Population Biology, Reproductive Biology, Fisheries, and Future Perspective to Develop Three-Spot Swimming Crab *Portunus sanguinolentus* as New Aquaculture Candidate: A Review

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ABSTRACT

The three-spot swimming crab *Portunus sanguinolentus* is an easily recognisable portunid species owing to the three red spots on its carapace. Like other portunid swimming crabs, *P. sanguinolentus* is an edible species found across the Indo-Pacific region, and it is gaining attention as one of the important edible crabs in the coastal crab fishery sector of many countries. In addition to being one of the main crab species (along with *P. pelagicus* and *P. trituberculatus*) that support the livelihood of coastal communities, *P. sanguinolentus* also exhibits high aquaculture potential. This species is often associated with coastal intertidal and subtidal zones, with juveniles and males preferably inhabiting depths up to 30 m, whereas females may be found as deep as 80 m. As *P. sanguinolentus* is a highly exploited portunid species with great aquaculture potential, this review summarises the available literature to provide a holistic compilation of the current knowledge, ranging from taxonomy and phylogeny, growth and life cycle, reproductive maturity and breeding, to feeding behaviour and food preference; we also highlight the knowledge gaps that require future emphasis. This is the first comprehensive review of the life history and other biological information of *P. sanguinolentus*. This review serves as an essential baseline for sustainable fishery management and aquaculture development of this species.

Keywords: Crab aquaculture, Crab fishery, Life history, *Portunus sanguinolentus*, Three-spot swimming crab

INTRODUCTION

Portunid crabs (Brachyura: Portunidae) are among the most valuable crustacean species after penaeid shrimps. Their delicate meat and exquisite flavour make them sought-after delicacies in the global seafood industry. As such, the fisheries and aquaculture of portunid crabs play a crucial role in supporting the livelihood of coastal communities, especially in the Indo-Pacific region, where they are mostly concentrated (Alberts-Hubatsch *et al*., 2016). Among portunid species with economic importance, those of the genus *Portunus* and *Scylla* dominate global fishery production, with a combined global capture and aquaculture production of 889,139.8 t and 365,140.1 t, respectively, in 2019 (FAO, 2021).

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The three-spot swimming crab, *Portunus sanguinolentus* (Herbst, 1783), is one of the commonly fished portunid species with high aquaculture potential (Figure 1b). Its contribution to the average annual crab landings of some countries, such as India, can reach up to 46 % (Dineshbabu *et al*., 2007). It is considered a cosmopolitan species that can be found in all major waters of the world, from India (Dineshbabu *et al*., 2007) to China (Zhang *et al*., 2021b), Hong Kong (Wu and Shin, 1997), and as far north as the Sea of Japan (Kepel and Tsareva, 2005). The landings of swimming crabs in most countries are not reported to species level, but instead are simply classified as *Portunus* spp. (Williams and Primavera, 2001). Such practice highlights that *P. sanguinolentus* is just as valuable as *Portunus pelagicus* (Figure 1c) and *Portunus trituberculatus* (Figure 1a), and that all are equally sought-after species. *Portunus* spp., including *P. sanguinolentus*, are often sold as fresh, canned, and frozen products (Takween and Qureshi, 2005). Additionally, the global crab industry is dominated by a few species from only four genera, i.e., *Scylla*, *Portunus*, *Charybdis*, and *Callinectes* (Waiho *et al*., 2022). Most of these species, including *P. trituberculatus, P. pelagicus,* and *Scylla* spp. are expensive and of limited supply (Duan *et al*., 2022; Fazhan *et al*., 2022). Therefore, *P. sanguinolentus* could serve as an alternative economic crab species due to its lower market price.

Biological information about an aquatic species is essential for its fishery management and aquaculture production. Among species within the genus *Portunus*, most of the research, ranging from population dynamics, reproduction and development characterisation to molecular physiological changes, focuses heavily on two main species, *P. pelagicus* and *P. trituberculatus* (Wang *et al*., 2018; Gao *et al*., 2019; Madduppa *et al*., 2021; Yu *et al*., 2021). The recently published chromosome-level assembly of *P. trituberculatus* further provides an important baseline for the molecular understanding of other *Portunus* species (Tang *et al*., 2020). In contrast, and despite its economic importance, *P. sanguinolentus* has gained less attention and its studies are scattered. The lack of a published review article hinders progress and knowledge gap identification in various fields related to *P. sanguinolentus*.

This review compiles the available information on the life history, population dynamics, and reproductive biology of *P. sanguinolentus*. To facilitate a thorough representation of the literature, articles were sourced from three public databases, namely Scopus, Web of Science, and Google Scholar, using the keyword “*Portunus sanguinolentus*”. A total of 202 papers were retrieved, of which 70 were from Scopus, 38 from Web of Science, and 94 from Google Scholar. Duplicates among the search results were removed, resulting in a total of 133 papers. Articles that were not directly related to the biological information or life history of *P. sanguinolentus* were also filtered out; these include papers that do not focus on taxonomy, geographical distribution, larval development, juveniles and adults, size at sexual maturity, breeding season, food and feeding, growth or mortality of *P. sanguinolentus*. Additional literature was added by screening the reference list of each *P. sanguinolentus*-related

(a) *Portunus trituberculatus* (b) *Portunus sanguinolentus* (c) *Portunus pelagicus*

Figure 1. Male of the three commonly harvested *Portunus* species: (a) *Portunus trituberculatus*, (b) *Portunus sanguinolentus*, and (c) *Portunus pelagicus*. The three species can be easily distinguished by their different patterning and coloration.

article. The final number of papers used in this review was 32. To avoid confusion with other *Portunus* crab species, either the species name or common name 'three-spot swimming crab' is used throughout the review.

TAXONOMY AND PHYLOGENY CLASSIFICATION

Taxonomic status

The three-spot swimming crab *Portunus sanguinolentus* is a portunid swimming crab under the family Portunidae. *P. sanguinolentus* was first described by Herbst in 1783 as *Portunus sanguinolentus sanguinolentus*, a subspecies under *P. sanguinolentus*. A second subspecies was originally named *Portunus sanguinolentus hawaiiensis* Stephenson, 1968, but is now accepted as *Portunus hawaiiensis* Stephenson, 1968 (WoRMS, 2022). *Portunus sanguinolentus* is among the 139 species under the genus *Portunus*, many of which, including *P. sanguinolentus*, are edible and commonly harvested marine crustacean species (Sukumaran and Neelakantan, 1997b).

In addition to the common name 'three-spot swimming crab', it is also known as 'blood-spotted swimming crab'. Its common names are derived from a very distinctive character only found in this species-a group of three red spots on the posterior half of its fairly plainly coloured carapace. In addition to the distinctive red spots, *P. sanguinolentus* also exhibits clear mesogastric, epibranchial, and metagastric ridges on its carapace (Sumpton *et al*., 1989; Rasheed and Mustaquim, 2010). Like other portunid swimming crabs, *P. sanguinolentus* has five pairs of appendages, the first pair being the chelipeds and the last pair being the swimming legs. There are no other spots or patterning on any of the appendages or carapace of *P. sanguinolentus*.

Molecular identification of a species relies heavily on its mitochondrial sequences as DNA barcodes (Yang *et al*., 2014b). For example, the use of cytochrome oxidase I subunit (COI) and 16S rRNA allows the identification of megalopas belonging to 15 brachyuran species (Marco-Herrero *et al*., 2021). The full mitochondrial genome of *P. sanguinolentus* has already been made available (Meng *et al*., 2016). The genome of *P. sanuginolentus* is approximately 16,024-16,027 bp, encoding 13 protein coding genes, 22 transfer RNA genes, two ribosomal RNA genes, and a control region (Meng *et al*., 2016). The phylogenetic comparison of 13 concatenated protein coding genes of *P. sanguinolentus* (Meng *et al*., 2016), and specifically cytochrome oxidase I (COI) gene (Figure 2), with other crustaceans placed it into Brachyura and under the genus *Portunus* as expected, conforming with its taxonomic characterisation based on morphology (Liu, 2008). Additionally, *P. sanguinolentus* was grouped with its congeneric species (*P. pelagicus* and *P. trituberculatus*).

Global distribution

Portunus sanguinolentus is widely distributed in the Indo-Pacific, from East Africa to French Polynesia, north to Japan, and south to Australia (Stephenson and Campbell, 1959) (Figure 3a). This species can be found in 48 countries ranging from tropical to temperate regions. For instance, *P. sanguinolentus* populations were reported in tropical regions such as Karachi, Malaysia (Ng, 1998), Taiwan (Lee and Hsu, 2003), Pakistan (Rasheed and Mustaquim, 2010), Thailand and Indonesia and. A subtropical population was reported in Honghai Bay, China (Yang *et al*., 2014a). Among temperate regions, *P. sanguinolentus* can be found from the intertidal to the subtidal zone in Queensland, Australia (Windsor *et al*., 2019). However, with the increase in global temperature due to climate change, it is expected that the native range of *P. sanguinolentus* would expand along with the increase in suitable living habitat (Figure 3b).

Based on the available phylogenetic study of *P. sanguinolentus*, Naz *et al*. (2016) revealed that the genetic diversity was minimal among populations (India, Vietnam, China, and Pakistan) as inferred from the partial mitochondrial 16S rRNA region. Haplotype diversity, but not nucleotide diversity, was significantly different among populations. Coupled with insignificant deviation from the mutation-drift equilibrium, the study of

Naz *et al*. (2016) highlighted the relatedness of *P. sanguinolentus* within the Indo-Pacific region. However, it is important to note that their inference was based on very low sample size, i.e., five or fewer per location. Future study with a larger sample size would allow a better characterisation of the genetic differentiation and genetic diversity at the population level (Macedo *et al*., 2019; Madduppa *et al*., 2021). Specifically focusing on the population genetic diversity of *P. sanguinolentus* along the China coast, Ren *et al*. (2017) found that individuals sampled from four distinct localities could be grouped into 68 haplotypes based on their COI gene. High gene flow was observed among haplotypes, and this was attributed to the high dispersal ability of *P. sanguinolentus* larvae and the lack of physical barriers within the marine environment (Ren *et al*., 2017). A thorough and global study of *P. sanguinolentus* populations in various tropical and subtropical regions would give an even more holistic representation of its connectivity and larval dispersal strategy.

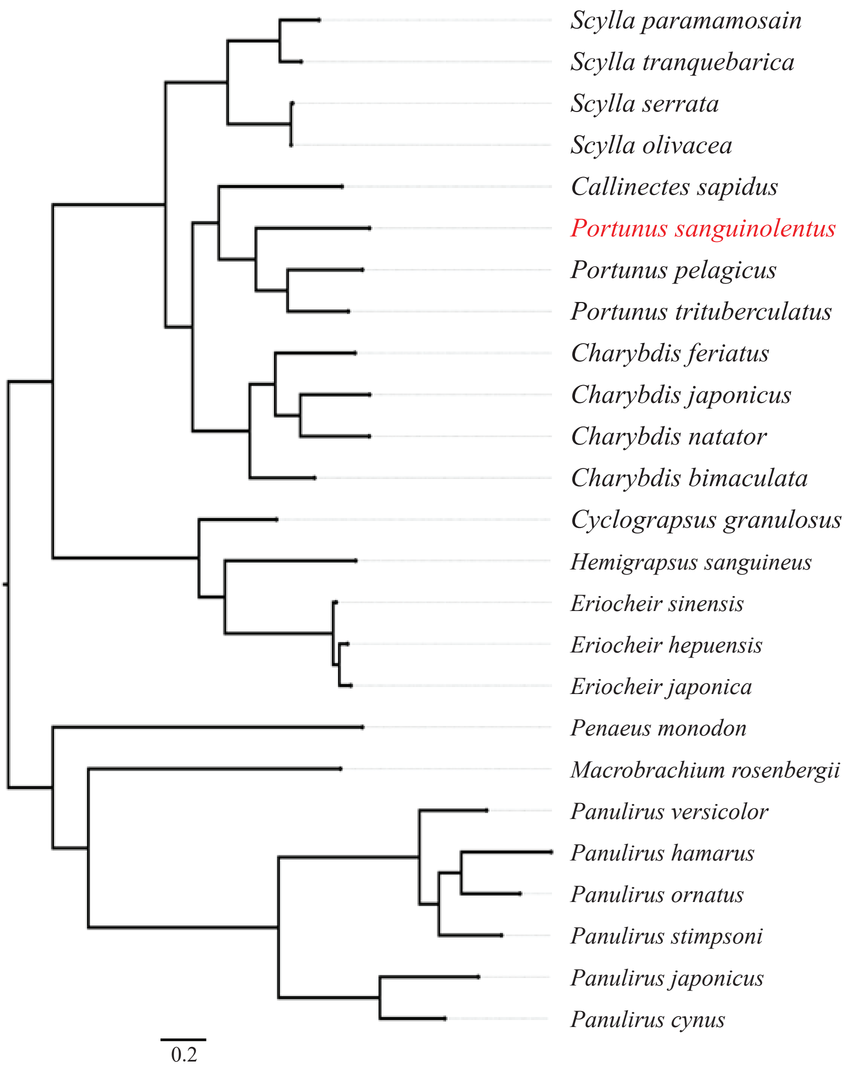

Figure 2. Phylogenetic analysis of the Cytochrome Oxidase I (COI) gene of *Portunus sanguinolentus* and 11 closely related species and several outgroups, based on the maximum likelihood method by RAxMLGUI 2.0.

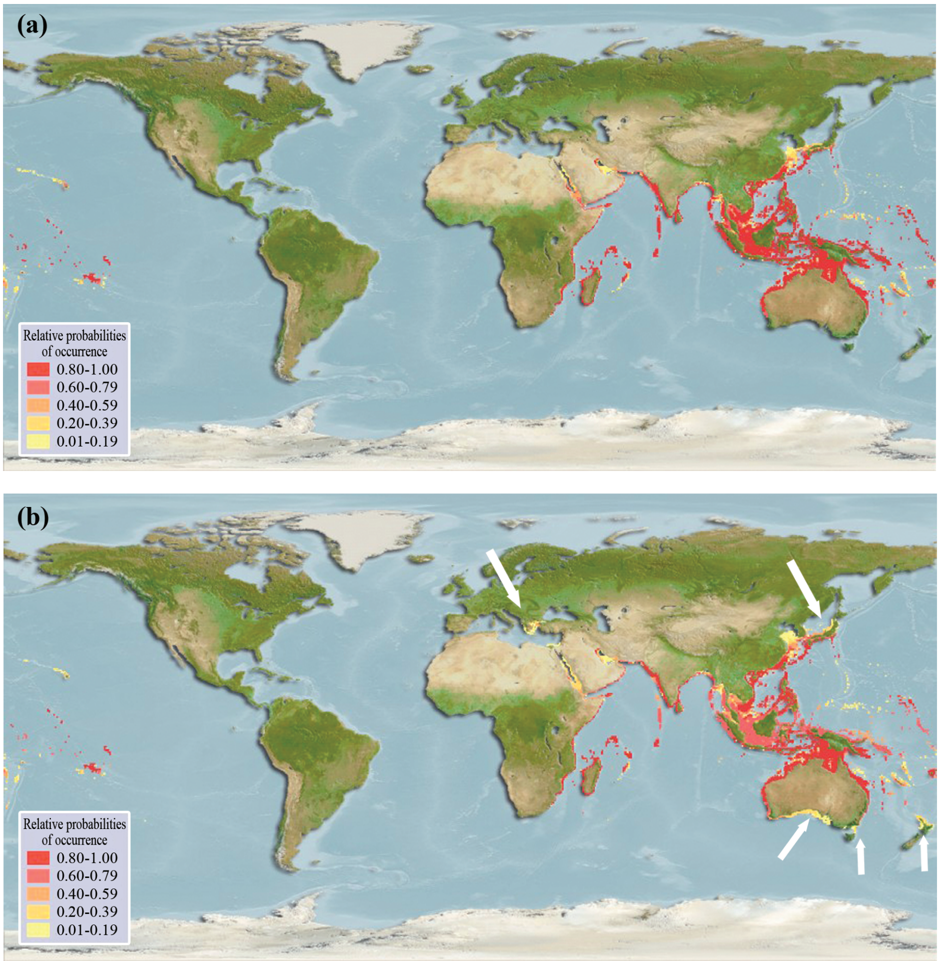

Figure 3. (a) Native distribution range of *Portunus sanguinolentus* and (b) predicted range of *P. sanguinolentus* modelled for year 2050 based on IPCC RCP8.5 emissions scenario (AquaMaps, 2019). Expansions in native range of *P. sanguinolentus* are marked by white arrows in Figure 3b.

GROWTH AND LIFE CYCLE

Similar to other portunid crab species (Ates *et al*., 2012; Ikhwanuddin *et al*., 2016; Yu *et al*., 2021), the newly deposited eggs of *Portunus sanguinolentus* go through a series of colour changes throughout embryonic developmental stages, i.e., from bright yellow to brown and eventually black shortly before hatching (Samuel and Soundarapandian, 2009). Based on the changes occurring in developmental stages and egg size increment, Samuel and Soundarapandian (2009) divided the embryonic development of *P. sanguinolentus* into six clear stages, with an incubation period between 8 and 11 days. Detailed description of each embryonic development stage can be found in Table 1. A common characteristic of the embryonic development of brachyurans is the almost linear increase in egg size as the brachyuran embryo develops (Ates *et al*., 2012). Such increment in size, however, is not related to the female size but to the ontogenetic development of the embryo itself (Samuel and Soundarapandian, 2009). The incubation period reported in *P. sanguinolentus* (8-11 days) is similar to that in other portunid species, such as 10 days in *P. pelagicus* (Ikhwanuddin *et al*., 2016), 9-13 days in *P. trituberculatus* (Hamasaki *et al*., 1992; 2003), 9-11 days in *Scylla serrata*, and 8-9 days in *S. tranquebarica* and *S. olivacea* (Ates *et al*., 2012). It is worth noting that external environmental factors such as temperature and salinity significantly affect the egg incubation period of portunids (Hamasaki *et al*., 1992; Ikhwanuddin *et al*., 2016). Some portunid species, such as the intertidal mud crab *Scylla* spp. migrate from the coastal zone to the open sea for spawning (Koolkalya *et al*., 2006; Meynecke and Richards, 2014; Alberts-Hubatsch *et al*., 2016). However, the spawning biology and migration of marine portunid species, especially *P. sanguinolentus*, is still unclear.

The larval development of *P. sanguinolentus* can be categorised into four planktonic zoeal stages and one intermediate megalopal stage before metamorphosis into the first crab instar (Kurata and Midorikawa, 1975; Samuel *et al*., 2011). Detailed description of zoeal, megalopal and first instar stages can be found in Samuel *et al*. (2011) (Table 2). Similarly, four zoeal stages and one megalopal stage were reported in *P. pelagicus* (Josileen and Menon, 2004) and *Portunus segnis* (Al-Aidaroos *et al*., 2019). However, the number of zoeal and megalopal stages vary within the Portunidae family; some species such as *Portunus rubromarginatus* have only three zoeal stages (Greenwood and Fielder, 1979), whereas mud crab *Scylla* spp. has five distinct zoeal stages and one megalopal stage (Jantrarotai *et al*., 2006; Alberts-Hubatsch *et al*., 2016; Waiho *et al*., 2018), and six zoeal stages and one megalopal stage were observed in swimming crab *Charybdis natator* (Islam *et al*., 2000).

To date, there is no study that characterises the optimised water quality parameters for *P. sanguinolentus* in its early stages, from larvae to crablet. Thus, little is known of the early life history and preferred habitat of this species, except that *P. sanguinolentus* also transitions from a planktonic to benthic lifestyle as it metamorphoses into the megalopa (Samuel and Soundarapandian, 2009). However, based on the larval biology of other

Table 1. Embryonic development of *Portunus sanguinolentus* (Samuel and Soundarapandian, 2009).

Stage of development	**Colour**	**Egg shape; diameter (mm)**	**Description**
Stage 1-Newly spawned egg	Golden yellow	Round; 0.34	Eggs are undeveloped; Undifferentiated cells with dense yolk granules. Unclear cleavage and gastrulation stages.
Stage II-Multicell stage	Yellow to yellowish orange	Round; 0.41	Egg division started. Space between the egg wall and the inner developing embryo is clearly visible.
Stage III-Eye stage	Orange	Round; 0.48	Yolk granules reduced in density. Segmentation and organogenesis are clear, including the characteristic scarlet crescent-shaped eye spots.
Stage IV-Pigment stage	Brown	Slightly elliptical; 0.57	Pigmented appendages of the embryonic larvae are visible.
Stage V-Heartbeat stage	Dark brown to black	Slightly elliptical; 0.64	Eyes are round in shape and heartbeats are visible.
Stage VI-Prehatching stage	Dark brown to black	Slightly elliptical; 0.73	Increase in chromatophores throughout the body and in rate of heartbeat.

Table 2. Larval development of *Portunus sanguinolentus* (Samuel *et al*., 2011).

Stage of development	**Duration (days)**	**Carapace length (mm); abdomen-telson length (mm)**	**Description**
Zoea I	3	0.46-0.55; 1.09-1.24	Eyes are sessile. Abdomen is divided into five segments and a telson. A pair of short setae on the dorsal surface of the first abdominal segment. Antennule is short and conical in shape, bears two long aesthetes and two short setae.
Zoea II	3	0.74-0.79; 1.46-1.54	Eyes are stalked. Abdomen is divided into five segments and a telson. A pair of medium or short setae on the dorsal surface of the first abdominal segment. Third to fifth abdominal segments have more distinct lateral spines. Antennule bears five long aesthetes and one seta.
Zoea III	2	0.82-0.89; 2.06-2.24	Eyes are stalked. Abdomen is divided into six segments and a telson. Three medium or short setae on the dorsal surface of the first abdominal segment, a single median seta on the dorsal surface of the second to sixth abdominal segments. Abdomen develops paired pleopod buds at the ventral posterior end of the second to fifth segments. Antennule increases in size.
Zoea IV	2	1.03-1.12; 2.67-3.11	Eyes are stalked. Abdomen is divided into six segments and a telson. Four median setae on the dorsal surface of the first abdominal segment, two median setae on the dorsal surface of the second to sixth abdominal segments. Clear segmentation can be seen on second to fifth pereiopod buds. Pleopod buds on second to fifth segments are large and biramous; those on sixth segment are uniramous. First pereiopod bud developed into chela. Antennule bears aesthetes in two tiers.
Megalopa	6	1.81-1.93; 1.38-1.43	Presence of rostral spine. Eyes projected to the lateral margin of the carapace. Abdomen has six segments with a dorsoventrally flattened telson. First abdomen segment has no pleopod. First pereiopod has 5 segments that are well developed. Second to fifth pereiopods have well-developed, 5-segmented endopods. Antennule has 3 segmented peduncles and two rami. Antenna is elongated.
Crablet (first instar)	-	2.8-3.6 (carapace width, mm)	Pereiopods well developed with setae, especially on the propodus and dactylus of the swimming legs. Carapace is laterally inflated, with eyes projecting laterally. Flat frontal region with 27 unequal lobes and 10 spines. Abdomen has six somites with simple setae and a semicircular telson. First pereiopods developed into chelipeds; second to fourth pereiopods developed into elongated dactyls with spiny tips; fifth pereiopods developed into dorsoventrally flattened swimming legs.

portunids (Azra and Ikhwanuddin, 2015; Waiho *et al*., 2018), it can be assumed that the larvae of *P. sanguinolentus* also occupy open ocean with salinity of 30-35 psu and temperature above 25 °C. Ariyama (1996) reported that *P. sanguinolentus* could not survive in water below 12 °C. Juveniles of *P. sanguinolentus* are known to inhabit the intertidal and subtidal zones up to a depth of 30 m. Both juveniles and adults show high preference towards sandy to muddy substrates in brackish to coastal waters (Ng, 1998). There is a stark contrast in depth preference of *P. sanguinolentus* according to sex, with adult females preferably inhabiting deeper waters of 40-80 m depth while adult males are commonly found together with juveniles nearshore in 10-30 m depth (Campbell and Fielder, 1986; Sumpton *et al*., 1989).

REPRODUCTIVE MATURITY AND BREEDING

Gonadal development

Understanding of the reproductive biology of an organism, especially age at maturity and spawning/breeding, which links directly to species recruitment (Zairion *et al*., 2015; Waiho *et al*., 2017a), aids in fishery management and informs policy-making decisions. Therefore, detailed characterisation of the gonadal development of a species is especially important for both fishery and aquaculture sectors. The gonadal development of *Portunus sanguinolentus* has been described by Soundarapandian *et al*. (2013) and Wimalasiri and Dissanayake (2016).

The male reproductive system of *P. sanguinolentus* conforms with that of other portunids (Nascimento and Zara, 2013; Waiho *et al*., 2017b), i.e., a bilaterally symmetrical structure made up of testes, anterior vas deferens, median vas deferens, posterior vas deferens, and ejaculatory duct. Soundarapandian *et al*. (2013) divided the gonadal development of *P. sanguinolentus* into three stages (immature, maturing, mature) based on the external size and morphology of the testes and vas deferens. In contrast, Wimalasiri and Dissanayake (2016) only used 'immature' and 'mature' stages to classify the male gonadal development of *P. sanguinolentus*. They described immature male gonads as small, creamy white testes; the vas deferens is not clearly differentiated; and spermatogonia and primary spermatocytes are the main germ cells in the testes. The mature male gonads are characterised by large testes, coiled and swollen vas deferens, and the presence of spermatozoa and spermatids in the testes. As in other members of the family Portunidae, testes of *P. sanguinolentus* are responsible for the production of germ cells, such as spermatogonia, spermatocytes, spermatids, and spermatozoa. Mature spermatozoa are transferred from the testes to anterior vas deferens, where they are packed into spermatophores. Subsequently, spermatophores are stored in the median vas deferens. In addition to acting as storage for spermatophores, the median vas deferens is also responsible for producing seminal fluid. The posterior vas deferens mainly has a secretory role by producing most of the seminal fluid to ease the transfer of spermatophores to the female's seminal receptacle during copulation (Beninger *et al*., 1988; Waiho *et al*., 2015). The increase in overall size and the volume of spermatophores once male crabs reach maturity leads to the use of gonadosomatic index as one of the gonadal development staging criteria in portunids (Waiho *et al*., 2015; Ali *et al*., 2021). There is, however, a lack of detailed histological and histochemical characterisation of the male reproductive system, thereby hindering the characterisation of the spermatogenesis and spermiogenesis of *P. sanguinolentus*.

Similar to other portunids, the female reproductive system of *P. sanguinolentus* is composed of a pair of ovaries, seminal receptacles, and oviduct (Soundarapandian *et al*., 2013). The gonopore is an opening that connects to the exterior of the female, located on the left and right sternites of the sixth thoracic segment (Ryan, 1967; Babu *et al*., 1989). The process of gonadal development in female *P. sanguinolentus* can be divided into the classical five stages found in portunids (Waiho *et al*., 2017a), i.e., immature, early maturing, late maturing, ripe, and spent (Wimalasiri and Dissanayake, 2016). An immature ovary is characterised by small, flattened, ribbon-like appearance, and whitish yellow coloration. Early maturing ovaries grow in size but do not yet reach the hepatopancreatic region, and are yellowish orange in colour. Limited perinucleolar oocytes and abundant yolkless oocytes can be found in the ovaries. The transition from early to late maturing ovaries is accompanied by further increase in size, whereby now the ovarian tissues can be found in the hepatopancreatic region. Ovaries are considered to be in the ripe stage if they appear bright yellow/orange in colour and occupy almost all areas of the body cavity and are highly nodulated. Mature oocytes dominate the ovarian tissues. After egg extrusion, spent ovaries are noted by their change in colour-from bright yellow/orange to pinkish white-and a significant reduction in ovarian mass size. The ovarian tissues now contain only limited mature oocytes. The gonadosomatic index (GSI) of *P. sanguinolentus* females was reported to range from 0.60-0.94 (Immature), 1.00-1.90 (Early Maturing), 1.70-5.40 (Late Maturing), and 6.90-14.81 (Ripe) (Jacob *et al*., 1990). Future research into the physiological changes during vitellogenesis of *P. sanguinolentus* females would be useful for understanding the internal regulatory mechanisms that govern ovarian development and oocyte maturation in brachyurans.

Population structure and size at maturity

Portunus sanguinolentus is a considerably large-bodied portunid crab. In Honghai Bay, China, the largest male recorded had a carapace width (CW) of 144.4 mm (Yang *et al*., 2014a), while a size of 175 mm CW was reported along the Calicut coast of India (Sarada, 1998). The largest reported male and female were in Taiwan, with CW of 193 mm and 182 mm, respectively (Lee and Hsu, 2003). In some regions, such as Honghai Bay, the sex ratio was male-biased (the average male to female ratio was 1.26:1), except for in February and June (Yang *et al*., 2014a). Similar male-biased sex ratios were found in *P. sanguinolentus* populations in Queensland, Australia (Sumpton *et al*., 1989), the west coast of Sri Lanka (Wimalasiri and Dissanayake, 2016), and Hawaii, USA (Wenner, 1972). Among Indian populations, the average sex ratios were balanced (1:1) at the south Karnataka Coast (Dineshbabu *et al*., 2007) and at Kozhikode (Sarada, 1998), whereas a female-biased sex ratio (1.41:1) was reported along the coast of Chennai (Pillai and Thirumilu, 2012). The difference in sex ratios might be attributed to the variation in mortality among populations, sex-specific habitat segregation, and possible single-sex migration (Wenner, 1972; Yang *et al*., 2014a). The depth and physical parameters at the sampling location could affect the sex of *P. sanguinolentus* captured, thus resulting in the skewness of reported sex ratios. Like other marine portunid species, the females of *P. sanguinolentus* prefer higher salinity than males and are often found in deeper water (Campbell and Fielder, 1986). Berried females also migrate to more inshore waters during breeding season to seek sandy substrate that aids the egg extrusion process.

Size at sexual maturity is a powerful tool to assess the general health of a stock population and for future comparisons (Waiho *et al*., 2017a). Among the three measures of maturity (morphometric, physiological and functional), the estimation of size at physiological maturity based on gonadal maturation is often preferred due to the accurate determination of gonadal development status. The size at maturity (CW_{50}) of *P. sanguinolentus* estimated using gonad maturation ranged from 76.4-100.0 mm CW in males and 82.2-96.9 mm CW in females (Table 3). Size at sexual maturity is population dependent, and wide geographical variation has been observed in other brachyuran crab species (Hines, 1989; Fisher, 1999; Waiho *et al*., 2016). Additionally, size at sexual maturity also shows temporal variation, as it is influenced by factors such as temperature and salinity (Fisher, 1999), fishing pressure and the size-selective removal of larger individuals (Olsen *et al*., 2005; Hamasaki *et al*., 2011), food availability, and other hydrodynamic conditions (Hill *et al*., 1997).

Growth and mortality

Due to the presence of their protective exoskeleton, growth in crustaceans is discontinuous and occurs during successive moulting events (Hartnoll, 1985; Abdullah-Zawawi *et al*., 2021). Two of the commonly estimated parameters for growth are asymptotic length (L_∞) and annual growth constant (K) (Froese and Binohlan, 2000). Mortality can be characterised by instantaneous total mortality rate (Z), based on size-converted catch curve using seasonal von Bertalanffy growth estimates (King, 1995); instantaneous natural mortality rate (M), estimated using Pauly's empirical equation (Pauly, 1980); fishing mortality (F), derived from Z-M; and exploitation rate (E), which is the ratio of F/Z (Quinn and Deriso, 1999). The growth and mortality parameters for *P. sanguinolentus* are presented in Table 4. It is notable that *P. sanguinolentus* populations exhibiting larger L_∞ have lower K values. Additionally, the K values within the same population are all skewed towards males, except for the population from Kozhikode, India (Table 4). Since growth parameters such as L_∞ and K are affected by various intrinsic and extrinsic factors (e.g., cohort, sex, physical parameters, fishing pressure), they are deemed unsuitable for comparing populations (Haukioja and Hakala, 1979). They are, however, useful tools that are crucial for effective fishery and conservation management of economically important species (Rouf *et al*., 2021), including *P. sanguinolentus*. Further analysis of the growth parameters by Lee and Hsu (2003) shows that although both sexes of *P. sangnuinolentus* exhibit the same growth rate, females achieve their smaller maximum size in a significantly shorter time than males. The smaller size at maturity of females compared to males is a common phenomenon among portunids (Fazhan *et al*., 2021; Waiho *et al*., 2021), whereby females divert their energy into reproductive output instead of somatic growth. Such information is crucial for the incorporation of *P. sanguinolentus* into the aquaculture sector and to aid in trait selection strategy.

The total mortality rates (Z) of *P. sanguinolentus* differed among populations (Table 4). Among the possible explanations for the variation are the difference in temperature and estimation methods (Leffler, 1972; Lee and Hsu, 2003). However, the exploitation rates (E) indicated that the reduction in *P. sanguinolentus* in most populations was due equally to natural and fishing losses, except in Karnataka and Gujarat, India, where females exhibited high E values (>0.59) (Table 4). The high M values of *P. sanguinolentus* in all populations were expected, as this is considered a common characteristic of species with r-strategy that mature in a short period, exhibit high fecundity and small body size, have a relatively short life span, and lack parental care (Gunderson, 1980; Kornienko, 2020). It is also worthy to note that the estimation of mortality parameters is based heavily on the size-converted catch curve, which in turn is influenced by the sample size and population structure of sampled populations (Lee and Hsu, 2003).

Table 3. Size at maturity (CW_{50}) of *Portunus sanguinolentus*.

Sex	**Size at maturity, CW_{50} (mm)**	**Sampling location**	**Reference**
Male	76.4	Honghai Bay, China	Yang *et al*., 2014a
Female	82.2	Honghai Bay, China	
Female	90.0	Karnataka, India	Dineshbabu *et al*., 2007
Male	60.8*	Karachi, Pakistan	Rasheed and Mustaquim, 2010
Female	63.5*	Karachi, Pakistan	
Male	100.0	Karwar, India	Reeby *et al*., 1990
Female	87.0	Chennai, India	Pillai and Thirumilu, 2012
Female	83.0	Calicut, India	Sarada, 1998
Female	96.9	Gujarat, India	Dash *et al*., 2013
Male	97.5	Negombo, Sri Lanka	Wimalasiri and Dissanayake, 2016
Female	94.0	Negombo, Sri Lanka	

Note: * indicates short carapace width (distance between the bases of the ninth anterolateral teeth)

Table 4. Growth and mortality parameters of *Portunus sanguinolentus*.

Sex	**Sampling location**	**Growth parameters**			**Mortality parameters**			**Reference**
		L_∞ (mm CW)	**K ($year^{-1}$)**	**Z ($year^{-1}$)**	**M ($year^{-1}$)**	**F ($year^{-1}$)**	**E**	
Male	Northern Taiwan	204.75*	0.97*	3.16*	1.65	1.51	0.48	Lee and Hsu, 2003
Female	Northern Taiwan	194.25*	0.87*	3.37*	1.8	1.57	0.47	
Male	Karnataka, India	169.00	1.60	5.96	$2.80^{\wedge}$	3.20	0.53	Dineshbabu *et al*., 2007
Female	Karnataka, India	170.00	1.60	6.84	-	4.00	0.59	
Male	Southwest coast, India	195.00	0.99	-	-	-	-	Sukumaran and Neelakantan, 1997a
Female	Southwest coast, India	188.00	0.82	-	-	-	-	
Male	Gujarat, India	174.20	1.40	4.19	2.15	2.04	0.49	Dash *et al*., 2013
Female	Gujarat, India	181.00	1.10	4.44	1.69	2.75	0.62	
Pooled	Gujarat, India	178.72	1.20	4.69	1.84	2.85	0.61	
Male	Kozhikode, India	161.80	1.49	-	-	-	-	Sarada, 1998
Female	Kozhikode, India	172.90	1.57	-	-	-	-	
Male	Kanara, India	173.00	-	-	-	-	-	Sukumaran *et al*., 1986
Female	Kanara, India	163.00	-	-	-	-	-	

Note: L_∞ = asymptotic length; K = annual growth constant; Z = instantaneous total mortality rate; M = instantaneous natural mortality rate; F = fishing mortality; E = exploitation rate; * indicates significant different ($p<0.05$) between sexes at the same sampling location; ^ indicates M value estimated without specifying sex.

Spawning season and fecundity

The presence of berried crabs throughout the year is classified as continuous breeding, whereas the presence of berried crabs in only a few months is considered discontinuous or seasonal breeding (Rasheed and Mustaquim, 2010). Brachyuran crabs that inhabit tropical waters tend to spawn year-round because the environmental conditions are consistently favourable for gonadal development (Yang *et al*., 2014a). However, brachyuran crabs that inhabit temperate waters only spawn in certain months, when the water temperatures are higher and more suitable for gonadal development (Warner, 1977). Warner (1977) also suggests that brachyuran crabs that inhabit subtropical and tropical regions show both continuous and seasonal reproductive patterns. The study by Rasheed and Mustaquim (2010) showed that berried females of *P. sanguinolentus* could be found throughout the year, except in June, in the coastal waters of Pakistan, and that the breeding activity was highest in May, July, and September. On the other hand, a study by Sukumaran and Neelakantan (1999) in Karnataka Coast showed that ovigerous females could be found throughout the year, although their numbers were higher from December to March and lower in September. Similar results were shown from a study by Yang *et al*. (2014a) in Honghai Bay, South China Sea, where the peak season of *P. sanguinolentus* berried females occurred from January to March. In Japan, ovigerous *P. sanguinolentus* females were found in more abundance from August to January (Ariyama, 1996). The results from these studies suggest that *P. sanguinolentus* exhibits continuous spawning, but with differences in spawning rate that may be associated with seasonal factors such as variation of temperature, salinity, food availability, photoperiod, health condition, and rainfall (Pillai and Thirumilu, 2012; Yang *et al*., 2014a).

Similar to most other brachyurans (Gardner, 1997; Danielsen *et al*., 2019), the body size (body weight and carapace width) of *P. sanguinolentus* females is highly correlated with the number and size of eggs produced (Lee and Hsu, 2003). This suggests that the presence of a higher percentage of large females will increase the maximum individual fecundity estimates of a population (Danielsen *et al*., 2019). The fecundity of gravid females was 4.1×10^5 to 2.44×10^6 eggs in the waters of Taiwan (Lee and Hsu, 2003), 2.7×10^5 to 1.4×10^6 eggs in the coastal zones of Karachi, Pakistan (Rasheed and Mustaquim, 2010), 5.9×10^4 to 5.7×10^5 eggs in Honghai Bay, China (Yang *et al*., 2014a), and 1.1×10^5 to 1.4×10^6 eggs along the west coast of Sri Lanka (Wimalasiri and Dissanayake, 2016). Similar to the factors that affect spawning, factors such as seasonal variation, geographical range and physical parameters, crab body size, and food availability may explain the discrepancy in fecundity among *P. sanguinolentus* populations (Yang *et al*., 2014a; Wimalasiri and Dissanayake, 2016). Additionally, the loss rate of eggs from gravid females during commercial catches employing different fishing gears could also impact the overall estimated fecundity. It is important to have a continuous record of the spawning season and fecundity of *P. sanguinolentus* females in each population to better inform the reproductive potential of spawning stock biomass and the health and exploitation potential of crab stocks.

FEEDING BEHAVIOUR AND FOOD PREFERENCE

Brachyuran crabs, including swimming crabs such as *Portunus sanguinolentus*, use their chelipeds to handle and crush their prey for feeding (Fazhan *et al*., 2022). The dominant cheliped is used to crush the prey, such as crustaceans and molluscs, while the minor cheliped is used as a cutter and to transfer food to the mouth. Three-spot swimming crabs are bottom feeders and opportunistic omnivores that feed on sessile invertebrates, slow-moving benthic macroinvertebrates such as bivalves, crustaceans and gastropods, and carcasses (Sukumaran and Neelakantan, 1997b). They appear to be opportunistic predators, but the absence of prey does not affect their diet as they are also scavengers. Based on stomach contents of *P. sanguinolentus*, Rasheed and Mustaquim (2018) showed that their diet mainly consists of crustaceans such as small crabs and shrimps, followed by bivalves and gastropods. Furthermore, detritus found in the stomachs suggested that the mouthparts of *P. sanguinolentus* are not morphologically adapted for deposit feeding; thus, the detritus was probably derived from prey or it was consumed along with other food items. In addition to their main diet of crustaceans, bivalves and gastropods, small quantities of plant material, fish, polychaetes, brittle stars and starfish were also found in the *P. sanguinolentus* stomachs (Rasheed and Mustaquim, 2018). It is doubtful that *Portunus* spp. are able to capture live swimming fish in their natural environment. Thus, it is suggested that the fish content in the stomachs of these crabs are from carrion (Wu and Shin, 1997). Although crustaceans are the most preferred food of adult *P. sanguinolentus*, the juveniles prefer various items such as polychaetes (*Nereis* sp. and *Glycera* sp.) instead of crustaceans. Their diet begins to change during the sub-adult phase, from these miscellaneous items to crustaceans as their main food source (Sukumaran and Neelakantan, 1997a). It is assumed that *P. sanguinolentus* ceases feeding prior to and during the moulting process, as has been shown in other brachyuran crabs such as *P. pelagicus* (Williams, 1982; Sugumar *et al*., 2013), *Chionoecetes opilio* (O’Halloran and O’Dor, 1988), and *Scylla paramamosain* (Zhang *et al*., 2021a). Since *P. sanguinolentus* is opportunistic in its feeding and is widely distributed across the Indo-Pacific region, it would be interesting to investigate their diet dependency on the local availability of prey types.

ECONOMIC IMPORTANCE

As with other *Portunus* swimming crab species, *P. sanguinolentus* forms an integral part of swimming crab fisheries in most of the countries where it occurs naturally, as the market price for swimming crabs is high and continues to increase. Previously, however, swimming crabs were not considered as targeted resources but only as incidental bycatch (Pillai and Thirumilu, 2012). The swimming crab fishery is now considered a high value industry in most subtropical and tropical Asian countries, and the increase in catch rate of *P. sanguinolentus* (>8 $\text{kg}\cdot\text{h}^{-1}$) is often linked with autumn (September to October) and the occurrence of La Niña and El Niño events in the Taiwan Strait

(Naimullah *et al*., 2021). Specific fishery landing data of *P. sanguinolentus* in India shows that on average, a decreasing trend of average annual landings was observed in most locations (Dineshbabu *et al*., 2007; Pillai and Thirumilu, 2012). The reported average landing of *P. sanguinolentus* varied among locations, with Karnataka coast recording the highest landing of 416 t (1998-2005; Dineshbabu *et al*., 2007), followed by Chennai (half of 765.8 t, the total landing of swimming crabs) from 1998-2007 (Pillai and Thirumilu, 2012), and 322 t at Gujarat (2006-2010; Dash *et al*., 2013). The catch per unit effort (CPUE) was higher at Karnataka coast (7.20 $kg{\cdot}unit^{-1}$) (Dineshbabu *et al*., 2007) than at Gujarat (6.3 $kg{\cdot}unit^{-1}$) (Dash *et al*., 2013). The catch per hour of *P. sanguinolentus* in India, however, was much lower (0.23-2.01 $kg{\cdot}h^{-1}$) (Dineshbabu *et al*., 2007; Pillai and Thirumilu, 2012) compared to that of the Taiwan Strait (>8.00 $kg{\cdot}h^{-1}$) (Naimullah *et al*., 2021). The lack of consistent landing data from most *P. sanguinolentus*-producing countries hinders the comprehensive comparison of its landings and economic importance to the national and international crustacean fishery sectors. Nevertheless, the available data from India and Taiwan Strait highlight the reliance of the local coastal communities on *P. sanguinolentus* capture fisheries as a source of income and livelihood.

CONCLUSIONS AND FUTURE CHALLENGES

Portunus sanguinolentus experiences classic ontogenetic shifts found in other brachyuran crabs, as they develop from planktonic larvae to benthic crablets. Although the early life stages of *P. sanguinolentus* have been characterised, there is still a huge knowledge gap regarding the sex determination and differentiation processes of this portunid species. Uncovering when and how sex determination and differentiation occur in *P. sanguinolentus* would provide a critical foundation for the future development of sex-manipulation techniques in *P. sanguinolentus* and its incorporation into the aquaculture sector. As species survival is highly dependent on its successful recruitment, knowledge of larval transport and dispersal, settlement during transitioning life stages, habitat preference, recruitment mechanisms, and adaptability to environmental changes is essential. The sustainable management of the *P. sanguinolentus* fishery sector relies on adequate information on their population structure, fishing effort and pressure, and the influence of this species on the socio-economic status of local communities. Therefore, their population structure,fishing effort and pressure, and the influence of this species on the socio-economic status of local communities. Therefore, biological, ecological, and socio-economic data of *P. sanguinolentus* populations are needed to develop a conceptual model framework for resource sustainability and to guide fishery management strategies.

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