaw 2011; Azra & Ikhwanuddin 2016). The primary focus in designing dietary strategies for broodstock is gonadal maturation, with nutrient profiles such as high protein and amino acids like alanine, cystine and leucine (Keenan & Blackshaw 2011; Early Septiningsih & Herlinah 2015). These feeds, commonly sourced from untreated wild catches, pose a potential risk for disease and pathogen transmission. Frequently identified agents of transmission pathogens within genus *Vibrio* included *V. parahaemolyticus*, *V. vulnificus*, *V. cholerae*, *V. alginolyticus*, *V. splendidus* and *V. haryeiyi* (Austin & Austin 2007; Jones & Oliver 2009; Jithendran et al. 2010; Deng et al. 2019; Cheng et al. 2020).

DISEASES MANAGEMENT

Mud Crab Diseases

It poses a critical risk of disrupting the immune defences of the host through direct host-pathogen interactions or worsening the situation via horizontal gene transfer among the vibrios to the host (Jithendran et al. 2010; Le Roux & Blokesch 2018; Deng et al. 2019 Zhang et al. 2020). It also increases susceptibility to fungal infections, including those caused by *Lagenidium* spp., which induce egg mortality and larval mycosis in shrimp and crab (Jithendran et al. 2010).

Mud crab rely on their innate immune system to counteract pathogen, such risk may result in the immune system prioritising pathogen resistance over reproductive performance (Chen & Wang 2019). The application of formalin as a disinfectant prior to broodstock captivity culture may

affect immune response ability due to its electrophilic character, which enables interaction with several biological molecules, such as proteins, DNA and RNA (McDonnell & Russell 1999; Leal *et al.* 2018b). Formalin not only eliminates native bacteria cells from the carapace of wild-caught broodstock but may also harm the broodstock's innate immune system, such as disrupting antimicrobial peptide that enhance phagocytosis and Antimicrobial Peptide (AMP) synthesis (Denyer & Stewart 1998). The potential risk on over exposure to formalin can lead to oxidative stress, resulting in imbalance in Reactive Oxygen Species (ROS) production and antioxidant defence (Cheng *et al.* 2021).

Bacterial infection in mud crabs can suppress hemocyte activity, allowing pathogens to invade (Zhou *et al.* 2018). Hemocytes are the key immune cell in crustaceans and play a crucial role in pathogen defence through phagocytosis, melanisation, phenoloxidase activity and regulation of immune gene expression (Mangkalanan *et al.* 2014; Kankamol & Salaenoi 2018). The stimulation of exosome secretion and modulation of anti-lipopolysaccharide factor (ALF) expression can impair immune recognition and binding to pathogens, potentially weakening the host's ability to initiate an effective defense against infections (Sun *et al.* 2022).

Specific Pathogen Free (SPF) Approach

The cultivation of broodstock mud crab in a closed recirculating system that meets the Specific Pathogen Free (SPF) requirements potentially providing a novel approach to optimise its performance. The remarkable success of SPF broodstock and larval of *Penaeus monodon* and *Litopenaeus vannamei* in the industry adds tremendous economic value (Lightner *et al.* 2009; Wyban 2009).

Unlike vertebrates, crustaceans lack an adaptive immune system and do not produce antibodies (Cerenius *et al.* 2010; Wang *et al.* 2014), yet they can still transmit pathogen to their offspring, leading to high morbidity and mortality rates. The development of SPF broodstock and larvae for crustacean like *P. monodon* and *L. vannamei* fundamentally follows strict biosecurity protocols for two consecutive years at a certified rearing facility to ensure the absence of specific pathogen listed by the Office International des Epizooties and is maintained on biosecure feeds (Lightner 2007; Lightner *et al.* 2009; Murray *et al.* 2022). Complying with high-level biosecurity protocols, as documented for SPF, not only safeguards pathogen exclusion but also contributes to genetic improvement (Lightner *et al.* 2009). Genetic characterisation involves Specific Pathogen Resistant (SPR) and Specific Pathogen Tolerant (SPT), where SPR refers to individuals genetically selected to resist specific pathogens, while SPT indicates that they may still become infected but exhibit minimal symptoms or performance loss (Alday-Sanz 2018).

Biosecure Transitional Broodstock and Hatchery System

Nevertheless, practical gaps exist in achieving SPF status for mud crab broodstock and larvae. Unlike shrimp, where SPF programs are well-established, the research and development of SPF mud crab remain limited (Alday-Sanz *et al.* 2018). Enforcing biosecurity is challenging due to their agonistic and cannibalistic behaviour, which makes them more difficult to manage in confined system compared to shrimp (Mirera & Moksnes 2013; Junaidi Zakaria & Agustina Saragih 2021; Liew *et al.* 2023).

Additionally, the dietary needs of mud crab also increase the risk of pathogen introduction, as artificial sterile feeds for *Scylla* spp. are not readily available. The primary consideration in establishing and maintaining SPF is the significant financial investment required due to several key factors, including infrastructure development, comprehensive biosecurity measures, high-quality water treatment systems, continuous health monitoring and disease screening. The development of SPF shrimp broodstock involves domestication, selective breeding, rigorous quarantine procedures and a highly sterilised environment (Lightner 2007; Lightner *et al.* 2009). The most critical aspect of this process is the strict prevention of pathogen exposure to ensure the health and biosecurity of the broodstock. By applying these criteria, the broodstock potentially miss out on immune priming and microbiome diversity, possibly leaving the offspring or the broodstock less equipped to combat real-world disease during the grow-out phase (Pope *et al.* 2011). Juveniles of mud crab need more space compared to shrimp due to their natural living behaviours, including territoriality and cannibalism, as they live a benthic lifestyle (Mirera & Moksnes 2013; Hannan *et al.* 2024). Moreover, their grow-out process is typically carried out in a diverse range of uncontrolled farms or earthen pond where environmental conditions and biosecurity measures may be challenging to regulate (Ut *et al.* 2007; Mirera & Moksnes 2015). Wild-caught crabs, naturally resilient from their environment, probably have a more robust innate immune response, even if they possess pathogens (Zhang *et al.* 2020).

To bridge the gaps, a hybrid approach involving the design of SPF-like conditions for wild-caught mud crab broodstock could balance the natural immune resilience of wild population with the disease-free advantages of SPF systems and biosecure feed. The breeding process would start by leveraging the benefits of wild-caught mud crabs, which would likely possess robust innate immunity derived from diverse microbiomes acquired through natural pathogen exposure, and transitioning them to a controlled, pathogen-free environment that mimics SPF conditions (Jiang *et al.* 2023).

This resilience might also contribute to a reduction in the time required for breeding SPF broodstock, as wild-caught crabs would have a robust immune system that could enhance their adaptability and resistance to pathogens in SPF-like conditions. As a result, the offspring might exhibit improved growth rates and higher disease resistance (Hamasaki & Hatai 1993). Based on broodstock aquaculture principles, capture and initial quarantine could be used in this hybrid approach, which would isolate crabs to assess their health, including PCR screening to identify microbial presence and potential virulence factors. The wild-caught broodstock would be placed in a quarantine tank with SPF-like conditions, such as filtered and UV-treated seawater, with water salinity of 32 psu–35 psu, pH of 7.5–8.5, and alkalinity of 120 mg/L–180 mg/L, within a high-biosecurity-level hatchery (Lovatelli *et al.* 2025).

Since wild-caught broodstock often host pathogen, to minimise disease threats, after the initial quarantine, they can be disinfected with formalin as practice in documented mud crab aquaculture protocols, which might also help achieve SPF-like conditions (Hamasaki & Hatai 1993; Jithendran *et al.* 2010; Keenan & Blackshaw 2011). The formalin exposure duration and concentration would need to be carefully assessed to minimise potential stress, which could impair the immune system while still effectively clearing latent infections. A detachable microbiome test would be conducted with rigorous screening and thorough risk assessment after the disinfectant treatment. Comprehensive screening for White Spot Syndrome Virus (WSSV), Mud Crab Reovirus (MCRV) and *Vibrio* species would be performed using PCR (Jithendran *et al.* 2010). A follow-up screening would assess pathogen clearance and confirm pathogen-free status prior to the initiation of breeding. A post-treatment recovery period could be implemented, allowing the crab to recover in a well-oxygenated, biosecurity water with nutritionally enriched feeds.

The treated broodstock individuals would be transitioned to biosecure holdings that mimic SPF conditions, utilising screened natural feeds and potential sterilisation methods such as ozone treatment, UV radiation or high-temperature processing. Strict biosecurity measures, including footbaths, equipment disinfection and restricted access, would be implemented to prevent recontamination. The broodstock gut microbiome would be stimulated with probiotics, for example, *Lactobacillus* or *Bacillus* spp., to enhance haemocyte activity and improve infection response (Wu *et al.* 2014). SPF-like water conditions and biosecurity feeding protocol would be maintained for the zoea and megalopa stages, using an enriched diet such as artemia with HUFA (highly unsaturated fatty acids) to provide a high nutritional profile essential for growth and to establish a strong foundation for the immune system (Suprayudi *et al.* 2004).

This hybrid approach would be practical as it would leverages existing aquaculture practices, including quarantine and treatment, which are commonly practiced in broodstock management (Keenan & Blackshaw 2011). This method could reduce the duration required for broodstock conditioning compared to the time needed for breeding traditional SPF lines. This innovative strategy might offer significant cost-effectiveness and high scalability, potentially closing gaps in underdeveloped protocols, biosecurity challenges and economic barriers.

CONCLUSION

Optimising broodstock management for mud crab is essential to improving the sustainability and productivity of tropical aquaculture, supporting coastal livelihoods and promoting environmental conservation through integration with mangrove ecosystem. However, challenges such as biosecurity risks and pathogen transmission have disrupted production consistency, particularly during the early stages from broodstock to larval rearing. Current practices, including broodstock selection based on ovarian maturation from wild-caught individuals, prophylactic formalin treatments and nutritional strategies, aim to mitigate these issues but also introduce risks, such as immune suppression and disease transmission from untreated feeds. The suggested hybrid strategy, which integrates the natural immune resilience of wild-caught broodstock with SPF-like condition, propose a practical solution for improving broodstock management. This approach involves implementing rigorous quarantine, disinfection, PCR screening and biosecure feeding strategies enriched with probiotics and nutritionally optimised diets. Together, these measures aim to mitigate pathogen risks while preserving innate immunity. This method not only targets existing biosecurity and economic challenges but also enhances reproductive performance and larval quality, laying the foundation for a more resilient and scalable mud crab aquaculture industry. Future research should focus on optimising formalin exposure, developing sterile feeds, and scaling SPF-like systems to ensure long-term sustainability and economic viability.

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AUTHORS' CONTRIBUTIONS

Sor Chin Siang: Conceptualisation, Methodology, stakeholder input, writing.

Chiar Yu Shan: Stakeholder input, data curation, writing.

Hanafiah Fazhan: Supervision, investigation.

Khor Waiho: Conceptualisation, validation, funding.

REFERENCES

- Alday-Sanz V. (2018). Specific pathogen-free (SPF), specific pathogen-resistant (SPR), and specific pathogen-tolerant (SPT) as part of the biosecurity strategy for whiteleg shrimp (*Penaeus vannamei* Boone 1931). *Asian Fisheries Science* 31(S1): 112–120. <https://doi.org/10.33997/j.afs.2018.31.S1.008>
- Alday-Sanz V, Brock J, Flegel T W, McIntosh R, Bondad-Reantaso M, Salazar M and Subasinghe R. (2018). Facts, truths and myths about SPF shrimp in aquaculture. *Reviews in Aquaculture*, 1–9. <https://doi.org/10.1111/raq.12305>
- Asmat-Ullah M, Waiho K, Azra M N, Norainy M H, Syafaat M N, Al Nahid S A, Fazhan H and Ikhwanuddin M. (2020). Induced mating of newly molted females of orange mud crab, *Scylla olivacea* (Herbst, 1796), in captivity. *Aquaculture* 533: 736159. <https://doi.org/10.1016/j.aquaculture.2020.736159>
- Austin B and Austin D A. (2007). Characteristics of the pathogens: Gram-negative bacteria. In *Bacterial fish pathogens*, 4th ed. Springer, 61–158. https://doi.org/10.1007/978-1-4020-6069-4_4
- Azra M N and Ikhwanuddin M. (2016). A review of maturation diets for mud crab genus *Scylla* broodstock: Present research, problems and future perspective. *Saudi Journal of Biological Sciences* 23(2): 257–267. <https://doi.org/10.1016/j.sjbs.2015.03.011>
- Bhuiyan M S, Shamsuzzaman M M, Hossain M M, Mitu S J and Mozumder M M H. (2021). Mud crab (*Scylla serrata* Forsskal 1775) value chain analysis in the Khulna region of Bangladesh. *Aquaculture and Fisheries* 6(3): 330–336. <https://doi.org/10.1016/j.aaf.2021.01.004>
- Bir J. (2016). *Mud crab's (Scylla serrata) reproduction and breeding technique course*. University of the Basque Country (UPV/EHU).
- Broadhurst M K, Butcher P A and Cullis B R. (2014). Effects of mesh size and escape gaps on discarding in an Australian giant mud crab (*Scylla serrata*) trap fishery. *PLoS ONE* 9(9): e106414. <https://doi.org/10.1371/journal.pone.0106414>
- Bromage N. (1998). Broodstock management and the optimisation of seed supplies. *Suisan Zoshoku* 46(3): 395–401.
- Butcher P A, Leland J C, Broadhurst M K, Paterson B D and Mayer D G. (2012). Giant mud crab (*Scylla serrata*): Relative efficiencies of common baited traps and impacts on discards. *ICES Journal of Marine Science* 69(8): 1511–1522. <https://doi.org/10.1093/icesjms/fss109>

- Chen F and Wang K. (2019). Characterization of the innate immunity in the mud crab *Scylla paramamosain*. *Fish & Shellfish Immunology* 93: 436–448. <https://doi.org/10.1016/j.fsi.2019.07.076>
- Cheng C -H, Ma H -L, Deng Y -Q, Feng J, Jie Y -K and Guo Z -X. (2020). Effects of *Vibrio parahaemolyticus* infection on physiological response, histopathology and transcriptome changes in the mud crab (*Scylla paramamosain*). *Fish & Shellfish Immunology* 106: 197–204. <https://doi.org/10.1016/j.fsi.2020.07.061>
- Cheng C -H, Ma H -L, Liu G -X, Deng Y -Q, Feng J, Jie Y -K and Guo Z -X. (2021). Oxidative stress, DNA damage, and cellular response in hydrogen peroxide-induced cell injury of mud crab (*Scylla paramamosain*). *Fish & Shellfish Immunology* 114: 82–89. <https://doi.org/10.1016/j.fsi.2021.04.015>
- Cerenius L, Jiravanichpaisal P, Liu H and Söderhäll I. (2010). Crustacean immunity. In K Söderhäll (ed.), *Invertebrate immunity*. Springer, 239–259. https://doi.org/10.1007/978-1-4419-8059-5_13
- Deng Y, Xu H, Su Y, Liu S, Xu L, Guo Z, Wu J, Cheng C and Feng J. (2019). Horizontal gene transfer contributes to virulence and antibiotic resistance of *Vibrio harveyi* 345 based on complete genome sequence analysis. *BMC Genomics* 20(1): 761. <https://doi.org/10.1186/s12864-019-6137-8>
- Denyer S P and Stewart G S A B. (1998). Mechanisms of action of disinfectants. *International Biodeterioration & Biodegradation* 41(3–4): 261–268. [https://doi.org/10.1016/S0964-8305\(98\)00023-7](https://doi.org/10.1016/S0964-8305(98)00023-7)
- Duncan N J, Sonesson A K and Chavanne H. (2013). Principles of finfish broodstock management in aquaculture: Control of reproduction and genetic improvement. In G Allan and G Burnell (Eds.), *Advances in Aquaculture Hatchery Technology*. Cambridge, UK: Woodhead Publishing, 23–75. <https://doi.org/10.1533/9780857097460.1.23>
- Early Septiningsih and Herlinah. (2015). Reproduction performances of mud crab (*Scylla olivacea*) broodstocks with different feeds. *International Journal of Agriculture System* 3(2): 157–168.
- Fazhan H, Waiho K, Shu-Chien A C, Wang Y, Ikhwanuddin M, Abualreesh M H, Kasan N A, Wu Q, Muda S, Sor C S and Jalilah M. (2022). Fine sand facilitates egg extrusion and improves reproductive output in female mud crab genus *Scylla*. *PeerJ* 10: e13961. <https://doi.org/10.7717/peerj.13961>
- Fitri A D P, Boesono H, Sabdono A, Supadminingsih F N and Adlina N. (2017). The mud crab (*Scylla serrata*) behavior in different inclination angles of funnel and escape vent for trap net. *AACL Bioflux* 10(2): 191–199.
- Funde A B, Naik S D, Pawar A S and Hotekar S P. (2013). Comparative efficiency of mudcrab fishing methods in and around Ratnagiri, Maharashtra. *Aquaculture* 14(1&2): 25–34.
- Hajisamae S, Waiho K, Khongpuang S, Yeesin P, Chaimongkol S, Suwanmala J, Chema H and Pholrat T. (2025). Broodstock management for mud crab. In A Lovatelli, C Shelley, E Tobias-Quinitio, K Waiho and D Chan (eds.), *Status, technological innovations, and industry development needs of mud crab (Scylla spp.) aquaculture: FAO Expert Workshop, 27–30 November 2023, Singapore*. Rome, Italy: Food & Agriculture Organization, 183–194.
- Hamasaki K and Hatai K. (1993). Prevention of fungal infection in the eggs and larvae of the swimming crab *Portunus trituberculatus* and the mud crab *Scylla serrata* by bath treatment with formalin. *Nippon Suisan Gakkaishi* 59(6): 1067–1072. <https://doi.org/10.2331/suisan.59.1067>
- Han W, Liu H and Wang Y. (2024). Changes of nutrient composition in the ovaries and hepatopancreas of mud crab *Scylla paramamosain* broodstock and their offspring performance at different salinities. *Aquaculture* 585: 740704. <https://doi.org/10.1016/j.aquaculture.2024.740704>

- Hannan M A, Munir M B, Jamy M, Habib K A, Hasan, M J, Asdari R, Nondi S, Eissa E S H and Eissa M E H. (2024). Natural breeding performance in different saline water pens, crablets rearing and cannibalism in juvenile phase of mangrove mud crab (*Scylla olivacea*) in earthen mangrove pens. *Desalination and Water Treatment* 319: 100500. <https://doi.org/10.1016/j.dwt.2024.100500>
- Holme M -H, Zeng C and Southgate P C. (2009). A review of recent progress toward development of a formulated microbound diet for mud crab, *Scylla serrata*, larvae and their nutritional requirements. *Aquaculture* 286(3–4): 164–175. <https://doi.org/10.1016/j.aquaculture.2008.09.021>
- Hoq M E, Sein A, Khan M S K, Debnath P P and Kabir Q A K E. (2014). Captive breeding of mud crab *Scylla serrata* (Forskål, 1975) in Bangladesh. *Bangladesh Journal of Zoology* 42(2): 295–299. <https://doi.org/10.3329/bjz.v42i2.23372>
- Jiang X, Niu M, Qin K, Hu Y, Li Y, Che C, Wang C, Mu C and Wang H. (2023). The shared microbiome in mud crab (*Scylla paramamosain*) of Sanmen Bay, China: Core gut microbiome. *Frontiers in Microbiology* 14: 1243334. <https://doi.org/10.3389/fmicb.2023.1243334>
- Jithendran K P, Poornima M, Balasubramanian C P and Kulasekarapandian S. (2010). Diseases of mud crabs (*Scylla* spp.): An overview. *Indian Journal of Fisheries* 57(3): 55–63.
- Jones M K and Oliver J D. (2009). *Vibrio vulnificus*: Disease and pathogenesis. *Infection and Immunity* 77(5): 1723–1733. <https://doi.org/10.1128/IAI.01046-08>
- Junaidi Zakaria I and Agustina Saragih D. (2021). Observation of behavior and daily activity of the mud crab, *Scylla serrata* (Forskål, 1775) under control condition. *Egyptian Journal of Aquatic Biology and Fisheries* 25(3): 1079–1093. <https://doi.org/10.21608/ejabf.2021.185135>
- Islam M L. (2015). *Breeding and larvae rearing of the green mud crab, Scylla Paramamosain (Estampador 1949) in captivity*. PhD diss., Universiti Sains Malaysia.
- Kankamol C and Salaenoi J. (2018). Enzymes involved in immunity and characteristics of hemolymph in red sternum syndrome mud crabs (*Scylla serrata*). *Agriculture and Natural Resources* 52(5): 489–496. <https://doi.org/10.1016/j.anres.2018.11.012>
- Keenan C P and Blackshaw A. (Eds.). (2011). *Mud crab aquaculture: A practical manual* (FAO Fisheries and Aquaculture Technical Paper No. 567). Food and Agriculture Organization of the United Nations. <https://www.fao.org/4/ba0110e/ba0110e.pdf>
- Le Roux F and Blokesch M. (2018). Eco-evolutionary dynamics linked to horizontal gene transfer in *Vibrios*. *Annual Review of Microbiology* 72(1): 89–110. <https://doi.org/10.1146/annurev-micro-090817-062148>
- Le Vay L, Ut V N and Walton M. (2007). Population ecology of the mud crab *Scylla paramamosain* (Estampador) in an estuarine mangrove system: A mark-recapture study. *Marine Biology* 151(3): 1127–1135. <https://doi.org/10.1007/s00227-006-0553-4>
- Leal J F, Neves M G P M S, Santos E B H and Esteves V I. (2018a). Use of formalin in intensive aquaculture: Properties, application and effects on fish and water quality. *Reviews in Aquaculture* 10(2): 281–295. <https://doi.org/10.1111/raq.12160>
- Leal J F, Neves M G P M S, Santos E B H and Esteves V I. (2018b). Use of formalin in intensive aquaculture: Properties, application and effects on fish and water quality. *Reviews in Aquaculture* 10(2): 281–295. <https://doi.org/10.1111/raq.12160>

- Liew K -S, Yong F K -B and Lim L -S. (2023). An overview of the major constraints in *Scylla* mud crabs grow-out culture and its mitigation methods. *Aquaculture Studies* 24(1): AQUAST993. <https://doi.org/10.4194/AQUAST993>
- Lightner D V. (2007). Biosecurity in shrimp farming: Pathogen exclusion through use of SPF stock and routine surveillance. *Journal of the World Aquaculture Society* 36(3): 229–248. <https://doi.org/10.1111/j.1749-7345.2005.tb00328.x>
- Lightner D V, Redman R M, Arce S and Moss S M. (2009). Specific pathogen-free shrimp stocks in shrimp farming facilities as a novel method for disease control in crustaceans. In S E Shumway and G E Rodrick (eds.), *Shellfish safety and quality*. Cambridge, UK: Woodhead Publishing, 384–424. <https://doi.org/10.1533/9781845695576.3.384>
- Lovatelli A, Shelley C, Tobias-Quinitio E, Waiho K and Chan D. (Eds.). (2025). *Status, technological innovations, and industry development needs of mud crab (Scylla spp.) aquaculture*. FAO Expert Workshop, 27–30 November 2023, Singapore (FAO Fisheries and Aquaculture Proceedings No. 73). Rome, Italy: Food and Agriculture Organization of the United Nations. <https://doi.org/10.4060/cd3976en>
- Mangkalanan S, Sanguanrat P, Utairangsri T, Sritunyalucksana K and Krittanai C. (2014). Characterization of the circulating hemocytes in mud crab (*Scylla olivacea*) revealed phenoloxidase activity. *Developmental & Comparative Immunology* 44(1): 116–123. <https://doi.org/10.1016/j.dci.2013.11.018>
- McDonnell G and Russell A D. (1999). Antiseptics and disinfectants: Activity, action, and resistance. *Clinical Microbiology Reviews* 12(1): 147–179. <https://doi.org/10.1128/CMR.12.1.147>
- Millamena O M and Quinitio E. (2000). The effects of diets on reproductive performance of eyestalk ablated and intact mud crab *Scylla serrata*. *Aquaculture* 181(1–2): 81–90. [https://doi.org/10.1016/S0044-8486\(99\)00214-8](https://doi.org/10.1016/S0044-8486(99)00214-8)
- Mirera O D and Moksnes P -O. (2013). Cannibalistic interactions of juvenile mud crabs *Scylla serrata*: The effect of shelter and crab size. *African Journal of Marine Science* 35(4): 545–553. <https://doi.org/10.2989/1814232X.2013.865677>
- Mirera O D and Moksnes P -O. (2015). Comparative performance of wild juvenile mud crab (*Scylla serrata*) in different culture systems in East Africa: Effect of shelter, crab size and stocking density. *Aquaculture International* 23(1): 155–173. <https://doi.org/10.1007/s10499-014-9805-3>
- Murray K N, Clark T S, Kebus M J and Kent M L. (2022). Specific pathogen free: A review of strategies in agriculture, aquaculture, and laboratory mammals and how they inform new recommendations for laboratory zebrafish. *Research in Veterinary Science* 142: 78–93. <https://doi.org/10.1016/j.rvsc.2021.11.005>
- Ngoc U V. (2002). *Assessment of the feasibility of stock enhancement of mud crabs, Scylla paramamosain, in the Mekong Delta, Vietnam*. PhD diss., Bangor University, United Kingdom.
- Oniam V, Arkronrat W, Suwanmala J, Leearam C and Konsantad R. (2025). Comparative analysis of growth and reproductive performance in domesticated mud crab (*Scylla paramamosain*) across generations in grow-out ponds versus wild broodstock. *Aquaculture Studies* 25: 278–285. <http://doi.org/10.4194/AQUAST2407>
- Overton J L and Macintosh D J. (2002). Estimated size at sexual maturity for female mud crabs (*Scylla*) from two sympatric species within Ban Don Bay, Thailand. *Journal of Crustacean Biology* 22(4): 790–797. <https://doi.org/10.1163/20021975-99990293>

- Pattiasina B J, Jamal E, Pattinasarany A Y and Masrikat N. (2016). Improving quality of broodstock and early larval stage of mud crab *Scylla serrata* through rearing and feeding methods. *AACL Bioflux* 9(3): 662–669.
- Petersen E H, Phuong T H, Van Dung N, Giang P T, Dat N K, Tuan V A, Nghi T V and Glencross B D. (2013). Bioeconomics of mud crab, *Scylla paramamosain*, culture in Vietnam. *Reviews in Aquaculture* 5(1): 1–9. <https://doi.org/10.1111/j.1753-5131.2012.01073.x>
- Pope E C, Powell A, Roberts E C, Shields R J, Wardle R and Rowley A F. (2011). Enhanced cellular immunity in shrimp (*Litopenaeus vannamei*) after ‘vaccination’. *PLoS ONE* 6(6): e20960. <https://doi.org/10.1371/journal.pone.0020960>
- Quinitio E T. (2015). Status of mud crab industry in the Philippines. In *Proceedings of the International Seminar-Workshop on Mud Crab Aquaculture and Fisheries Management, 10-12 April 2013, Tamil Nadu, India*. Rajiv Gandhi Centre for Aquaculture (MPEDA), 27–35.
- Rouf M A, Shahriar S I M, Sarower M G and Ahsan M N. (2016). Taxonomic clarification of mud crab species of Genus *Scylla* (Brachyura: Portunidae) available in the coastal regions of Bangladesh. *Asian Fisheries Science* 29: 124–136. <https://doi.org/10.33997/j.afs.2016.29.3.001>
- Shaiful Kahar N A, Mohd Sharif N A, Syed Hussein M A, Ransangan J and Seok Kian Yong A. (2022). Reproductive cycle and size at maturity of wild mud crab, *Scylla tranquebarica* (Fabricius, 1798) in Marudu Bay, Sabah. *Borneo Journal of Marine Science and Aquaculture* 6: 20–29. <https://doi.org/10.51200/bjomsa.v6i1.1543>
- Shelley C. (2008). Capture-based aquaculture of mud crabs (*Scylla* spp.). In A Lovatelli and P F Holthus (eds). *Capture-based aquaculture. Global overview*. FAO Fisheries Technical Paper. No. 508. Rome, FAO. pp. 255–269.
- Sun Q, Lin S, Zhang M, Gong Y, Ma H, Tran N T, Zhang Y and Li S. (2022). SpRab11a-regulated exosomes inhibit bacterial infection through the activation of antilipopolysaccharide factors in crustaceans. *The Journal of Immunology* 209(4): 710–722. <https://doi.org/10.4049/jimmunol.2200094>
- Suprayudi M A, Takeuchi T and Hamasaki K. (2004). Effects of Artemia enriched with eicosapentaenoic and docosahexaenoic acid on survival and occurrence of molting failure in megalop larvae of the mud crab *Scylla serrata*. *Fisheries Science* 70(4): 650–658. <https://doi.org/10.1111/j.1444-2906.2004.00853.x>
- Syafaat M N, Azra M N, Waiho K, Fazhan H, Abol-Munafi A B, Ishak S D, Syahnon M, Ghazali A, Ma H and Ikhwanuddin M. (2021). A review of the nursery culture of mud crabs, genus *Scylla*: Current progress and future directions. *Animals* 11(7): 2034. <https://doi.org/10.3390/ani11072034>
- Ut V N, Le Vay L, Nghia T T and Hanh T T H. (2007). Development of nursery culture techniques for the mud crab *Scylla paramamosain* (Estampador). *Aquaculture Research* 38(14): 1563–1568. <https://doi.org/10.1111/j.1365-2109.2006.01608.x>
- Waiho K, Fazhan H, Quinitio E T, Baylon J C, Fujaya Y, Azmie G, Wu Q, Shi X, Ikhwanuddin M and Ma H. (2018). Larval rearing of mud crab (*Scylla*): What lies ahead. *Aquaculture* 493: 37–50. <https://doi.org/10.1016/j.aquaculture.2018.04.047>
- Wang P -H, Huang T, Zhang X and He J -G. (2014). Antiviral defense in shrimp: From innate immunity to viral infection. *Antiviral Research* 108: 129–141. <https://doi.org/10.1016/j.antiviral.2014.05.013>

- Wu H -J, Sun L -B, Li C -B, Li Z -Z, Zhang Z, Wen X -B, Hu Z, Zhang Y -L and Li S -K. (2014). Enhancement of the immune response and protection against *Vibrio parahaemolyticus* by indigenous probiotic *Bacillus* strains in mud crab (*Scylla paramamosain*). *Fish & Shellfish Immunology* 41(2): 156–162. <https://doi.org/10.1016/j.fsi.2014.08.027>
- Wyban J. (2009). World shrimp farming revolution: Industry impact of domestication, breeding, and widespread use of specific pathogen-free *Penaeus vannamei*. In C L Browdy and D E Jory (eds.), *The rising tide: Proceedings of the Special Session on Sustainable Shrimp Farming, World Aquaculture 2009*. The World Aquaculture Society, 12–21. <https://www.researchgate.net/publication/308052439>
- Zhang X, Zeng X, Sun Y, Wang Y and Zhang Z. (2020). Enhanced immune protection of mud crab *Scylla paramamosain* in response to the secondary challenge by *Vibrio parahaemolyticus*. *Frontiers in Immunology* 11: 565958. <https://doi.org/10.3389/fimmu.2020.565958>
- Zhou Y -L, Gu W -B, Tu D -D, Zhu Q -H, Zhou Z -K, Chen Y -Y and Shu M -A. (2018). Hemocytes of the mud crab *Scylla paramamosain*: Cytometric, morphological characterization and involvement in immune responses. *Fish & Shellfish Immunology* 72: 459–469. <https://doi.org/10.1016/j.fsi.2017.10.055>