

Life-history, movement, and habitat use of *Scylla serrata* (Decapoda, Portunidae): current knowledge and future challenges

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Abstract The mud crab *Scylla serrata* is a highly exploited species, associated to mangrove ecosystems in the Indo-West-Pacific. It has a complex life cycle with a dispersing larvae phase, and benthic juveniles and adults. The former are stenohaline depending on high-salinity conditions to survive, whereas the latter are physiologically well adapted to changing temperatures and salinities, conditions that typically occur in mangrove habitats. Movement and habitat use of large juveniles and adults are well studied, and these life stages are known to utilize and move between various habitats within the mangrove ecosystem: intertidal flats as well as subtidal channels and flats. Females undertake long movements from brackish inshore

waters to waters with oceanic conditions for spawning. Sensory abilities—of early stages and adult stages—have hardly been studied, and little is known about larval and early benthic stages in the wild. Summarizing, the literature revealed substantial gaps in the understanding of the spatiotemporal dynamics of the different life stages and of the clues that trigger recruitment, movement, and other behavior. This is the first comprehensive review on the life history, movement patterns, habitat use, and systemic role of *S. serrata* with emphasis on the respective life stages and geographic differences. We emphasize the need for further research into these processes as a basis for the sustainable management and conservation of this species.

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Introduction

The highly valued mud crab *Scylla serrata* (Forskål, 1775) (Portunidae) is widely distributed throughout the Indo-West-Pacific (IWP) region (Keenan et al., 1998), where it is closely associated with mangrove forests. *S. serrata* has a substantial share in industrial and artisanal fisheries throughout its distribution, and fishing effort and landings have drastically increased in the last decades (Allan & Fielder, 2003; FAO, 2012). The global catch rose from approx. 10,000 t in

1990 to 40,000 t in 2012, and there was a concurrent increase in aquaculture production from approx. 4000 to 175,000 t (FAO, 2012). Despite efforts taken to establish sustainable aquaculture of this species, indications of overfishing (Naylor et al., 2002; Ewel, 2008) have led to the establishment of protected areas and fishery limitations in some countries (Australia; Butcher et al., 2003).

Scylla serrata has been studied since the 1940s, and more than 590 research papers, theses, and reports have been published, the majority (67%) after the revision of the genus in 1998 (Keenan et al., 1998). Until then, *S. serrata* and its co-species *S. tranquebariqua*, *S. paramamosain*, and *S. olivacea* that often occur in the same habitats were frequently mistaken as one species (see “Taxonomy” section). Despite its economic importance and the vast number of publications, basic aspects of the biology and ecology of *S. serrata* for optimizing its conservation and management, e.g., larval dispersal and habitat choice, are not yet well understood. There is also no peer-reviewed review focusing on the general biology and ecology of *S. serrata* that would help identify gaps of knowledge and guide future efforts of researchers and managers. Many publications have been published as non-peer-reviewed reports or technical papers with limited circulation.

This review presents available information on life-history, population dynamics, movement, and habitat use of *S. serrata* with an emphasis on regional differences to facilitate predictions on possible changes due to climate change and facilitate local management. Information from both peer-reviewed publications and unpublished reports (i.e., theses and technical reports) is included. The term “*S. serrata*” was used to search in ‘title’ or ‘topic’ in the database ISI Web of Science, resulting in >1100 publications. These were sorted, and publications not containing *S. serrata* in the title or abstract were discarded. Due to the long confusion of the classification of the genus *Scylla*, it is often difficult to ascertain the species in publications prior to 1998 (see “Taxonomy” section). To avoid stating information that may relate to other *Scylla* species instead of *S. serrata*, we only considered publications from early years from study regions where this particular species is the only *Scylla* species known to occur, i.e., South-East Africa, southern East Australia, South Indo-Pacific Islands (“Geographical distribution” section; Fig. 1; Appendix Table 1). Only *S. serrata* is considered here and referred

to as the “mud crab”. A great proportion of the literature available is about physiological aspects and topics related to aquaculture, which is not in the focus of our work and thus not included in this review, except few technical papers dealing with aspects of development (life-history) and tolerances toward natural parameters.

Taxonomy

The portunid crab *S. serrata* was first described by Forskål in 1775 as *Cancer serratus* from Jiddah, Red Sea. It is a widespread species occurring in coastal tropical and subtropical regions in the whole Indo-Pacific region. Estampador (1949) was the first to recognize three different species within the genus *Scylla* in the Philippines on the basis of variations in size, color, and shape: *S. serrata* (Forskål, 1775), *S. oceanica* (Herbst, 1796), and *S. tranquebarica* (Fabricius, 1798). *S. serrata* var. *paramamosain* was regarded as a variation of *S. serrata*. This classification was accepted for several decades, except for some obscurities regarding the clear differentiation of species and variations (Serene, 1952). Kathirvel & Srinivasagam (1992) also noticed the occurrence of several species of *Scylla* in India, but considered *S. oceanica* as a synonym of *S. tranquebarica*. Others recognized *S. paramamosain* as an additional species in Papua New Guinea (Quinn & Kojis, 1987) and Western Australia (Taylor, 1984). Due to these uncertainties some authors referred to *S. serrata* as a single species with different morphs (Stephenson & Campbell, 1959; Perrine, 1978).

The existence of three distinct species (*S. serrata*, *S. tranquebarica*, and *S. oceanica*) was already noted by Fuseya and Watanabe (1996) in Japan on the basis of differences in three genetic loci (EST, LAP-2, and SOD). Keenan et al. (1998) revised the genus *Scylla*, combining genetic and morphometric data. Allozyme electrophoresis and analysis of mitochondrial DNA sequences (COI I and 16 S RNA) revealed four distinct species of *Scylla*, which are now generally accepted: *S. serrata* (Forskål, 1775), *S. tranquebarica* (Fabricius, 1789), *S. olivacea* (Herbst, 1796), and *S. paramamosain* (Estampador, 1949) (Fuseya & Watanabe, 1996; Keenan et al., 1998; Klinbunga et al., 2000; Imai et al., 2004; Fuseya et al., 2007; Lin et al., 2007; Ogawa et al., 2011; Mandal et al., 2014).

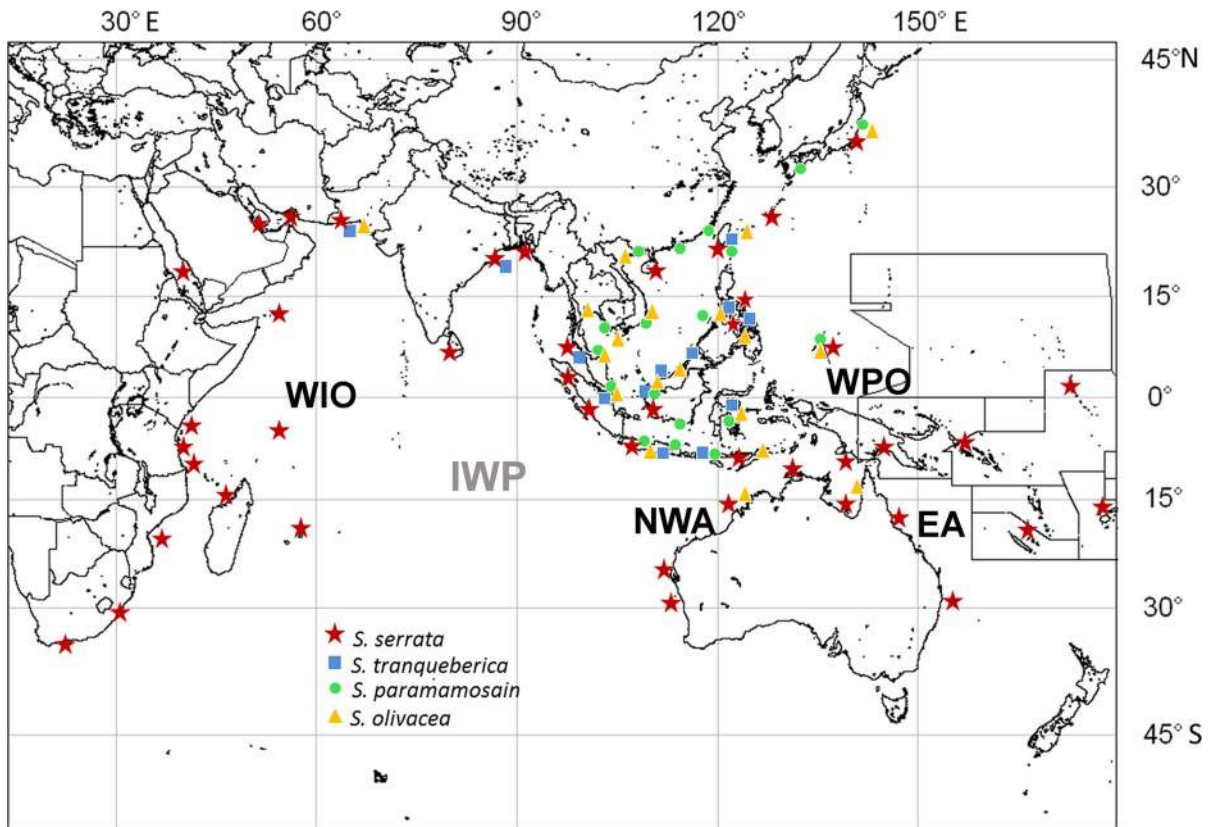


Fig. 1 Distribution of the four *Scylla* species. Not shown: Hawaii with *Scylla serrata* populations. IWP: Indo-West-Pacific (whole area), WPO: Western Pacific Ocean, EA: Eastern

Australia, NWA: North-Western Australia, WIO: Western Indian Ocean. Scale: 1: 11,000,000 at latitude 0°; a table with references can be found in Appendix 1

Despite the existence of identification keys, morphological identification fails in some cases. A presumed *Scylla* hybrid from Japan with ambiguous morphological characters was identified to be an offspring of female *S. olivacea* and a male *S. serrata* by analyzing mitochondrial and nuclear DNA (Imai & Takeda, 2005). Individuals from Indonesia are also sometimes hard to be identified due to the lack of distinct morphological features (I. Nordhaus, *pers. observation*).

Geographic distribution

Scylla serrata is the widest spread species of the genus *Scylla*. It can be found in tropical and subtropical coastal regions of the IWP including the southern coast of South Africa (34°S) (Du Plessis, 1971), the east coast of Africa (Le Reste et al., 1976; Barnes

et al., 2002; Davis et al., 2004; Fondo et al., 2010; Macia et al., 2014), the Red Sea (Keenan et al., 1998), Gulf of Aden (Simões et al., 2001), the Arabian/Persian Gulf (Hogarth & Beech, 2001; Rezaie-Atagholipour et al., 2013), South-east and East Asia (Bight of Bengal, 19–21°N, Mohanty et al., 2006; Zafar et al., 2006; Indonesia, 5°N–10°S, Sugama and Hutapea, 1999; Nordhaus et al., 2009), the northern Philippine Sea, (34°N) (Imai et al., 2004), and Australia (Keenan et al., 1998). It also occurs around oceanic islands of the Indo-Pacific: Marianas, Fiji, Samoa Islands (Keenan et al., 1998), and Seychelles, Maldives, and Mauritius (Gopurenko et al., 1999; Anand et al., 2006; Fratini et al., 2010). The species was introduced to the Hawaiian Archipelago between 1926 and 1935 and has since then become an established population (DeFelice et al., 2001). *Scylla serrata* occurs in areas up to 38°S, whereas the other three species are centered around the equator. *Scylla*

tranquebarica, *S. olivacea*, and *S. paramamosain* are distributed on the Asian continental shelf, and only *S. olivacea* can be found in northern parts of Australia (Keenan et al., 1998; Fig. 1). Referring to the literature after 1998, the latter three species dominate the coastal areas of the southern China Sea and the Java Sea, whereas *S. serrata* is hardly found here (Keenan et al., 1998; Sugama & Hutapea, 1999; Overton, 2000; MacIntosh et al., 2002; Ikhwanuddin et al., 2011).

Analysis of mitochondrial *CoxI* genes revealed at least three distinct genetic stocks of *S. serrata* in the Indo-Pacific region: Western Indian Ocean, Eastern Australia; and Western Pacific Ocean (WPO), North-Western Australia (Fratini et al., 2010, Fig. 1). The Australian populations can be separated into two distinct clades (northern and eastern populations) divided by the Torres Strait (Gopurenko & Hughes, 2002). Local mud crab populations are not genetically distinct from each other, but can differ in phenotype (e.g., smaller sizes for southern distribution limit). The larvae have high dispersal potential during the planktonic life stages (16–75 days depending on environmental conditions, Baylon 2010), which is driven by regional and global currents. This enables *S. serrata* to connect with other geographic areas and expand to new habitats, resulting in panmixis of the species (Hill, 1994; Gopurenko et al., 1999, 2003).

Furthermore, genetic analyses suggest colonization by mud crabs of the IWP through propagules deriving from the WPO (Gopurenko et al., 1999; Fratini et al., 2010). The most ancestral haplotype is found in the Red Sea; the colonization of the IWP region seems to have its origin in a rapid single radiation through the Pleistocene (Gopurenko et al., 1999). The occurrence of a common haplotype from the eastern Australian clade in few individuals in the radically divergent north-western Australian clade as well as the existence of a haplotype in south-east China connecting these two Australian clades could be an indicator of human-mediated translocation (Fratini et al., 2010).

Larval development

The larvae of *S. serrata* hatch in offshore areas where they undergo five developmental stages (stage I–V; Delathiere, 1990). The survival and developmental time of the larvae strongly depend on water temperature and salinity (Hill, 1974; Hamasaki, 2003;

Nurdiani & Zeng, 2007; Baylon, 2010). Laboratory experiments showed that all larval stages of *S. serrata* need high salinities and intermediate-to-warm temperatures for survival, with optimum salinities of 25–30 (practical salinity units) and optimum temperatures of 26–30°C (Hamasaki, 2003; Nurdiani & Zeng, 2007; Baylon, 2010), as reported for other tropical and subtropical crab species (Anger, 2001). The first zoeal stage does not survive salinities below 15–17.5 (Hill, 1974; Baylon, 2010) and temperatures $\leq 20^\circ\text{C}$ (Baylon, 2010). This explains the offshore migration of the females as the salinity in estuaries often fall below 20 (see “Female spawning migration” section). The last zoeal stage (stage V) still needs higher salinities and temperatures to successfully metamorphose into the megalopa stage (Baylon, 2010). Even though the megalopa stage shows increased tolerance towards salinity (15–45) and low temperature (20°C), it still does not develop into the first crab stage at salinities below 15 (Baylon, 2010). The physiological optima suggest that settlement and metamorphosis into the first crab stage occur in waters with intermediate-to-high salinities.

The results of larval rearing studies in aquaculture suggest that the optima of temperature at optimal salinities (25–30) differ slightly for the larvae from different areas: Hill (1974) revealed higher larval mortality at temperatures above 25°C in South Africa, whereas in Japan (Hamasaki, 2003) and Indonesia (Nurdiani & Zeng, 2007), best survival rates were reached at 28 and 29°C, respectively. Whether these differences exist due to different sampling techniques or are actual differences in populations or phenotypic plasticity has not been investigated.

While dispersal and recruitment of many coastal brachyuran crab larvae are triggered by diurnal and tidal patterns as well as hydrological variables (DeVries et al., 1994; Macintosh et al., 1999; Pineda et al., 2007), no such patterns could be detected to date for *S. serrata*, due to insufficient sampling effort.

The behavior and ecology of mud crab larvae have been studied using hatchery-reared larvae. Webley et al. (2009) showed that laboratory-reared megalopae did not select between different habitats (mud, sand, seagrass), whereas early juveniles expressed strong preferences for seagrass. This suggests that megalopae do not benefit from preferring one of the habitats or do not depend on encountering these, whereas they seem to benefit from inhabiting seagrass as early juveniles

(Webley et al., 2009). This result can be seen as an indicator for post-settlement behavior, but this aspect should be further investigated, since the preference for seagrass could also be an indicator for preferences for structured or sheltered habitats in general.

Juvenile mud crabs

After molting into the first crab stage, the tolerance toward lower salinities increases (5–45; Ruscoe et al., 2004, Baylon 2010). The activity of early crab stages ceases at temperatures below 20°C, but the crab survives these temperatures ($\leq 20^\circ\text{C}$) and recovers when transferred back into warmer water (Baylon, 2010). The increased tolerance toward changes in salinity and low temperatures with size facilitates movement into estuarine habitats, where these factors vary substantially.

Juveniles (3–99 mm CW) are resident in the upper intertidal and remain there during low tide (Hill et al., 1982; Alberts-Hubatsch et al., 2014; Mirera, 2014, see Appendix Table 2). Heasman (1980) found crabs hiding under stones (tiles) in the upper intertidal zone in Moreton Bay, south-east Queensland. In the St. Lucia lagoon, South Africa, juvenile crabs (20–85 mm) were captured in shallow waters among macrophytes (Hill, 1979a), suggesting that juvenile *S. serrata* use habitats where they are protected from large aquatic predators. In northern New South Wales, Australia, early benthic stage *S. serrata* (3–30 mm CW, Fig. 2 III.) were found in upper intertidal areas between pneumatophores of *Avicennia marina* near the mangrove fringe at low tide, where they bury in the soft mud (Alberts-Hubatsch et al., 2014). In east Africa, this stage was predominantly found on upper intertidal flats landward from the mangrove belt at night moving to subtidal habitats during the day (Mirera, 2014). The very first juvenile stage (3–4 mm CW) was found on upper subtidal mud areas seaward to the mangrove fringe in Australia, which might indicate a settlement in subtidal areas and post-settlement relocation toward the mangrove habitat (Alberts-Hubatsch et al., 2014). In general, these ontogenetic shifts in habitat use, i.e., occupying different microhabitats within the adult habitat, can be seen as a mechanism to avoid interspecific predation and cannibalism by larger conspecifics (Alberts-Hubatsch et al., 2014).

Movement, habitat use, and activity of adult mud crabs

Adult mud crabs generally inhabit muddy estuaries and enclosures in mangrove ecosystems that are influenced by tidal waters (Arriola, 1940; Brown, 1993; Appendix Table 2). In Deception Bay, south-east Queensland, Hill et al. (1982) studied the use of different habitats by different life stages. Large adults (≥ 150 mm CW) were predominantly distributed in the subtidal with peak abundances in the summer season (January to April; Hill et al., 1982). Some were also found in intertidal areas where they occasionally inhabit burrows at low tide (Arriola, 1940; Le Reste et al., 1976; Brown, 1993). Female crabs rather bury in the mud than seeking shelter in burrows, so the majority of crabs found in burrows are males (Perrine, 1978; Ewel et al., 2009). The reason for the use of burrows remain unclear, since crabs do not return to the same burrows and do not seem to display homing behavior (Ewel et al., 2009). It has not been investigated, if burrowing mud crabs display different movement patterns from those of crabs living in subtidal creeks. Smaller crabs (100–149 mm CW) are hardly found in burrows and inhabit subtidal waters only at low tide and move into the intertidal zone at high tide with peak abundances from spring to autumn (September–March; Hill et al., 1982).

The movement of mud crabs seems to be closely related to the kind of habitat they live in (Hyland et al., 1984). In general, crabs (>100 mm CW) that live in enclosed habitats such as narrow mangrove-fringed creeks, normally do not move more than 1 km (Hill, 1975; Perrine, 1978; Hyland et al., 1984; Bonine et al., 2008), whereas in southern Moreton Bay, Queensland, crabs that are found in open environments like intertidal flats in open bays show larger movement (average 3.7 km) (Hyland et al., 1984). It is suggested that these different distances of routine movement (daily movements, e.g., foraging activity) are dependent on the availability of alternative feeding grounds at high tide. Isotope studies in Kosrae showed that even though the majority of local mud crab populations reside in their local mangrove area, some populations move regularly between mangrove forests and adjacent reef flats and seagrass meadows (<1 km distance) for feeding (Demopoulos et al., 2008). In narrow creeks, there is only a limited intertidal zone, whereas in the open environment, more and larger

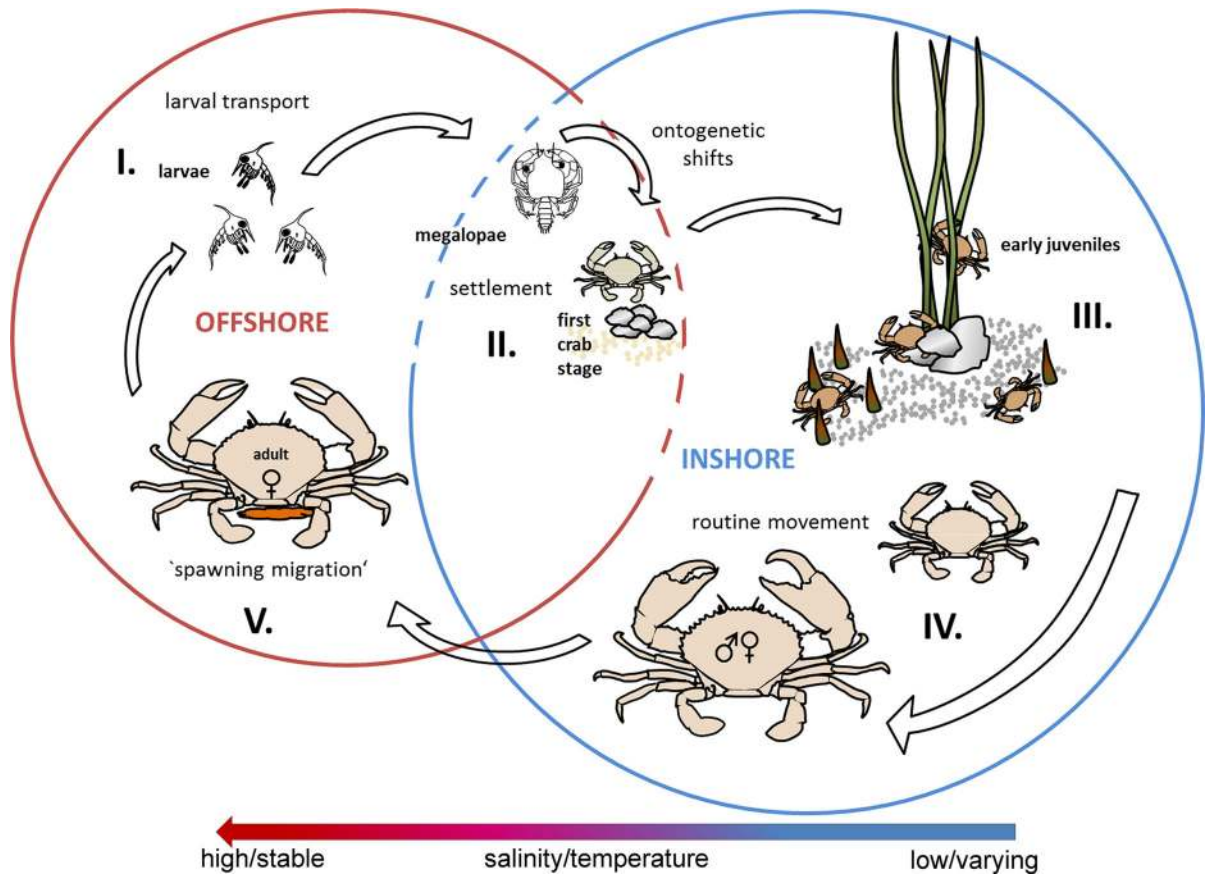


Fig. 2 Schematic drawing of the life cycle of *Scylla serrata*. The arrow indicates the gradient for salinity (from low/varying to high/stable) and temperature (from varying to stable)

intertidal flats are present, which provide alternative feeding grounds at high tide and help to avoid intraspecific competition (Hyland et al., 1984) and cannibalism. Recent studies show that movement can be influenced by the seascape and environmental conditions: Adult mud crabs may display stronger seaward movement from enclosed estuarine habitats toward open bay areas, to avoid conspecifics ('demographic diffusion'; Steneck, 2006; Alberts-Hubatsch, unpublished data). Increased freshwater flow during the rainy season may also enhance the activity of mud crabs and therefore trigger their movement (Butcher et al., 2003; Meynecke et al., 2010; Alberts-Hubatsch pers. observation).

Mud crabs are well adapted to warm temperatures (20–30°C) in the tropical and subtropical regions, but become inactive at low temperatures. Fishermen in Australia have recognized drastic decreases in catch

rates, when water temperatures drop to 20°C or exceed 35°C (Meynecke et al., 2010, unpubl. data). The majority of crabs showed decreased movement and general activity with decreasing temperatures (below 16°C), indicating that mud crabs stay inactive during the colder seasons in subtropical regions (Hill, 1980). An attempt of acclimating mud crabs to water temperatures of 10°C failed with most crabs dying (Hill, 1980).

Larger juveniles and adults are strongly euryhaline, thus tolerating broad ranges of temperature and salinity: adult mud crabs survived experimental salinities between 1 and 42 in Malaysia (Davenport & Wong 1987) and even remained active from 2 to 56 in a South African estuary (Hill, 1979a). The lethal experimental salinity was 64.9 (Hill, 1979a). Mud crabs show strong osmoregulatory responses to changing salinities (Davenport & Wong, 1987; Chen

& Chia, 1996b) and express metabolic responses toward extreme high or low salinities (e.g., nitrogen excretion; Chen & Chia, 1996b).

Dependence on large-scale climate patterns was shown in Australia where mud crab populations seem to be strongly influenced by the Southern Oscillation. A high Southern Oscillation Index (La Niña) causes cool temperatures and rainfall, inducing high productivity in coastal areas and estuaries that can positively affect the occurrence and reproduction of the mud crab (Meynecke et al., 2006, 2010, 2012; Meynecke & Lee, 2011).

Female spawning migration

The spawning migration (Fig. 2, V.) of mud crabs is poorly understood. The absence of ovigerous female mud crabs in brackish waters (Le Reste et al., 1976) indicates that they leave their usual habitat for spawning. In accordance with the findings of ovigerous mud crabs in bottom trawls while fishing for prawns offshore, it was concluded that female mud crabs move long distances (up to >95 km) offshore for spawning (Hill, 1994). Other studies noticed ovigerous females in shallow lagoons, bays, and inlets (Arriola, 1940; Brick, 1974; Prasad & Neelakantan, 1989), indicating that the spawning migration might depend on hydrological features rather than topographic features. However, to date it was not possible to track the exact movement of gravid females to their spawning grounds. It can only be assumed that female mud crabs seek habitats with stable abiotic conditions with high salinity and temperatures for hatching the larvae. The stable environment maximizes the survival rate of larvae, and the currents facilitate dispersal (see “Larval development” section).

The time of the spawning season varies over different geographic regions. Some authors suggested that the timing of the spawning season is related to latitude and there with the climate zones (tropics, subtropics), but a summary of the different spawning seasons does not reveal such a pattern (Table 1). In most regions, the spawning season coincides with the rainy season, but there are some exceptions (e.g., Madagascar and Hawaii, Brick 1974; Le Reste et al., 1976; Table 1), which makes a link with warm temperatures more likely (Perrine, 1978).

Maturity and mating

Maturity of *S. serrata* starts at different sizes in different geographic regions (Tables 2, 3). Some authors (Quinn & Kojis, 1987; Robertson & Kruger, 1994) suggested that the different maturation sizes depend on the latitudinal distribution of the crabs, resulting in a faster maturation in tropical regions. However, these conclusions might actually derive from the different size classes of the various *Scylla* species, since these assumptions were made before the revision of the species (see “Taxonomy” section). Nevertheless, in recent research, different sizes at maturity were observed for *S. serrata* at different locations. In both males and females, a distinction between physiological, morphological, and functional maturities can be made. Physiological maturity in males is characterized when spermatophores develop in the vas deferens after the pubertal molt, but the external appearance of the crab might still be the one of an adolescent/juvenile crab (Robertson & Kruger, 1994; Knuckey, 1996). Once the male develops large claws, morphological maturity is reached (Knuckey, 1996). Functional maturity describes the ability to successfully mate, which is indicated by ‘mating-scars’ on the sternum and first pair of walking legs of the male. Even though some adolescent males have mated, functional maturity was far more prevalent in morphologically mature males. In South Africa, males reach physiological maturity at smaller sizes than in Australia (92 vs. 110 mm CW, respectively), and size at functional maturity seems to vary due to the geographic region (Table 2).

In females, physiological maturity is reached during the last pubertal molt when the ovaries are fully developed. In contrast to males, the functional maturity is often reached at the same time as physiological maturity, since successful mating can already occur during the last pubertal molt when the female is soft-shelled (see below). Morphological maturity is characterized by the development of a mature abdominal flap (wider and more rounded than in adolescent females, Robertson & Kruger, 1994) and sometimes by the ability of extruding eggs (Hill, 1975). Therefore, comparing female sizes at maturity from different geographic regions can be confusing, since some authors use the shape of the abdominal flap as indicator for maturity, whereas others define maturity by the ability to mate or extrude eggs

Table 1 Different spawning seasons of *Scylla serrata* in relation to latitude

Location	Latitude	Peak spawning season	Year-round?	Reference
Hawaii	21°N	May–October (summer, dry season)	No	Brick (1974)
Philippines	15°N	End of May to middle of September	Yes	Arriola (1940)
Karwar, India	14°N	Two peaks: Dec–Mar and Sept–Nov	Yes	Prasad & Neelakantan (1989)
Andaman Sea, Thailand	8°N	Late rainy season (Oct–Feb)	Yes	Poovachiranon (1992)
Negombo, Sri Lanka	7°N	Two season: April and August	No	Jayamanna & Jinadasa (1993)
Ramisi River, Kenya	4°S	Possible peak in 2nd half of the year	Yes	Onyango (2002)
Labu estuary, Papua New Guinea	6–7°S	Two peaks: April–June and Sept–Oct	Yes	Quinn & Kojis (1987)
Tropical (North) Australia	11–15°S	Rainy season: November–February	No	Hill (1994)
Madagascar (North-West)	14°S	Two seasons: dry season (July/Aug), rainy season (Jan)	Not specified	Le Reste et al. (1976)
Queensland, Australia	28°S	October–March	No	Heasman et al. (1985)
Natal, South Africa	29°S	Late spring–early autumn	Yes	Robertson & Kruger (1994)
Natal, South Africa	29°S	July/August	Yes	Davis et al. (2004)
Knysna, South Africa	34°S	November–April	No	Du Plessis (1971)

Table 2 Size at physiological and functional maturity of male *Scylla serrata* in relation to latitude

Location	Latitude	Physiological maturity CW	Functional maturity CW	Source
Pohnpei	6–7°N		120–130 (130–150*)	Perrine (1978)
Tropical Australia (north)	11–14°S	110	125 (140–160*)	Knuckey (1996)
New Caledonia	20–22°S	129		Delathiere (1990)
Moreton Bay, Australia	28°S		145 (164*)	Heasman (1980)
South Africa	29°S	92	115–119	Robertson & Kruger (1994)
South Africa	32°S		123	Robertson (1996)
South Africa	34°S		141	Hill (1975)

Size measured as carapace width (CW) in mm

* Size at 50% maturity

(Table 3). However, there are differences depending on the geographic region, e.g., the smallest size at maturity (regarding the abdominal flap) is 102 mm CW in Madagascar (Le Reste et al., 1976), and the minimum size reported from Australia is 138 mm CW (Heasman, 1980, Table 3).

The gonads (ovaries/testes) of mud crabs lie below the carapace as paired H-shaped organs. The different developmental stages of the gonads are shown in Tables 4 and 5. In both sexes, the maturity stages can be identified by different size and coloration of the

gonads (Shanmugam & Bensam, 1980; Prasad & Neelakantan, 1989; Poovachiranon, 1992; Robertson & Kruger, 1994; Qunitio et al., 2007).

Mating occurs when the mature (or maturing) female is in the verge of molting. The male uses its walking legs to gently grab the female by its carapace and keeps hold to her until she molts and is soft-shelled. Then he turns her around, both open their ventral flap, and the male inseminates the female by depositing the spermatophore into the female's spermathecae by inserting his gonopodia into the female's

Table 3 Size of female *Scylla serrata* at different maturity classifications in relation to latitude

Location	Latitude	Ovary development	Ovigerous	Mating	Mature abdominal flap	Reference
Pohnpei	6–7°N		141–187	105		Perrine (1978)
New Guinea	6–7°S				85–190	Quinn & Kojis (1987)
Sri Lanka	7°N	120–130				Jayamanna & Jinadasa (1993)
Tropical Australia (north)	11–15°S		120–209			Hill (1994)
Madagascar	13°S				102–180	Le Reste et al. (1976)
New Caledonia	20–22°S	126 (140*)				Delathiere (1990)
Subtropical Australia	28°S				138 (147*)	Heasman (1980)
South Africa	28°S	116 (145*)				Davis et al. (2004)
South Africa	29°S				104 (123*)	Robertson & Kruger (1994)
South Africa	32–33°S				130–140	Robertson (1996)
South Africa	34°S		137–159	103–148		Hill (1975)
South Africa	34°S				131–141	Du Plessis (1971)

Size measured as carapace width in mm

* Size at 50% maturity

Table 4 Maturity stages of gonads in male *Scylla serrata* (adapted from Shanmugam & Bensam, 1980)

Stage	Color	External characteristics	Histology
I Immature	Transparent, creamy	Testes occupy $\leq 1/6$ th of haemocoel	Adhering to the lobes of hepatopancreas without prominent vas deferens
II Maturing	Creamy white	Testes occupy 1/4th to 1/3rd of haemocoel	
III Mature	Milky white	Testes occupy 1/2 to full haemocoel	With a thick vas deferens

genital openings (Du Plessis, 1971; Lavina, 1978b). Multiple spawning after a single mating has been observed in the female mud crab (Du Plessis, 1971; Brick, 1974), indicating that females can store sperm, which is a common feature in larger decapod crustaceans (Raviv et al., 2008).

Sex ratios and density

In unfished populations, female mud crabs can be three-fold outnumbered by males, for example in Kosrae, Micronesia the male: female ratio can be as high as 3:1 (Bonine et al., 2008). Similar ratios have been reported from other studies (Heasman, 1980). By contrast, in areas with a sex-biased fishery, a strong shift toward female-dominated populations is found. In Queensland, Australia, the fishing regulations only allow large (≥ 150 mm CW) males to be taken, which results in increasing numbers of large females compared to males. This shift can be reversed with the

implementation of marine protected areas (MPAs) where fishing is prohibited (Pillans et al., 2005; Butcher et al., 2014; Alberts-Hubatsch, pers. observation).

Population densities and biomass are often difficult to measure, and only few studies have addressed this issue. Abundances and biomass can be important indicators for the health of the species as well as the whole ecosystem (Butcher et al., 2003; Walton et al., 2007). Low densities from 0.2 to 2.4 crabs per hectare were reported from North Australia, depending on the season and the activity of the mud crabs (Tait et al., 1985), while densities as high as 40 crabs per hectare were observed in Palau (Ewel et al., 2009). This report coincides with earlier studies, which reported densities of 44–53 crabs per hectare for Natal, South Africa (Robertson & Piper, 1991) and 80 crabs per hectare for another South African estuary (Kleinmond estuary, Hill, 1975). Maximum densities were found in Tanzania with 1228 ± 7.3 crabs per hectare (\pm SD) at the mangrove fringe and 324 ± 10 crabs per hectare in the

Table 5 Ovary development female *Scylla serrata*, GSI = gonadosomatic index. (adapted from Prasad & Neelakantan, 1989; Poovachiranon, 1992; Robertson & Kruger, 1994; Quinitio et al., 2007)

Stage	Color	GSI	Ova diameter (mm)	External characteristics	Histology
0	Translucent				Clusters of oogonia, primary oocytes surrounded by follicle cells apparent in the ovarian lobe; pre-vitellogenic stage in some developing oocytes
I Immature	Transparent, white	≤0.5	0.01–0.06	Ovaries thin strips, covering 10% of haemocoel	Cluster of oogonia and primary oocytes, surrounded by connective tissue; more advanced oocytes in the periphery; first yolk globules previtellogenic oocytes
II Early maturing	Yellow to orange/pinkish	0.5–1.5	0.10–0.30	Ovaries increase in size, covering 20% of haemocoel	Most bigger oocytes yolk-filled; follicle cells surround each oocyte
III Late maturing	Orange	2.5–8.0	0.40–0.90	Ovaries extending into anterolateral region of carapace, covering 50% of haemocoel	Yolk globules occur in the cytoplasm, follicle cells hardly discernible; some atretic cells evident
IV Fully mature	Orange to deep orange/reddish	15.85	0.70–1.30	Ovaries covering 80–100% of haemocoel; eggs visible to the naked eye	Large yolk globules in entire cytoplasm; nucleus small; follicle cells hardly discernible; some atretic cells evident
V Spent	Yellow, orange to brown			Flaccid ovary	Some unspawned oocytes of various stages present, some atretic cells evident

inner mangroves, resulting in biomass estimates of 604 and 188 kg per hectare, respectively (Barnes et al., 2002). The high discrepancies in abundances might be due to both different sampling techniques (catching technique and effort, sampling intertidal or subtidal areas or both, sampling time) and/or actual differences in densities induced by habitat or environmental conditions.

Feeding and trophic role

Mud crabs are top benthic predators and feed on sessile or slow-moving benthic macroinvertebrates, mainly gastropods, crustaceans, and molluscs, as shown by foregut content analyses conducted on populations in Australia, Africa, and India (Hill, 1976; McLaren, 1977; Prasad & Neelakantan, 1988). The composition of food items changes as the mud crab grows (Prasad & Neelakantan, 1988). In small juveniles (<70 mm CW), foregut contents were dominated by detritus while in larger juveniles (>80 mm CW) and adults, crustaceans and fish were the dominant food

items. This change in the food composition was confirmed by stable isotope analyses in Thailand (Thimdee et al., 2001). Small mud crabs are omnivorous, feeding opportunistically on smaller crabs and plants, whereas medium- and large-sized crabs are carnivorous, feeding on benthic invertebrates (Thimdee et al., 2001) or being opportunistic scavengers (Webley, 2008).

Some authors suggested that mud crabs are predominantly feeding at night, and in laboratory experiments, mud crabs spend the daytime buried in sand and became active during the night (Hill, 1976, 1979b). In the wild, the catchability of mud crabs does not change over the day's cycle probably due to turbid waters, which suggests no periodicity in the feeding activity (e.g., south-east Australia; Alberts-Hubatsch, pers. observation).

Endo- and epibenthic food items are detected by the chemoreceptors in the mud crabs walking legs. Mud crabs seem to exhibit responses toward olfactory cues of prey items by displaying searching behavior (mainly locomotion and tactile investigation; Wall et al., 2009) to find the approximate location of the food item.

Laboratory observations revealed that the crab then starts drilling in the sand with the dactyls of its walking legs until it finds the exact location of a food item, and pushes it out of the sand with its chela (Hill, 1979b). Compared with other portunid crabs, mud crabs have relatively heavy and blunt chelae (Heasman, 1980), which allow them to crush the hard shells of bivalves and gastropods to feed on them (Williams, 1978).

In most regions, the activity, and therewith the feeding of mud crabs, is strongly linked to the wet season, which is the most productive season in the tropics (summer). The feeding rate drops with decreasing temperatures during the winter and ceases when temperature is below 12°C (Du Plessis, 1971; Hill, 1980). Feeding increases again when the water becomes warmer in the spring and during summer (Du Plessis, 1971).

The feeding rate also ceases 2–14 days before molting. Shortly after molting (2–4 days), the crab starts feeding again, when the mouthparts have hardened (Du Plessis, 1971). Females do not feed when they are ovigerous, showing a similar behavior to that of molting crabs (Du Plessis, 1971).

Little is known about turnover rates of mud crabs and the systemic importance for mangrove ecosystems, i.e., the role of mud crab for ecosystem functioning (e.g., consumption and turnover of biomass). The monthly consumption rates for intermediate sized crabs (368–678 g wet weight) varies from 0.13 g food*g crab⁻¹ in winter to 0.41 g food*g crab⁻¹ in summer (average 0.29 g food*g crab⁻¹ per month) at ambient water temperatures in the laboratory (Du Plessis, 1971). Taken these experimental numbers to the field, mud crabs increase their weight from 360 to 680 g within a year while consuming 1.74 kg of prey. Combining this number with the lowest estimate for biomass of 188 kg/hectare inside the mangrove forest (Barnes et al., 2002) would result in 654.2 kg biomass consumed by mud crabs per hectare and year. At the mangrove fringe, the amount of biomass consumed by mud crabs per hectare per year would be even greater, at 2101.9 kg (604 kg of crab biomass per hectare; Barnes et al., 2002). These figures are likely to vary strongly between regions and can only provide guidance on the potential importance of mud crabs in estuarine ecosystems. However, the significance of the trophic role of mud crabs for mangrove ecosystem functioning has rarely been studied. Only one study investigated the scavenging potential of mud crabs, and estimated its

role rather insignificant, assuming that it could be easily replaced by other scavenging or decomposing organisms (Webley, 2008). However, that study only estimated the role of *S. serrata* as scavenger, not as a predator in general.

The predation on mud crabs is the highest when they are juveniles and decreases with the increase of size (Palmqvist, 2009), but even large mud crabs are preyed upon by aquatic top predators such as crocodiles and sharks (Hill, 1979a). In South Africa, the water mongoose *Atilax paludinosus* has been found to feed on mud crabs as well (Whitfield & Blaber, 1980). In the intertidal zone, birds like the Grey Heron (e.g., *Egretta novaehollandiae*, *Butorides striatus*) are common predators on small crabs (Hill, 1979a). Many mud crabs are also subject to intraspecific predation—mud crabs are well known for their cannibalistic behavior, which hinders rearing them in high densities in aquaculture (Quinitio et al., 2001; Allan & Fielder, 2003; Mann et al., 2007).

Growth

Like all decapod crustaceans, *S. serrata* has an exoskeleton (cuticle), which makes molting a prerequisite for growth. Prior to molting (4–6 h before) the crab reduces all activities and completely stops feeding (Lavina, 1978a; Mirera & Mtile, 2009), and experiences a general weight decrease (Mirera & Mtile, 2009). The loss of weight can be allocated to the extrusion of water prior to molting. This also applies to protein levels in the hemolymph (i.e., oxyhemocyanin), which increase before molting as do the osmolality levels (Chen & Chia, 1997). In the reverse direction, hemolymph protein and electrolyte levels decrease after molting, which is associated with post-molt water uptake (Chen & Chia, 1997).

The molting follows a rhythmic pattern and is closely related to the lunar and tidal cycles (Le Reste et al., 1976; Mirera & Mtile, 2009), most crabs molt during the neap high tide during night (Mirera & Mtile, 2009). In the intertidal zone, mud crabs exclusively molt at high tide, so they are covered with water. Molting is an important factor for the reproduction process as female crabs need to be soft-shelled to be inseminated (see reproduction). The process of molting is necessary for growth, but also poses a high risk for the mud crabs. The molting crab is very

vulnerable to predators, and especially during the larval stages, there are high mortality rates due to molting (Hamasaki, 2003).

Mud crabs can easily reach sizes above 200 mm CW, and maximum reported sizes seem to be slightly different in the different regions (228 mm in Pohnpei, Perrine, 1978; 230 mm in Kosrae, Bonine et al., 2008; 206 and 209 mm in Australia, Heasman, 1980; Hill, 1994; 200 mm in South Africa, Robertson & Kruger, 1994). Growth rates of males and females are similar (Mirera & Mtile, 2009), but as in many other brachyuran crab species, adult male mud crabs are generally heavier than females of the same size due to their bigger chelae (sexual dimorphism; Schenk & Wainwright 2001). Juvenile mud crabs molt frequently which results in a high growth rate, but there is a decrease in molt frequency with the increase of age. Intermolt duration of four to seven days was observed for instar III mud crabs (8–13 mm CW) under optimal conditions (Ruscoe et al., 2004) and 18 days intermolt duration between the first two molts of larger juveniles (initial size approx. 40 mm CW) increasing to 50–60 days between 2nd and 3rd molts (from 50 to 65 mm CW; Catacutan, 2002). In the Philippines, mud crabs reached maturity in captivity within 146 days after hatching into the first crab stage and the calculated duration from egg to mature crab covered approx. 186 days with twelve–fifteen molts (Arriola, 1940).

With the increase of intermolt duration with the increasing age, there is an increase of growth increments. Mud crabs with a mean initial size of 67 mm CW are growing by an average of 15 mm CW after each molt, whereas crabs with mean sizes of 103 and 131 mm CW are growing by 20 and 23 mm, respectively (Du Plessis, 1971).

Conclusions and future challenges

Throughout its life, *S. serrata* undergoes several ontogenetic shifts, expressing different behaviors and occupying different habitats at each stage (Fig. 2): I.) the larvae are (presumably) released offshore, and undergo five larval stages before returning to coastal areas; II.) The larvae metamorphose into the megalopa stage in these coastal areas and subsequently settle and transform into the first juvenile stage in supposedly inshore areas; III.) Early juvenile mud crabs inhabit sheltered

mangrove areas, and IV.) they expand their habitat to larger subtidal and intertidal areas in or adjacent to mangrove habitat when growing into an adult crabs. V.) After mating, the male resides in inshore waters, whereas the female sets out to spawn at sea ('spawning migration'). The differences in habitat use are mainly driven by life-stage-dependent tolerances as well as intraspecific competition (cannibalism).

Although a number of publications discuss the biology of developmental stages, these are mainly interested in aquaculture purposes, e.g., best survival rates. Little information is available about the behavior and habitat use of the early life stages in the wild. Recent studies were able to detect the habitat use of small crabs, but it is also crucial to know how small juvenile crabs would react to alterations of this environment (e.g., habitat fragmentation). The survival of the species depends greatly on successful recruitment to the adult population, and therefore more knowledge is needed on larval transport, settlement process, habitat use, adaptability to changing environment, and recruitment mechanisms.

There are still some gaps in knowledge about adult habitat use and behavior. It is still not clear how and why burrows are used, and if there are different types of mud crab behavior (i.e., mud crabs using burrows vs. mud crabs not using burrows) or if there is even a shift in behavior from use of burrows to non-use of burrows depending on, e.g., the crab size or changes in environmental conditions. Furthermore, knowledge of spawning behavior of female crabs is vague, and it is not known if females only migrate when gravid; where their spawning grounds are, and which orientation mechanisms (e.g., rheotaxis, use of olfactory, auditory or celestial cues) are used to find appropriate spawning grounds.

Finally, upon reviewing the systemic role of mud crabs, it became evident that many facts on this topic remain undefined. Abundances seem to vary substantially between areas, but it is not known why and what this means for the persistence or status of the mud crab population or the ecosystem. In the light of this information gap, the development of a standardized sampling method for determining mud crab abundances is necessary to compare the role of the mud crab over (geographic) different ecosystems. Even though it is known that the mud crab is a top benthic predator, not much is known about its systemic role. Besides the suggested insignificant systemic role as a

scavenger (Webley, 2008), it is not known what consequences the absence of mud crabs on the estuarine ecosystem would have. Therefore a number of different variables would have to be investigated, starting with maximum and average size of mud crabs in the respective geographic area, as well as densities, biomass, food composition, and food intake.

Most studies neglect the fact that the species shows high variations in terms of size, maturity, spawning seasonality, and also exposure to human exploitation at different locations throughout its range. *Scylla serrata* occurs on three different continents, but to date no comparative studies have been conducted among the different locations. Regarding the apparent differences (e.g., size at maturity, thermal tolerances of larvae, abundances) it is not known if these can be attributed to differences in sampling methods, actual genetic differentiation, or phenotypic plasticity. Unraveling the geographic differences could also help to predict changes in mud crab populations and their reactions toward changing environmental parameters, as these may have already been reflected in another geographic area where mud crabs occur.

While climate change and global warming are widely accepted to cause significant changes to ecosystems globally and may impact on the persistence of marine species (Vitousek, 1994; Walther et al., 2002; Harley et al., 2006), this subject is hardly discussed in mud crab research, except few papers discussing annual variations (Meynecke et al., 2010, 2012). Rising temperatures are known to be a problem for many crustacean species from temperate regions (e.g., Walther et al., 2010). However, *S. serrata* might not be affected given that all life stages are highly tolerant toward warm and increasing temperatures, as it is typical for warm water crustaceans (Anger, 2001). Yet, the absorption of atmospheric CO₂ lowers pH in seawater ('ocean acidification') and can have negative effects on calcification rates of a variety of marine species, including crustaceans (Ries et al., 2009; Byrne, 2011). Even though crustaceans with a relative thick epicuticle seem to be less affected (e.g., Ries et al., 2009; Small et al., 2010), this has not been investigated to date for *S. serrata* and could be of particular concern for larvae and early life stages. Further, ocean acidification is known to alter the sensory abilities and therefore the behavior of marine organisms. Tropical fish larvae, for which larval sensory abilities are well studied, showed diminished

olfactory discrimination abilities under elevated CO₂ concentrations, and therefore loss of crucial cognitive abilities (Munday et al., 2009; Simpson et al., 2011; Ferrari et al., 2012). So far, these issues have received no attention in mud crab research.

Mangrove ecosystems as the primary habitat of mud crabs might experience a decline in total area due to sea-level rise (Gilman et al., 2008), potentially resulting in habitat loss for mud crabs. However, non-climate-related anthropogenic stressors such as habitat loss and fragmentation due to logging and urbanization and pollution (e.g., urban discards, toxins, microplastics) might have a greater impact on mangrove ecosystems and therefore mud crabs. Water pollution for example may also influence settlement behavior and success of mud crab larvae by altering olfactory settlement cues, as known to be the case with fish larvae (Olsén, 2011; Siebeck et al., 2015).

This review covers a number of aspects relating to the ecology of *S. serrata*. It becomes evident that there are still essential gaps in knowledge about life history, behavior, habitat use, and the significance for the inhabited ecosystem. In summarizing apparent knowledge gaps, we emphasize the pressing need for further research in a multitude of areas relating to *S. serrata*. The information gained from addressing these missing links is vital for researchers, decision-makers, and practitioners in order to develop appropriate and effective mangrove and mud crab management strategies.

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