

**Movement patterns and habitat use of the exploited swimming  
crab *Scylla serrata* (Forskål, 1775)**



Dissertation

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“That's an endangered species at most. What would be the scientific purpose of killing it?”

“Revenge”

Steve Zissou, Life Aquatic



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## Summary

Mangrove ecosystems are highly productive, providing habitat for a variety of species, of which many are harvested. In times of rapid global change, due to natural as well as anthropogenic drivers, these ecosystems are increasingly placed at risk, and so are the species living within them.

The mud crab *Scylla serrata* (Portunidae) (Forskål, 1775) is a highly valued and exploited species associated with mangrove ecosystems in the Indo-West-Pacific. Its complex life-cycle includes a dispersing larval phase and a benthic phase as juveniles and adults. The planktonic larvae are restricted to oceanic waters, since they are stenohaline and therefore dependent on stable, high salinity conditions in order to survive. Benthic juveniles and adults are physiologically adapted to changing temperatures and varying 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 move between various mangrove habitats including intertidal mangrove area flats as well as subtidal channels and flats. Females undertake long distance movements from brackish inshore waters to waters with oceanic conditions for (supposed) spawning. However, little is known about larval stages, and early benthic stages are underrepresented in the literature. The aim of this thesis is to provide deeper insights into movement patterns and habitat use at these particular life stages and to understand how these characteristics might be affected by environmental factors, such as seascape and rainfall.

Microhabitat use by the early benthic stage (EBS) mud crabs was studied at two sites in eastern Australia. The two sampling sites were mangrove fringed, one with muddy and the other with sandy sediments. The majority of EBS mud crabs were found in intertidal areas within the mangrove fringe in muddy habitats and few crabs were found in the sandy mangroves. Few individuals were found on unvegetated mud flats seawards to mangroves. Crabs from the mudflat (including first instars of 3-4 mm CW) were significantly smaller than those found in the mangrove habitat. This indicates an active migration from the mud flat towards the mangrove fringe as the crabs grow. Cannibalism is considered a major driver in the distribution patterns of EBS mud crabs, which may explain why EBS individuals stay in more sheltered areas near the mangrove fringe.

The movement of large juvenile and adult mud crabs was studied in a marine protected area (MPA) and an adjacent unprotected zone in an enclosed seascape. The aim was to determine whether the enclosed seascape facilitates directional movement of mud crabs and also if therefore the MPA has a positive spill-over effect on the mud crab fishery in adjacent waters. I assessed the effect of the banned fishery inside the MPA on the structure of the crab population by comparing sizes and sex-ratios between the two zones. Tagging crabs with a combination of T-bar/passive-integrated-transponder(PIT)-tags, allowed both physical recaptures and automated detections through an

underwater antennae system set in the creek leading to the MPA. I detected predominant seaward movement of adults, compared to the less pronounced movement in the opposite direction or sedentary behavior. Due to the predominant seaward movement and the landwards location of the MPA from the fishery zone, this resulted in spill-over. This behavior may be caused by increasing crab densities in the limited area of the MPA, so large crabs moved out of the system to avoid constant aggressive encounters. While a positive effect of the MPA on sex-ratio and size of the crabs was detectable, the effect of the fishery in the adjacent unprotected area was also found. The largest captured specimens both inside and outside the MPA were smaller than formerly reported, most likely due to the effect of downfishing.

In the third study, I tracked movements of female *S. serrata* in a river system during the supposed spawning season. Here, female *S. serrata* were tagged with acoustic transmitters 7-17 km upstream in a river in south-east Queensland, Australia. A static receiver array deployed in the river and the adjacent bay allowed for continuous tracking irrespective daytime or weather conditions. The majority of females was found to move downstream, whereas some moved upstream. The movement was supported by the tides (tidal stream transport) and crabs reached maximum speeds of 56 cm/sec for downstream and 57 cm/sec for upstream movement, both supported by high river velocity. Downstream and upstream movements ranged between 0.4 and 21.4 km and 1 and 11.4 km, respectively. Contrary to previous reports, a diurnal movement pattern of the crabs was not observed, which could be attributed to the turbid waters in the study area. Nine crabs reached the mouth of the river and five of them were detected later by receivers deployed in the bay area. Of these, only one crab was detected near the inlet leading to the open ocean. This suggests that *S. serrata* does not necessarily move offshore for spawning if oceanic conditions prevail in nearshore waters.

In summary, the results from the three independent studies contributed to knowledge about habitat use of different life stages of *S. serrata*. The studies show that mud crabs use different habitats at different life stages, every habitat providing the best conditions for growth and predator avoidance. However, there are still essential gaps in knowledge in the life cycle of *S. serrata*. I summarized the current state as well as the gaps of knowledge by compiling a literature review at the end of my thesis, which can be used to guide future efforts of researchers and managers.

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## Zusammenfassung

Mangroven Ökosysteme sind hochproduktiv und bieten einer Vielzahl von Arten – von denen viele kommerziell genutzt und befischt werden - einen Lebensraum. Aktuelle globale Veränderung, sowohl durch natürliche als auch anthropogene Ursachen, bedrohen diese Ökosysteme, sowie die unterschiedlichen Arten die in ihnen leben.

Die Mangroven-Krabbe *Scylla serrata* (Portunidae) (Forskål, 1775) ist eine Schwimmkrabbe die in den Mangroven-Ökosystem des Indo-West-Pazifiks vorkommt und hier stark befischt wird. Ihr komplexer Lebenszyklus beinhaltet eine Larvenphase, in der sie durch Meeresströmungen verdriftet wird, und eine juvenile und adulte Zeit, in der sie eine benthisch Lebensweise annimmt. Die planktonische Larve ist auf ozeanische Verhältnisse angewiesen, da sie stenohalin ist und somit stabile, hochsaline Gewässer zum Überleben braucht. Die am Boden lebenden juvenilen und adulten Krabben hingegen sind perfekt an schwankende Umweltbedingungen, wie sie in gezeitenabhängigen Mangrovenwäldern vorkommen, angepasst und können stark schwankende (hohe) Temperaturen, sowie Salzgehalte überstehen. Die Nutzung der Mangrovenwälder durch die größeren Krabben sowie die Bewegungsmuster zwischen den einzelnen Habitaten ist gut untersucht und es ist bekannt, dass sie sowohl die Gezeitenzone und Wattflächen in der Gezeitenzone nutzen, als auch die ständig überfluteten Priele, Kanäle und Untiefen. Die Weibchen dieser Art unternehmen Laichwanderungen aus den Brackwasserzonen der Flüsse und Ästuar in Gewässer höheren Salzgehaltes um dort (vermutlich) zu laichen. Auch wenn schon Vieles bekannt ist, ist das Wissen um den Lebensraum und das Verhalten der frühen benthischen Lebensstadien eher begrenzt. Das Ziel dieser Dissertation ist es, tiefer Einblicke in die habitatsabhängigen Bewegungsmuster dieser Krabben zu bekommen und vor allem welches Habitat von den jüngsten Lebensstadien genutzt wird. Weiter möchte ich herausfinden, welchen Einfluss äußere Begebenheiten, wie z.B. Regen oder die Beschaffenheit der Unterwasserlandschaft auf diese Bewegungsmuster haben.

In meiner ersten Studie habe ich das Habitat der jüngsten Krabbenstadien untersucht und habe dabei zwei verschiedene Mangrovenstandorte miteinander verglichen. An dem einen Standort war die Bodenbeschaffenheit eher sandig, während an dem anderen Standort Schlick vorherrschte. Die große Mehrheit der Krabben kam an dem schlickigen Standort vor, während an dem sandigen nur wenige vorzufinden waren. An dem schlickigen Standort fanden sich die kleinen Krabben nicht nur am Rand der Mangrove, zwischen den Wurzeln, sondern einige auch im Wattbereich davor. Unter diesen waren auch die allerersten benthischen Stadien, die 3 - 4 mm groß sind. Damit waren die Krabben aus dem Wattbereich signifikant kleiner als die aus dem mangrovennahen Bereich, was auf eine

Wanderung der kleinsten Krabben Richtung Mangrove hindeutet. Die Verteilung der kleinen Krabben wird vermutlich hauptsächlich durch das aggressive Verhalten und Kannibalismus gesteuert, was erklären könnte, dass die kleinen Krabben sich im Schutze von Wurzeln und ähnlichem im Randbereich der Mangroven aufhalten.

Die Bewegungsmuster der größeren Krabben habe ich in meiner zweiten Studie untersucht, die ich in einer marinen Schutzzone und der angrenzenden Zone, die der Fischerei offen war, durchgeführt habe. Das Ziel hierbei war herauszufinden, ob die Art der Unterwasserlandschaft die Bewegungsmuster der Krabben beeinflusst und ihre Bewegungen dadurch in eine bestimmte Richtung gelenkt werden, was unter Umständen zu sogenanntem „Spill-Over“ (Überlaufen) in die der Fischerei offenen Zone führen kann. Des Weiteren habe ich hierbei die Unterschiede der Krabben in Hinsicht auf Geschlechterverteilung und Größenzusammensetzung in den beiden Gebieten verglichen. Die Krabben wurden mit kombinierten T-bar/passive-integrated-transponder-tags markiert, die es ermöglichten die Krabben entweder direkt wiederzufangen oder durch ein automatisiertes Unterwasser-Antennensystem zu erfassen. Bei dieser Studie konnte ich überwiegend seewärts gerichtete Bewegungen feststellen im Gegensatz zu deutlich weniger Bewegungen landeinwärts oder Standorttreue. Dadurch dass die Fischereizone seewärts der Schutzzone lag, ließ sich dabei der Spill-Over-Effekt beobachten. Während sich ein positiver Effekt der Schutzzone auf die Größe und der Geschlechterverteilung der Krabben bemerkbar machte, ließen sich doch auch die Fischereieffekte der benachbarten ungeschützten Zone nicht übersehen: die Maximalgrößen der Krabben innerhalb wie außerhalb der Schutzzone war deutlich kleiner als aus anderen Gebieten bekannt, was auf eine zu starke Befischung großer Größenklassen schließen lässt.

In meiner dritten Studie habe ich die Bewegungen weiblicher Krabben während ihrer Laichwanderung untersucht. Hierfür wurden die Weibchen in einem Fluss gefangen und mit akustischen Transpondern ausgestattet, die es ermöglichten die Krabben über ein automatisiertes Netz aus Hydrophonen zu verfolgen, die unabhängig von Wetter oder Sichtverhältnissen operierten. Die Mehrheit der Weibchen zog flussabwärts Richtung Bucht, während sich einige flussaufwärts bewegten. In jedem Fall wurde die Bewegungsrichtung durch die Gezeiten unterstützt. Die größte Strecke die bei der Abwärtswanderung verfolgt werden konnte war über 21 km lange und für Wanderung flussaufwärts über 11 km. Im Gegensatz zu früheren Berichten konnte keine tageszeitabhängige Aktivität festgestellt werden. Auch wenn einige Krabben die Flussmündung erreichten, wurde nur eine einzige Krabbe in unmittelbarer Nähe zum Meer gefunden, während sich einige wenige andere tiefer in die Bucht bewegten. Dieses Verhalten ließ vermuten, dass die Krabben zwar in Gewässern mit höherem Salzgehalt schwimmen, jedoch nicht unbedingt ins offene Meer.

Die drei Studien meiner Thesis konnten zu dem Wissen um die Habitatsnutzung der unterschiedlichen Lebensstadien von *S. serrata* beitragen und konnten zeigen, dass die jeweiligen

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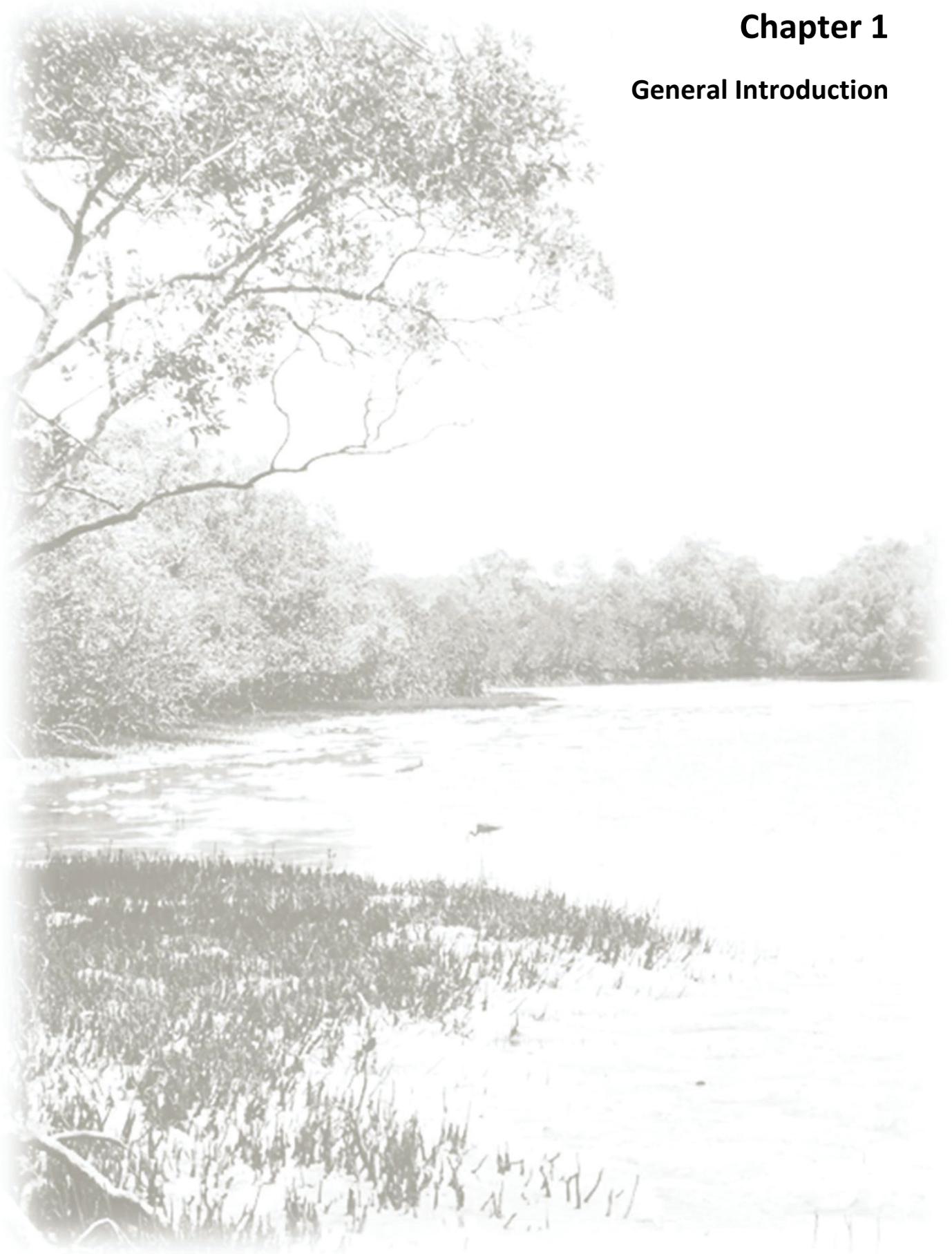
Habitats dem jeweiligen Nutzen nach ausgesucht werden. Während kleinere Krabben den Schutz durch feste Strukturen aufsuchen um optimal vor Prädatoren geschützt zu sein, bewegen sich die durch ihren Panzer geschützten größeren Krabben frei durch die Gewässer, wobei sie jedoch auch auf äußeren Druck durch Artgenossen reagieren und gegebenenfalls in andere Gewässer ausweichen.

Zusammengefasst lassen sich aber immer noch große Wissenslücken in der Ökologie dieser Mangroven-Krabbe finden. Den aktuellen Stand des Wissen sowie auch die Lücken habe ich am Ende meiner Thesis in einem Review Paper zusammen gefasst, welches zukünftige Bestrebungen sowohl in der Wissenschaft als auch im Umweltmanagement unterstützen und anleiten kann.



# Chapter 1

## General Introduction



## **Mangrove ecosystems**

Mangrove forests occur in tropical and subtropical regions all around the world, with a poleward extension to approx. 25-30° N and S; globally they cover an area of approx. 137760 km<sup>2</sup> (in 2000; Giri *et al.*, 2011). They form a transitional zone between terrestrial and marine environments and grow in sheltered (i.e., protected by coral reefs or islands) marine shores, bays, coastal rivers and estuaries (Macnae 1968). Mangroves are able to tolerate regular flooding by seawater and have developed special adaptations to the marine environment, of which the aerial root system is the most obvious. Since mangroves predominantly occur in coastal areas that are influenced by tides, the species distribution follows certain zonation patterns which are predominantly defined by the frequency of tidal flooding as well as water and soil salinity (Macnae 1968, Tomlinson 1986). The root structure of mangroves is complex, providing sheltering habitats and feeding grounds for a variety of aquatic and semi-aquatic animals (*see below*). Thereby it slows down currents and traps sediments, as well as 'filtering' pollutants from coastal runoff (e.g., river discharge). Mangroves also support nearby ecosystems such as coral reefs or seagrass-beds by providing nutrients. In their function as fringing forests, mangroves prevent erosion, slow down wave surge and can buffer the impact of tsunamis.

Mangroves are highly productive and accumulate large amounts of above-ground biomass and even higher below-ground biomass, which exceed those of terrestrial forests (Komiyama *et al.* 2008). Mangroves are considered one of the most carbon-rich ecosystems, and although they occupy only 0.5 % of the global coastline they are responsible for storing 10-15 % of global coastal sediment carbon (Alongi 2014).

Despite the great ecological value of mangrove ecosystems, approx. 2 % of global mangrove area is lost each year (Valiela *et al.* 2001). Even though rising sea levels due to climate change as well as ocean acidification may affect mangrove ecosystems, human activity is generally considered to have a greater impact on mangrove ecosystem health (Gilman *et al.* 2008). Increasing urbanization of coastlines due to an ever-growing human population drives the degradation of mangrove swamps by pollution, logging and conversion into areas for aqua- and agriculture (Valiela *et al.* 2001).

### *Australian mangroves*

Australia's mangroves are highly diverse and consist of 41 species (22 genera, 19 families), representing 57 % of global mangrove species. At the same time, Australia has the second largest extent of mangroves worldwide, with 977,975 ha or 7.1% of total mangroves worldwide (in 2000; Giri *et al.*, 2011). The distribution of mangroves in Australia is limited by temperature (sea surface temperature, SST) and moisture/rainfall (Duke 2006). As a result, mangrove abundance and diversity is higher in the warm, tropical northern regions in comparison to the temperate southern areas.

In contrast to tropical regions in northern Queensland, there are defined seasons in south-east Queensland and southern regions, represented by cool winters with little rainfall (dry season) and a hot summers, with high rainfall and tropical storms (rainy season). Due to the relative cold months in winter, the biodiversity of mangroves is low: only eight mangrove species are found in this region, mainly *Avicennia marina* and *Aegiceras corniculatum* (Duke et al. 2003).

### *Mangrove fauna*

Mangrove forests provide habitat to a variety of terrestrial, semi-terrestrial, aquatic and semi-aquatic species. Aquatic animals living in mangroves are predominantly marine species, some living permanently within mangrove forests, whereas others use them as temporary habitat as feeding ground or for shelter or at a certain point of their life cycle, i.e., as nursery sites (Sheridan and Hays 2003, Dahlgren et al. 2006, Nagelkerken 2009).

Species permanently living in mangroves are mainly invertebrates and can be categorized into epi- and endobenthic species. Generally, the diversity and abundance of endobenthic meiobenthos is estimated to be lower than in temperate regions (Alongi 1987, Dittmann 2001), supposedly due to the harsh conditions in the soil caused by deoxygenation and high temperatures. Species richness of the macrobenthos is also estimated to be lower than in temperate regions or adjacent habitats (e.g., seagrass meadows or mud flats). However, the abundance of macrobenthic species is high. The macrobenthic community is dominated by crustaceans and gastropods (Lee 2008). Burrowing crabs (e.g., Ocypodoidea and Grapsoidea) are seen as keystone species for ecosystem functioning (Lee 1998, Wang et al. 2010), as they are assumed to trigger soil oxygenation by building burrows, and nutrient enrichment in mangrove soils through leaf litter turnover .

Many species associated with mangroves, such as prawns, cockles, and crabs, are of commercial importance and therefore harvested. Indeed, nearby coastal fisheries have been shown to be enhanced by mangrove ecosystems (Manson et al. 2005, Mohapatra et al. 2007, Hutchison et al. 2014). Brachyuran crabs are common in mangrove forests and are dominated by crabs of the families Sesamidae, Ocypodidae and Portunidae. Three genera of large portunid crabs are common in the mangrove habitat (*Thalamita* spp., *Portunus* spp. and *Scylla* spp.) and fished almost everywhere throughout their range.

The complex root structure, which is inundated at high tides, provide sheltering habitat for a variety of marine and estuarine species, often including those of commercial value. Animals from adjacent nearshore ecosystems often utilize mangroves occasionally for feeding, for example many reef fish undergo daily migrations from their subtidal resting ground to the intertidal mangrove habitat at high tide for feeding (Nagelkerken et al. 2008, Krumme 2009, Davy et al. 2014).

### *Mangroves and animal movement*

Many species respond to the intertidal character of the mangroves by moving in and out of the habitat, either on a regular basis (routine movement) or by ontogenetic migrations. This movement is often a response to changing favorable conditions like food-availability, predator-avoidance and environmental conditions. Pittman and McAlpine (2003) summarized different types of movement during a life-cycle and distinguished three phases: “(1) the movement of planktonic eggs and larvae to nursery areas; (2) a range of routine shelter and foraging movements that maintain a home range; and (3) spawning migrations away from the home range to close the life cycle.” Species associated with mangroves often express these three types of life-cycle related movement. Invertebrates, as well as some fish species living in the mangroves, have a biphasic life with a pelagic larval phase and a benthic or demersal juvenile and adult life. The larvae are typically dispersed over long distances and, for some species, the ability of steering movement towards suitable habitat for settlement by the supposedly drifting larvae using tidal stream transport has been documented (Kingsford et al. 2002, Pineda et al. 2007). The dispersive potential also depends on a variety of biotic and abiotic factors such as advection, dispersion, larval survival, duration and behavior, as well as spawning time and location (Edwards et al. 2007, Shanks 2009). The spawning of some species occurs in inshore waters, within their home sites (e.g., gastropods and bivalves; Broom, 1983; Sanpanich *et al.*, 2008), whereas others (e.g., crabs, prawns and fish) undertake spawning migrations that can cover great distances. These spawning migrations are well documented for a number of species and transport mechanisms are well studied (e.g., *Callinectes sapidus*; Carr *et al.*, 2004; Hench *et al.*, 2004). For other species, it is only known that they exhibit a form of spawning migration behavior (e.g., *Scylla serrata*; Hill, 1994).

Routine movements of adults generally occur on smaller spatio-temporal scales compared to larval movement and spawning migration (Pittman and McAlpine 2003). In such cases, the movement range is limited to a species-specific home range, connecting areas utilized for different activities such as feeding, resting or maintaining the territory. In intertidal areas, such as the mangrove habitat, movement of animals often follows the tidal rhythm, meaning that habitat utilization is different at low or high tide, respectively. Fishes from nearby habitats (e.g., seagrass, coral reefs) move into the mangroves at high tide for feeding or in order to use the protection of mangrove roots as nursery habitats (Nagelkerken and van der Velde 2004, Dahlgren et al. 2006, Nagelkerken 2009, Jones et al. 2010). Other species, such as sesarimid crabs, rest in their burrows during high tide and become active at low tide and search for leaf litter.

**Tracking animal movement**

Following animal movement - especially in aquatic environments – can be challenging. Since visual census is often not applicable to marine mobile organisms due to depth, currents, or simply turbid waters, a variety of methods have been developed, including external or internal tagging with artificial tags, acoustic telemetry or the use of natural chemical markers (Gillanders 2009). Each of these methods has its advantages and disadvantages: tagging or marking aquatic animals is cheap, but only feasible if the target species can be easily retrieved. Therefore this method is only suitable for either slow-moving organisms or easy-to-catch species that reside in predictable habitats. Additionally, the repeated physical recovering of tagged animals can be time consuming. Acoustic tracking, a relatively novel but well established tracking technique, is becoming increasingly popular in aquatic research (Cooke et al. 2004, Heupel et al. 2006). Here, an acoustic tag (transmitter) is attached to or implanted into the target species and can be either actively tracked by the use of portable hydrophones or passively tracked using an array or network of submerged acoustic receivers (Heupel et al. 2006). Once the animal is tagged, it will be automatically recorded by all receivers of the same frequency that it passes. This approach allows for simultaneous tracking of several individuals. Compared to t-bar tagging or marking, this method is relatively cost-intensive and requires regular maintenance of receivers.

All these methods are feasible for large crustacean species and some have already been used for tagging brachyuran crabs (e.g., *Callinectes sapidus*, Carr et al., 2004)

For *Scylla* spp., several tagging methods have been used in previous studies. Simple non- invasive methods, such as gluing colored buttons to the carapace have been used to identify individuals (Bonine et al. 2008, Mirera 2014) and provided good results. However, this method is not feasible for long term studies, since the mud crab molts as it grows and therewith loses its shell, including the mark. Hill (1979) used t-bar tags as externally visible markers, which also showed good retention and survival rates and is also externally visible. In this method a T-shaped anchor-tag is inserted between the carapace and first abdominal segment of the crab, so that the tag is incorporated into crab's cavity.

### **The mangrove crab *Scylla serrata***

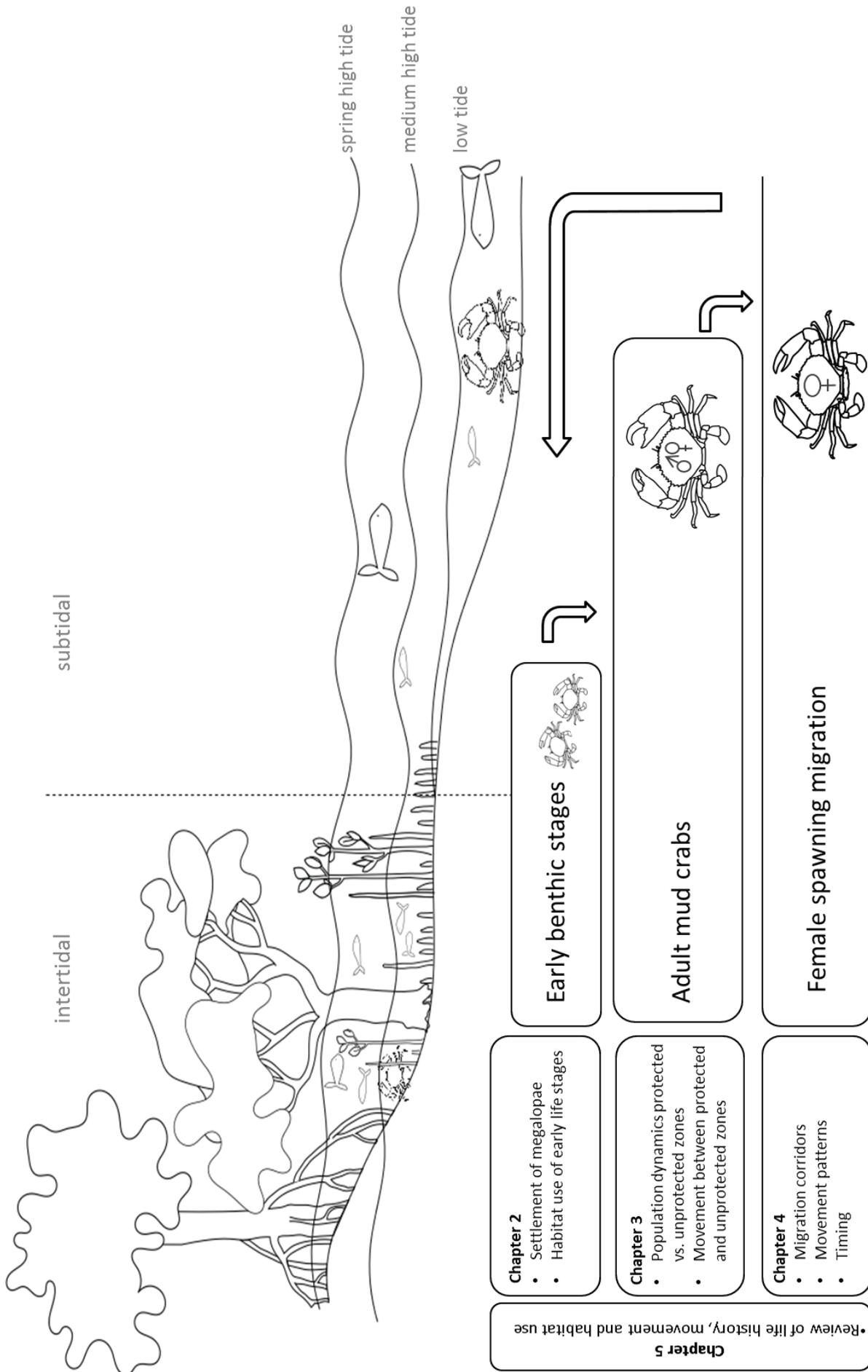
The objective of this thesis is to investigate the movement patterns at different life stages of *Scylla serrata* (Forskål, 1775), which is a large portunid crab associated with mangrove habitats throughout the Indo-West-Pacific region. There are four cryptic species, *S. serrata* (Forskål 1775), *S. tranqueberica* (Fabricius 1789), *S. olivacea* (Herbst 1796) and *S. paramamosain* (Estampador 1949) which were considered as one species (*S. serrata*) before the revision of the species in 1998 (Keenan et al., 1998). *S. serrata* is the largest and widest spread of the four species (hereafter referred to as ‘mud crab’) and can be found throughout the whole Indo-West-Pacific (IWP) region including the Red and Arabian Sea, whereas the other three species are mainly found on the Asian shelf.

*Scylla serrata* can attain sizes > 240 mm carapace width (CW) and weights of over 2 kg (Heasman 1980). It is a fast growing species and size at maturity (123 mm CW in South Africa, Robertson and Kruger 1995; 147 mm CW in Southern Queensland, Heasman 1980) can be reached within less than a year (Arriola 1940). As adults, mud crabs are generalists that are perfectly adapted to the life in mangrove areas. They are very tolerant to the constantly changing conditions, withstanding salinities from 2 – 64 (Practical Salinity Scale; Davenport and Wong, 1987; Hill, 1979). Alike many other crab species they are also able to survive dry conditions during low tide as long as their gills do not dry out. They are opportunistic omnivores, being more omnivore during their early juveniles phase and more carnivore as adults (Hill 1976, McLaren 1977, Prasad and Neelakantan 1988). As early juveniles they mainly feed on algae and detritus, whereas late juveniles and adults feed on slow moving or sessile benthic invertebrates, other crustaceans as well as conspecifics and carrion (Prasad and Neelakantan 1988, Thimdee et al. 2001).

As a portunid crab, *S. serrata* has a biphasic life with a dispersive larval phase and a benthic juvenile and adult phase. The benthic adults live in the inter- and subtidal areas in mangrove forests and swamps and are predominantly found in subtidal channels within mangroves and adjacent mud flats (Arriola 1940, Brown 1993). Here they routinely move between different microhabitats (mangroves, mud flats, channels (Heasman 1980, Hyland et al. 1984). This behavior changes for the females after mating: since the larvae need constantly high water salinity and ideally stable temperatures for survival and development, the female mud crabs has to move from inshore to offshore waters for spawning (Le Reste et al. 1976, Hyland et al. 1984, Robertson and Kruger 1994). This spawning migration has been reported from several geographic areas, and it is known that during spawning season, females can be found as far as 95 km off the coast, but also in coastal bay areas with oceanic conditions (Hill 1994). The process of spawning itself in the wild has never been reported in the literature, and there is only indirect evidence for the ontogenetic movement of larval *S. serrata* on their way back to coastal waters.

*Scylla* spp. in general and *S. serrata* in particular are seen as delicacies and fetch high prices in local as well as international markets (Angell 1992). In Asia, ovigerous females are particularly expensive and therefore sought after (Le Vay 1998), whereas in Queensland, Australia, females are banned from fisheries to protect the local stocks and prevent recruitment overfishing. So far, Australia is the only country with legal restriction on mud crab fisheries, but these vary from state to state (Butcher et al. 2012).

The commercial value of *S. serrata* combined with their fast growth and generalist behavior makes them a most suitable species for aquaculture. In Asian countries it is common practice to collect juvenile mud crabs for fattening in culture ponds, pen and cage cultures (Angell 1992, Keenan and Blackshaw 1999). Since hatching mud crabs in the laboratory is difficult and has not been commercially feasible until recently (Quinitio et al. 2001, Davis 2004a), early juveniles are being collected in the wild for aquaculture purposes (so-called 'seed-collection', Agbayani, 2001). This high fishing pressure on all life stages of *S. serrata* poses a threat to the species, and in some parts of Asia effects of overfishing are clearly visible.



**Figure 1** Schematic drawing of thesis outline

## Scope and structure of the thesis

The objectives of this thesis are to investigate movement patterns and habitat use of the different life stages of *S. serrata*. For the effective management of exploited species, such as *S. serrata*, it is important to have a sound understanding of its ecology and especially, its behavior in the wild. In the face of global change, with an increasing human population, climate change and thus increasing pressure on coastal ecosystems, it is important to know how the species may react to anticipated alterations to their habitat. Despite the high public and scientific interest in these issues, knowledge about the life history characteristics of *Scylla serrata* is still limited and deeper insights into the habitat use and movement patterns are needed.

By reviewing the current knowledge on the species, I identified gaps in knowledge regarding habitat use and movement at different ontogenetic stages. I found several discrepancies in the literature regarding geographical differences, which may be due to the ambiguity regarding species identification. Therefore, I summarized the knowledge gathered to-date in a review paper in **Chapter 5**. Here, I presented data on *S. serrata* from studies where the species could be clearly identified due to the identification key provided by Keenan et al. (1998) with emphasis on movement and habitat use in light of global change and anthropogenic impacts. Further, I addressed some of the open questions in my own research (**Chapters 2 – 4**, Figure 2) and included them in the review.

In **Chapter 2** I studied the different possible nursery habitats (sandy vs. muddy mangroves) of early benthic stage (EBS) *S. serrata* and determined ontogenetic movements as part of the post-settlement behavior. Further, I present the methods I used as a novel approach for sampling juvenile mud crabs in turbid waters.

Adult *S. serrata* are important for commercial and recreational fisheries, and many marine protected areas (MPAs) have been created in the Moreton Bay area as general protected zones. I investigated the effects of the marine park zoning on the population dynamics of mud crabs in **Chapter 3**. Another important aim of this study was to determine the routine movement of mud crabs in and between the MPA and non-MPA areas in an enclosed seascape, with emphasis on possible spill-over effects and benefits for adjacent fisheries. I used a novel approach of combined t-bar/passive-integrated-transponder (PIT) tagging to follow mud crab movement patterns.

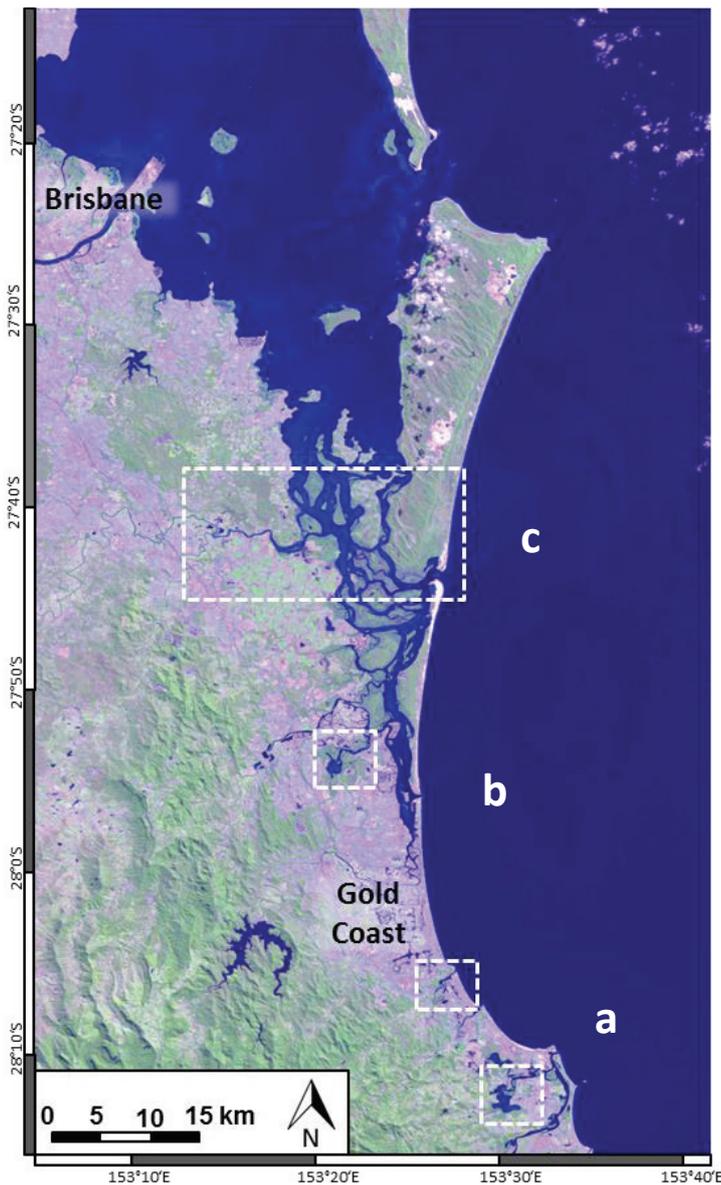
In **Chapter 4**, I studied the ontogenetic movement of female *S. serrata* during the spawning season, using acoustic telemetry. Twenty-four mature female mud crabs were tagged and tracked over four months using a receiver array that was set up in a subtropical estuary and the adjacent bay. This static receiver array followed the paths and timing of females during spawning migration and gave new insights into their swimming behavior.

## Study site and research approach

### *Study site*

All studies were conducted in the greater Gold Coast/Moreton Bay region in Queensland, eastern Australia (from 27°38'36"S 153°21'14"E to 28°12'51"S 153°30'14"E, Figure 2). Since the three studies carried out during my thesis slightly varied in their scope and therefore requirement on the seascape, a different area was chosen for each. However, the different sites are situated within a <100 km stretch along the coast (Figure 2). In general, the species composition of the mangroves at this site concurs with the typical pattern mentioned in the general introduction. The shallow intertidal areas are dominated by *Avicennia marina* with saplings and pneumatophores spreading into the shoals adjacent to mangrove forest. In the areas of high salinity, this species is accompanied by predominantly *Rhizophora stylosa*, whereas the mangrove community in the upper tidal reaches (upper Logan River, figure 2c) is dominated by the river mangrove *Aegiceras corniculatum*. The whole eastern Australian coast is under tidal influence, with semi-diurnal tides and a meso-tidal range of approx. 2 meters. The seasons in subtropical Queensland are defined by colder winters with little rainfall (dry season) and warmer summers with high rainfall (rainy/wet season, Figure 3). Southern Queensland is the southernmost area of monsoonal activity and can experience extended times of increased rainfall (up to 300 mm per day; BOM). Rainfall is correlated to sea surface temperature (SST), and therefore the El Nino Southern Oscillation Index (ENSO), with below average seasonal rainfall in El Nino years (high SST) and above-average seasonal rainfall in La Nina years (low SST, Murphy and Ribbe, 2004). Annual variation in SST is between 20-28 °C with a mean annual temperature of 24.07 °C (Meynecke and Lee 2011). However, the temperature can easily exceed 30°C in shallow coastal waters (pers. observation). Air temperatures are typically around 21 °C in winter and 28 °C in summer (Figure 3).

The whole area Moreton Bay area is under substantial urban influence and all study sites are located in close proximity to urbanized areas, with some areas being subject to commercial fisheries as well as recreational activities (e.g., fishing, boating, canoeing).

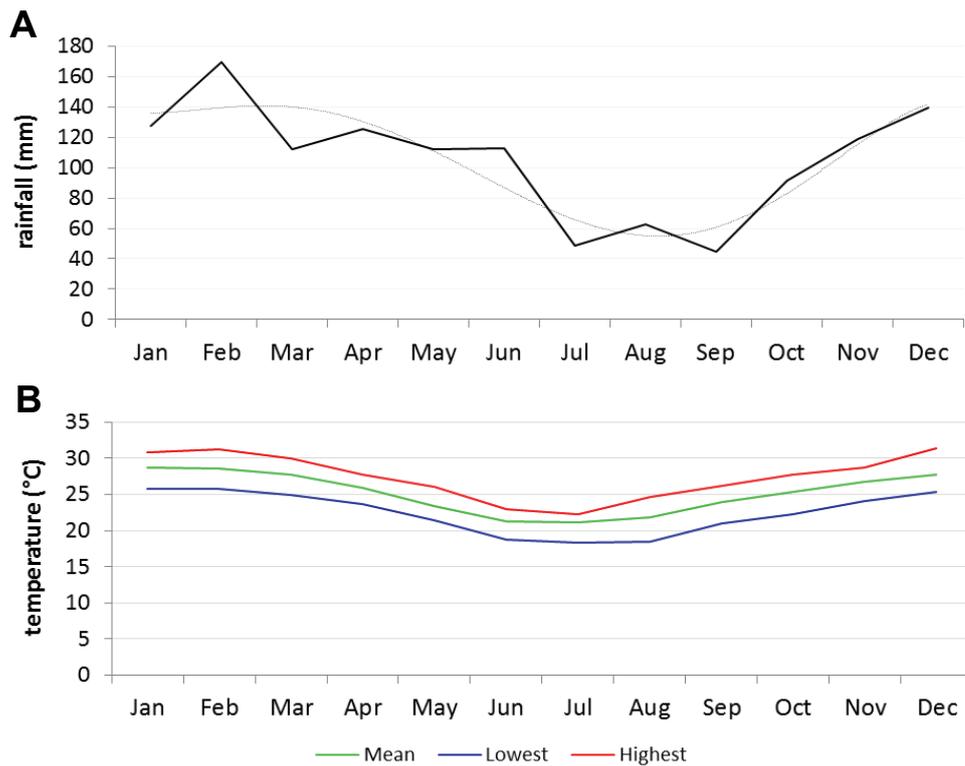


**Figure 2** Satellite image of the study area, southern Queensland/northern New South Wales, Australia. The first study (Chapter 3) was conducted in the southernmost part of the study area (a), in Tallebudgera Creek, Queensland and Terranora Broadwater, New South Wales. The second study (Chapter 4) was in Coombabah Creek and Lake in the southern part of Moreton Bay Park, Queensland (b). The third study (Chapter 5) was conducted in Logan River and the southern Moreton Bay area between Logan River and Jumpinpin bar (c). (adapted from Landsat Imagery)

### Research approach

Several approaches for tagging *S. serrata* were used in my thesis, depending on the life stage and scope of the study. Early benthic stage mud crabs were tagged using Visible Implant Elastomer (VIE, **Chapter 2**). Using this method, smallest proportions (< 0.01 ml) of colored elastomer are injected into tissue right underneath the crab's shell where it can easily be spotted in bright daylight or in UV-light in the dark. The advantage of this tagging is that the color is maintained through several molts (Liu et al. 2011), but if applied to hard-shell crabs it is only visible in early stage specimens since the shell thickens with growth and becomes impervious to color. Additionally, considering the welfare of small crabs, the process of injecting the tag is complicated and delicate. (for more see appendix)

In **Chapter 3**, I conducted a mark-and-recapture study using t-bar tagging combined with passive-integrated-transponder (PIT) tagging. Frusher et al. (2009) elaborated this method to improve



**Figure 3** Monthly average rainfall with adjusted moving averages (dashed line, **A**) and temperature with lowest and highest average (**B**), measured between 1992 and 2014 at the Gold Coast Seaway (source: BOM)

reporting rates in a lobster (*Jasus edwardsii*) trap fishery. To avoid ingestion of the PIT tag (if conventionally inserted into the crab's tissue) by consumers, the PIT tag was attached to the shaft of the t-bar tag, which stayed outside the body cavity. I used this approach, with a slight variation on Hill's t-bar tagging method (1978). In my study, the insertion angle was altered in the way, that the tag is anchored in the muscle of the rear leg of the crab (Meynecke et al., in prep., **Chapter 3.2**). For the detection of the PIT, an underwater antennae system was installed in the creek leading to the MPA. (for more details see appendix)

In **Chapter 4**, I tracked the spawning migration of female mud crab using acoustic telemetry. Hill (1976) already used acoustic tags to track fine scale movement of *Scylla serrata* in an estuary in South Africa (Hill 1978). In his study, handheld hydrophones were used and the crab's position triangulated. In my study, the tracks of *S. serrata* were detected by an automated receiver network that was deployed in the Logan River and adjacent Moreton Bay. Acoustic tracking in general and automated tracking in particular has been used previously to track movement of several other crustacean species (Heupel et al., 2006; *Maja squinado*, González-Gurriarán et al., 2002; *Panulirus argus*, Bertelsen and Hornbeck, 2009; horseshoecrab, Brousseau et al., 2004). A static array, such as used in my study, continuously tracks the female's movement disregarding harsh environmental conditions and provides data to calculate speed and distances over several months.

**Publication outline:**

The following chapters (**Chapter 2- 5**) contain the manuscripts of five publications originating from this thesis

**Chapter 2:**

**Alberts-Hubatsch, H.**, Lee, S. Y., Diele, K., Wolff, M., and Nordhaus, I.

**Microhabitat use of early benthic stage mud crabs, *Scylla serrata* (Forskål, 1775), in eastern Australia.**

Journal of Crustacean Biology, 2014, 34: 604–610. This study was conducted in collaboration with the Australian Rivers Institute, Griffith University, Australia. Study design was developed by H. Alberts-Hubatsch with support of S.Y. Lee, K. Diele and I. Nordhaus. The study was carried out by H. Alberts-Hubatsch in the field. Data analysis was conducted by H. Alberts-Hubatsch. The manuscript was prepared by H. Alberts-Hubatsch and co-authored by S.Y. Lee, K. Diele, M. Wolff and I. Nordhaus.

**Chapter 3:**

**Alberts-Hubatsch, H.**, Meynecke, J.-O., Lee, S Y, Nordhaus, I., Wolff, M., Diele, K.

**Population structure and movement of the mud crab *Scylla serrata* in and between protected and unprotected zones in a tidal lake system in eastern Australia: implications for management**

Submitted to ICES Journal of Marine Science. This study was conducted in collaboration with the Australian Rivers Institute, Griffith University, Australia. Study design was developed and field study conducted by H. Alberts-Hubatsch with support of J.-O. Meynecke. Data analysis was conducted by H. Alberts-Hubatsch. The manuscript was prepared by H. Alberts-Hubatsch and co-authored by J.-O. Meynecke, S.Y. Lee, I. Nordhaus, M. Wolff and K. Diele.

**Performance and physiological responses of combined t-bar and PIT tagged mud crabs (*Scylla serrata*)**

Meynecke J.-O., J. Mayze, **H. Alberts-Hubatsch**

In preparation. This study was conducted by the Australian Rivers Institute, Griffith University, Australia in collaboration with Johns Institute? and the Leibniz Center for Tropical Marine Ecology. Study design was developed and study conducted by J.-O. Meynecke. Field data was supported by data derived from this thesis. Data analysis was conducted by J.-O. Meynecke. The manuscript was prepared by J.-O. Meynecke and co-authored by J. Mayze and H. Alberts-Hubatsch.

**Chapter 4****Going with the tide: Movement patterns of the female mud crab *Scylla serrata* (Forskål, 1775)**

**Alberts-Hubatsch, H.**, I. Nordhaus, K. Diele, J.-O. Meynecke, S.Y. Lee, R. Babcock, R. Pillans, M. Wolff

In preparation. . This study was conducted in collaboration with the Australian Rivers Institute, Griffith University, Australia and CSIRO Brisbane. Study design was developed by H. Alberts-Hubatsch. Field study was carried out by H. Alberts-Hubatsch, receivers were deployed by CSIRO. Data analysis was conducted by H. Alberts-Hubatsch. The manuscript was prepared by H. Alberts-Hubatsch and co-authored by I. Nordhaus, K. Diele, J.-O. Meynecke, S.Y. Lee, R. Babcock, R. Pillans, M. Wolff.

**Chapter 5****Life-history, movement and habitat use of *Scylla serrata* – current knowledge and future challenges**

**Alberts-Hubatsch, H.**, S.Y. Lee, J.-O. Meynecke, K. Diele, I. Nordhaus, M. Wolff

Submitted to Hydrobiologia. The data was compiled and manuscript prepared by H. Alberts-Hubatsch. The manuscript was co-authored by S.Y. Lee, J.-O. Meynecke, K. Diele, I. Nordhaus, M. Wolff.



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## Chapter 2

### Microhabitat use of early benthic stage mud crabs, *Scylla serrata* (Forskål, 1775), in eastern Australia



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*Journal of Crustacean Biology*, 34(5), 604-610, 2014

## **Abstract**

The mud crab *Scylla serrata* (Forskål, 1775) (Portunidae) is a commercial species in the Indo-West-Pacific. Despite its high fishery value, the microhabitat of its early juvenile stages remains unknown. We studied microhabitat use by the 'early benthic stage' (EBS, between 3 and 30 mm carapace width, CW) at two sites in eastern Australia by two types of artificial benthic collectors and baited traps. 92% of EBS mud crabs were captured in muddy areas, compared to 8% on sandy habitats. The majority of the EBS mud crabs (87%) was found in intertidal areas within the mangrove fringe, only few individuals (13%) were found on unvegetated mud flats seawards to the mangroves. EBS from the mudflat (including first instars of 3-4 mm CW) were significantly smaller ( $p < 0.001$ ) than those from the mangrove habitat. This indicates an active migration from the mud flat towards the mangrove fringe as the crabs grow. The recapture of mud crabs in close proximity to their tagging site at the mangrove fringe suggest that EBS-crabs have a small home range. Cannibalism is considered a major driver in the distribution patterns of EBS mud crabs, which may explain, why EBS-crabs stay at the more sheltered site near the mangrove fringe. By identifying the microhabitat of the critical early benthic stages of *S. serrata* in eastern Australia, our findings may contribute to the development of appropriate management and conservation strategies for this commercially important species.

Key words: early benthic stage (EBS), nursery, recruitment, post-settlement movement, settlement habitat

## Introduction

Many estuarine decapod species have a complex larval phase in which the pelagic stages disperse over long distances in marine/offshore waters and the later stages return to brackish estuaries prior to the first settlement (DeVries et al., 1994; Hill, 1994; van Montfrans et al., 1995). Recruitment to juvenile habitat is a critical process in the life cycle of estuarine nekton affecting the abundance, distribution and structure of estuarine communities and may thus be settlement regulated (Connell, 1985). Settlement can be described as a behavioral process, which includes the active movement of the larvae from the water column to a potential settlement site (Forward Jr. et al., 2001). Finding appropriate settlement grounds within the time window of metamorphosis, within which settlement is possible, is crucial for the survival of juvenile decapods such as brachyuran crabs (Pineda et al., 2007). During this phase the larvae are highly vulnerable to predation (Hunt and Scheibling, 1997; Doherty et al., 2004) and even if the larvae reach the settlement habitat their survival is not guaranteed. The settlement process can be steered by many sensory cues such as light, sound, tactile or olfactory cues (Kingsford et al., 2002; Stanley et al., 2011) and it is clear that settlement is directional rather than random, unless adequate cues are absent (Lecchini et al., 2010; Simith and Diele, 2008). Not only can pre-settlement and settlement processes (larval transport and dispersal as pre-settlement process, reviewed by Pineda et al., 2007 and Fraschetti et al., 2003) alter the abundance of recruits, post-settlement processes particularly have a great effect on the abundances of populations (Hunt and Scheibling, 1997; Fraschetti et al., 2003). In the last two decades, attention was drawn to the role of post-settlement processes in regulating adult populations (Connell, 1985; Orth and Montfrans, 1987; Eggleston and Armstrong, 1995; van Montfrans et al., 1995; Hunt and Scheibling, 1997; Wahle and Incze, 1997; Heck Jr and Spitzer, 2001), but knowledge about habitat requirements and behavior of the early post-settlement stage is still scarce.

Several methods are being used to identify the settlement habitats of small benthic crustaceans. The least invasive method employs passive collectors, which can be easily deployed and retrieved without excessive disturbance to the surrounding environment. Settlement rates of blue crabs, *Callinectes sapidus* (Rathbun, 1896), megalopae were investigated in several estuaries of the western Atlantic using artificial benthic 'hog's hair collectors' (van Montfrans et al. 1990, 1995), which have been demonstrated to be also efficient in estimating settlement rates of brachyuran megalopae in mangrove areas (Paula et al., 2001). For sampling late larval stages or early juvenile stages, a variety of collectors has been designed to imitate natural habitats. For example puerulus and post-puerulus of spiny lobster, *Panulirus argus* (Latreille, 1804), were caught with seagrass-imitating traps (Phillips, 1972) and early juvenile clawed lobster, *Homarus gammarus* (Linnaeus, 1758), can be sampled using artificial cobble substratum collectors (Wahle et al., 2009). Despite the diversity in sampling gears for

**Table 1.** Habitat of different age classes of *Scylla serrata*. CW = carapace width.

Life stage	Age	Size (CW, mm)	Habitat	Reference
Larvae I - V	15 - 22 days	1 - 3	Pelagic, offshore	Ong 1964, Heasman and Fielder 1983
Megalopa	22-34 days	3 - 4	Subtidal, inshore (assumed)	Heasman et al. 1985; Brown 1993
Early benthic stage (EBS)/crablet	4-12 weeks	3 - 30	Intertidal, mud flat, mangrove fringe	this study
- 1st crablet/instar	4-5 weeks	3 - 5	Inter/subtidal, mud flat	this study
juvenile (immature)	> 12 weeks	> 30	Mangrove fringe, intertidal channels	Hill et al. 1982; Hyland et al. 1984
adult (mature)	12 months	> 130	Intertidal channels, subtidal channels	Hill et al. 1982; Quinn and Kojis 1987

larval or juvenile stages of decapods, some of these methods have turned out to be inefficient for some species and the settlement habitats of many brachyuran species are still elusive.

The giant mud crab *Scylla serrata* (Forskål, 1775) is a portunid crab associated with mangroves (hereafter referred to as mud crab) in the tropical and subtropical regions of the Indo-west Pacific. Adults and older juvenile mud crabs (> 60 mm carapace width, CW) live in muddy inter- and sub-tidal areas of coasts and estuaries where they are commonly caught using crab pots, dip nets, or other capture methods (Hill et al., 1982; Brown, 1993). *S. serrata* has high commercial value, and is therefore heavily exploited as well as farmed. In the last decade, the main farming practice has switched from just fattening larger juveniles to market size to pond-rearing of wild-caught crablets. Even though commercial seed production is now achievable (Quinitio and Parado-Esteva, 2008), the massive collection of early juvenile stages in the wild is often a more feasible and cost effective alternative and often poses a threat to the sustainability of some wild populations in several places (Keenan and Blackshaw, 1999; Shelley, 2008). Despite the fact that wild crablets of congeners, e.g., *S. paramamosain* (Estampador, 1949), are routinely collected in Asian countries for aquaculture, sampling early juvenile mud crabs of *S. serrata* has as yet been difficult. Hill et al. (1982) sampled juvenile mud crabs in Moreton Bay, Australia in the upper intertidal using artificial collectors made out of roofing tiles, which were supposed to imitate the crab's natural habitat. Using the methods described above only individuals  $\geq 2$  cm CW were caught and the results were not replicable (Webley et al., 2009; personal observation). Parkes et al. (2011) mentioned that they captured juvenile *S. serrata* > 2.8 cm CW using 'seed collectors', but did not specify the seed collector or the habitat where juveniles were found. To date, no successful capture of early juvenile (< 2 cm CW) *S. serrata* in the wild has been reported in the literature.

In this study, we searched for early benthic stages (EBS, Table 1) of *S. serrata* in different potential habitats of subtropical mangroves in eastern Australia. We introduce the term 'EBS' to describe the sensitive life stages of juvenile mud crabs. While major morphological changes do not occur during

these life stages, they are ecologically and behaviorally distinct from adult crabs (compare American lobster: Wahle and Steneck, 1991) as well as being a potential 'bottleneck' in the life cycle.

This research aimed at improving our understanding of settlement, a key ecological process, of juvenile mud crabs. In view of the muddy habitats of adults, we hypothesized that the EBS mud crabs prefer sheltered intertidal and/or subtidal substrates for settlement and use mangroves as primary nursery areas. We compared muddy and sandy habitat sites that differed in distances to the mangrove fringe to identify the preferred settlement habitat. We also tested the feasibility of three non-invasive methods for sampling EBS of *S. serrata* in these habitats and assessed their range of movement within their preferred habitat.

## Material and Methods

### *Sampling Sites*

We collected EBS of *S. serrata* at two locations: Tallebudgera Creek (28°6'22"S, 153°26'49"E) in southeast Queensland and Terranora Broadwater (28°13'3"S, 153°30'47"E) in northern New South Wales. The two sampling sites were approximately 20 km apart and were both fringed with mangroves. The mangrove forests of both sites are dominated by mature *Avicennia marina*, *Aegiceras corniculatum*, and *Rhizophora stylosa*, and are fringed by saplings of *A. marina* that spread into the mid intertidal areas.

Tallebudgera Creek (TC) is a tidal river opening into the Coral Sea, with a sandy substrate and only few muddy areas enclosed by the mangrove forest. The sampling sites were located in a small bay near the mouth of the creek, where stream flow is reduced and tidal influence is strong. Terranora Broadwater (TB) is a shallow protected tidal lake with little freshwater input from small local creeks. Due to the sheltered condition the substrate is dominated by soft mud.

At both localities, the tides are semi-diurnal with amplitude of around 100 cm at neap tides and 160 cm at spring tides.

Two sites were sampled at each location: 1) directly at the mangrove fringe (intertidal mangrove site, IMS), and 2) 30 m (at TC) or 100 m (at TB) seaward from the mangrove fringe (upper subtidal site, USS), roughly corresponding to the lower tidal limit. In the IMS, the traps were placed in small tidal creeks or surface puddles, so they would not fall completely dry during low tide. All sample sites (IMS and USS) remained inundated during low tide (10-30 cm water). The IMS sites were surrounded by pneumatophores and saplings of *Avicennia marina* whereas the USS sites were unvegetated. Sampling inside the mangrove forest was considered not appropriate as the sediment here was only inundated during spring high tides and EBS-crabs were expected to stay in permanently inundated areas.

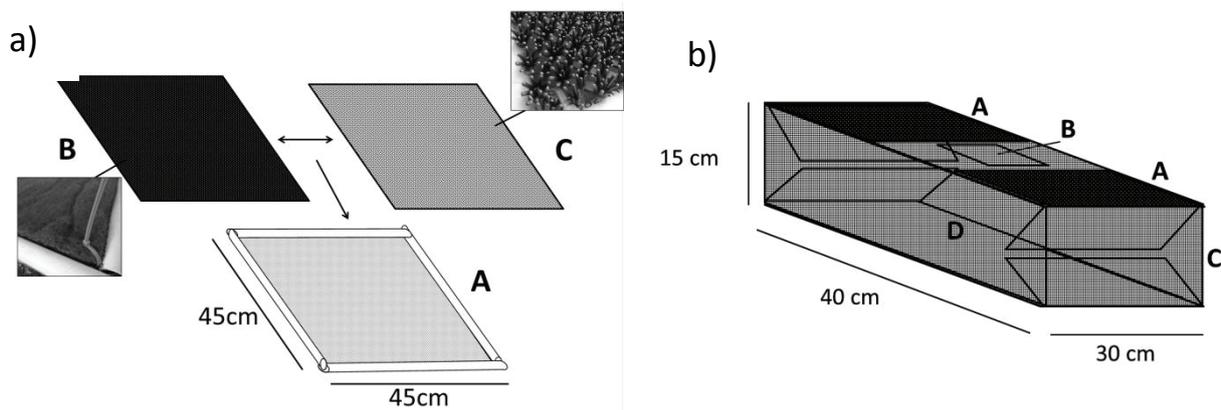
Sampling was conducted from December 2012 to March 2013, which falls into the rainy season (summer) in Australia. The spawning season of *S. serrata* in subtropical Australia occurs from early spring to early autumn when the water temperature exceeds 22°C and peaks in mid-spring and late summer (Heasman et al., 1985), so early juvenile mud crabs were expected to be present during this period.

### Sampling Design

Two different types of artificial benthic collectors were used: 1) ‘hog’s hair’ filter mats (aquarium filter mats) and 2) modified simple plastic doormats with the bristles directed upwards (Fig. 1). Each collector was attached to a 45 x 45 cm frame made out of concrete-filled PVC pipes (2 cm in diameter) to prevent movement of the collectors. The collection frame was supported by a 1 mm mesh on the bottom so no specimen would be lost when the collector was lifted.

In December 2012, three collectors of each type were deployed at each sampling site, i.e., a total of six collectors per location. From January 2013 on, the number of collectors was increased to five per sampling site, i.e., a total of ten collectors per location. The collectors were emptied and redeployed at low tide during daytime three times a week whenever possible. At the end of January sampling could not be done due to severe flooding in the sampling areas.

Additionally, five baited traps made out of wire mesh (40 x 30 x 15 cm; mesh size 6.5 mm), covered on the top with shading cloth (Fig. 2), were deployed at the mangrove fringe among the pneumatophores (IMS) in the Terranora Broadwater site only. The traps were baited with pieces of pilchard, *Sardinops sagax*. At Tallebudgera Creek, the relatively high human disturbance precluded the use of baited traps and only benthic collectors were used.



**Figure 1.** a) **A**, Artificial benthic collector with two different types of cover; **B**, hog’s hair filter mats; **C**, doormat. b) Funnel trap to capture early benthic stage *Scylla serrata*. Dimensions 40 x 30 x 15 cm, funnel length 10 cm; made from wire mesh with a mesh size of 6.5 mm; covered with jute fabric. **A** indicates the jute cover, **B**, opening flap of the trap; **C**, the funnel through which the crabs enter; **D**, position of the bait inside the trap

### *Tagging*

To test the site fidelity and home range of EBS mud crabs, two groups of crabs < 20 mm CW (each of 20 and 44 specimens) collected from the sampling described above were tagged with Visible Implant Elastomer (VIE)-tags (Liu et al. 2011, Northwest Marine Technologies Inc.) and released on February 10 and March 12 2013, respectively. Both groups were released in the IMS site in Terranora Broadwater and the collectors were checked for tagged crabs during the subsequent sampling events.

### *Statistical Analysis*

We used catch per unit effort (CPUE) data to compare abundance of crabs between a) the locations (TB vs. TC) and b) between the sites (IMS vs. USS) at each location using one-way ANOVA in PAST (version 3.01). For detecting differences in size of captured crabs in different habitats, we chose TB as the representative location, as only few crabs were found in TC. Differences in size were also analyzed using one-way-ANOVA.

## **Results**

### *Crab Collection Using Benthic Collectors*

From December 2012 to March 2013, some 101 juvenile mud crabs were found in the artificial collectors at the Tallebudgera Creek and Terranora Broadwater locations, but no megalopae were recorded. Differences in juvenile abundance were found with regard to proximity to the mangrove fringe and the type of collector used: the great majority of juveniles ( $n = 81$ , 87 %) were found at the mangrove fringe (IMS), while only 12 individuals (13 %) were recorded on the mud flat (USS). Only eight percent ( $n = 8$ ) of all juveniles caught were from the collectors on sandy substrates of Tallebudgera Creek (Table 2).

During the three-month sampling period (31 sampling events in total) EBS mud crabs were recorded with CPUEs of 0-0.83 crabs per trap per sampling day. CPUE was highest in the TB IMS site (mean =  $0.33 \pm 0.19$  SD), followed by TB USS ( $0.05 \pm 0.1$  SD) and TC IMS ( $0.02 \pm 0.08$  SD). No crabs were recorded at TC USS, therefore this site was excluded from the one-way ANOVA. Significant differences in CPUE exist across sample sites (ANOVA:  $F(2, 53) = 31.05$ ,  $p < 0.001$ ). Post-hoc comparisons using the Tukey HSD test indicated that the mean CPUE at TB IMS was significantly higher than those at TB USS ( $p < 0.001$ ) and TC IMS ( $p < 0.001$ ). However, TB USS did not differ from TC IMS ( $p = 0.84$ ). These results suggest that EBS mud crabs are most abundant in habitats with muddy sediments (TB) in the upper intertidal near the mangrove fringe (IMS).

At Terranora Broadwater, crabs were significantly larger near the mangrove fringe ( $10.5 \text{ mm} \pm 0.6 \text{ SE}$ ; ANOVA:  $F(1,77) = 9.19$ ,  $p = 0.003$ ) than on the mud flat ( $5.9 \text{ mm} \pm 0.2 \text{ SE}$ ) (Table 1). During the whole sampling period, three first crablet stages of 3-4 mm CW were found in the benthic collectors on the mud flat and one in the collectors at the mangrove fringe.

The majority of EBS mud crabs (80%) preferred the doormat collectors over hog's hair collectors (20%) with a CPUE of  $0.49 \pm 0.04 \text{ SE}$  for the former compared to  $0.1 \pm 0.03 \text{ SE}$  for the latter (One-way ANOVA:  $F(1, 51) = 54.1$ ,  $p < 0.001$ ).

#### *Crab Collection Using Baited Traps*

The baited traps at the fringe of the pneumatophores in Terranora Broadwater captured 48 juveniles ranging from 6 to 36 mm CW (average of  $14.2 \text{ mm CW} \pm 1.4 \text{ SE}$ ). The CPUE was  $0.29 \pm 0.5 \text{ SE}$  crabs per trap per sampling day.

#### *Recapture of Tagged Crabs*

Five of the VIE-tagged juveniles (7.8 %) were recaptured 4 to 17 days after their release in the benthic collectors < 5 m away from the release site. Two of those had molted as reflected by their size increment. The VIE-tags were still clearly visible in these crabs.

Crabs were observed to bury in the mud within seconds after release to the water (10-20 cm water depth). Most of them started burying backwards in the sediment as soon as they touched ground and were only visible by the antennae, eyes and exhalant openings (Fig.3).

**Table 2.** Total numbers (n), average size (CW in mm) and Catch per unit effort (CPUE) of early benthic stage *S. serrata* at different sample sites collected from December 2012 to March 2013 (IMS= intertidal mangrove area, USS= upper subtidal site)

	IMS			USS			baited traps (IMS)		
	average size			average size			average size		
	n	mm $\pm$ SE	CPUE $\pm$ SE	n	mm $\pm$ SE	CPUE $\pm$ SE	n	mm $\pm$ SE	CPUE $\pm$ SE
Tallebudgera Creek (sandy)	8	$8 \pm 0.11$	$0.02 \pm 0.08$	0	0	0	-	-	-
Terranora Broadwater (muddy)	81	$10.5 \pm 0.6$	$0.33 \pm 0.2$	12	$5.9 \pm 0.2$	$0.05 \pm 0.1$	48	$14.2 \pm 0.14$	$0.29 \pm 0.5$

## Discussion

### *First Habitat of EBS Mud Crabs*

Our results suggest that: 1) EBS-crabs prefer muddy over sandy sediments for settlement, but sandy substrates were not completely avoided as shown by 8 % of small mud crabs that were found on this sediment type; 2) EBS-crabs are more abundant in close proximity to the mangrove fringe and among pneumatophores than on mud flats; and 3) first instar specimens appear to be more abundant in the mud flat area, crab size therefore increases with proximity to the mangrove fringe.

Mud flats probably play an important role as a transient habitat for EBS mud crabs, which then migrate into the mangrove area with increasing age. Moreover, the VIE tagging revealed short movement distances of a few meters only of the EBS crabs, which stay within a relatively small area inside the mangrove-belt, presumably to reduce predation risk. However, since only five of the tagged specimens were recaptured, additional data need to be gathered to confirm these findings.

Observations in the laboratory and in the field showed that EBS mud crabs hide by burying quickly into the soft substratum (Fig. 3), following a general behavior described for hatchery-reared *S. serrata* (Parkes et al., 2011), other crab species (Mclay and Osborne, 1985; Mcgaw 2005) and for other young portunid crabs (*Ovalipes ocellatus* (Herbst, 1799) 15-35 mm CW, Barshaw and Able, 1990). This behavior could explain the overall low number of EBS encountered in our study, including the low recapture rate of tagged EBS.

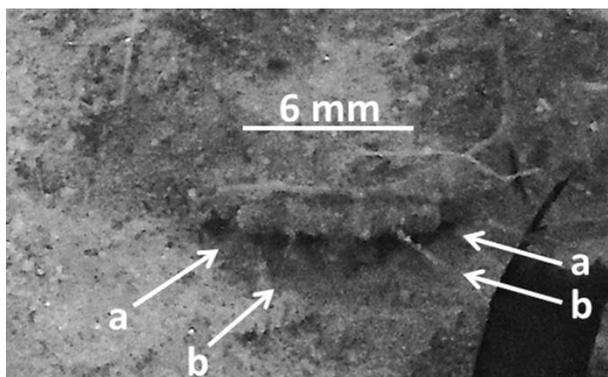
Baylon and Failaman (1999) tested the survival of small juvenile mud crabs in the presence of conspecifics of the same size under different shelter and substrate treatments (shelter/no shelter, mud/no mud). The highest survival rates were observed on plain mud without shelters compared to mud with sheltering structures (coconut leaves and mangrove twigs). However, lower survival rates in the sheltered treatment may have been due to fouling of the mud underneath the shelters, these findings suggest that a muddy substratum may be crucial for successful recruitment of *S. serrata* by reducing the risk of cannibalism. This assumed recruitment-pattern for the mud crab contradicts a variety of studies dealing with decapod settlement, which suggest that megalopae preferentially settle in habitats with hard structures (rocks, seagrass) where early juveniles are also found, e.g., American lobster (Wahle and Incze, 1997); shore crab (Hedvall et al., 1998; Moksnes et al., 2003); Dungeness crab (Eggleston and Armstrong, 1995); blue crab (van Montfrans et al., 2003), and *Romaleon polyodon* (Poeppig, 1836) (Wolff and Soto, 1992). While these complex habitats are considered to provide better refuge from predators, they are usually patchily distributed and densely occupied. Their capacity for supporting successful settlement is then regulated by density-dependent processes (Pile et al., 1996). However, most of the decapod species described in the literature occur

on hard substrates, for which the settlement may differ from those species adapted to soft bottom habitats such as *S. serrata* (see review by Frascchetti et al., 2003).

In previous studies, small mud crabs (>20 mm CW) were found in macro-algae beds and under stones (Hill, 1979; Heasman, 1980), but results were not reproducible using the described sampling methods (Webley et al., 2009; personal observation). While the reported findings suggest that early juvenile mud crabs may be associated with hard structures, our results suggest that the most important condition for successful settlement is a penetrable muddy substrate, which offers protection from predation, cannibalism, and extreme physical conditions.

Since the EBS-crabs captured on the mud flat were significantly smaller than those at the mangrove fringe, and first stage crablets were found in higher numbers on the mud flat, primary settlement of *S. serrata* appears to occur inside the estuary in subtidal muddy areas. This contradicts Webley and Connolly (2007), who hypothesized that *S. serrata* megalopae settle in offshore subtidal areas, and then move into the estuary with increasing age. Given the fact that the first crablet stages in our study were found more than 7 km upstream from the creek mouth and considering that it takes 7-12 days for the megalopae to develop into the first crablet stage (Table 1), it seems unlikely that the megalopae had settled outside the estuary in offshore areas, where settlement cues are weaker (odors, sound, hydrological features, for summary see Kingsford et al., 2002). Ong (1964) observed that megalopae of *Scylla* spp. develop faster when reared in low salinities (21-27 ppt) rather than high salinity (31 ppt) and postulated that this may be an indicator for megalopae moving towards brackish waters and molting into the first crab stage as soon as they sense suitable habitat (inshore waters). This is also supported by Nurdiani and Zeng (2007), who found similar trends in developmental durations in relation to salinity for megalopae of *S. serrata*. Additionally, Forbes and Hay (1988) were able to capture megalopae inside a mangrove fringed South African estuary, which also indicates that the first settlement of the megalopae occurs close to the mangroves.

In Vietnam, first instars of the congener *S. paramamosain* were found to recruit into the mangrove fringe, where they live on the surface around pneumatophores and shallow tidal pools during low tide (Walton et al., 2006), but no megalopa of this species were found, and mud flats were not sampled.



**Figure 2.** Picture of an EBS *Scylla serrata* (12 mm CW) buried in mud. The major part of the body remains invisible. a = eyestalks, b = antennae

*Post-settlement Redistribution*

Le Reste et al. (1976) proposed that small *S. serrata* recruit from subtidal waters into intertidal waters below the mangrove area at sizes between 20 and 100 mm CW. Our results do not support this assumption, as we found EBS-juveniles < 20 mm CW between the pneumatophores and in a small creek within the mangroves. Instead, the redistribution of the small juveniles from the mud flat to the mangrove area probably happens quickly (during the first and second juvenile stages) after the initial settlement. The early redistribution of different stages of *S. serrata* could explain why we did not find any small juveniles in the subtidal and only few crabs were recorded in the sandy intertidal of Tallebudgera Creek. While moving from the subtidal to the upper intertidal on sandy substrates, juvenile crabs become an easy target for predators and cannot hide as quickly in sand as on muddy substrates. When sandy substrates prevail, movement between habitats could pose a risk for the EBS mud crab and their abundance might decrease due to predation.

Rapid habitat transition has been observed in the post-settlement period of several brachyurans. Etherington and Eggleston (2000) observed changes in habitat during the first life stages of *Callinectes sapidus*. Hedvall et al. (1998), Moksnes (2002) and Moksnes et al. (2003) discussed post-settlement movement in juvenile shore crabs, *Carcinus maenas* (Linnaeus, 1758). On the other hand, Bell and Westoby (1986) suggested a “settle and stay model” for competent crustacean larvae. According to this model, larvae and early juveniles stay in the first habitat they encounter, e.g., a seagrass meadow, thus avoiding exposure to predation when moving between sites even though the first habitat might be a poor choice in terms of food availability and competition. In contrast, the “settle-and-move” behavior was considered more suitable for fishes, e.g. reef fishes (Pittman and McAlpine, 2003). Two settlement-models may thus be distinguished for crustaceans: 1) settle-and-stay-model, where the early juveniles identify a certain site where they settle and show no extension of home range to additional habitats; 2) settle-and-move model, where larvae settle in one microhabitat, metamorphose, and relocate to another microhabitat. In the settle-and-move-model, the different benthic life stages occupy different habitats after leaving the water column to avoid intraspecific competition as well as predation and relocate to other habitats with increasing age. In our case, it seems that the settle-and-move model is applicable, since the first stage crablet moves from subtidal settling-grounds into protected intertidal habitats. As soon as the EBS crab reaches appropriate nursery grounds the behavior seems to shift and it establishes site-fidelity.

In summary, this study has shed some light on the elusive habits of early juvenile *Scylla serrata*. Using artificial benthic collectors with either doormat or hog’s hair cover it was possible to catch first instar crablets and early juvenile *S. serrata*. We could detect an ontogenetic shift, in which different stages occupy different microhabitats within the adult habitat. Since juveniles seem to prefer muddy

substrates, future studies should concentrate on areas with muddy mangroves and extended mud flats. An extended sampling period and increased sampling effort beyond this preliminary study would provide additional information about settlement and recruitment processes and nursery areas of *S. serrata*.

### **Acknowledgements**

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## Chapter 3.1

### Population structure and movement of mud crab *Scylla serrata* (Forskål, 1775) in and between protected and unprotected zones in a tidal lake system in eastern Australia: implications for management



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## Abstract

*Scylla serrata* is an exploited portunid crab that occurs in mangrove associated areas in the Indo-west Pacific. We studied its movement within and between a marine protected area (MPA) and an unprotected zone in an enclosed seascape in south-east Queensland, Australia, to determine whether the MPA has a positive spill-over effect on the mud crab fishery in adjacent waters. To assess the effect of the banned fishery inside the MPA on the structure of the crab population, we compared sizes and sex-ratios between the two zones. A total of 852 crabs was tagged with a combination of T-bar/passive-integrated-transponder(PIT)-tags, allowing both physical recaptures and automated detections through an underwater antennae system set in the creek leading to the MPA. Between January 2012 and March 2013, 9.6% of the tagged crabs were recaptured. The predominant seaward movement of adults (46% of recaptures), compared to the less pronounced movement in the opposite direction (25%), and sedentary behavior (28%) indicates spill-over. In fishery-relevant males ( $\geq 150$ mm carapace width, CW) spill-over was 13%. Sex-ratio was male-dominated in the MPA (2:1), whereas it was shifted towards equal proportions in the unprotected zone. While a positive effect of the MPA on sex-ratio and size of the crabs was detectable, the effect of the fishery in the adjacent unprotected area was also recognizable. The largest captured specimens (max. 174mm CW) both inside and outside the MPA were smaller than formerly reported, most likely due to the effect of downfishing. Furthermore, the sex-ratio in the MPA was less skewed compared to undisturbed populations. We suggest follow-up studies to determine the magnitude of downfishing and its potential effects on the reproductive output of *S. serrata*. Monitoring the legal as well as ongoing illegal fishing activities will also provide data to support measures to improve fisheries law compliance.

## Introduction

The global trend of declining fish stocks (Pauly et al. 2002) has drawn attention towards the importance of Marine Protected Areas (MPAs) as a tool for conservation and fisheries management (Roberts et al. 2001). No-take marine reserves have been shown to increase the abundance and average size of the target species inside the protected area (e.g., Babcock *et al.* 1999, Côté *et al.* 2001, Abesamis and Russ 2005) and impart positive effects on adjacent fisheries outside MPAs through biomass spill-over (e.g., Hilborn 1994, Halpern *et al.* 2010, Gaines *et al.* 2010, Grüss *et al.* 2011a, Russ *et al.* 2013). While some studies have monitored the increase in abundances of exploited species inside and adjacent to MPAs over time, few were able to quantify the export of biomass from an MPA to fishery areas, e.g. by tracking the movement of individuals (see review by Abesamis and Russ 2005).

For the effective management and protection of mobile fishery species, knowledge of the spatial scales of their movements (Palumbi 2004, Grüss *et al.* 2011b) as well as their response towards changing environmental conditions (e.g., seascape, extreme events such as flooding, general fluctuations in water quality) is crucial. In particular, knowledge about the habitat and home range of different life stages is essential in evaluating the effectiveness of an MPA for a target species (Halpern and Warner 2003).

*Scylla serrata* (Forsk., 1775; hereafter referred to as 'mud crab') is a large commercial portunid crab that occurs in estuaries and coasts associated with mangroves in east Africa, (South-) Asia and Australia. It is a high-value species in local and international markets, with an annual global catch of 4.7 million t (FAO, 2012). In the last decades, the fishing pressure on this species has increased drastically; not only on large individuals for direct consumption, but also on juveniles for aquaculture ('fattening') purposes (Angell 1992, Sivasubramaniam and Angell 1992, Shelley 2008). *S. serrata* is a very suited species for fattening in aquaculture ponds due to its fast growth rate (market size within a year) and high tolerance towards changes in environmental parameters such as salinity (0-64; Davenport and Wong 1987) and temperatures (active 12- 35°C; Hill 1980, Meynecke *et al.* 2008).

Throughout its range, the maximum size and abundance of mud crabs are decreasing in heavily exploited areas (Naylor et al. 2002, Ewel 2008, Lebata et al. 2009) and even in areas with fishing restrictions the population structure tends to change towards smaller size-classes and a shift in sex-ratio towards a higher proportion of protected female crabs (Pillans et al. 2005). Generally, sustainable management of this species is still lacking or only in development, but in some countries management practices such as minimal legal sizes are already enforced. For example, in Queensland (Qld), Australia, the Qld Fisheries Act 1994 stipulates that only male crabs  $\geq 150$  mm carapace width (CW) can be collected while females and undersized males ( $< 150$  mm CW) are protected. Mud crabs can grow to sizes exceeding 240 mm CW in southern Queensland (Heasman 1980). Recent studies in southeast Queensland showed that *S. serrata* populations recover quickly in MPAs (Pillans et al.

2005, Butcher et al. 2014), but the implementation of MPAs is more seen as a tool for the conservation and protection of the species rather than to increase fishery benefits.

Meynecke *et al.* (2012) showed that the catch rates of *S. serrata* in Australia vary with the Southern Oscillation Index (SOI) and, therefore, the occurrence of dry and wet periods. Anecdotal data (Butcher *et al.* 2002, H. Alberts-Hubatsch, pers. comm.) suggests highest crab activity (as shown by highest catch rates) during the wet season in Australia, but it remains unclear if rain and therefore salinity is the major driver in this pattern. Rainfall might increase the activity of mud crabs by either triggering movement with decreasing salinities or by just flushing mud crabs out of mangrove habitats through increased water flow.

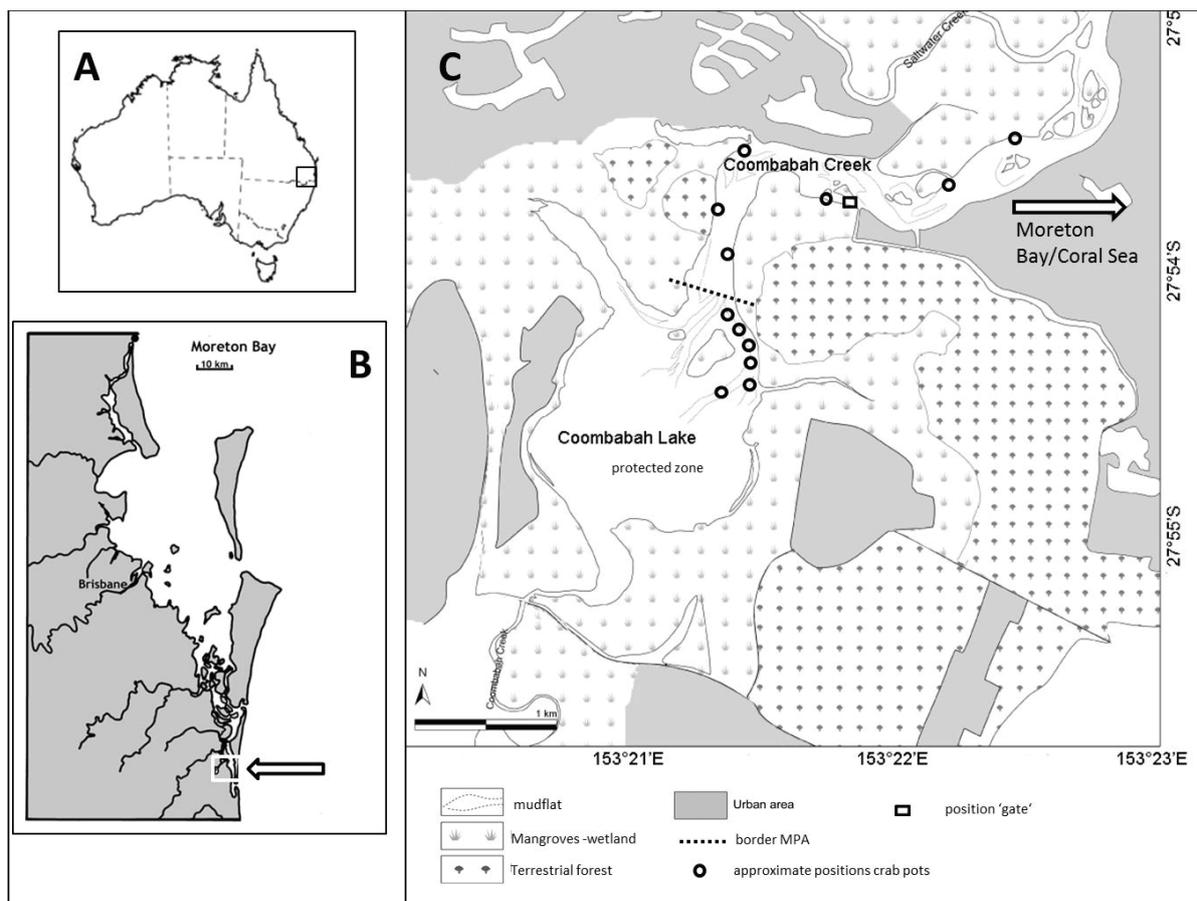
*S. serrata* has been reported to demonstrate limited routine movement and to have a relatively small home range (Hill 1978, Hill et al. 1982, Hyland et al. 1984, Pillans et al. 2005), only ovigerous females migrate over long distances to offshore areas for spawning (Hill 1994). Many studies have neglected the significance of seascapes in movement studies. Seascapes can be highly diverse (e.g., inshore-offshore, open-closed, marine-estuarine-riverine), so is the diversity of the types of movement associated with them. Hyland *et al.* (1984) acknowledge that the range and directions of movement of *S. serrata* seem to be affected by the structure of the local seascape. Further, the scales of movement can differ widely even between individuals of the same species (Pittman and McAlpine 2003).

This study aims to measure the movement of tagged *Scylla serrata* in a partial enclosed, protected, tidal lake in Queensland, Australia, and the implication of this movement for the effectiveness of the protected zone in support of adjacent local fisheries ('spill-over'). The effect of rainfall/flooding events on the crabs' movement was also assessed, in order to evaluate possible seasonal restrictions on fisheries as a management measure for this species. Further, we investigated the seasonal variation in population structure of *S. serrata* between protected and unprotected areas in this specific seascape. We hypothesize that a) population structure in the MPA and fished zones demonstrate different size distributions and sex-ratios (Hypothesis 1); b) the movement of *S. serrata* exceeds the boundaries between the protected and unprotected zones, resulting in a spill-over to adjacent fisheries (Hypothesis 2); and c) increased activity (catchability) of *S. serrata* occurs at times of reduced salinity, i.e., during the rainy season (Hypothesis 3).

## Material and Methods

### Study site

The study was carried out in the subtropical Coombabah Lake and Creek, southern Moreton Bay, Queensland, Australia (27°54'5.48"S, 153°21'16.20"E). The study area (Figure 1) is part of the Moreton Bay Marine Park (Queensland Fisheries Act 1994), which includes Coombabah Lake, a declared no-take zone, and Coombabah Creek, a partially protected area, which is open to most fisheries including mud crab fishery (hereafter referred to as 'unprotected'). Coombabah Creek connects Coombabah Lake with polyhaline southern Moreton Bay. Hypersaline conditions (up to 42, practical salinity scale) can occur in the Coombabah area during the dry season in winter (Benfer et al. 2007) whereas very low salinity ( $\leq 2$ , H. Alberts-Hubatsch, pers. obs.) can prevail during heavy rain events in the wet season. The dry season normally occurs from late autumn (May/June) to early summer (October/November) with lowest rainfall from July to September (average 95 mm); the rainy ('wet') season is during the summer months until early autumn with highest rainfall in February and March (average 410 mm) (Benfer et al. 2007). Three main factors influence the salinity dynamics in



**Figure 1.** Map of the study area. **A** Map of Australia, box indicates the location of the study site. **B** Map of Moreton Bay, Southeast Queensland, white box and arrow indicate the location of the study site. **C** Detailed map of the study site: Coombabah Lake (protected/no-take area) and Coombabah Creek (unprotected area), which connects Coombabah Lake with the adjacent southern Moreton Bay.

this area: rainfall/runoff, evaporation and tidal exchange (Benfer et al. 2007). Coombabah Lake is shallow and small (2 km<sup>2</sup>) with average depth < 1m and a muddy bottom (Benfer et al. 2007). Coombabah Creek broadens towards the entry of the Lake with an approximate width of 200 m and an average water depth of 1 m with many sand banks and mud flats exposed at low tide. Further towards the ocean the Creek becomes narrower (approx. 100 m) with steeper banks, has an average depth of 4 m and few sand banks exposed at low tide. Both Coombabah Lake and Creek are fringed by mangroves (mainly *Avicennia marina*, *Rhizophora stylosa* and *Aegiceras corniculatum*), the southern bank of the Creek is lined by concrete and rock walls of residential developments (Benfer et al. 2007). The whole area is influenced by semi-diurnal tides with a range of 1 - 1.8 m.

#### *Collection and tagging of crabs*

Mud crabs were captured year-round from January 2012 to April 2013, randomly regardless of lunar cycle or weather conditions. Sampling was generally done on 2-4 days per month, with the exception of June to September 2012 when traps were deployed only one day per month. Activity of mud crabs is low in these winter months, when they are hardly fished in Queensland (Heasman and Fielder 1977).

Mud crabs were caught with round “pop-up” pots (60 cm in diameter) made of galvanized steel, covered with a 55 mm mesh, commonly used for commercial fisheries. The pots were baited with either mullet (*Mugil cephalus*) or heads of snapper (*Pagrus auratus*). Six pots each were deployed in the Lake and in the Creek (protected and unprotected zones, respectively). At the beginning of the sampling in January 2012, the pots were left soaking for 24 h, but trapping was restricted to day-time after some pots were stolen by poachers at night-time in February 2012. Therefore, night catches were excluded from the analysis of catch-per-unit-effort (CPUE) data. During day-time, the pots were checked for crabs every 1-3 hours. In the Lake, the deployment of pots was restricted to the main channel at the entry of the Lake as the major part was too shallow for fishing from a boat. The bathymetry of the Creek allowed for more flexible sampling and the pots were deployed at varying sites in the channel and along the bank.

The captured mud crabs were checked for recaptures, their sex determined and their size measured. Size was measured as inner carapace width (CW), which is the distance across the notches between the eighth and ninth antero-lateral spines of the carapace. Injuries and deformations were recorded. After assuring that the crab had no major injuries (e.g., loss of appendages), a T-bar-tag combined with a passive-integrated-transponder-tag (T-bar/PIT-tag) was inserted into the small gap between the carapace and the first abdominal segment (Meynecke et al. submitted). This placement has little effect on the survival and the movement of the crab and prevents the tag from being lost when the crab molts (Hill 1975, Frusher et al. 2009, Meynecke et al. submitted). Each PIT-tag number was

checked using a handheld PIT-tag reader (BIOMARK 601) before releasing the crab. The T-bar tag (Infofish/Suntag) was imprinted with an ID and a toll-free phone number to report recaptures by the public. The tagged crabs were released at the same site as and within half an hour after the initial capture.

In Coombabah Creek, an automated underwater antenna system (the “Gate”) was installed approximately 4.5 km downstream from the protected zone (Figure 1), to read the identity of the tagged crabs’ swimming through the gate and to record the time and date of passage using RFID technology (Meynecke et al. 2008). The Gate consisted of two copper coils (antennae) in water-tight seals, each enclosing an area of 25 m width and 1 m height, extending along the bottom of Coombabah Creek from the bank to the middle of the channel. The two antennae were placed 10 m away from each other, enabling the detection of speed and direction of movement of the tagged crabs (Meynecke 2013).

Different aspects of the movement were investigated. The movement of all tagged mud crabs (all males and females in Coombabah Lake and Creek) was assessed and an additional analysis focused on the fishery relevant male crabs  $\geq 150$  mm. The direction of movement was divided into upstream, same site and downstream. Since Coombabah Creek is not a river, but a tidal creek, the terms ‘upstream’ and ‘downstream’ refer to the geographical position in relation to the ocean and not to the actual direction of currents.

Water temperature and salinity were recorded on each sampling day using combined conductivity, temperature, and depth sensors (RBR XR 420 CTD) and/or a manual water sampling kit (WTW Multi 3430) at the entry of Coombabah Lake and in the Creek at the position of the Gate. Daily rainfall data was obtained from the bureau of meteorology (BOM 2014), collected at the Coombabah treatment plant right next to the sampling area.

#### *Data analysis*

Data exploration was performed in R (version 3.0.1) following the protocol of Zuur et al. (2010) with the “nlme” and “ggplot2” - packages. Abundance data of mud crabs (as total number of crabs caught in the traps) were normally distributed in the protected and in the unprotected zone and compared by one-way ANOVA. The abundance of male and female mud crabs as well as the distances moved by the two sexes were also compared by one-way ANOVA. Sex-ratios were calculated for a) the total catch containing all sizes and b) only mature mud crabs  $> 145$  mm CW; bias in the sex-ratios in the protected and unprotected zones was assessed using a binomial test to estimate the deviance from the predicted ratio.

Generalized additive mixed-effect modeling (GAMM, Zuur et al. 2009) was used to model the response in catch-per-unit-effort to measured environmental parameters (rainfall, water temperature and salinity). GAMM allows modeling of non-linear trends with a smoothing function for

the predictor variables and implement random effects. The Akaike information criterion (AIC) was used to choose the best fit model. The variable “Trap” was set as a random term as the traps in our sampling were dependent on each other (e.g., traps upstream may have reduced the catch downstream in the direction of the crab movement). Salinity values were smoothed in the GAM (generalized additive model) as part of the GAMM to reduce influence of extreme values recorded during the sampling period.

## Results

### *Size and sex-ratio*

Between January 2012 and April 2013, a total of 852 mud crabs were caught, tagged and released in Coombabah Lake and Creek (Table 1). Catching effort was similar in both the protected (six traps) and the unprotected zone (six traps). During the winter months traps were only deployed in the unprotected zone. In the latter, a total of 458 crabs were caught while 394 crabs were captured in the protected zone.

One-way ANOVA revealed significant differences between size (CW) of male and female mud crabs in the protected and unprotected zone (Table 1): male size (CW) ranged between 82 and 174 mm ( $133 \pm 1.2$  mm, average + SE) in the protected zone and 64 – 173 mm ( $129 \pm 1.3$  mm) in the unprotected zone (Table 1), with the former group being significantly larger ( $F(1,501)=7.12$ ,  $p = 0.0079$ ). The average sizes of large legal-sized males ( $\geq 150$ mm) did not differ between the protected ( $157 \pm 0.8$  mm) and unprotected zone ( $158 \pm 1.2$  mm,  $F(1,96) = 0.716$ ,  $p = 0.39$ ), but more large males were captured in the former ( $n = 62$ ) than in the latter ( $n = 36$ ). In the protected and unprotected zones, 24.2% and 14.5% of all male mud crabs were equal or larger than legal size (Figure 3). The CW of female mud crabs ranged between 87 – 183 mm ( $145 \pm 1.9$  mm) in the protected zone and 87 – 187 mm CW ( $140 \pm 1.6$  mm) in the unprotected zone (Table 1), but size was not significantly different ( $F(1,347)=3.51$ ,  $p=0.061$ ). At both sites, high abundances of large females ( $\geq 150$  mm CW) were

**Table 1.** Comparison of numbers and mean sizes of *Scylla serrata* captured in Coombabah Creek and Coombabah Lake

Location	total				male				female		
	n	mean size (CW in mm)	SD	% legal	n	mean size (CW in mm)	SD	% legal	n	mean size (CW in mm)	SD
Coombabah Creek - unprotected	458	133	22	7.75	249	129	20	14.5	209	140	23
Coombabah Lake - protected	394	137	21	15.5	254	133	19	24.2	140	145	23

found, making up 49% of all females in the protected and 40.6% in the unprotected zone.

A binomial test revealed differences in the sex-ratio between the two sites. In the protected zone, males outnumbered females with a sex-ratio (M:F) of 2:1 ( $H(0) = 0.66$ ;  $p = 0.53$ ) whereas the sex-ratio in the unprotected zone was 1:1 ( $H(0) = 0.5$ ;  $p = 0.07$ ). When regarding only mature individuals (> 145 mm CW in Qld; both sexes, Heasman 1980), their sex-ratio shifted towards dominance of female mud crabs and was 1:1 ( $p = 1$ ) in the protected and 1:2 ( $p = 0.735$ ) in the unprotected area.

### *Movement*

Of the 852 crabs tagged in this study, 82 were recaptured in the trapping program or recorded by the gate system, yielding a 'recapture' rate of 9.6% (both will be referred to as recaptured crabs). The gate system detected 20 crabs in the summer of 2012 (24% of all recaptures), but stopped working by the end of 2012 due to flooding and corrosion of its technical parts. Of the 62 crabs recaptured from traps, 48 (58%) were recaptured by traps set in this study and another 14 (18%) were recaptured and reported by recreational fishermen. None of the crabs were recaptured more than once and none showed size increment that indicated molting.

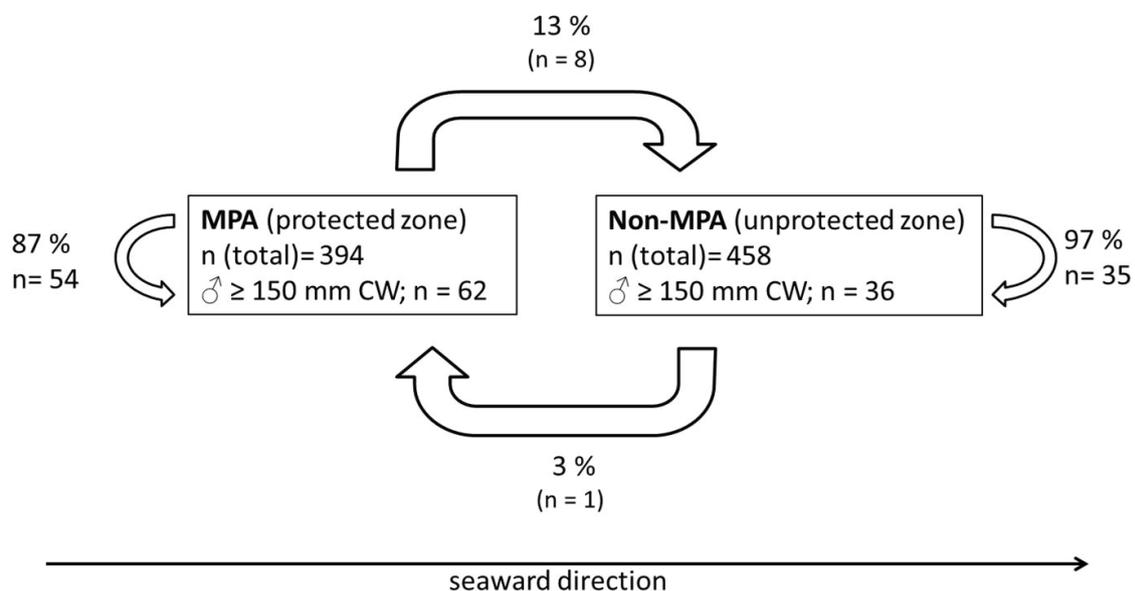
**Table 2.** Mean distance between release and recapture sites and time at liberty of *Scylla serrata* in Coombabah Lake and Creek, Australia. 'same site' indicates the proportions of mud crabs, that were recaptured in the same site as release, 'upstream' movement indicates proportions of crabs moving in landward direction and 'downstream' movement the proportion of crabs moving in seaward direction. Overall number from both zones combined are given (all recaptures), and zones were analyzed separately (protected/unprotected zone). The proportions are relating to the n in the respective columns, numbers in brackets indicate the respective proportion of crabs that crossed the border from one zone to the other).

	n	mean distance (in m)	SE	mean time in liberty (days)	SE	same site %	upstream movement %	downstream movement %
all recaptures	82	413	83	14	2.2	28	25 (6)	47 (13.4)
males	60	475	108	15	2.8	30	25 (17)	45 (12)
legal males	23	563	179	14	3.3	28	24 (1)	48 (35)
females	22	242	82	13	3.3	23	27 (14)	50 (4)
protected zone								
total	42	464	127	19	3	21	31	48 (26)
males	33	550	159	19	3.6	21	30	49 (30)
legal males	16	746	267	23	5	6	31	63 (50)
females	9	150	54	17	5.1	22	33	44 (33)
unprotected zone								
total	40	358	106	10	3.1	35	20 (13)	45
males	27	383	144	9	4.2	40.5	19 (11)	40.5
legal males	7	537	412	2	0.5	57	29 (14)	14
females	13	306	134	11	4.3	23	23 (15)	54

The recaptured crabs originated equally from the unprotected (n=40) and the protected zones (n=42). Regarding all recaptured crabs from both zones, 46 % (n=38) moved downstream (in seaward direction) and 13% (n=11) crossed the border from the protected into the unprotected zone in seaward direction, with 10% (n=8) being legal-sized males (> 150mm CW). Movement in the landward direction ('upstream') was less frequent (25%, n=20) and only 6 % (n=5) crossed the border from the unprotected zone into the protected zone. Only one legal-sized male was observed to enter the protected zone this way. The proportion of crabs recaptured at the same site as released ("sedentary crabs") was 28%.

The longest distance moved was by a male crab (158 mm CW), which was originally released in the protected Coombabah Lake. It was recaptured after 25 days in liberty 4000 m downstream the creek by a recreational fisherman. The average days in liberty at the time of recapture was  $14 \pm 2.2$  (Table 2), the longest time in liberty was 87 days (male, 137 mm CW). This crab was recaptured 410 m away from its release site. Table 2 shows a summary of mean distances moved, days in liberty and direction of movement of the recaptured crabs.

Regarding the separate analysis of the two zones (Table 2), there are major differences in the direction of movement and time in liberty of legal sized males in the protected and unprotected



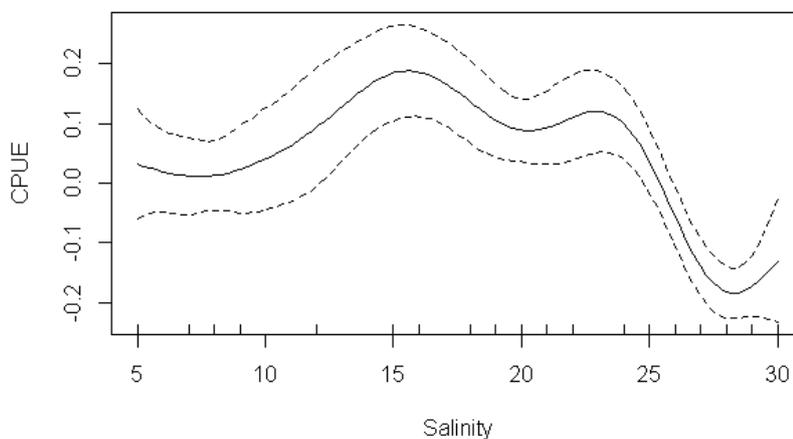
**Figure 4.** Movement of *Scylla serrata* relevant to fisheries (large males  $\geq 150$  mm CW) in and between the protected (no-take) and unprotected zone (recreational zone). All numbers outside the two rectangles refer to the total number of large male crabs caught in the respective zone (protected/unprotected). Total number of crabs is the number of all crabs in the respective zone, including females and undersized; arrows indicate direction of movement. \* is the maximum number of large males that resided in the respective zone, actual numbers could be smaller as not all of them were recovered.

zone. Firstly, we recaptured fewer males in the unprotected ( $n=7$ ) than in the protected zone ( $n=16$ ). In the protected zone, the majority of large males (63%) moved in seaward direction. In contrast, in the unprotected zone only 14% moved in this direction and 57% were recaptured at the same site as release, versus 21% in the protected zone (Table 2). The time in liberty also differs between the two zones. In the protected zone, large males were recaptured in average  $23 \pm 5$  days after release, whereas the time in liberty in the unprotected zone was only  $2 \pm 0.5$  days.

#### *Effects of rainfall and temperature*

The catch-per-unit-effort data showed a seasonal pattern with significantly higher (ANOVA,  $p < 0.001$ ) mean rates ( $0.42 \pm 0.017$ , mean  $\pm$  SE) during the wet season in summer (December to April) and lower rates ( $0.14 \pm 0.016$ ) during the dry season in winter (May to November).

The best GAMM for the CPUE data was found to be the model with salinity as a smoothed term ( $p < 0.001$ ) and only rainfall as an additional explanatory variable, even though rainfall was non-significant ( $F = 14$ ,  $df=7$ ,  $p < 0.001$ ,  $AIC = -24.43$ ). Including temperature as an explanatory variable did not improve the model ( $F = 12$ ,  $df=7$ ,  $p < 0.001$ ,  $AIC = -22.39$ ). Applying this model to our data shows that the effect of salinity is significant and moderate salinity (10-25) resulted in highest catch rates and low salinities ( $<10$ ) still resulted in higher catch rates than high salinities ( $> 25$ , Figure 5).



**Figure 5.** Catch-per-unit-effort (number of crabs per hour per trap) of *Scylla serrata* in relation to salinity in Coombabah Lake and Creek, eastern Australia in 2012/13. The dashed line indicates the 95 % confidence interval of CPUE.

#### **Discussion**

Basing upon the results of our study on the capture and movement of adult *Scylla serrata* within and between the Coombabah Lake MPA and the adjacent unprotected Creek zone, all three initially stated hypotheses can be accepted, i.e., a) the population structure in the MPA and fished zones differ in mud crab size distributions and sex-ratios (Hypothesis 1); b) the movement of the crabs exceeded the boundaries between the protected and unprotected zones, resulting in a spill-over to adjacent fisheries (Hypothesis 2); and c) incidences of high crab activity co-occurred with decreasing salinities (Hypothesis 3).

### *Size and sex-ratio*

As predicted by Hypothesis 1, significant differences in size and sex-ratio of *Scylla serrata* existed between the protected and unprotected zones in Coombabah Lake and Creek. The mud crab fishery in Queensland is sex-biased and only male mud crabs > 150 mm CW may be legally collected. Our findings support previous reports of differences in sex-ratio and sizes of mud crabs in protected and unprotected areas in the Moreton Bay Park (Pillans et al., 2005) and a nearby site in New South Wales (Paul A Butcher et al., 2003). The largest female caught in the protected zone of our study measured 183 mm and the largest male was 174 mm. Mud crabs can grow to sizes above 240 mm (Heasman, 1980), and Hill et al., (1982) found as many male crabs in the size range of 180-190 mm as they found crabs in the size from 150 160 mm in Northern Queensland and also Heasman (1980) found crabs in this size range in his study in Moreton Bay, whereas we were not able to detect any crabs in this range. The fishing pressure for male crabs in the unprotected zone is high and in the crabbing season recreational fishers are “fishing the line” (Grüss, Kaplan, Guénette, et al., 2011), i.e. crab pots are deployed right at the border to the protected zone, to catch the big males as soon as they leave this zone. The fact that we did not find any males > 174 mm in the protected zone and fewer males in the unprotected than in the protected zone indicates that there is a constant downstream movement of large males, with most of them being caught shortly after leaving the protected zone, supporting hypothesis 2.

Even though management measures towards the sustainability of *S. serrata* are implemented in our study area, this is an alarming trend towards decreasing sizes which is also observed in areas without any fishing restrictions (e.g., Philippines). Current management strategies and exploitation rates allow the population to persist. However, consideration should be given to the fact that maximum crab sizes are decreasing. The high fishing pressure in the unprotected zone at our study sites is also reflected by the differences in the sex-ratio due to the sex-biased fishery. In the protected zone, males are outnumbering female crabs (sex-ratio 2:1), whereas the number of females and males in the fishing zone is even (1:1). Regarding the mature mud crabs only ( $\geq 145$  mm CW; Heasman, 1980), the sex-ratio is shifted towards female predominance in the unprotected zone (1:2) but is even in the protected zone. The skewed sex-ratio for mature mud crabs in the protected and unprotected zone poses the question whether big females are still able to reproduce due to the lack of appropriate-sized mating partners. However, there is yet no data to indicate decreased reproductive output, such as an overall decrease in mud crab abundance (DAFF 2014). In the Dungeness crab, *Cancer magister*, where the sex-specific harvest regulations are similar to those for mud crabs in Queensland, no effect was seen on the reproductive output of female crabs by removing male crabs (Dunn & Shanks, 2012; Hankin, Butler, Wild, & Xue, 1997).

Males usually dominate in natural populations of *S. serrata*, with sex-ratios of 3:1 in the Philippines (Bonine, Bjorkstedt, Ewel, & Palik, 2008) and also 3:1 in undisturbed (unfished) populations elsewhere in Australia (Heasman, 1980). Pillans et al. (2005) found sex-ratios of 2:1 for mature crabs in MPAs within fished areas in Moreton Bay, Australia, which is the same as in our study, but still less male-biased than those reported in the literature for natural or protected populations. We also have to take into account that actual number and maximum size of large males in the protected zone might be reduced due to illegal fishing in that area. Our crab pots were subjected to poaching in the protected area and anecdotal reports from residents around the Lake indicate that the no-take zone is sometimes being poached at night.

#### *Cross-boundary crab movement and possible triggers*

Our recapture rate of tagged crabs was 9.6 %, which is comparable to recapture rates in other studies (10.6 %: Butcher et al. 2002; 9 and 13 % in two different areas: Pillans et al. 2005). No differences in distance moved by male and female *S. serrata* were observed in our study. However, only few female crabs were tagged during the spawning season, when they are known to move long distances to spawn offshore (Hill 1994). In the protected zone, 13 % of tagged large males ( $\geq 150$  mm) moved into the unprotected zone where they became available to fisheries (Figure 4). To the contrary, only one legal-sized crab moved in the opposite landward direction from the unprotected zone into the protected zone. Overall, the greater proportion of mud crabs (47%) moved downstream, supporting Hypothesis 2, whereas only 25% moved upstream (Table 2) and the other 28% stayed on site.

None of the crabs tagged during the first year (2012) were recaptured in the second year (2013). We know from previous studies (Hill 1975, Perrine 1978, Tait et al. 1985, Meynecke et al. submitted) that tag retention is good and that tags can stay in place even after a second molt. The absence of tagged crabs from the previous season might also indicate that the crabs had left the system towards Moreton Bay, further supporting Hypothesis 2 of downstream movement. Alternatively, male crabs might have been fished out of the system.

Hill (1978) tracked the movement of individual mud crabs in a South African estuary and found only minor and slow foraging movement. In his study, mud crabs were predominantly moving against the current, which was seen as a foraging strategy since mud crabs use olfactory cognition/information for orientation towards possible prey items. The upstream and on-site movement in our study may reflect foraging activities while other triggers might be responsible for the larger scale downstream movement, e.g. change in salinity/current flow during rainy periods.

Hyland et al. (1984) compared the movement of mud crabs in different areas (narrow creeks and open bay area/mud flats) and concluded that their movement depends on the seascape. Movement on the mud flat seemed to occur over longer distances whereas movement within the channels was

limited to hundreds of meters. However, in either case the crabs' movement seemed to be non-directional. When designing protected areas and implementing species-specific management measures, one has to bear in mind that concepts that work in one particular land- or seascape setting may not necessarily be applicable to another. Concerning mud crabs conservation, the implementation of MPA should incorporate aspects of the particular seascape. Coombabah Lake for example is semi-enclosed and only a small MPA (2 km<sup>2</sup>), furthermore located upstream to a fishable zone, hence favouring spill-over. In contrast, in bigger MPAs biomass export of mud crabs was estimated to be low (Pillans et al., 2005), as the boundary extend might exceed the movement range.

We hypothesized that the movement range of *S. serrata* traverses the boundaries from the protected to the unprotected zone, which is supported by our results (Hypothesis 2). The observed export of mud crabs from the MPA suggests that Coombabah Lake serves as a source of *S. serrata* for the adjacent unprotected area, since the range and direction of an animal's movement can determine if a MPA serves as source or sink (Pulliam 1988). However, to unequivocally determine source-sink dynamics for *S. serrata* in Coombabah Lake, an estimate of crab recruitment and mortality is necessary. While the process by which larvae of *S. serrata* recruit to inshore populations from offshore areas is still obscure (Alberts-Hubatsch, Lee, Diele, Wolff, & Nordhaus, 2014), Coombabah Lake does support a high density of juvenile and adult crabs, suggesting a regular successful recruitment of early juveniles to the area.

The movement from the protected into the unprotected zone observed in our study might reflect density-dependent processes, as mud crabs react strongly to the presence of conspecifics (Beattie, Pitt, & Connolly, 2012) and are highly aggressive. Seaward movement could be seen as a reaction to avoid intraspecific competition. On the other hand, mangroves and adjacent areas are highly productive – especially during the rainy season - and provide habitat for a variety of potential prey items of *S. serrata*. Additionally, many of these potential prey items are marine species, which are not adapted to changing salinities (e.g., barnacles) and may be immobilized or killed due to the drastically decreasing salinities (Goodbody 1961, H. Alberts-Hubatsch, pers. obs.) during the rainy season. These become easily available to the mud crabs that are known to feed on carrion as well as on slow moving and sessile benthic invertebrates (Hill, 1976; Webley, 2008). Since food availability should be favorable during this period, the trigger for the observed downstream movement of the mud crabs may thus be a density threshold. A similar behavior has been observed in American lobster (*Homarus americanus*), where intraspecific superior lobster leave crowded areas, even though other factors (e.g., food) might be favorable (Cobb & Wahle, 1994; Steneck, 2006). This process was defined as 'demographic diffusion' by Steneck (2006), which "occurs when an identifiable segment of the population moves from habitats of high population density to habitats of

low population density". It appears that mud crabs – similar to the American lobsters – are seeking areas of low densities and relaxed competition instead of constantly investing energy in aggressive behavior.

We hypothesized that high crab activity co-occurs with decreasing salinity (Hypothesis 3). Our model supports this hypothesis since salinity was the explanatory factor for mud crab activity. However, it is not possible to say whether salinity is a direct or indirect factor in triggering the observed increased activity levels since other potential factors such as increased nutrient levels, prey abundance, currents due to flushing may also be important. To disentangle the effects of these co-occurring factors on the activity of the mud crab, carefully designed experimental studies should be performed.

#### *Conclusions and management implications*

Our study highlights the importance of comprehensive biological knowledge of a species such as the movement pattern of individuals for effective management of fished species and for the set-up of a protected area for their conservation in the context of a given location. The Coombabah Lake MPA serves both the conservation of mud crabs and the mud crab fishery. While the boundaries of the MPA are static in time and space, the mud crabs therein are not since, e.g., the spatial scale of their habitat use exceeds the area protected by the MPA. This caused the observed trans-boundary movements of some individuals, and, when involving large-legal sized males, results in a spill-over effect that benefits the fishery. The relatively small size of the Coombabah Lake MPA in combination with the range, direction and frequency of movements of the vulnerable part of the mud crab population (i.e. legal-sized males  $\geq 150$  mm CW) and the ongoing "fishing on the line" at the seaward opening of the otherwise enclosed lake probably drives the observed downfishing of male sizes, which suggests the dangers of growth-overfishing.

While management measures in Queensland are the strictest in the world in terms of the definition of minimum sizes of mud crabs and seem to prevent recruitment overfishing, the observed downfishing of male sizes and potential detrimental effects thereof need to be investigated. For example, we must know whether the unfished large female crabs are still (and for how much longer) able to find appropriate sized mating partners, and if not, whether this would affect the quality of reproductive output. We further suggest to review the size at maturity of the local mud crab population, last studied in the 1970's (Heasman, 1980), since this value and the circumstances of the fishery may have changed over time. It is important to assure that the harvested male crabs are morphologically, physiologically and behaviourally mature before being caught, and have had the chance to mate at least once (Knuckey, 1996). Finally, during our field study we observed incidences of poaching in the Coombabah Lake MPA, and mud crab fisheries law non-compliance is in fact a well-known problem in this area. Given the simultaneous occurrence of decreasing crab sizes due to high

fishing pressure and poaching , we strongly advocate regular assessments of the population structure and capture sizes of the local mud crab population, involving both fisheries dependent and, ideally, fishery-independent data. Furthermore, the frequency of poaching events should be determined. Given the likely limited resources to do this in an effective way, an alternative option could be to involve citizens inhabiting the shores of Coombabah Lake in collecting data. Quantifying the magnitude of poaching would help to evaluate the need for measures to improve law compliance in this frequently fished mud crab habitat.

### **Acknowledgements**

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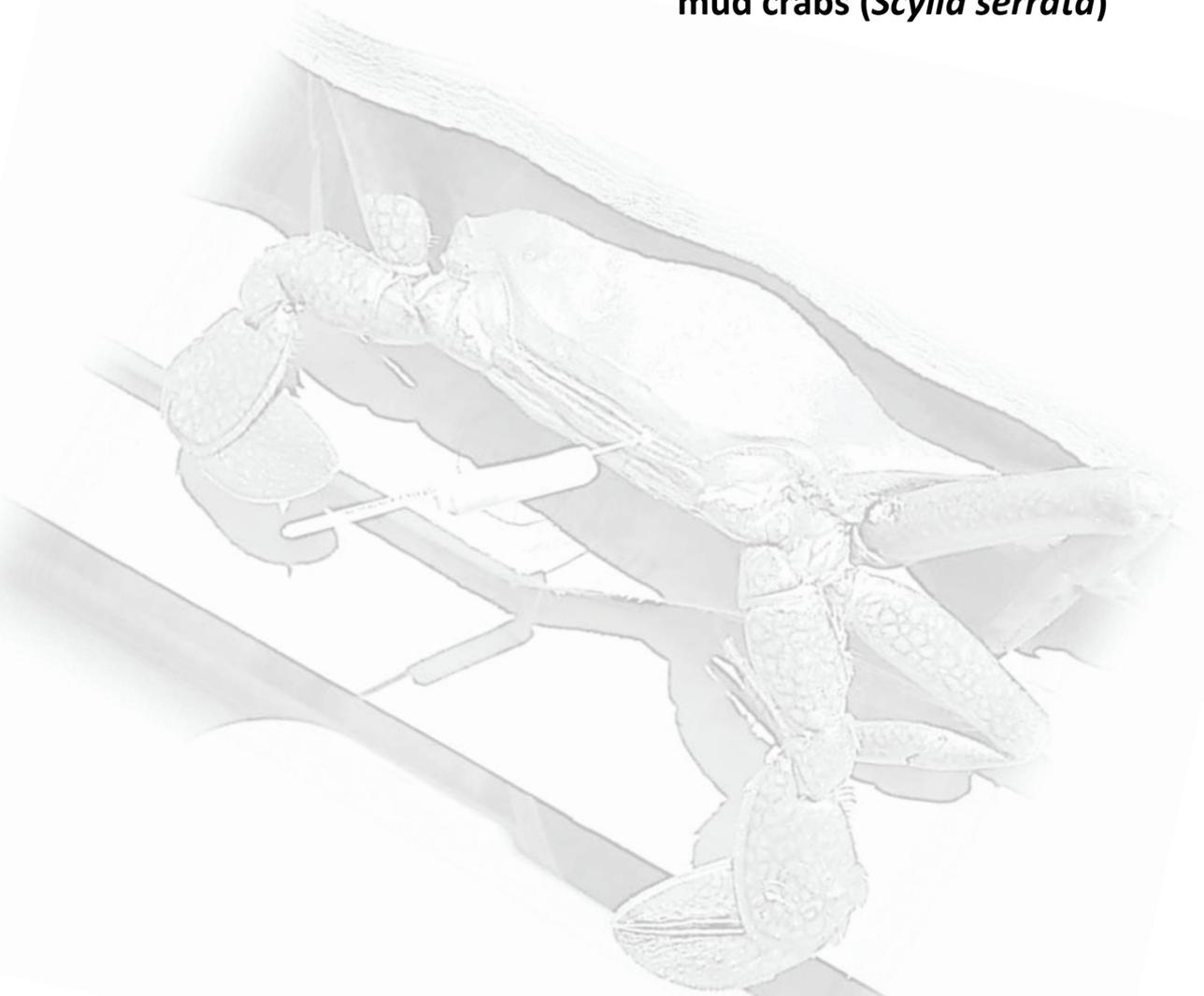
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## Chapter 3.2

### Performance and physiological responses of combined t-bar and PIT tagged mud crabs (*Scylla serrata*)



Jan-Olaf Meynecke

John Mayze

Hilke Alberts-Hubatsch

*In preperation*

## **Abstract**

Mud crabs (*Scylla* spp.) are intensively caught throughout South-East Asia and support a million dollar commercial, recreational fishing and aquaculture industry. Enabling individual identification for wild and aquaculture research is important to improve understanding and management of this species. However, tagging of crustaceans is difficult as they frequently moult and internal tags can pose a hazard to consumers. In this study we tested a method combining passive integrated transponder tags and t-bar tags externally. 45 crabs (carapace width 80mm to 130 mm) were subject to treatment in two separate trials and tank environments. Firstly we inserted tags into the abdomen of 30 mud crabs as described in previous studies and then tested the modified method. The crabs were kept for a total of 10 month. Tagged crabs with the modified method showed 85% tag retention for moulting crabs. Secondly we tested the same method in the field where 852 individuals were tagged with combined t-bar and PIT tags of which 82 were successfully recaptured. This method has major implications for mud crab monitoring for wild and aquaculture populations and can be deployed widely.

## Introduction

Crabs of the genus *Scylla* are widely distributed throughout the Asia-Pacific region, representing a valuable fishery resource. Fisheries currently exist in South Africa, Pakistan, Japan, Taiwan, Philippines, Malaysia and Australia (Knuckey 1999). Though not formally reported or reviewed, significant fisheries are also present in Vietnam, China, and other parts of Southeast Asia. Mud crabs are an important component of small-scale coastal fisheries, particularly in tropical and subtropical Asia, where their capture generates significant revenue for coastal communities (Le Vay 2001). Due to its fast growth, large size and extended distribution, *Scylla serrata* (Forskål, 1775) is generally favored by fisheries and for aquaculture. Mud crab farming is largely based on the capture and fattening of wild caught juvenile crabs (Nurdiani and Zeng 2007). However, aquaculture studies have demonstrated potential for breeding (Quinitio et al. 2010). Identification of individuals is important for selective breeding but also to determine habitat preference, improving growth and management of wild stocks. Mark and recapture approaches allow studying mud crab population dynamics including population size, distribution, migration, mortality, growth and maturity (Barnes et al. 2002, Lebata et al. 2007). Identifying mud crabs contributing to the fishery is required for a better management.

There are a number of existing external tagging methods. They include rostrum ablation, branding, anchor tags and more advanced internal methods such as fluorescent elastomer, fluorescent alphanumeric, passive integrated transponder and microwire tags. Each method has its advantages and disadvantages. Anchor tags can cause death, especially in the case of juveniles (McPherson 2002) and passive integrated transponders can be costly albeit being more reliable than anchor tags (Jefferts et al. 1963, Le Vay et al. 2007). Visible implant elastomers (Liu et al. 2011) are difficult to see in larger individuals and are not practical to follow through to adult stage. Overall it is desirable to have a fast and reliable way of identification without impacting on consumer safety (e.g. internal PIT tags) (Frusher et al. 2009).

T-bar or anchor tags have been used previously to tag the mud crab *S. serrata* (Hill 1975, Perrine 1978, Hyland et al. 1984, Tait et al. 1985, Hay and Calogeras 2000, Pillans et al. 2005). Tagging of *S. serrata* with t-bar tags is a method first described by Hill in 1975. Hill (1975) tagged mud crabs with Floy FD67 anchor tags and a Dennison tagging gun. Tags were placed slightly off center at the junction of the carapace and the abdomen in the hope that this would reduce any effects of the tag at moult. Later, Hill et al. (1982) used Floy FD68B anchor tags with a Dennison tagging gun to tag mud crabs. Recapture data suggested that tags remained with the crabs after moulting, but outcomes were highly variable and dependent on the number of individuals tagged, their size and duration of study. During a field study Hill (1975) tagged 2500 *S. serrata* and recaptured 23 moulted crabs with the t-bar tag. The same method used by Hill 1975 was also applied in other studies. However, as Hill (1975) mentioned he "...hoped the tags would stay in..." but no study on the effectiveness of his

method has been undertaken to date. Perrine (1978) slightly altered the method. “Instead of puncturing the abdominal plate at the point of juncture with the carapace, the needle of the tagging gun was forced up along the underside of the carapace until it was completely free of that portion of the abdominal plate which extends up under the carapace, before squeezing the trigger to insert the tag” (Perrine 1978). A summary of t-bar tag studies for *S. serrata* is provided in Table 1.

Here we aim to test the deployment of combined t-bar and PIT tags and compare the method described by Hill 1975 with a slightly altered deployment method in a controlled tank environment.

**Table 1** Overview of t-bar tagging studies on *S. serrata*.

Reference	Method	Number tagged individuals	Size CW (mm)	Time in liberty	Moulting	Comments
Hill, 1975	anchor tags inserted with a tagging gun into the posterior region at junction of carapace and abdomen; put in slightly off-centre	2100	>80	1 day - 13.5 months /mean 99 days	14%	moulted crabs 23 - 414 days in liberty, up to two moults (40mm CW growth increment)
Perrine, 1978	Same as Hill, 1975, but tagging gun was forced up along the underside of the carapace	502	>100	up to 7 month	2%	reported scars from lost tags; moulted crabs 71 - 90 days in liberty, ~ 20mm CW growth increments
Hyland, 1984	same as Hill, 1975	6233	>100	36 weeks/ mean 28 days	no	
Tait et al., 1985	same as Hill 1975	3059	>80	up to 8 month	yes	longer times in liberty with growth: ♂ = 300 days; ♀ = 170 days
Hay and Calogeras, 2001	not described	2519	>120	9 - 11 months	no	
Pillans et al., 2005	same as Hill 1975	472	>100	8- 223 days/ mean 80 days	no	one male 17 cm CW = 300 days (no moulting)
Butcher et al., 2002	same as Hill 1975	1412	>70		N.A.	

## Methods

### *Sampling*

A total of 45 *S. serrata* were captured from the wild and kept in aerated seawater tanks for up to 7 days prior tagging to look for any abnormalities and allow the animals to adjust. Only crabs between 80 mm and 130 mm carapace width (CW) were selected. The impact of t-bar tagging on crabs smaller than 80 mm was likely to cause major harm and even death (McPherson 2002) and animals larger than 130 mm were unlikely to moult within a short time frame (3 month).

Crabs were kept in two different environments to see if the tank environment would influence overall survival. 15 (9 males, M, and 6 females, F) crabs were kept in a temperature controlled room at 27°C, in separate 20 l glass tanks with a half cut plastic tube for shelter. An air bubbler was inserted into each tank and the seawater (30 ppt) was changed every 3-4 days. Half a prawn (Penaeidae) or one pipi (*Plebidonax deltoides*) was fed daily. Another 30 crabs (17 M, 13 F) were kept in a flow through system in separate plastic containers (20 x 20 x 24 cm). They were fed approximately 20 % of their body weight and food included also prawns and pipis once every day (except weekends).

### *Treatment*

Prior to tagging the animals serum was tested. A sample was taken from the rear leg near the carapace and tested for Refractive Index (RI) values greater than 1.355 as an indication for moulting within a few weeks (Mayze et al. 2014). T-bar tags were combined with PIT tags by using heat shrink tubes (similar to Frusher et al. 2009). A first trial using Hills method (treatment 1) with the modified t-bar tags was run for 90 days. It consisted of 11 tagged crabs, 9 control and untagged crabs in the flow through system. Another 4 tagged crabs and 1 control were set in aerated tanks. In a second trial (treatment 2) a variation of Hills method was tested. The t-bar tag was inserted into the abdomen towards the right side and actively placed in the muscular tissue of the back rear leg determined by triggered movement of the rear leg. Size and weight of animals were determined at the start and end of each treatment and infections, tag and moulting status were checked and recorded frequently.

### *Field study*

A total of 852 *S. serrata* were tagged with the modified method between January 2012 and March 2013. *S. serrata* were caught with round “pop-up” pots made out of galvanized steel, covered with a 55 mm mesh, commonly used for commercial fisheries. The pots were baited. The captured *S. serrata* were sexed and their size and weight measured. Only *S. serrata* without major injuries (e.g.,

loss of appendages) were tagged with a combined t-bar/PIT-tag inserted between the carapace and the first abdominal segment using the modified method (Alberts-Hubatsch et al. *in prep.*).

### *Statistics*

Preliminary data exploration were undertaken using Minitab 16 (Minitab 2010) and Primer 6 (Clarke and Gorley 2006). Analyses were performed using the PERMANOVA+ add on for Primer (Anderson et al. 2008). Permutational multivariate analysis of variance (PERMANOVA) was used to determine whether differences in PIT tag retention rates existed for crabs across treatment groups. An Euclidean distance matrix was created for the response variable 'Tag presence or absence'. The three factor reduced model included the variables 'Treatment group', 'Tank environment', 'Moulting status' and the interaction terms 'Tank\*Treatment' and 'Moult\*Treatment'. All factors were treated as fixed with the analysis performed using Type III sums of squares and 999 permutations of the residuals under a reduced model. Pairwise tests were also performed for the factor 'Treatment'.

The size of the treatment effect was further investigated using distance based linear modeling (DistLM). Predictor variables included in the analysis were 'Original CW', 'Sex', 'Moulting status', 'Treatment' and 'Tank environment'. A stepwise selection procedure was applied using the adjusted  $R^2$  criteria.

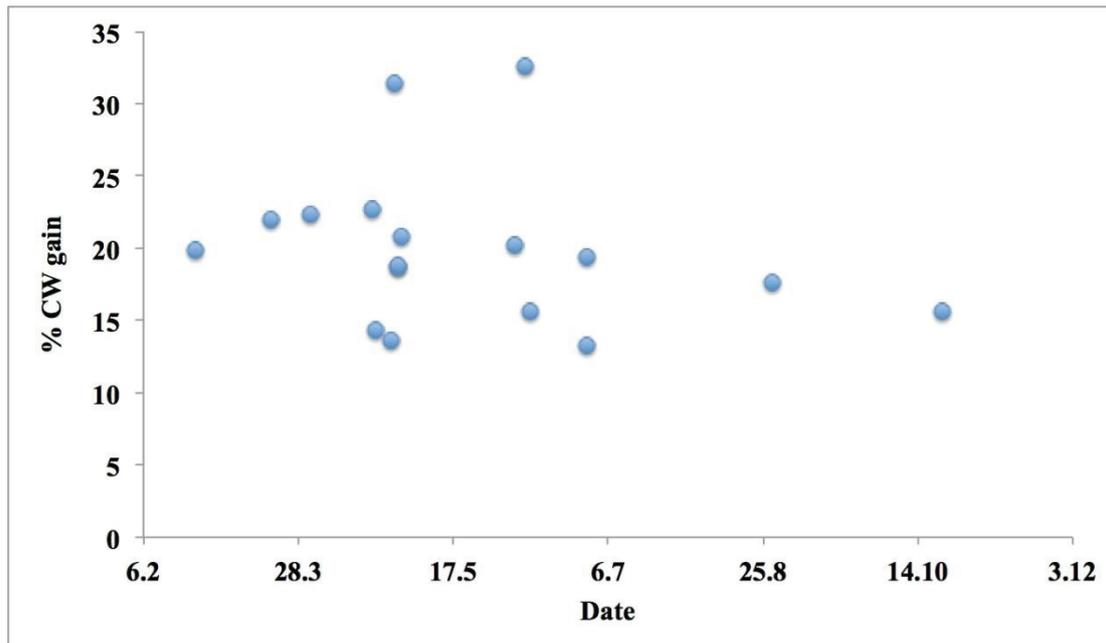
### **Results**

A summary of results is presented in Table 2. Tag retention was 77 % higher in the modified treatment compared to the method described by Hill. Moulting occurred in average after 75 days and for 42 % of all *S. serrata* during the study time. Successful moult was seen as evidence for growth and subsequently good health of the crabs. Moulting only occurred in the flow through system (60 % of *S. serrata* moulted) but not in aerated tanks and mortality was doubled in the aerated tanks compared to the flow through system. The average CW increase after moulting was 20 % with the smallest increase being 13 % and the largest being 33 % (Figure 1 shows CW increase for 16 *S. serrata* excluding one that died shortly after moulting)

#### *Treatment 1*

Hill's method was tested on 15 *S. serrata* (CW between 84-130 mm, 6 F, 9 M) and another 10 were kept as control for a total of 90 days. The tag was lost 12 times and remained with 2 *S. serrata* and 1 individual died during the study period. In the control 1 animal died. Overall tag retention was 13 % with a mortality of 7 %.

The flow through system was fitted with 11 tagged *S. serrata* and 9 control, untagged *S. serrata*. 8 individuals moulted but lost their tags during moulting. Out of the 3 that did not moult 2 also lost their tags. The individuals showed no signs of infections but scars occurred where the tagging took place. The aerated tanks were fitted with 4 tagged *S. serrata* and 1 control (CW 117-130 mm). The animals did not moult with 1 tag remaining after 90 days and 2 individuals that died including in the control.



**Figure 1.** Increase in carapace width (%) after moulting for 16 individuals of *S. serrata*.

### Treatment 2

The modified method was tested on 20 *S. serrata* (CW between 86 – 132 mm, 9 F, 11 M) for 90 days in aerated tanks and 213 days in the flow through system. A control with untagged *S. serrata* was not introduced for this treatment as there were no changes to the environment following the first experiment. At the end of the experiment the tags were present in 17 *S. serrata* and 3 individuals died. Overall tag retention for treatment 2 was 85 % with a mortality of 15 %. Figure 2 shows a *S. serrata* after successful moult with a modified t-bar and PIT tag inserted into the abdomen.



**Figure 2.** *S. serrata* B5 after successful moulting with exoskeleton on the left. Picture shows PIT tag attached to t-bar tag injected into right swimmer muscle tissue avoiding abdominal artery damage. Tag was inserted midway of the right side at the joint between the carapace and tail where moult separation occurs, angling slightly upward toward upper carapace but avoiding interference with the soft intermoult carapace.

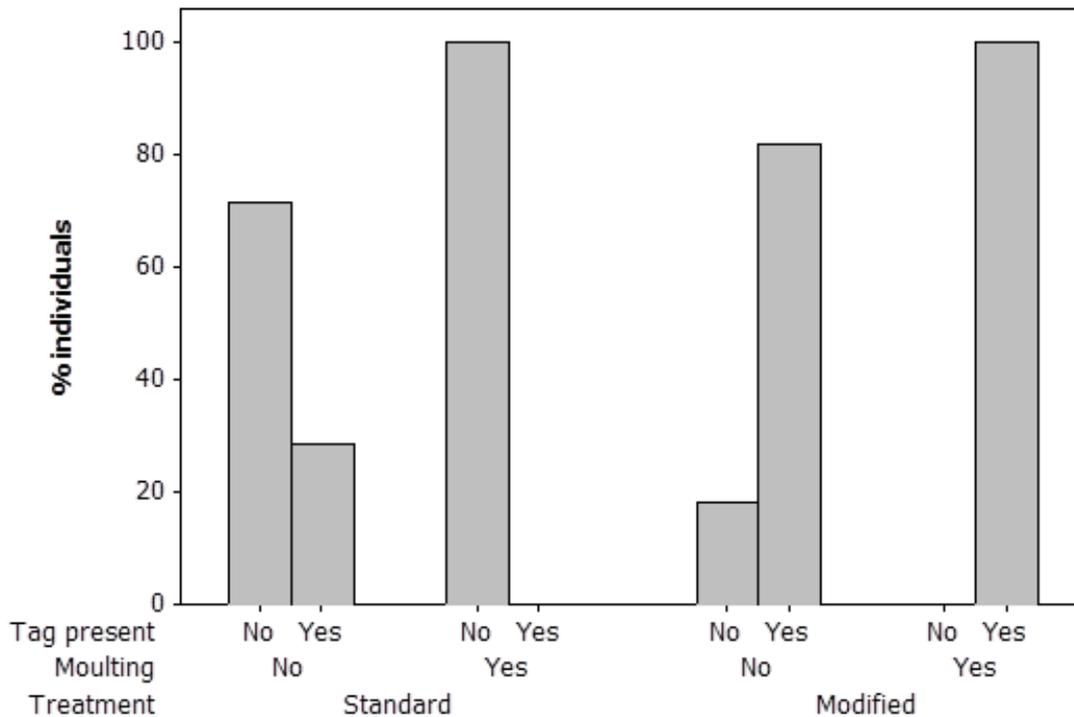
The tagging was also undertaken in 2 different environments. The flow through system was fitted with 10 tagged *S. serrata* of which 9 moulted with their tags remaining and 1 died. The aerated tanks were also fitted with 10 tagged *S. serrata* of which 8 still had their tags at the end of the trial and two died. However, no moulting occurred (Fig. 3).

A reduced model PERMANOVA found that the only variable to be a significant predictor of tag retention was 'treatment' ( $p=0.001$ ;  $df=2$ ). Pairwise tests for differences between treatment groups found that tags were significantly more likely to be retained in Treatment group 2 than group 1 ( $p=0.001$ ). Tag retention in group 1 was not found to be significantly greater than the control group that had not been tagged ( $p=0.465$ ).

The DistLM analysis found that the differential allocation of crabs to treatment group was responsible for 60 % of the variability in tag retention. The best model suggested by the DistLM analysis also included the variables 'Original CW' and 'Moulting status', accounting for only a small amount of variability in the results (~3%).

### *Field study*

The modified method was also tested on 852 *S. serrata* in the field. The individuals were tagged with combined t-bar/PIT tags of which 82 individuals (9.6%) were recaptured but no moulting was recorded. However, the tags were in place and functional and no signs of infection were visible but some scarring occurred where the tags were inserted.



**Figure 3.** The number of individuals of *Scylla serrata* that moulted in each treatment and tag presence at the end of treatment.

### Discussion

The study presented here showed that a combined t-bar/PIT-tag inserted into the muscle tissue of the rear leg between the dorsal carapace plate and the top of the abdominal flap has significantly higher tag retention after moulting than the method described in Hill (1975) ( $p=0.001$ ;  $df=2$ ). The method described by Hill 1975 where tags were also inserted at the posterior end did not actively deploy the tag into the muscle tissue. As our lab study demonstrated if tags are not inserted into the muscle tissue of the rear leg there is a high likelihood that the tags will not remain with the animal when moulting. Previously, no assessment was made of the potential effect of the impact of t-bar tagging method on the survival of *S. serrate*, posing a problem population estimates. The results also have implications for other studies on similar species such as *Metacarcinus magister* (Dungeness crab) where floy t-bar anchor tags were used to conduct mark-recovery population assessments (Smith and Jamieson 1991).

### *Development and growth*

Using two types of aquaculture environments (flow system and aerated tanks) indicated that growth and development can depend on the type of aquaculture system. No growth was recorded in aerated tanks and moulting only occurred in the flow system. Du Plessis (1971) cultured *S. serrata* and suggested an annual growth from 39 to 145 mm CW within a year with an increase of 18-19 % per moult for crabs between 80-160 mm CW. This is supported by our results, which showed a 20 % increase in CW over a 3 month period. Perrine (1978) also cultured *S. serrata*. In this study *S. serrata* moulted after an average of 82 days with an average CW increase of 16.9 % (average 20,1 mm CW increase), which is very similar to our results. Hill (1975) provided records of 16 recaptures that moulted. Their average CW increase was 26 mm or 21.5 % over an average of 193 days. This is the double amount of time for growth than in aquaculture, which seems reasonable considering food and environmental restrictions limiting fast growth in the wild (Hill 1975).

### *Survival and retention*

During the first treatment using the method described in Hill (1975) a number of tags were lost after a few weeks or came off during moulting. Perrine (1978) using the same method also mentioned poor tag retention (only 5 recaptures showing growth). The second treatment with the modified method resulted in no tag loss, but some mortality (10%). Tag retention was significantly higher ( $p=0.001$ ) using treatment 2 than the treatment 1 method. Tags were not found in significantly ( $p=0.465$ ) more individuals in the type 1 treatment group than in the control group (which had not been tagged). Other factors (sex, CW and tank environment) were not found to impact tag retention likelihood.

A minor increase in mortality is expected due to tagging. Incorrect insertion of the t-tag can damage the soft carapace tissue inside the crab. When the animal moults the tag can catch on the old shell. This can slow the moulting process and the animal's exoskeleton begins to harden prior to all body parts being released from the old shell. The rear leg can get caught in the old shell and has to be auto excised. A higher mortality and infection was reported in aerated tanks likely due to high values of Ammonium and related water quality issues. In this study, it is likely that the type of system has strongly influenced moulting and infection rates. However, other influencing factors such as size may also play a role but could not be tested in this study. Some tag loss needs to be considered when deploying combined t-bar/PIT tags. For instance, internal PIT tagging on the red king crab *Paralithodes camtschaticus* resulted in 4.8% loss (Watson et al. 1991). The field study indicated no major infections. The low recapture rate, which was similar to previous studies (Butcher et al. 2003,

Pillans et al. 2005) suggests that both number of samples and catch effort have to be higher for population estimates.

### **Conclusion**

Using a combination of t-bar and PIT tags can provide essential data for population or migration studies for *S. serrata*. Their influence on *S. serrata* survival seems negligible. In addition, tags are visible and easily read. This method has implications for future tagging of *S. serrata* and how population estimates and movement studies can be undertaken. Further testing of tag implantation and moulting likelihood is suggested for *S. serrata* of a variety of sizes under different environmental conditions.

By using PIT tags externally, injury to *S. serrata* is reduced, better consumer safety provided but it still allows for the benefits of PIT tags such as fast and secure identification. Furthermore, this technology can then also be combined with advanced telemetry to monitor movement (Meynecke 2013, Alberts-Hubatsch et al. *in prep.*). We recommend a combination of tagging methods to follow life history starting with visible implant elastomer (Liu et al. 2011, Alberts-Hubatsch et al. 2014) then anchor tag and PIT tags and for advanced individual assessment biotelemetry using acoustic tags (González-Gurriarán et al. 2002).

### **Acknowledgements**

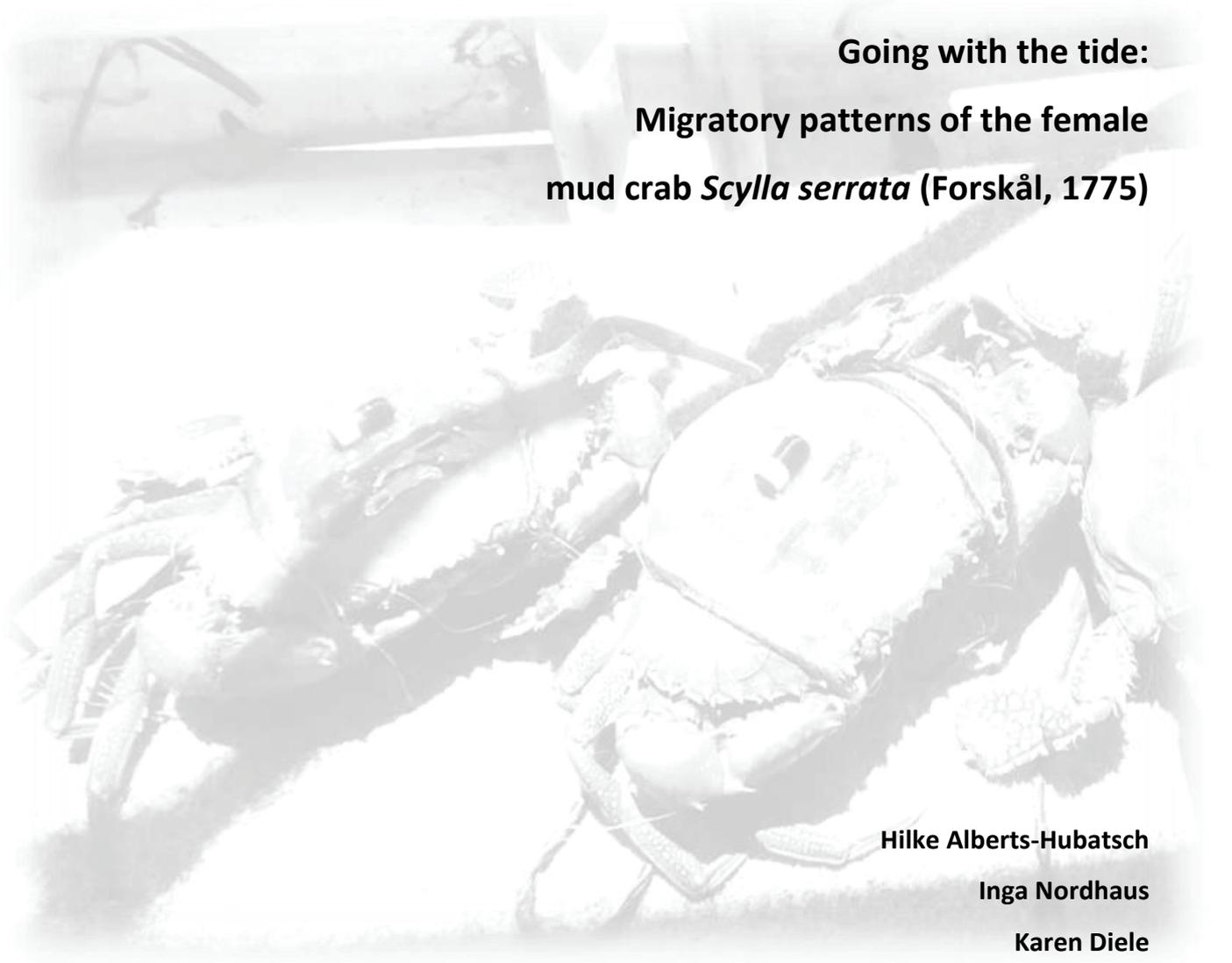
The principle investigator thanks Dirk and Wilhelmina Meynecke for their outstanding support that allowed this study to be completed. Sue Pool for support and access to aquaculture facilities. Jason Pallot for comment and contribution to statistics. Collection of specimen was undertaken under Queensland Fisheries permit no. 158794.

**Table 2.** Overview of treatments and results. Treatment 0 = control, 1 = Hill, 1975, 2 = modified Hill 1975. Crabs A-C were set up in flow through system and crabs E-G kept in aerated tanks only. Crabs A, B, E, F kept from 01.02. to 30.04.09 and C kept from 01.05. to 30.11.09; G,H kept from 01.02.-29.07.09.

ID	Treatment	Days in treatment	Sex	Refrac.	O CW in mm	F CW mm	PIT tag ID	Moult Date	Tag present
A1	0	90	M	1.355	113	115	-	-	-
A2	0	90	M	1.345	102	106	-	-	-
A3	0	90	F	1.344	119	136	-	22.04.09	-
A4	0	90	F	1.346	130	130	-	-	-
A5	0	90	M	1.345	115	115	-	-	-
A6	0	90	M	1.354	100	108	-	-	-
A7	0	90	M	1.359	89	117	-	28.04.09	-
A8	0	90	F	1.350	95	98	-	-	-
A9	0	90	F	1.355	115	115	-	-	-
B1	1	90	F	1.357	117	139	268	29.04.09	no
B2	1	90	M	1.354	121	145	489	23.02.09	no
B3	1	90	M	1.363	118	140	620	29.04.09	no
B4	1	90	F	1.354	100	122	708	19.03.09	no
B5	1	90	M	1.358	84	84	472	-	no
B6	1	90	F	1.364	110	135	671	21.04.09	no
B7	1	90	M	1.358	103	117	618	27.04.09	no
B8	1	90	F	1.358	85	104	696	01.04.09	no
B9	1	90	M	1.357	95	98	281	-	no
B10	1	90	F	1.353	101	122	630	30.04.09	no
B11	1	90	M	1.357	110	110	666	-	yes
C1	2	213	M	1.356	105	119	757	29.06.09	yes
C2	2	213	M	1.354	115	133	319	22.10.09	yes
C3	2	213	F	1.356	108	108	426	18.06.09	yes
C4	2	213	F	1.352	102	118	604	11.06.09	yes
C5	2	213	M	1.352	94	113	454	06.06.09	yes
C6	2	213	M	1.350	112	116	660	-	yes
C7	2	213	F	1.351	119	140	364	28.08.09	yes
C8	2	213	M	1.355	109	109	321	23.06.09	yes
C9	2	213	M	1.351	86	114	369	09.06.09	yes
C10	2	213	F	1.355	98	117	651	29.06.09	yes
E2	1	90	M	1.356	120	120	723	-	-
E3	1	90	F	1.353	130	130	432	-	no
E4	1	90	M	1.356	125	125	316	-	no
E5	1	90	M	1.357	117	117	275	-	yes
F1	0	90	F	1.355	130	130	-	-	-
G1	2	90	M	1.355	117	117	400	-	yes
G2	2	90	M	1.356	125	125	547	-	yes
G3	2	90	M	1.346	125	125	303	-	yes
G4	2	90	M	1.346	130	130	536	-	yes
G5	2	90	F	1.348	130	130	591	-	yes
G6	2	90	F	1.354	132	132	623	-	yes
G7	2	90	F	1.361	110	110	326	-	yes
G8	2	90	F	1.362	122	122	316	-	yes
G9	2	90	M	1.365	112	112	530	-	-
G10	2	90	M	1.357	129	129	531	-	-
H11	0	90	F	1.351	195	195	-	-	-

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## Chapter 4



**Going with the tide:  
Migratory patterns of the female  
mud crab *Scylla serrata* (Forskål, 1775)**

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*in preparation*

### **Abstract**

Spawning migrations from brackish to oceanic waters play a major role in the life history of female *Scylla serrata* (Forskål, 1775). To determine migratory paths and movement patterns during this migration, 24 female *S. serrata* were tagged with acoustic transmitters 7-17 km upstream a river in south-east Queensland, Australia. Detection was by a static receiver array deployed in the river and the adjacent bay. Of the 24 crabs, 22 were relocated at least once and 15 showed movement between receivers. 77% of these moved downstream, whereas 23% moved upstream. The movement was supported by the tides (tidal stream transport) and crabs reached maximum speeds of 56 cm/sec for downstream and 57 cm/sec for upstream movement, both supported by high river velocity. Downstream and upstream movements ranged between 0.4 and 21.4 km and 1 and 11.4 km, respectively. Contrary to previous reports, a diurnal movement pattern of the crabs was not observed, possibly attributing to the turbid waters in the study area. Nine crabs reached the mouth of the river and five of them were detected later by receivers deployed in the bay area. Of these only one crab was detected near the inlet leading to the open ocean. This suggests that *S. serrata* does not necessarily move offshore for spawning, if oceanic conditions prevail in nearshore waters.

## Introduction

*Scylla serrata* (Forskål, 1775) is a large portunid crab that occurs in mangrove associated waters in the Indo-West Pacific. Its high exploitation rate raises concerns about the sustainability of the fishery and calls for on a sound understanding of the mud crab's behavior and movement in natural environments to inform management measures.

The spawning migration from brackish inshore waters to offshore marine environments plays an important role in the life cycle of *S. serrata* (hereafter referred to as "mud crab"). However, this aspect of the life history is poorly understood. *S. serrata* has a bipartite life cycle with a pelagic larval phase and a benthic juvenile/adult phase. During its larval life, the mud crab is stenohaline and its survival depends on oceanic conditions (salinity > 25; Baylon 2010). With the metamorphosis into a juvenile it develops a benthic life style and becomes increasingly euryhaline with age (Wang et al. 2005, Baylon 2010). Due to the dependency on high salinities of the larvae, the female mud crab has to find oceanic conditions prior to spawning. Therefore it sometimes migrates tens to hundreds kilometers offshore for spawning, e.g., in Northern Territory, Australia (Hill 1994). That study showed that almost all mud crabs found offshore were females (97.1%) and more than half of these (61.5%) were ovigerous. In contrast to this, hardly any ovigerous females were found in inshore waters, but dissecting mature females in inshore waters revealed a large number of individuals with spent ovaries, indicating that these had returned to coastal waters after spawning (Heasman et al. 1985). Other studies also give accounts of ovigerous females in inshore waters with oceanic conditions, such as estuaries and bays (e.g., Arriola 1940, Pillai and Nair 1968, Brick 1974, Perrine 1978). Hill (1994) as well as local fishermen in the Moreton Bay, Queensland (*pers. communication*) report that ovigerous females are occasionally found in inshore waters, indicating that mud crabs may also be spawning in bay areas with oceanic conditions and not exclusively in offshore areas. Anecdotal reports from the same area describe females swimming at the surface in an offshore direction or in offshore waters.

*S. serrata* is reported to have a distinct spawning season in Australia (Heasman et al. 1985, Hill 1994), Papua New Guinea (Quinn and Kojis 1987), Sri Lanka (Jayamanna and Jinadasa 1993), Hawaii (Brick 1974) and South-Africa (Du Plessis 1971), whereas in other Asian and African countries the spawning occurs throughout the whole year (Arriola 1940, Prasad and Neelakantan 1989, Poovachiranon 1992, Robertson and Kruger 1994, Onyango 2002, Davis 2004b). A dependency of spawning latitude or longitude is not detectable, but correlates with the beginning of the rainy season in most regions (e.g., Arriola 1940, Quinn and Kojis 1987, Poovachiranon 1992, Hill 1994, Robertson and Kruger 1994, Onyango 2002, Davis 2004), except Madagascar and Hawaii (Brick 1974, Le Reste 1976).

Acoustic tracking gives new possibilities for understanding the movement of invertebrates and fishes over long spatio-temporal scales in their natural habitat. To date, this method has been successfully used to track the movement of a variety of fish and crustacean species and marine mammals (e.g., Klimley et al. 1992, Kelly et al. 1999, Cooke et al. 2004, Heupel et al. 2006, Gillanders 2009). In

acoustic tracking, two types of telemetry can be distinguished: either manual tracking, in which a tagged species is tracked actively by using ultrasonic receivers and directional hydrophones or automated tracking, in which moored acoustic receivers equipped with omnidirectional hydrophones continuously record tagged animals in range. The use of acoustic tracking technology to study crustacean movement was incorporated in the early 1970's in a study on the movement of spiny lobsters in the U.S. (Barr et al. 1971) and later on mud crabs in South Africa (Hill 1978). In both studies the specimens were tracked individually, using handheld ultrasonic receivers and hydrophones. This kind of tracking is useful to study animal movement and behavior on small spatio-temporal scales and can identify even small changes in direction and speed of movement. This method has advanced since then, is now well established and has been used to study behavior in a variety of other large decapod species (e.g., *Maja squinado*, González-Gurriarán et al. 2002; *Callinectes sapidus* Carr et al. 2004; *Homarus gammarus* Moland et al. 2011; *Cancer magister*, Stone and Clair 2001 and *Limulus polyphemus*, Brousseau et al. 2004). To study movement patterns of marine animals on greater spatio-temporal scales, the use of automated tracking systems with a fixed (moored) array of hydrophones is expedient (Klimley et al. 1992, Heupel et al. 2006). After initial tagging, less manpower is needed compared to the manual tracking method, since submerged receivers have a long battery life (> one year), data can be downloaded to the own convenience and tagged specimen are continuously recorded regardless weather or daytime. In crustaceans, this method has been used to track the behavior and use of habitat within a predetermined area (e.g., *Homarus gammarus*, Bowlby et al. 2007; *Cancer irrogatus*, Comeau et al. 2012; *Cancer pagurus*, Skajaa et al. 1998) or long-distance migrations, such as spawning-migrations (e.g., *Limulus polyphemus*, Smith et al. 2010; *Panulirus argus*, Bertelsen and Hornbeck 2009).

Since female mud crabs are known to migrate over long distances to their spawning grounds, we used automated acoustic telemetry to track their movement patterns during spawning migration in the southern Moreton bay region, Australia. Mud crabs are known, to inhabit euryhaline areas in upper estuarine and riverine seascapes, so the use of this habitat for tracking animal migration is almost ideal, due to “the almost linear nature of habitat, which restricts the direction of possible movements” (Comeau et al. 2012). Prior to the spawning season in 2012, we tagged 24 female mud crabs and tracked them using a receiver array deployed in the Logan River and adjacent southern Moreton Bay. We hypothesize that female mud crabs are mainly active at night and use tidal stream transport for migration. Further, we suggest that the females spawn offshore as they do in the Northern Territory (Hill 1994) and use the shortest way towards the ocean supported by the tides. Characterizing the migration patterns of *S. serrata* will give new insights into the ecology of mud crabs, which can help to understand possible implications of future management decisions on the protection of the species.

## Material and Methods

### Study area

The study was conducted in the Logan River (27°41'33"S, 153°15'40"E) and the adjacent southern Moreton Bay (27°43'58"S, 153°24'5"E), southeast Queensland, Australia (Figure 1) between October 2012 and March 2013. The Logan River has a total length of 191 km, with 60 km under tidal influence (Loneragan and Bunn 1999) and opens into the southern Moreton Bay. Here it drains into the open ocean through the Jumpinpin Inlet, which separates North and South Stradbroke Island (Maxwell 1970).

The Logan River has a thin fringe of riparian vegetation dominated by mangroves (mainly *Avicennia marina* and *Aegiceras corniculatum*) and some extended mangrove forests at the lower river banks. The southern section of Moreton Bay is rather shallow (0-10 m), with many small mangrove-dominated islands and extended mud flats.

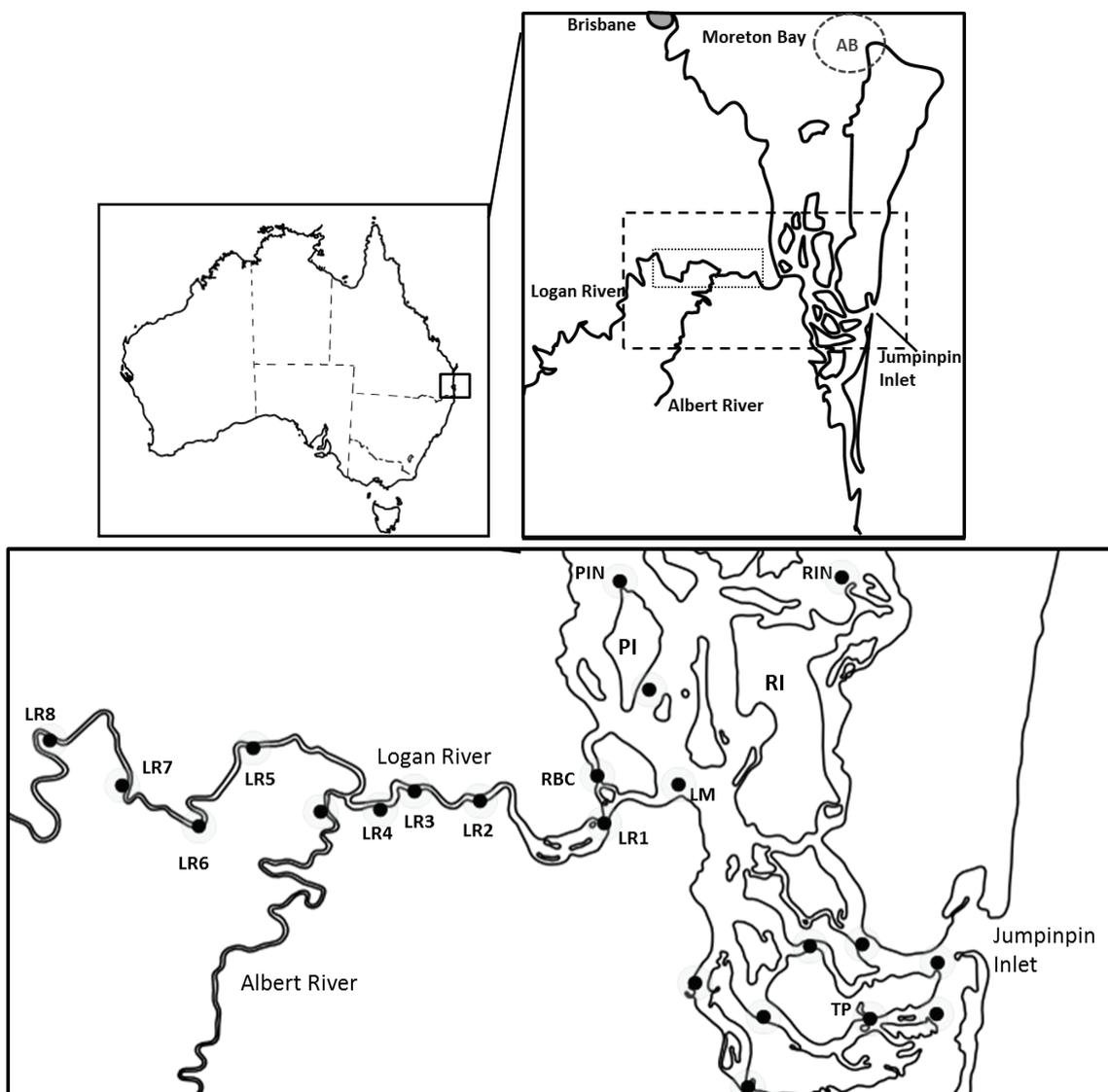
Both the Logan River and southern Moreton Bay, have a semidiurnal tide with ranges of 0.6 –2 m. Southern Moreton bay is under oceanic influence and salinities normally range between 27 and 31 in the rainy season (summer, December to March) and 31 to 34 in the dry season (winter and autumn, June to November). Going upstream the river, mean salinities decrease and vary with the tidal cycle. In the lower Logan River (approx. 7-8 km from the mouth), salinity can vary between 16 and 34 whereas in the upper regions (approx. 16-17 km from the mouth) it can vary between 1.5 and 25, both depending on rainfall and tidal cycle.

Prior to the supposed spawning migration in spring (October/November), we captured and tagged female *S. serrata* in the Logan River in an area 7 – 17 km upstream the mouth using baited crab pots. Fertilization of eggs is internal in mud crabs, so there is non-invasive method to make sure the females are carrying fertilized eggs. Therefore, the animals were selected regarding their molting stage and size (freshly molted: light ventral side and joints, no barnacles/epiphytes; mature > 130 mm carapace width (CW)) so they were likely to migrate. Two types of ultrasonic transmitters were used: 20 female mud crabs were equipped with ultrasonic transmitters (V9, Vemco) and four females with transmitters with integrated depth sensors (V9-TP, Vemco). The tags were attached to the dorsal surface of crab's the carapace, in the slight depression in the center, using premixed epoxy glue (Loctite® easy repair). Prior to that the crab's carapace was roughened with sandpaper, cleaned with water and dried to ensure good adhesion. The crabs were placed into a shaded bucket with little water, to let the glue dry for one hour before releasing them at the same site as initial capture. The movement of the tagged crabs was monitored by an array of 21 acoustic receivers (V2WR, Vemco) in the Logan and Albert River (n=10) and Southern Moreton Bay (n=11, Figure 1). At the same time, another receiver array was deployed at Amity Banks, covering the passage between North Stradbroke and Moreton Island, approx. 15 - 25 km north of from our receiver array. Receiver data

was uploaded to and processed by the Australian Animal Tagging and Monitoring System (IMOS 2013).

We calculated the distance moved as the shortest distance between the receivers. For each crab, the direction of movement and the distances moved between the receivers as well as total distance was recorded. Additional depth was recorded for the four crabs equipped with the V9-TP tags. The status of the tide for each track segment was registered as 'in' for incoming/flood tide and 'out' as outgoing/ebb tide. Diurnal and nocturnal activity was assigned to each track segment as 'day' if it occurred from 0600h to 1800h and 'night' if it occurred from 1800h to 0600h (Table1).

Speeds were calculated only where movements between receivers were recorded within < 4 hours on the same tidal cycle.



**Figure 1** Location of the Logan River within adjacent southern Moreton Bay (A, B), southern Queensland, Australia (A). The small box (dotted line) indicates the area of capture, tagging and release of *S. serrata*. Dots indicate the approximate receiver locations, 'AB' is the receiver array at Amity Banks (B). Receiver ID's are only indicated for receivers producing data in our study. PI and RI (C) indicate Pannikin and Russel Island, respectively.

Water quality (temperature, salinity, water depth and river velocity) was continuously monitored at two stations of the lower and the upper Logan River and data was obtained from TERN (Terrestrial Ecosystem Research Network; Steven and Carlin 2014a, 2014b). Direction and speed of crab movement was plotted against river velocity.

A Pearson correlation was run to detect relationships between the direction of movement, tide (in/out) and day/night activity (PAST, vers. 3.02). Comparisons of use of depth by the TP-tagged crabs were done using One-Way Anova for unequal sample sizes using R (vers. 3.1.0).

## Results

Twenty-two of the tagged crabs were detected by the receivers in the Logan River and southern Moreton Bay between October 2012 and February 2013, no crabs were detected by receivers deployed in the Albert River or by the northward receivers at Amity Banks. A table was compiled for all crabs recorded, showing the number of receivers that registered the crab, direction of movement and the tide (Table 1). Fifteen crabs showed movement between receivers, 77.3% of these moved downstream and 22.7% moved upstream. In 85% of the cases, downstream movement occurred during ebb tides, whereas 94% of upstream movement was supported by incoming tides, resulting in a significant relationship between tides and direction of movement (Pearson correlation: 0.68,  $p < 0.001$ ). Plotting river velocity and movement speed (Figure 3) did not reveal significant correlation, maybe due to unpredictable movement behavior of mud crabs during the swimming intervals (discontinuous movement). Movement during night and day occurred in 59% and 41% of detections respectively. No significant correlation was detected between activity and day/nighttime (Pearson correlation: 0.14,  $p = 0.21$ ).

Downstream movement ranged between 0.4 and 21.4 km ( $9.3 \text{ km} \pm 1.6 \text{ SE}$ ) and upstream movement ranged between 1 and 11.4 km ( $4.6 \pm 2.0 \text{ km SE}$ ) as far as it could be tracked by the receiver array (examples of tracks: Figure 2). There was no difference in size of crabs moving upstream ( $151 \text{ cm CW} \pm 6.1 \text{ SE}$ ) or downstream ( $155 \text{ cm CW} \pm 2.7 \text{ SE}$ ; Anova:  $F(1,20)=0.58$ ,  $p=0.484$ ). Rainfall most likely had no impact on these movements as precipitation was low during this time. Top speed for the downstream movement was 56 cm/s for a crab that covered 7 km within 3.5 hours supported by an average river velocity of 36 cm/s, and 57 cm/s for upstream movement by a crab that moved 3.1 km within 1.5 hours supported by an average velocity of -46 cm/s. In 58 % of the cases the mud crab stayed within a certain range (receiver) for days or even weeks before taking off and moving quickly downstream. The upstream movement took up immediately after releasing the crab (Crab 8,9,10 and 21, Table 1). 73 % of female mud crabs were exclusively registered by the receivers in the Logan River (up to the mouth), whereas 27% did leave the river and could be tracked by receivers deployed in the bay. No tagged crab was found in offshore regions.

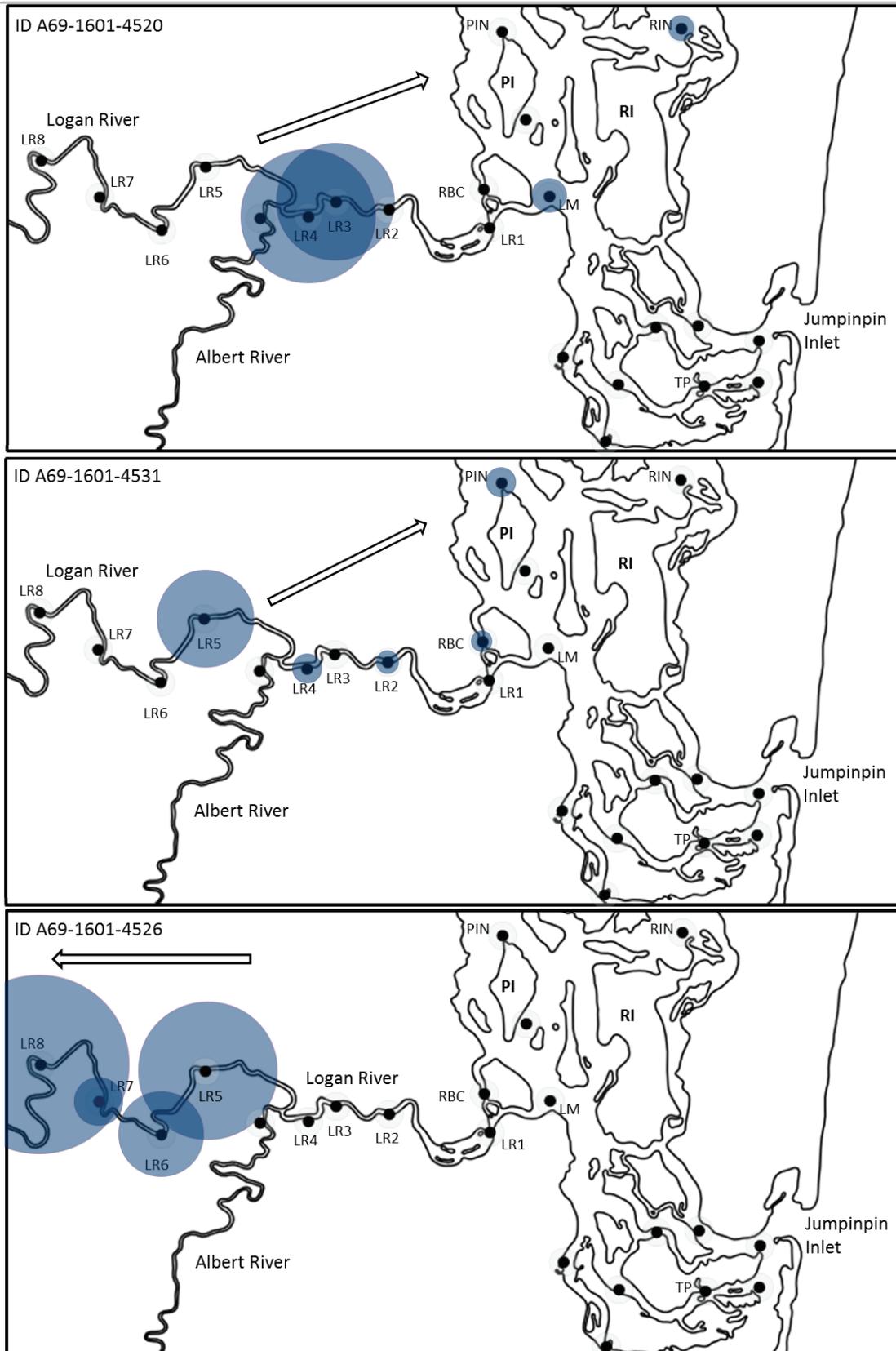
**Table 1** Movement of female *Scylla serrata* between receivers in Logan River and southern Moreton Bay. Arrows (-->/<--) indicate downstream/upstream movement between receivers, \* indicate crabs. in which movement was not exclusively supported by tides.

Crab No.	ID	Size (mm CW)	distance		total distance tracked	time from release to last record	direction	tide in/out
			release to first receiver	receiver				
1	4517	155		LR4 --> LR2 -->	9.3 km	30	down	out
2	4518	149	0.5 km -->	LR5 --> LR4 --> LR2 -->	11.8 km	54	down	out
3	4519	160	2.3 km -->	LR4 --> LR2 -->	5.4 km	49	down	out
4	4520	165	0.2 km -->	LR4 --> LR2 --> LM-->	21 km	49	down	both*
5	4521	162	2.8 km -->	LR4 --> LR2 -->	5.9 km	6	down	out
6	4522	153	1.2 km -->	LR4 --> LR2 --> LR1	9.4 km	30	down	out
7	4523	135	1.4 km <--	LR4 <--	1.4 km	40	-	in
8	4524	170	1.8 km <--	LR5 <--	1.8 km	1	up	in
9	4525	149		LR5 <-- LR6 <-- LR7 <--	7.6 km	3	up	in
10	4526	142		LR5 <-- LR6 <-- LR7 <-- LR8 <--	11.4 km	2	up	in
11	4527	149	4.8 km -->	RBC	4.8 km	1	down	in*
12	4528	138	0.4 km -->	LR6	0.4 km	8	down	out
13	4529	170	17 km -->	TP	17 km	14	down	out
14	4531	134	0.4 km -->	LR5 --> LR4 --> LR2 -->	21.4 km	36	down	out
15	4532	142	0.5 km -->	LR4 --> LR2 -->	3.6 km	1	down	out
16	4533	163	2.2 km -->	LR4 --> LM	11.3 km	26	down	out
17	4534	140	1.4 km -->	LR4 --> LR2 -->	4.5 km	43	down	both*
18	4535	165	0.8 km -->	LR2	0.8 km	1	down	out
19	4536	162	1.0 km -->	LR4 --> LR2 --> PIN	17.3 km	55	down	out
20	07/08	167	1.0 km -->	LR4 --> LR2 --> LM-->	10.1 km	61	down	both*
21	09/10	158	1.0 km <--	LR2	1.0 km	1	up	in
22	13/14	162	1.0 km -->	LR4 --> LR2 -->	4.1 km	1	down	out

The depth sensors revealed only little changes in the use of depth. The first female stayed in an average depth of  $171.7 \text{ cm} \pm 0.14 \text{ SE}$  and the other two in an average depth of  $161 \pm 0.15 \text{ cm}$  and  $146 \pm 0.24 \text{ cm}$  respectively. Even though the statistical comparisons revealed differences between the three crabs (Anova:  $F(2,2468): 637.5, p < 0.001$ ), this might be due to the differences in number of sampling events and low sample size: one of these female could be tracked over the period of three month, resulting in 2341 data points, whereas the other two stayed in the range of the receivers for less than a day, resulting in 40 and 90 detections, respectively.

## Discussion

Our study showed that female *S. serrata* are highly mobile and use tidal stream transport for their spawning migration. The use of ebb-tide-transport for seaward migration has been demonstrated in several studies for other crab species, such as the blue crab *Callinectes sapidus* (Tankersley et al. 1998, Forward et al. 2003). Since the spawning migration for *S. serrata* is reported to occur between September - November (Heasman et al. 1985), it is likely that some female mud crabs already returned to inshore waters, ascending the river. As a consequence, we found five tagged crabs moving upstream, whereas the others expressed downstream movement, all supported by the tides.



**Figure 2** Migratory paths of female *Scylla serrata* in Logan River and southern Moreton Bay, Qld, Australia. **A** Crab ID A 69-1601-4520 (165 mm CW) travelled downstream the river, then north in the bay (21 km within 49 days). **B** Crab ID A 69-1601-4531 (134 mm CW) expressed downstream movement in the river then northward movement in the bay (21.4 km within 36 days) **C** Crab ID A 69-1601-4526 (142 mm CW) expressing upstream movement (11.4 km within 2 days). Sizes of bubbles (blue) indicate approx. number of detections.

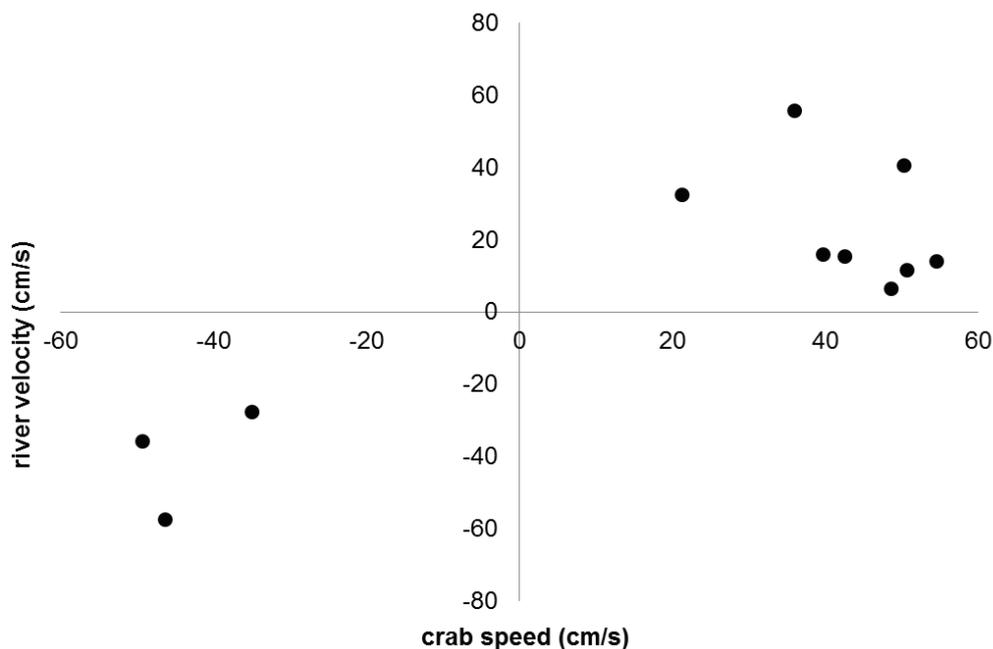
Selective tidal stream transport is known for a variety of crustacean species, including larvae (e.g., Kingsford et al. 2002, Pineda et al. 2007) and adults (e.g., Tankersley et al. 1998, Forward et al. 2003), and is defined by active vertical positioning in the water column depending on the current direction (Hill 1991). Even though we found significant differences in the use of depth by three females, our data is limited and therefore should be considered carefully when drawing conclusions on the whole population. Despite the significant differences, all three crabs stayed in a depth range between 1.4 and 1.85 m, even though the depth of the river and bay is often up to 10 m. This could indicate that the females remain in intermediate depths at the slope of the river bank or on subtidal flats or ascend in the water column to use the tidal current. However, our data does not reveal data on the position of the crab in relation to the river bank. Personal observations and anecdotal reports witnessed female mud crabs swimming on the surface for some time and only descending in the water column when approaching the crab, which would also indicate an active selection of tidal currents. Still, how female mud crabs use vertical movement for migration needs further investigation.

It is known for some crustacean species that movement predominantly occurs during night times (e.g., *Callinectes sapidus*; Tankersley et al. 1998, Carr et al. 2004; *Romaleon polyodon*; Wolff and Cerda 1992). The female *S. serrata* in our study did not show such a pattern. Even though there was slightly more movement during night, all our crabs were initially caught during day time and 41 % of recorded movement events occurred during day. Another movement study conducted on female and male mud crabs indicate both diurnal and nocturnal movement (Alberts-Hubatsch et al., *under review*). Instead of claiming daytime preferences for the activity of *S. serrata*, we rather suggest increased activity as a matter of 'being seen'; i.e., if the inhabited waters are more turbid with little visibility, the mud crab may display less nocturnal dependency than in clear waters. Since the Logan River as well as the adjacent bay is tide-dominated with muddy bottoms, the turbidity is naturally high and would support movement independent of daytime. Juveniles of some tropical estuarine fish species are also known to actively seek turbid waters, which might be linked to reduced predation pressure (Blaber and Blaber 1980).

Even though we had a spacious array of receivers, we were not able to detect the full extent of female mud crab migration in the Moreton Bay. We hypothesized, that the females use the shortest way towards the sea, which would have been Jumpinpin Inlet. We only recorded one female in Tiplers Passage (TP, Figure 1), which is nearby the Inlet, but in contrast four other females turned north after leaving the river and were recorded at the northern tip of Pannikin and Russel Island (Figure 2 A,B). These were the northernmost locations covered by our receiver array, so we were not able to detect movement further northwards. However, we did not expect our crabs to migrate this direction since this is not the shortest tide-supported way offshore and this raises new questions

about the underlying mechanisms of female mud crab migration. One possibility could be, that female mud crabs do not only use tidal streams for seaward migration in the open bay, but olfactory cues in the water column or the use of the sun orientation as it has been proven for fish (Schwassmann and Hasler 1964, Bisazza 1996, Mouritsen et al. 2013) and also some crabs (Horridge 1966, Nishimoto and Herrnkind 1982). It is also possible that the spawning does indeed occur in the Moreton Bay and once the female mud crabs sensed appropriate spawning grounds, they stopped migrating seawards. In that case, the crabs may prefer the wider areas of the northern bay for spawning since the water currents are not as strong as in the narrow channels of the southern bay area.

In comparison with the only other portunid crab, *Callinectes sapidus*, for which the patterns of spawning migration are investigated in detail, there are some similarities. Both crabs live in estuarine and riverine habitats and move downstream into waters with high salinities for spawning. In our study, female *S. serrata* were found to express discontinuous movements once they started migrating. Rapid movements were disrupted by reoccurring pauses during which the female stayed within a certain area without showing directional movement. Some of these pauses reflect changes in tide, i.e., the crab stayed inactive as long as unfavorable currents prevail, but others did not follow any obvious patterns. This episodic swimming behavior was also observed in free roaming *C. sapidus* ("swimming bouts", Forward Jr. 2003, Forward Jr et al. 2004, Carr et al. 2004) and it was suggested that the stationary periods may be resting periods for the negatively buoyant crab and helps the crab to sense other environmental changes (Carr et al. 2004).



**Figure 3** Direction and speed of movement of female *S. serrata* in relation to river velocity (Logan River, SE Queensland, Australia)

Despite the similarities, there is one behavioral feature that is not alike and rejected one of our hypotheses. We hypothesized predominant nocturnal movement as it was observed in *C. sapidus*, but it seems like *S. serrata* does not have diel preferences with regards to movement. However, this behavior should be reevaluated, when studying *S. serrata* stocks from areas with less turbid waters.

Our findings can be considered for management decisions on the conservation of the species, but we have to take into account that our study was conducted in the subtropics where mud crabs express seasonal spawning. In other areas, mud crabs spawn the whole year through and as a consequence, management decisions need to be adapted to the regional conditions.

In Queensland, Australia, female mud crabs are protected, but there is a re-occurring discussion on abandoning the ban on fishing female mud crabs. Even though a single-sex harvest policy is not regarded ecologically necessary for *S. serrata* (Brown 2010), no actions have been taken in that direction. If no changes are made, the major concern is that females grow to large sizes, but male sizes are decreasing since large males are being fished. It is not known, if small males can still successfully reproduce with the large females, as the male has to grab the female crabs by the carapace with its legs during mating (Lavina 1978b). The exploitation of the cancrid crab *Metacarcinus magister* raised similar concerns (big females – small males) in the Pacific Northwest, but studies showed that females of this species still had good mating success regardless their size (Dunn and Shanks 2012). There are no indications (such as diminishing stocks), that the mud crab population in Queensland suffers from recruitment overfishing, but a study on mating success of large *S. serrata* females in this area could clarify this issue.

Many marine species are protected with seasonal restrictions and size limitations, which should support at least one reproductive cycle, supporting the sustainability of the species. This study could encourage future management decisions, by identifying the migration paths of female mud crabs, which allow more precise predictions about the end of the reproductive cycle. Even though spawning season starts in early spring, our females showed migratory behavior until mid-summer. When considering lifting or loosening the ban from taking female mud crabs, one should contemplate not to lift it completely but maybe have seasonal restrictions, e.g., lifting the ban by the end of the summer after the females spawned at sea. Due to the long migration routes of females, the implication of protected areas for females is not ecologically worthwhile, as the females will sooner or later leave the area.

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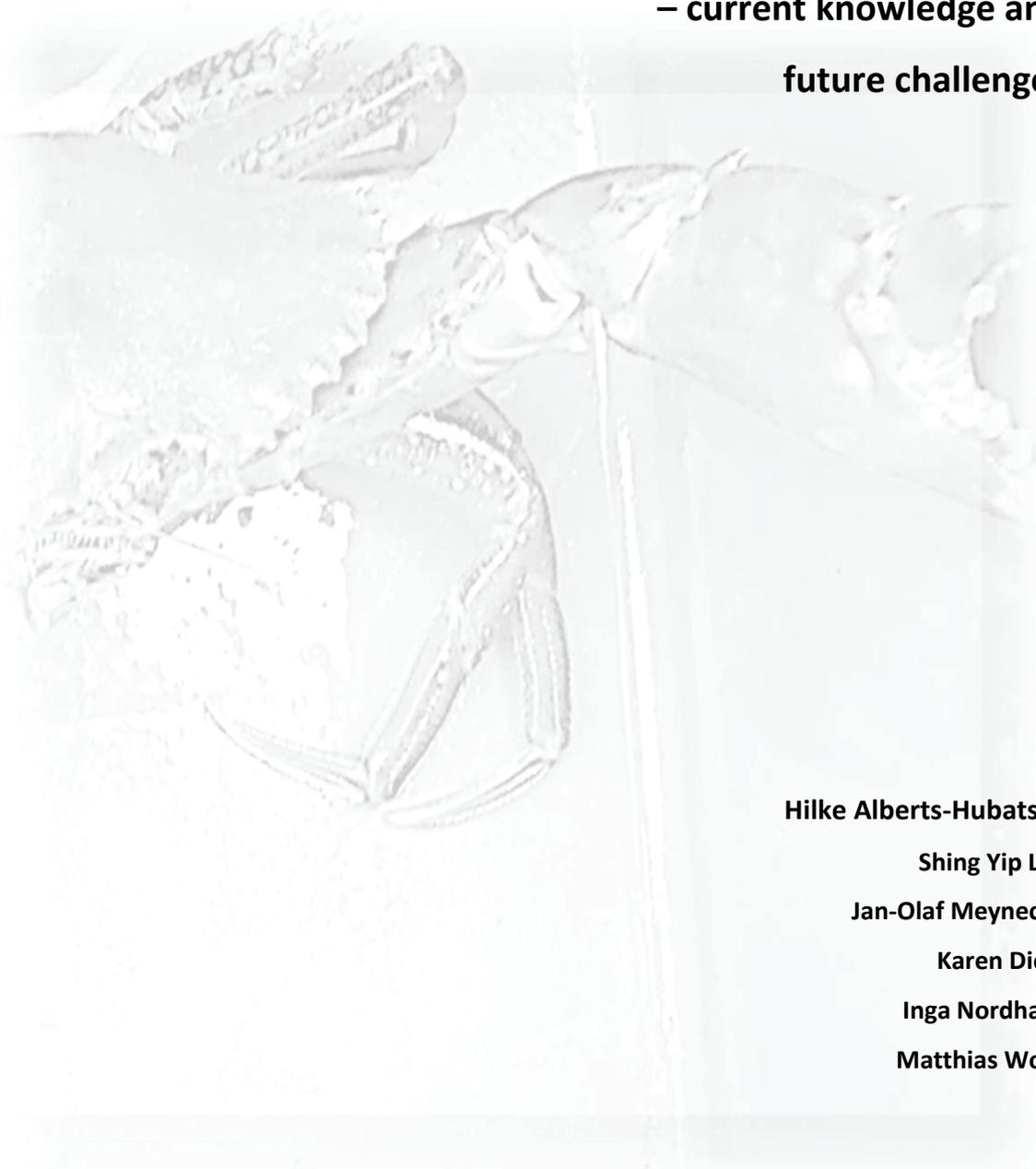
The Australian Animal Tagging and Monitoring System (AATAMS) was a substantial help for collecting and organizing data. This data was sourced as part of the Integrated Marine Observing System (IMOS) - IMOS is supported by the Australian Government through the National Collaborative Research Infrastructure Strategy and the Super Science Initiative. K.D. received funding from the MASTS pooling initiative (The Marine Alliance for Science and Technology for Scotland) and its support is gratefully acknowledged. MASTS is funded by the Scottish funding Council (grant reference HR09011) and contributing institutions.



## Chapter 5

### Life-history, movement and habitat use of *Scylla serrata*

– current knowledge and  
future challenges



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## **Abstract**

The mud crab *Scylla serrata* is a highly valued 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 making use of different parts of the onshore-offshore continuum of the mangrove system. The former are stenohaline and depend on stable high salinity conditions to survive, whereas the latter are physiologically well adapted to changing temperatures and varying 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 mangrove area flats as well as subtidal channels and flats. Females undertake long movements from brackish inshore waters to waters with oceanic conditions for spawning. However, little is known about larval stages and also early benthic stages are underrepresented in the literature. Especially sensory abilities – of early stages as well as adult stages – have hardly been studied. A picture of this species emerged, which still lacks a complete understanding of the spatio-temporal 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.

## Introduction

The highly valued mud crabs *Scylla serrata* (Forskål, 1775) (Portunidae) is widely distributed throughout the Indo-West-Pacific (IWP) region, 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. The global catch rose from approx. 10,000 t in 1990 to 40,000 t in 2012 and there was a contaminant increase in aquaculture production from approx. 4,000 t 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., 2012).

*S. serrata* has been studied since the 1940's 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. tranqueberiqua*, *S. paramamosain* and *S. olivacea* that often occur in the same habitats were frequently mistaken as one species (see 'Taxonomy'). Despite its economic importance and the vast number of publications, basic aspects of the biology and ecology of *S. serrata* important in 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 the 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 the available information on the life-history, population dynamics, movement and habitat use of *S. serrata* with an emphasis on regional differences. Information from both peer-reviewed publications and unpublished reports (i.e., theses and technical reports) is included. Two terms ('*Scylla serrata*' and 'mud crab') were used to search in 'title' or 'topic' in the database ISI Web of Science, resulting in > 1,1000 publications. These were sorted and publications not containing *Scylla 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'). 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, South Australia, South Indo-Pacific Islands ('Geographical distribution' and Figure 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.

## Taxonomy

The portunid crab *Scylla 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 borders of species and variations (Serene, 1951). 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 and Kojis 1987) and Western Australia (Taylor 1984). Due to these uncertainties other authors referred to *Scylla serrata* a single species with different morphs (Stephenson and Campbell 1959, Perrine 1978).

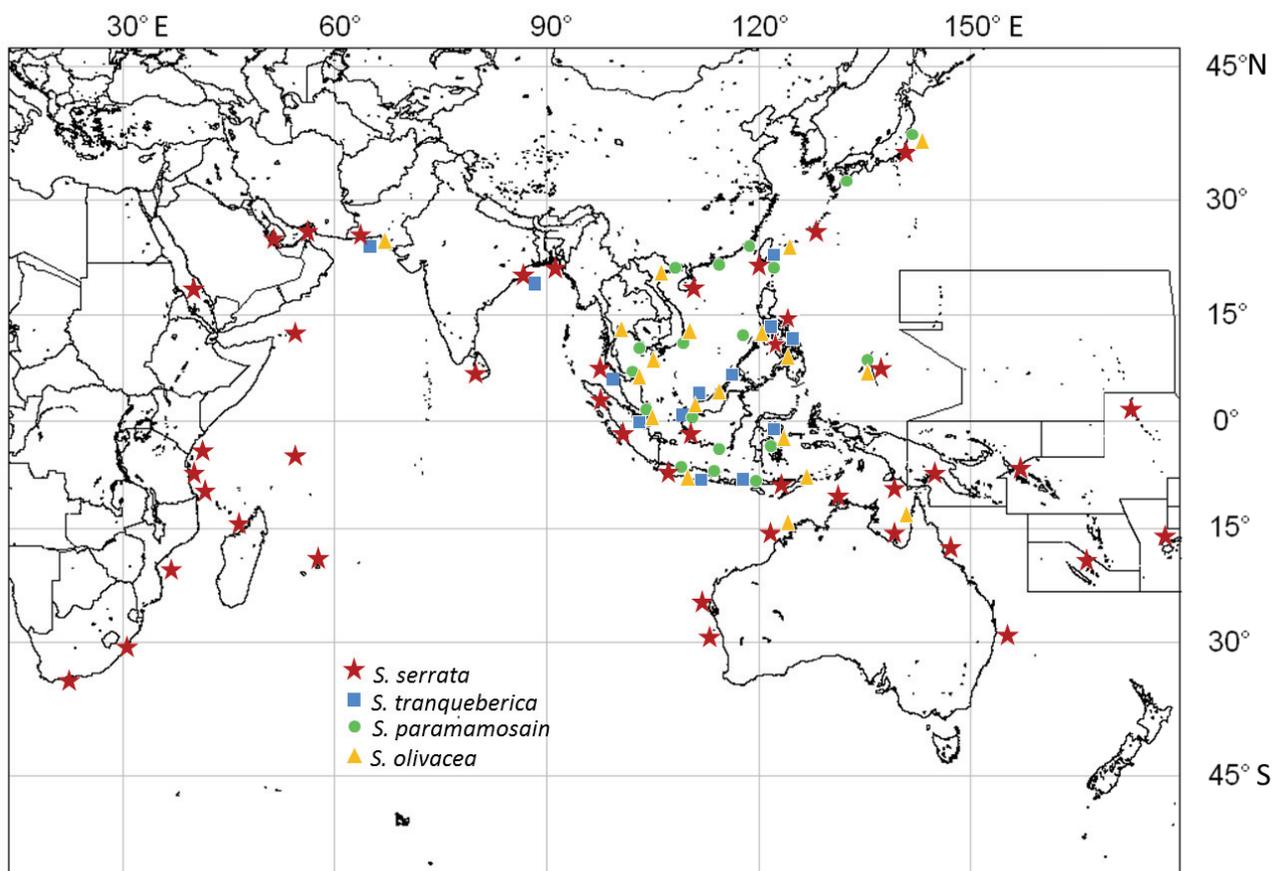
The existence of three distinct species (*S. serrata*, *S. tranquebarica*, and *S. oceanica*) was later noted by Fuseya and Watanabe (1996) in Japan on the basis of differences in three genetic loci (EST, LAP-2, and SOD). In 1998, Keenan et al. revised the genus *Scylla*, combining genetic and morphometric 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 and Watanabe 1996, Klinbunga et al. 2000, Imai et al. 2004, Lin et al. 2007, Fuseya et al. 2007, Ogawa et al. 2011, Mandal et al. 2014).

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 and Takeda 2005). Individuals from Indonesia are also sometimes hard to be identified due to the lack of distinct morphological features (I. Nordhaus *pers. observation*).

### **Geographical distribution**

*S. 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 and 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. 1998b) 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). *S. serrata* occurs in areas up to 38° S, whereas the other three species are centered around the equator. *S. 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, Figure 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. 1998b, Sugama and Hutapea 1999, Overton 2000, MacIntosh et al. 2002, Ikhwanuddin et al. 2011).



**Figure 1** Distribution of the four *Scylla* species. Not shown: Hawaii with *S. serrata* populations. Scale: 1: 11,000,000 at latitude 0°; a table with references can be found in supplement Table 1.

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). The Australian populations can be separated into two distinct clades (northern and eastern populations) divided by the Torres Strait (Gopurenko and 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 geographical areas and expand to new habitats, resulting in panmixis of the species (Hill 1994, Gopurenko et al. 1999, 2003).

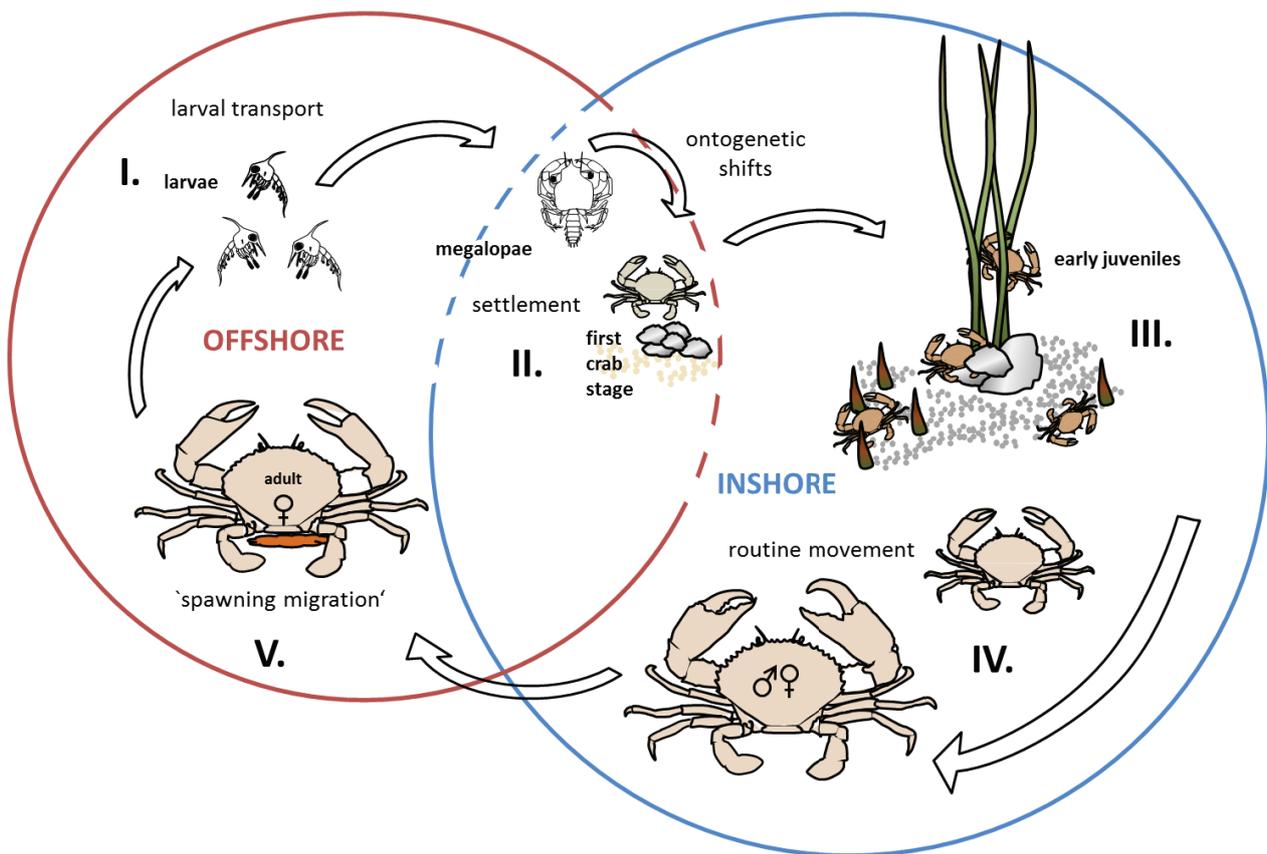
Furthermore, genetic analyses suggest colonization by mud crabs of the IWP through propagules deriving from the WPO (Gopurenko et al. 1999, Fratini et al. 2010). The most ancestral haplotype is found in the Red Sea; the colonization of the Indo-West-Pacific region seems to have its origin in a rapid 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).

### **General life-cycle**

Throughout its life, *S. serrata* undergoes several ontogenetic shifts, expressing different behavior and occupying different habitats at each stage: I.) the larvae are (presumably) released offshore, and undergo five larval stages (Delathiere 1990) before returning to coastal areas. II.) There the larvae metamorphose into the megalopae stage and subsequently settle and transform into the first juvenile stages. III.) Early juvenile mud crabs live in sheltered mangrove habitat and IV.) 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 individual steps of this life cycle (I-V) are illustrated in Figure 2 and will be discussed in detail in the following section.

### **Larval Development**

The survival and developmental time of the larvae strongly depends on water temperature and salinity (Hill 1974, Hamasaki 2003, Nurdiani and 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 scale) and optimum temperatures of 26-30 °C (Hamasaki 2003, Nurdiani and 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'). 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 ( $20^{\circ}\text{C}$ ), it still does not develop into the first crab stage at salinities below 15 (Baylon 2010).



**Figure 2** Schematic drawing of life cycle of *Scylla serrata*.

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 and 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 is 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 has 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 crablets (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. The physiological optima suggest that settlement and metamorphosis into the first crab stage occur in waters with high salinities.

### **Juvenile mud crabs**

After molting into the first crab stage, the tolerance towards 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 this temperature and recovers when transferred into warmer water (Baylon 2010). The increased tolerance towards 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, Figure 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 landwards 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 flats seaward to the mangrove fringe in Australia, which might indicate a settlement in subtidal areas and post-settlement relocation towards the mangrove habitat (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 (1982) studied the use of different habitats by different life stages. Large adults ( $\geq 150$  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 than 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 to 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). Generally, 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), whereas in southern Moreton Bay, Queensland, crabs that are found in open environments like intertidal flats in open bays show larger routine movement (average 3.7 km) (Hyland et al. 1984). It is suggested that these different distances of routine movement are dependent on the availability of alternative feeding grounds at high tide. In narrow creeks, there is only a limited intertidal zone whereas in the open environment more and larger intertidal flats are present that provide alternative feeding grounds at high tide and help to avoid intraspecific competition (Hyland et al. 1984) and cannibalism. Recent studies indeed show that movement can be influenced by the seascape and environmental conditions: Adult mud crabs may display stronger seaward movement from enclosed estuarine habitats towards open bay areas, to avoid conspecifics ('demographic diffusion'; Steneck 2006, Alberts-Hubatsch, pers. observation). Increased freshwater flow during the rainy season may also enhance the activity of mud crabs and therefore trigger their movement (Meynecke et al. 2010, Alberts-Hubatsch pers. observation).

Mud crabs 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, emerging and feeding 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).

While the larvae of mud crabs are very sensitive to changing salinities (Hill 1974, Baylon 2010, see 'Larval development'), the larger juveniles and adults are strongly euhaline, tolerating broad ranges of temperature and salinity: adult mud crabs survived experimental salinities between 1 and 42 in Malaysia (Davenport and 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 and Wong 1987, Chen and Chia 1996) and express metabolic responses towards extreme high or low salinities (e.g., nitrogen excretion; Chen and Chia 1996).

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, 2012a, Meynecke and Lee 2011).

### Female spawning migration

The spawning migration (Figure 2, V.) of mud crabs is poorly understood. The absence of berried 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 berried 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 lagoon, bay and inlets (Arriola 1940, Brick 1974, Prasad and Neelakantan 1989), indicating that the spawning migration might depend on hydrological features rather than topographical 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).

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

location	latitude	peak spawning season	year-round?	
Hawaii	20°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 and 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 and Jinadasa 1993
Ramisi River, Kenya	4°S	possible peak in 2nd half of the year	yes	Onyango 2002
Labu estuary, Papua New Guinea	7°S	two peaks: April-June and Sept-Oct	yes	Quinn and Kojis 1987
Tropical Australia (North)	11-15°S	rainy season: November-February	no	Hill 1994
Madagascar (North-West)	14°S	two seasons: dry season (July/Aug), rainy season (Jan)	n.n.	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 and 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

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 therewith 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, Le Reste et al., 1976; Brick 1974, Table 1), which makes a link with warm temperatures more likely (Perrine 1978).

### **Maturity and Mating**

Maturity of *Scylla serrata* starts at different sizes in different geographic regions (Table 2, 3). Some authors (Quinn and Kojis 1987, Robertson and 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, it seems more likely that these assumptions are actually derived from the different size classes of the different *Scylla* species, since these assumptions were made before the revision of the species (see Taxonomy). Nevertheless, in recent research, different sizes at maturity were observed for *Scylla serrata* at different locations. In both, males and females, a distinction between physiological, morphological and functional maturity 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 and 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 morphological mature males. In South Africa, males reach physiological maturity at smaller sizes than in Australia (92 vs. 110 mm CW, respectively), and also size at functional maturity seems to vary due to the geographical region (Table 2).

In females, physiological maturity is reached during the last pubertal molt and the ovaries fully develop. 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 geographical 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 3). However, there are differences depending on the geographical region, e.g., smallest size at maturity (regarding the abdominal flap) is 102 mm CW in Madagascar (Le Reste et al. 1976) and minimum size reported from Australia is 138 mm CW (Heasman, 1980, Table 3).

**Table 3** Size at physiological and functional maturity of male *S. serrata* in relation to latitude

Location	Latitude	physiological maturity CW (mm)	functional maturity CW (mm)	Source
Ponape	4°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 (south-east)	28°S		145 (164*)	Heasman, 1980
South Africa	29°S	92	115-119	Robertson and Kruger, 1994
South Africa	32°S		123	Robertson, 1996
South Africa	34°S		141	Hill, 1975

\*size at 50% maturity

**Table 2** Size female *S. serrata* at different maturity classifications of in relation to latitude

Location	latitude	ovary development	ovigerous	mating	mature abdominal flap	Source
Ponape	5°N		141-187	105		Perrine, 1978
New Guinea	6°S				85-190	Quinn and Kojis, 1987
Sri Lanka	7°N	120-130				Jayamanna and 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 (south-east)	28°S				138 (147*)	Heasman, 1980
South Africa	28°S	116 (145*)				Davis et al., 2004
South Africa	29°S				104 (123*)	Robertson and 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 at 50% maturity

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 table 4 and 5. In both sexes the maturity stages can be identified by different size and coloration of the gonads (Shanmugam and Bensam 1980, Prasad and Neelakantan 1989, Poovachiranon 1992, Robertson and Kruger 1994, Quinitio 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 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).

**Table 4** Maturity stages of gonads in male *S. serrata* (adapted from Shanmugam 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

### 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 towards female dominated populations is found. In Queensland, Australia, the fishing regulations only allow large ( $\geq 150$  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 the Philippines (Ewel et al. 2009). This report coincides with earlier studies, which reported densities of 44 – 53 crabs per hectare for Natal, South Africa (Robertson and Piper 1991) and 80 crabs per hectare for another South African estuary (Kleinmond estuary, Hill 1975). Maximum densities were found in Tanzania with  $1,228 \pm 7.3$  crabs at the mangrove fringe and  $324 \pm 10$  crabs per hectare in the inner mangroves, resulting in a biomass estimate 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 real differences in densities induced by habitat or environmental conditions.

**Table 5** Ovary development female mud crabs. GSI = ‘Gonadosomatic index’ (adapted from Quinito 2007, Poovachiranon 1991, Robertson & Kruger 1994, Prasad 1989)

Stage	Colour	GSI	ova diameter (mm)	External characteristics	Histology
0	translucent				Clusters of oogonia, primary oocytes surrounded by follicle cells apparent in the ovarian lobe; previttellogenic 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 discernable; 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 discernable; some atretic cells evident
V Spent	yellow, orange to brown			flaccid ovary	some unspawned oocytes of various stages present, some atretic cells evident

### 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 and Neelakantan 1988). The composition of food items changes as the mud crab grows (Prasad and 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 2009).

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. obs.).

Endo- and epibenthic food items are detected by the chemoreceptors in the mud crabs walking legs. Mud crabs seem to exhibit responses towards 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 bivalvae 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 ceased when temperature is below 12 °C (Du Plessis 1971, Hill 1980). Feeding increases again when the water becomes warmer in the spring and during the 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 also do not feed when they are in berry, showing a similar feeding rate to that of molting crabs (Du Plessis 1971). Little is known about turnover rates of mud crabs and the systemic importance for mangrove ecosystems. The monthly consumption rates for intermediate sized crabs (368 – 678 g wet weight) varies from 0.13 g food\*g crab<sup>-1</sup> in winter to 0.41 g food\*g crab<sup>-1</sup> in summer (average 0.29 g food\*g crab<sup>-1</sup> per month) at ambient water temperatures in the laboratory (Du Plessis 1971). Taken these

optimized numbers to the field, we would end up with a mud crab increasing 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), this 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 a guidance on the potential importance of mud crabs in estuarine ecosystems. However, the importance of the trophic role of mud crabs for mangrove ecosystem functioning have 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 highest when they are juveniles and decreases with increase of size (Palmqvist 2009), but even large mud crabs are preyed upon 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 and 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 and 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 to 6 hours before) the crab reduces all activities and completely stops feeding (Lavina 1978a, Mirera and Mtile 2009) and experiences a general weight decrease (Mirera and 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 and Chia 1997). In the reverse direction, hemolymph protein and electrolyte levels decrease after molting, which is associated with post-molt water uptake (Chen and Chia 1997).

The molting follows a rhythmic pattern and is closely related to the lunar and tidal cycle (Le Reste et al. 1976, Mirera and Mtile 2009), most crabs molt during the neap high tide during night (Mirera and 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 2002).

Mud crabs can easily reach sizes above 200 mm CW, and maximum reported sizes seems be slightly different in the different regions (228 mm in Ponape, 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 and 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 and Wainwright 2001). Juvenile mud crabs molt frequently which results in a high growth rate, but there is a decrease in molt frequency with increase of age. Intermolt duration of four to seven days were 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 2<sup>nd</sup> and 3<sup>rd</sup> molt (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 to fifteen molts (Arriola 1940).

With the increase of intermolt duration with 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 a mean size of 103 and 131 mm CW are growing by 20 and 23 mm respectively (Du Plessis 1971).

### **Conclusions and future challenges**

This review covers a number of aspects relating to the ecology of *Scylla serrata*. It becomes evident that there are still essential gaps in knowledge about life history, behavior and habitat use and the significance for the inhabited ecosystem. By addressing these and condensing existing literature, this review can give guidance for future research and management decision makers.

In particular, little information is available about the behavior and habitat use of the early life stages. 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 highly depends on a 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 lacking information, the development of a standardized sampling method for determining mud crab abundances is necessary to compare (geographical) different ecosystems and the role of the mud crab therein. 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 between 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 towards changing environmental parameters, as these may already be reflected in another geographic area where mud crabs occur.

While climate change and global warming is 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. 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 towards warm and increasing temperatures, as it is typical for warm water crustaceans (Anger 2001). Yet, the absorption of atmospheric CO<sub>2</sub> 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 live stages. Further, ocean acidification is known to alter the sensory abilities and therefore behavior of marine organisms. Tropical fish larvae, for which larval sensory abilities are well studied, showed diminished olfactory discrimination abilities under elevated CO<sub>2</sub> concentrations and therefore loss of crucial cognitive abilities (Munday et al. 2009, Simpson et al. 2011, Ferrari et al. 2012). To date, 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).

A number of publications are available to provide a good overview of the crabs' life cycle, needs and dependencies. 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.

## Supplements

**Table 1** Reference table global distribution of *S. serrata*

Region	Country	Regional location	<i>S. serrata</i>	<i>S. olivacea</i>	<i>S. paramamosain</i>	<i>S. tranquebarica</i>	
West Africa	South Africa	Knysa	X			Du Plessis, 1971	
		Kariega, Kowie, Kei estuary (Eastern Cape)	X			Davis, 2004	
		Umlalazi, Richards Bay, Kosi Bay (Kwazulu-Natal)	X			Davis, 2004	
		St. Lucia lagoon (Natal)	X			Hill, 1979	
		Kleinemonde estuary	X			Hill, 1975	
		Kowie estuary	X			Hill, 1975	
		Richards Bay, Mlalazie estuary (Natal)	X			Robertson and Kruger, 1994	
		Mossel Bay	X			MacNae, 1968	
		Mocambique	Ibo and Quirimba Island	X			Barnes et al., 2002
			Maputo Bay	X			
	Madagascar	Inhaca Island		X			Paula et al., 2001
			Morandava estuary	X			Davis, 2004
		Diégo-Suarez province general		X			Le Reste, 1976
				x			Crosnier, 1962
	Tanzania	Mafia, Chole and Juani Island	X			Barnes et al., 2002 Fratini and Vannini 2002	
		Zanzibar (Chwaka Bay)	X			Fratini and Vannini 2002	
	Kenya	Mida Creek, Gazi Bay, Lamu		X			Onyano, 2002
			Ramisi river	X			Mirera and Mtile 2009
		Mtwapa creek	X			Vannini and Innocenti 2000	
	Somalia			X			
Seychelles	Mahe Island		X			Fratini et al., 2010	
Maledives	Laamu Atoll		X			Anand et al., 2006	
Mauritius			X			Keenen et al., 1998	
Arabian Peninsular	Yemen	Socotra Island	X			Simões et al., 2001	
	Saudi Arabia	Jiddah	X			Forsk, 1775	
		United Arab Emirates	Ras al-Khaimah	X			Hogarth and Beech, 2001
	Iran	Persian Gulf		X			Rezaie-Atagholipour et al., 2013
		Gulf of Oman		X			Rezaie-Atagholipour et al., 2013

Region	Country	Regional location	<i>S. serrata</i>	<i>S. olivacea</i>	<i>S. paramamosain</i>	<i>S. tranquebarica</i>	
Asia	Pakistan		X				Saifullah, 2005
	India	Chilika lagoon (Odisha)	X			X	Keenan et al., 1998
						X	Mohanty et al., 2006
			X			X	Srinivasagam et al. 2000
			X				Zafar et al., 2006
	Sri Lanka	Negombo and Kalpitiya lagoon	X				Anas et al., 2009
	Bangladesh	Sunderbans					Ali et al., 2004;
		Ban Don Bay, Gulf of					Begum et al., 2009
	Thailand	Thailand		X	X		Overton, 2000
		Ranong		X			Koolkalya et al., 2006
				X	X		Tongdee, 2001
				X			Moser et al., 2005
		Chantaburi and Trat	X	X		X	Klinbunga et al., 2000
	Malaysia	Matang mangroves, Perak	X	X			Kosuge, 2001
		Sematan mangroves, Sarawak		X	X	X	Ikhwanuddin et al., 2011
	Indonesia	East Java, Lombok, South Sulawesi		X	X	X	Sugama and Hutapea, 1999
		Segara Anakan lagoon	X				Nordhaus et al., 2009
	Singapore			X	X	X	Keenan et al., 1998
	Papua New Guinea	Labu Estuary	X		X		Quinn & Koijs, 1987
	Philippines	Panay Island (Visayas)	X	X		X	Walton et al., 2006, Leбата et al., 2007
		Cagayan, Sorsogon (Luzon)	X				Gaillard and Morrissens, 2010
		Samar (Visayas)	X				
	Vietnam	Mekong Delta		X	X		Le Vay et al., 2001; MacIntosh et al., 2002
	China	Shanghai	X				Fang et al., 2008
		Hainan, Beibu Bay	X	X	X	X	Lin et al., 2007
		Xiamen		X	X		
	Taiwan	Ilian	X				Chen & Chia 1996
		Kaohsing		X	X		Keenan et al., 1998
	Japan	Iriomote Island	X	X			Ogawa et al., 2011
		Okinawa and Sakishima Island	X				Hamasaki 2003
Oceania and Australia	Federal States of Micronesia	Palau	X	X	X		Ewel et al., 2009

Region	Country	Regional location	<i>S. serrata</i>	<i>S. olivacea</i>	<i>S. paramamosain</i>	<i>S. tranquebarica</i>
		Kosrae	X			Bonine et al., 2008
	Northern Territory (Australia)	Elisabeth River, Darwin Harbour	X			Ruscoe et al., 2004
		around Darwin	X	X		Hay et al., 2005
		Van Diemen Gulf, Gulf of Carpentaria	X			Knuckey, 1996
				X		Keenan et al., 1998
	Western Australia		X		X	Taylor 1984*
				X		Keenan et al., 1998
		Shark Bay	X			Lee 1992
	Queensland (Australia)	Gulf of Carpentaria	X	X		DPI Qld., 2009
		Pumicestone Passage	X			Williams & Hill, 1982
		Deception Bay (Moreton Bay)	X			Hill et a., 1982
	New South Wales (Australia)	Wooli Estuary	X			Butcher et al., 2003
	New Caledonia		X			Delathiere 1990, Gopurenko et al. 1999
	Fiji		X			Gopurenko et al., 1999
	Solomon Islands		X			Gopurenko et al., 1999
	Hawaii (USA)		X			Atkinson 1971; DeFelice et al., 2001

\* obvious mix-up in the species

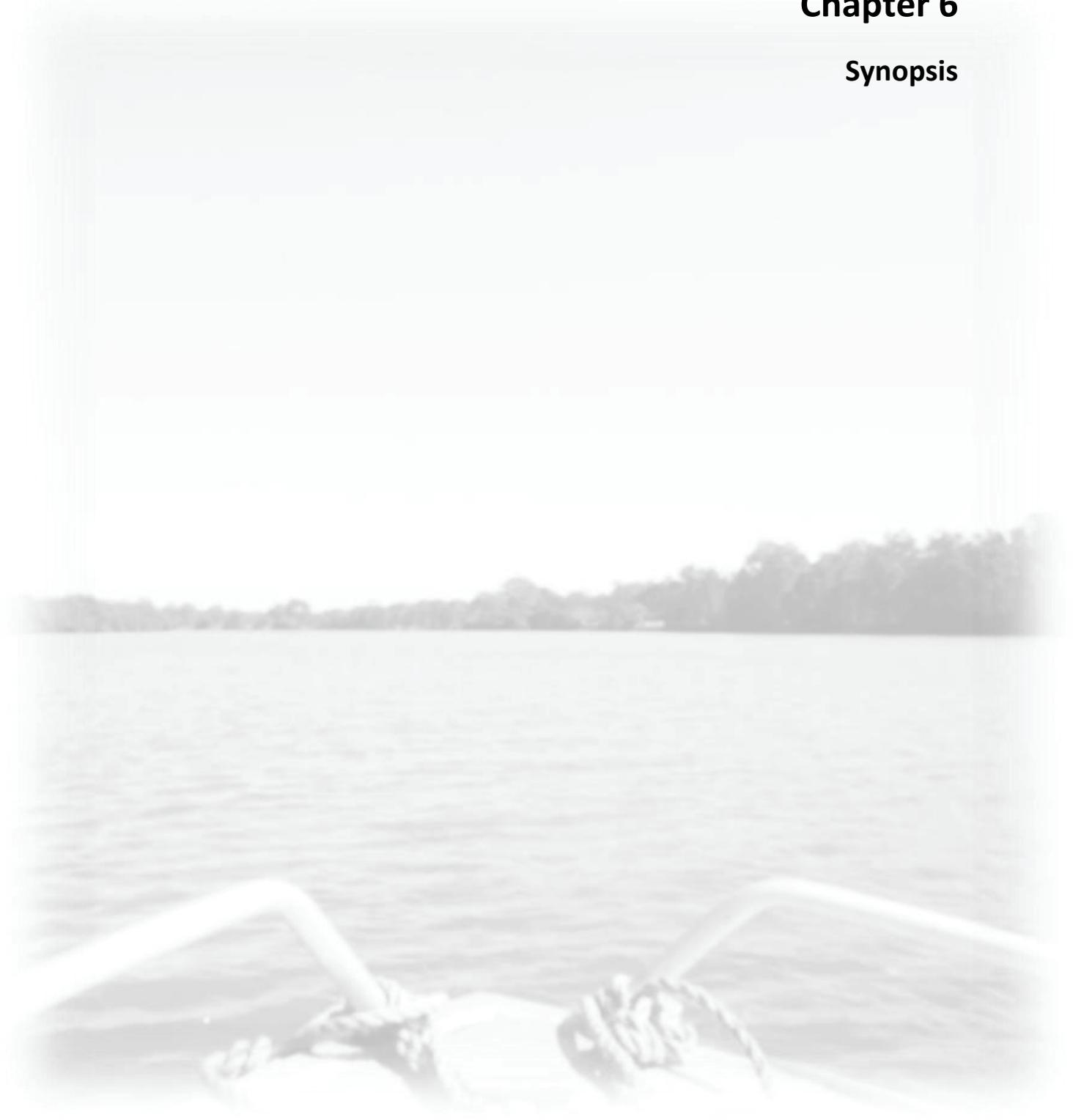
**Table 2** Habitat use of different life stages of *S. serrata*

Geographic location	Larvae	EBS	Inter-mediate juveniles	Large juveniles	adults m/f	Habitat	Distribution range	Comments	Habitat
South Africa					m/f	along the river	ø 1km, max. 3km long time		Hill, 1975
South Africa					m	10 km upstream, muddy grounds	219 - 910m, ø 461m		Hill, 1978
Queensland, Australia			yes ≥ 20 mm a)	yes b)	m/f c)	a) intertidal flats b) intertidal at high tide c) mostly subtidal		a) all year b) Sept.-March c) Jan.-April	Hill, 1982
Queensland, Australia				yes	m/f	a) narrow creek with mangroves b) intertidal flats no mangroves (high tide)	a) little movement b) more movement ø3.7 km	population exchange, but not when seperated by unsuitable habitat	Hyland, 1984
South Africa	yes					6 km inshore	watercolumn	megalopa and early stages, high abundance Nov.-May	Forbes and Hay 1988
Northern Australia					m/f, mostly females	offshore	10-60 m depth 3-95 km offshore, ø17,9km	spawning behaviour of females	Hill, 1995
Chilika lagoon, India			yes a)	yes b)	yes c)	a) no habitat specifications b),c) muddy bottoms with hydrophytes and seagrass meadows			Mohanty et al., 2006
Kosrae, Micronesia				yes a)	yes b)	subtidal areas: a) channels within mangrove forest b) mangrove fringe	general limited movement (average < 1 km, up to 2-3 km); single individual males up to 8.5 km		Bonine et al., 2008

Geographic location	Larvae	EBS	Inter-mediate juveniles	Large juveniles	adults m/f	Habitat	Distribution range	Comments
Palau				yes	occupying burrows in intertidal mangrove habitat		no homing behavior (no second encounter in same burrow), most abundant riverine with debris on ground (logs)	Ewel et al., 2009
Queensland, Australia	first stage				laboartory		habitat choice test: no preferences for habitat at settlement as larva, preferences for seagrass as megalopa	Webley, 2009
Tanzania, Mozambique and Kenya	yes < 40mm a)	yes 40-75 mm b)	yes >75 mm c)		a) tidal pools in mangrove backflats (high intertidal) b) tidal creeks and seaward mangrove fringe c) tidal creeks lower intertidal		a) continuous recruitment (Tanzania, Kenya), peak recruitment in rainy season (only Mafia Island)	Mirera, 2014
Queensland, Australia	yes < 30mm				marked crabs recaptured on shallow (10 cm) subtidal mudflat	marked crabs recaptured in same tidal pool after 4-17 days		Alberts-Hubatsch et al., 2014

## Chapter 6

### Synopsis



Mangrove habitats provide food and shelter for many marine and estuarine species. Many of these species have a complex life-cycle during which ontogenetic shifts co-occur with an associated change in behavior and therefore habitat use (Dahlgren and Eggleston 2000, Nagelkerken et al. 2000, Beck et al. 2001, Jones et al. 2010).

In this thesis, I studied movement patterns and habitat use of different life stages of the mud crab *Scylla serrata*. In **chapter 2**, I was able to find early benthic stage mud crabs in two different mangrove systems and could determine that substrate as well as distance to the mangrove fringe influences abundance at this stage. The movement of larger juveniles and adult mud crabs was studied in **chapter 3**, and I detected movement between protected and non-protected zones in an enclosed embayment with predominant seaward movement of large crabs. In **chapter 4**, I tracked the movement of female mud crabs during their spawning migration and identified tidal stream transport as the major transport mechanism. Reviewing the literature (**chapter 5**), I detected essential knowledge gaps regarding habitat use and movement patterns of *S. serrata*, of which some were already addressed in the former chapters. I was able to implement my own work in this review to close a number of these knowledge gaps, and highlighted the need for future research to fully understand the species and its interactions with mangrove ecosystems.

### **Habitat of early benthic stage crabs**

Early life-stages are highly vulnerable to environmental stressors, as well as predation. Estuaries in general and mangroves in particular often function as nursery habitats, since they provide refuge from predators and offer sheltered, calm waters that promote good retention for early life stages (Robertson and Duke 1987, Acosta and Butler IV 1997, Rönnbäck et al. 1999, Sheridan and Hays 2003, Nagelkerken 2009). I compared the abundances of early benthic stage (EBS) *S. serrata* at two different mangrove systems, one riverine with sandy bottoms and the other estuarine with muddy bottoms. Highest abundances of EBS were found on muddy substrates in pools within the mangrove fringe. Very few EBS were found in sandy habitats. This may either be due to an active preference of EBS for muddy mangrove habitats, or due to a higher predation rate on sandy substrates. EBS, including the very first crab stage, were also found on the mud flats adjacent to the mangrove habitat, which could be an indicator for post-settlement relocation. Similar behavior was observed in *Callinectes sapidus* and *Carcinus maenas* (Hedvall et al. 1998, Etherington and Eggleston 2000, Moksnes et al. 2003). A study on mud crabs from Kenya and Tanzania, which was conducted simultaneously to my study, found early benthic stage crabs in highest abundances in the upper intertidal areas on unvegetated flats between the mangrove and the shore (Mirera 2014). Here, diurnal tidal migrations of EBS were observed, with the crabs using the flats exclusively at ebb tides during night and moving into subtidal areas during the day (Mirera 2014). While the general

distribution pattern observed by Mirera (2014) seems to be similar to that of my study, variations may be allocated to differences in mangrove habitat. In my study, the mangrove fringe was in the upper intertidal area and the inner mangrove area was only inundated during spring high tides. Further, the water was relatively turbid, making visual census impossible. Therefore I had to use benthic collectors instead. In the East African study, the mangrove zonation seemed to be different, with another intertidal flat between the mangroves and land. In addition, the water may have been less turbid, since mud crabs were collected by hand. When considering distribution patterns in EBS mud crabs, differences in the local mangrove ecosystem should therefore be taken into account.

### **Movement patterns of adult mud crabs**

Movement of large juveniles and adult mud crabs is generally assumed to be limited in distance and non-directional (Hill 1978, Hyland et al. 1984). The movement of mud crabs seems to be closely related to the kind of habitat they live in (Hyland et al. 1984). Generally, crabs (> 100 mm CW) that live in enclosed habitats such as narrow creeks surrounded by mangroves, normally do not move over distances longer than 1 km (Hill 1975, Perrine 1978, Hyland et al. 1984), whereas in southern Moreton Bay, Queensland, crabs that are found in open environments like intertidal flats in open bays show larger routine movement ( $\phi$  3.7 km) (Hyland et al. 1984).

When I tracked the movement of large juvenile and adult mud crabs in an enclosed embayment, I detected a predominant seaward movement by large crabs. Since the study area included a protected and a non-protected area and the former was situated landwards from the latter, this seaward movement resulted in spill-over effects, benefitting adjacent fisheries. Mud crabs are considered aggressive, and the seaward movement of large crabs could be seen as a mechanism to avoid conspecifics, a process defined as 'demographic diffusion'. A similar behavior has been observed in American lobsters, where large lobsters move towards deeper waters to avoid spending too much energy in reoccurring intraspecific aggressive encounters (Steneck 2006).

Anecdotal reports (Butcher *et al.*, 2003, pers. communication) indicated that mud crabs are more active and therefore easier to catch during the rainy season. Since my study was conducted over two years (2012-2013) I was able to plot salinity and catchability of crabs in my sampling area and detect the co-occurrence of increased activity of crabs and rainfall.

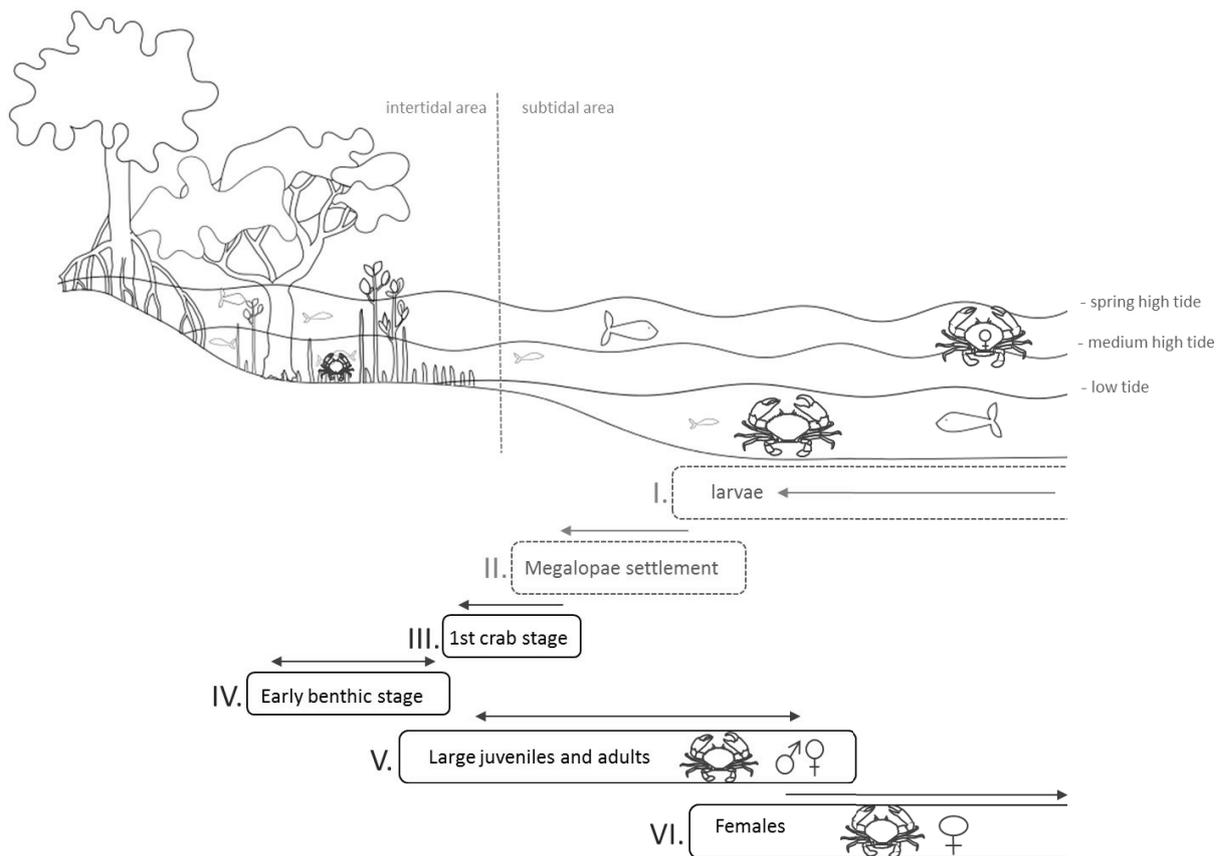
### **Female migration**

The patterns of female spawning migration are well studied for other portunid crustaceans, such as *Callinectes sapidus* (e.g., Carr *et al.*, 2004; Hensch *et al.*, 2004; Wolcott *et al.*, 2003). Female mud crabs are known to exhibit migratory behavior at the time of spawning and ovigerous females were found up to 95 km offshore (Hill 1994). Larvae of *S. serrata* are known to depend on high salinities and stable temperatures, which makes the migration of females to waters with oceanic conditions

necessary. To study the movement patterns during this spawning migration, acoustic tracking in a river system and the adjacent bay was used. I was mostly able to track the females over long distances, with the majority migrating downstream. Due to the constant monitoring by receiver deployed in the river and the bay, I was able to prove the use of tides for tidal stream transport, a mechanism also used by females of *C. sapidus* (Tankersley et al. 1998, Forward et al. 2003). Even though I conducted this study at the time of the supposed spawning season, it was not possible to detect the actual extrusion of eggs or even spawning. In fact there are some indicators that the long-distance migration of females might not be strictly restricted to the spawning season, meaning that female mud crabs routinely expand their habitats and generally move larger distances than male crabs.

Many crustacean species are known to be nocturnal (Wolff and Cerda 1992, Carr et al. 2004), but this behavior was not observed for the crabs in my study. Mud crabs live in mangrove habitats with muddy bottoms, often in combination with high turbidity in surrounding waters, which protects the animal from being seen by predators. This could in turn lead the mud crab to be active, irrespective day or night.

Combining the outcomes of my thesis and former studies on the movement of *S. serrata* results in a complex life cycle with several ontogenetic habitat shifts (Figure 1). A picture emerges, in which post-settlement processes relocate the first crab stages from the mud flat towards the mangrove fringe (**Chapter 2**), where they utilize the protection of mangroves' roots structures and pneumatophores, as well as macrophytes as nursery areas (Hill, 1979; Hill *et al.*, 1982; Mirera, 2014; **Chapter 2**). With increasing age (late juveniles) mud crabs start to expand their habitat towards the wider subtidal channels within the mangrove forests and to mud flats for foraging (Hyland et al. 1984). As adults, mud crabs use multiple habitats within or nearby mangrove forests: intertidal as well as subtidal mud flats, subtidal channels and the mangrove forest itself (e.g., Hill, 1979; Hyland *et al.*, 1984; **Chapter 3**). Here, the movement patterns are strongly linked to the seascape mud crabs reside in (**Chapter 3**). In open bay areas, mud crabs display more extended movement than in narrow seascapes shaped by riverbanks (Hill 1978, Hill et al. 1982). When mud crab densities increase, individuals start expanding their movement range and eventually leave the area to avoid the stress of aggressive encounters with conspecifics (**Chapter 3**). Females move larger distances than males, especially during the spawning season, connecting inshore mangrove habitats with other coastal and offshore areas (Hill, 1994; **Chapter 4**). There are some indicators that females also migrate irrespective of the spawning season, connecting different ecosystems, but this behavior has not yet been investigated in detail (R. Pillans, personal communication).



**Figure 1** Schematic drawing of ontogenetic shifts in habitat use and movement in *S. serrata*. Nothing is known about the first two steps (I. and II.), dotted-outline boxes indicate assumed behavior and habitat. The first crab stage (III.) moves from the upper subtidal mud flat towards the mangrove fringe. EBS crabs (IV.) use the mangrove fringe as nursery sites. Larger juveniles and adult crabs (V.) move back into subtidal areas, occasionally using mangroves for shelter and foraging. Adult female mud crabs migrate towards offshore regions with oceanic conditions during the spawning season (VI.)

Ontogenetic shifts in habitat use can be observed in several crab species, and are believed to optimize growth and survival, and to reduce intraspecific competition between size classes (Nagelkerken et al. 2000, Laegdsgaard and Johnson 2001, Manson et al. 2005, Hultgren and Stachowicz 2010, Kimirei et al. 2013). In *S. serrata*, the latter seems to be a major driving factor of distribution at all life stages, since mud crabs are known to be highly aggressive and cannibalistic. The early life stages occupy microhabitats within the adults' macrohabitat, where they can avoid intraspecific predation by hiding between complex structures (**Chapter 2**). Avoidance of intraspecific encounters has also been observed in large juvenile and adult crabs, with smaller crabs usually avoiding larger crabs, especially males (Beattie et al. 2012). In **Chapter 3** I observed and discussed another effect of this avoidance: predominantly large crabs are leaving areas with high crabs densities, trading the benefits of good resources against the costs of constant aggressive interactions ('demographic diffusion'; Steneck, 2006).

## Conclusion and Outlook

Understanding movement patterns and habitat use by animals contributes to the understanding of their spatial distribution, their connectivity and their impact on the structure and function of ecosystems (Lima and Zollner 1996). Knowledge of how species move through the landscape and which habitat they use at which life stage can increase the accuracy of predictions on the species' persistence in a changing world (Knowlton and Graham 2010). In a study from New South Wales *S. serrata* was already used to estimate the effectiveness of marine protected areas (Butcher et al. 2003) and its conspecific *S. olivacea* was used in the Philippines to assess the habitat-function of replanted mangroves (Walton et al. 2007). Even though there is a link between mud crabs and mangrove ecosystems, it is hard to estimate how exactly they are connected, and if the resilience of the former can be directly linked to the health of the latter. Adult mud crabs are relatively tolerant towards changing environmental conditions, whereas the early life stages are more vulnerable. These differences in response to environmental conditions should be considered when using the species as an indicator for ecosystem health, or when designing meaningful management strategies. In my thesis, I was able to detect the microhabitat of EBS mud crabs for the first time and was able to generate additional information on movement patterns as well as habitat use of different life stages of *S. serrata*. However, reviewing the current literature, it became evident, that there are still essential gaps in knowledge on the ecology of EBS *S. serrata*.

Regarding the early life stages, the underlying mechanisms and drivers for choosing a specific habitat need further investigation. There may be (inherited) developmental causes other than proximate predator avoidance and food availability that steer the crabs' behavior. Combining proximate and ultimate causes of behavior can improve our understanding of the ecology and evolution of these behaviors (Hultgren and Stachowicz 2010). Once we know more about sensory abilities and behavior, simulating anticipated future changes (e.g., ocean acidification, water and noise pollution, habitat fragmentation) and respective behavioral responses can help to shed light on the resilience of the species.

This study also emphasizes the importance of the seascape for movement and behavior in *S. serrata*. Given the vast possibilities of environmental settings (e.g. open vs. closed, sandy vs. muddy, macrotidal vs. microtidal) seascape-dependent habitat use and behavior require further exploration. In this context, human induced habitat fragmentation could play an important role. It is not yet known how mud crab populations may react towards habitat destruction or fragmentation. Behavioral landscape ecology can provide a strong theoretical background for predicting how animals react to landscape alterations (Knowlton and Graham 2010).

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## Eidesstattliche Erklärung

Gemäß §6 der Promotionsordnung der Universität Bremen für die mathematischen, natur- und ingenieurwissenschaftlichen Fachbereiche vom 14. März 2007 versichere ich, dass die Arbeit mit dem Titel

„Movement patterns and habitat use of the exploited swimming crab *Scylla serrata* (Forskål, 1775)“

1. ohne unerlaubte fremde Hilfe selbstständig verfasst und geschrieben wurde
2. keine anderen als die angegebenen Quellen und Hilfsmittel benutzt wurden
3. die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht wurden
4. es sich bei den von mir abgegebenen Arbeiten um 3 identische Exemplare handelt.

Bremen, Datum

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Hilke Alberts-Hubatsch