Nursery habitat of the mud crab (*Scylla serrata*) and the distribution of mobile epifauna in seagrass habitats on Mafia Island, Tanzania

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Abstract

Studies were performed inside Chole bay, Mafia Island, Tanzania in 2009 with the aim of locating the nursery habitat for the mud crab *Scylla serrata* and develop a method to collect juveniles for grow-out aquaculture. The aim was also to describe the distribution of mobile epifauna on the intertidal flat at low tide. Sampling was carried out in 4 different seagrass habitats (high intertidal seagrass, low intertidal seagrass, unvegetated intertidal and subtidal seagrass) and in 2 different mangrove habitats (mangrove fringe and inner mangrove) that were sampled both during day and night. Juvenile *S. serrata* was found only in the mangrove and only at night. Significantly more juveniles were found in the inner mangrove compared to the fringe (5.7 and 0.6 crabs transect\(^{-1}\) respectively). The mud cabs found at the inner mangrove was smaller than the ones found at the fringe (mean CW 32 and 68 mm respectively). The smallest crab collected was 4 mm CW. Two people could collect up to 30 juveniles in approximately one hour with little effort, by hands or by using a net. The seagrass samples from the intertidal displayed a rich faunal community. 46 taxa of mobile epibenthic animals were found in vegetated and unvegetated tidal pools at low tide. The highest diversity and abundance of animals were found in samples from the low intertidal seagrass. The results indicate the importance of intertidal mud flats as a "permanent" habitat for small epibenthic animals and as nurseries for certain animal groups.
1. INTRODUCTION

The mud crab, *Scylla serrata* is a large species of portunid crab that can reach a size well over 200 mm carapace width (CW) (Robertson 1996). The crab is an important food source and a commercially important species throughout the Indo-Pacific region. It is sought after because of its excellent taste and nutritional value (Triño and Rodriguez 2002, Keenan 2003). *Scylla serrata* inhabits intertidal and subtidal coastal mangrove habitats and can be found both free-ranging and in burrows (Hill *et al.* 1982, Hyland *et al.* 1984, Mahika *et al.* 2005). Chemical trace-analyses indicate that *S. serrata* mainly feed in mangrove habitats, but also in adjacent seagrass environments (Demopoulos *et al.* 2008). The crab is well suited for aquaculture and can stay alive out of water for 4-5 days (Keenan 2003), which enables export of live crabs to the national and international market, generating a higher price than frozen crabs.

Aquaculture of the mud crab has been successful in many parts of Southeast Asia and the crabs grow and survive well in earthen ponds and pen cultures (Triño and Rodriguez 2002, Rodriguez *et al.* 2007). However, the rapid increase in demand for the mud crabs and an expansion of the industry could potentially lead to overexploitation and a depletion of the natural population in many areas (Le Vay 2001, Keenan 2003, Rodriguez *et al.* 2007).

*Scylla serrata* is the only species in the genus *Scylla* that exists in East Africa (Keenan *et al.* 1998). Tanzania is believed to have a sustainable population of mud crabs (Barnes *et al.* 2002) but there are signs that some local populations off the coast of Tanzania has decreased significantly due to enhanced fishing efforts (Mahika *et al.* 2005). The fishery is still quite small in comparison to Southeast Asia but as the tourism grows, so will the demand for crabs (ASDI-VOCA 2005).

The aquaculture of mud crabs in East Africa and Tanzania is today still at a stage of development (Shipton and Hecht 2007). In Tanzania, small-scale pilot farms have recently been established by various NGOs. In contrast to Southeast Asia, were crabs generally are cultured from young juveniles (Triño and Rodriguez 2002) these farms are dependent on capturing of sub-adults or adult crabs (300-500 g) (seed-crabs) that are kept in cages and fed until they reach the market size of 700-1000 g (15-30 days) (Keenan 2003, Shipton and Hecht 2007, Mahika *et al.* 2005). This technique, called “crab-fattening” were developed to work under local conditions with material available for the villages, but a rapid extension of this fattening industry, would likely lead to a depletion of “seed-crabs” and trash-fish for feed (Mahika *et al.* 2005). No mud crab hatcheries have yet been successful in providing viable seeds of *S. serrata* for aquaculture farms (Keenan 2003). The average mortality of mud crabs in crab-fattening farms is 10% per month (ACDI-VOCA 2005). This mortality is higher than the estimated natural mortality of 2% per month in the wild (Mahika *et al.* 2005), which means that the fattening of sub-adults is even more unfavorable to the population of crabs than the fishing for adults. An extension of this aquaculture could also potentially lead to increased environmental costs, like the clearing of mangroves (Mahika *et al.* 2005).

A more sustainable and ecologically friendly way to farm these crabs would be in small-scale grow-out farms. This technique is based on the collection of small juvenile seed-crabs from the wild, which are kept in ponds or pens until they reach market size. These grow-out farms could be integrated into the mangrove, which would minimize the disturbance of the mangrove ecosystem (Triño and Rodriguez 2002, Mirera and Mtile 2009).

A bearing female can carry more than 7 million eggs and the mud crab seems to spawn during all months of the year with a peak around July to August (Le Vay 2001, Davis *et al.* 2004) and the predation of early juveniles is very high in many species of crabs (>99% per
month). When the crab grows, the predation levels decline as they obtain a size-refuge from predators (Moksnes and Heck 2006). If you could collect the crabs for grow-out farms, at a size where natural predation mortality is still high, the impact on the natural population in the area would be minimized.

Although mud crabs are an extremely important commercial species in the Indo-Pacific region, very little is known about the basic biology and ecology of the crabs (Keenan 2003 and Shipton and Hecht 2007). This is especially true for the juvenile mud crabs and newly settled juveniles of *Scylla serrata* have not yet been found in nature (Keenan 2003, Davis *et al.* 2004, Webley *et al.* 2009). Thus, the nursery habitat for the species is presently unknown. Studies have shown that many species of crabs actively select to settle and reside in structurally complex habitats (e.g. algae, mussel beds and seagrass) during their early juvenile stages (Moksnes 2002 and Moksnes and Heck 2006). If these nursery habitats for mud crabs could be located, juvenile crabs could be collected with little effort for grow-out aquaculture.

The seagrass meadows constitute a complex habitat, which could be an important nursery area for the juvenile mud crabs. These seagrass areas are also important habitats for other mobile epifauna, including juvenile stages of many fish and invertebrates (Heck *et al.* 2003, Lugendo *et al.* 2006). Most research of seagrass ecosystems in East Africa has been done in connection to the fish community (Gullström *et al.* 2002, Dorenbosch *et al.* 2005, Lugendo *et al.* 2006, Unsworth *et al.* 2007) and less is known about the diversity and abundance of small mobile epibenthic invertebrates in these habitats (de Boer and Prins 2002, Eklöf *et al.* 2005).

The aim of this study was to locate the nursery habitat for the mud crab, *S. serrata* and develop a low-tech method to collect newly settled individuals for grow-out aquaculture. The second aim was to describe the mobile epibenthic species that uses these seagrass habitat as their primary habitat and stay there during low tide (i.e. permanent species).

### 2. MATERIALS AND METHODS

#### 2.1 Study area

The mud crabs are an important resource on Mafia Island, and have the potential to evolve into a long-term alternative livelihood for the fishing villages around the island. The present study was conducted inside the marine park (Horrill *et al.* 1996) of Mafia Island off the coast of Tanzania. Mangroves are present around much of the Islands shoreline, with the dominant species being *Avicennia marina*, *Sonneratia alba* and *Rhizophora mucronata*. On Mafia Island, the mud crab is fished for by artisanal and commercial fishermen, and two different techniques are used on the Island when capturing crabs (Barnes *et al.* 2002). At some regions they fish during the day searching through burrows with curved sticks. The crab detaches its chelipeds when it grabs the stick and the fishermen can then extract the crab from the burrow by hand. In other parts of the island, crabs are fished for at night, while free-ranging. Torches are used and the crabs captured with hand-nets.

The tourism and the population on Mafia Island is growing (Horrill *et al.* 1996) and the demand for crabs by hotels is increasing. An expansion of the fisheries on the Island will most definitely have a negative impact on the natural populations of mud crabs around the Island.
The sampling was carried out in Jan to Feb of 2009 at four study sites inside Mafia Island Marine Park (MIMP) in the sheltered bay of Chole, Mafia Island, (7º 40´S, 40º 40´E: Fig. 1) Tanzania. The waters outside Mafia Island has an average surface salinity of 34.4 ppt and an average yearly temperature of 27°C (Newell 1959). Mafia Island is affected by a semi-diurnal tide with an average amplitude of 3.3 m (McClanahan 2000). The water depth inside Chole Bay rarely exceeds 10 meters and has its deepest channel at Kinasi Pass (20-27 m) in the east. Kinasi Pass is also the main point through which tidal currents enter the bay (McClanahan 2000). Mafia Island, in particularly Chole bay houses extensive intertidal and subtidal seagrass beds with a large number of seagrass species (Horriil and Ngoile 1991), typically with *Halodule sp.* and *Thalassia hemprichii* in the intertidal, *Enhalus acoroides* in the subtidal and *Thalassodentron ciliatum* in the deeper parts of the subtidal.

2.2. Study sites

Three study sites (Utende, Kilole and Kichangani; Fig. 1) were used in the sampling of seagrass and mangrove habitats. The sites were randomly selected based on the condition that they had mangroves at the shoreline and seagrass in the intertidal and subtidal. An additional 4th site (MIMP; Fig. 1) was used to sample mud crab abundance in the mangrove.

**Utende** (Fig. 1.) was sampled during the 28th and 29th of January. The mangroves at this site were dominated by *Sonneratia alba* in the fringe and *Rhizophora mucronata* further in. The width of the intertidal flat, from the mangrove fringe to the low-tide mark was approximately 150 m. During low tide at the intertidal flat, water remained in small tidal pools that contained a mix of *Thalassia hemprichii, Halodule sp.*, *Halimeda opuntia* and filamentous green algae. Juvenile moray eels and pufferfish were observed in some of the puddles during sampling. Closer to the mangrove fringe *Halodule sp.* was the dominating seagrass species. Further into the mangrove, no vegetation except mangroves was found. The subtidal contained large patches of *Enhalus acoroides* and separate patches with *T. hemprichii* and *Syringodium isoetifolium*. The seagrass and algae coverage in the subtidal was about 60%. The seagrass was healthy and relatively clear of epiphytes. Schools of small fish were observed amongst the seagrass. The site also had a lot of calcium algae in the subtidal, mainly *H. opuntia*, but also *Halimeda macroloba*, that grew amongst the seagrass. Small colonies of hard corals were observed in the subtidal. The substratum was muddy, with fine sand close to the mangrove fringe. The intertidal flat had a muddy to sandy substrate mixed with coarse sand and shell sand in some areas. The subtidal substratum was less compact and had more coarse sand and shell sand than the intertidal. During night transects around high tide, small/juvenile fish were observed in the mangrove fringe. Human activity was moderate in the area. People were seen collecting shells and mussels on the intertidal flat at low tide, but beside that the area seemed fairly undisturbed.

**Kilole** (Fig. 1.) was sampled on the 9th and 10th of February. The mangroves were dominated by *S. alba* all the way from the shore to the fringe. *Avicennia marina* grew in scarce numbers just by the shoreline. At this site there was an approximately 20 m wide back-flat (an open area) between the mangroves and the shoreline. The width of the intertidal zone was about 400 m. During low tide, water remained in small tidal pools containing *T. hemprichii* and a great number of sponges. *T. hemprichii* was the dominating seagrass species from the mangrove fringe to the low water mark. Closer to the mangrove fringe we also noted some filamentous green algae (*Caetomorpha crassa*), but deeper into
the mangrove no algae or seagrass was found. In the subtidal, *T. hemprichii* continued to be the dominating seagrass species, but smaller patches of *E. acoroides* were also seen (but not sampled) within the site. The subtidal seagrass covered around 40% of the seafloor and the seagrass showed signs of heavy grazing and was covered with epiphytes. Larger colonies of hard corals were observed between the patches of seagrass, and many species of fish seen during sampling. The substratum inside the mangrove and in the back-flat consisted of mud and fine sand. At low tide in the back-flat, water remained in small puddles that were filled with dead leaves and debris. These puddles were often anoxic without much animal activity. At the intertidal zone the substratum ranged from muddy close to the mangrove fringe to fine sand and shell sand closer to the low-water mark. The subtidal substratum was less compact with more coarse sand and shell sand. While conducting the night transects in this site we observed a lot of small/juvenile fish in the back-flat and in the mangrove fringe during falling tide. This site had a lot of human activity both during the day and night. During the day at low tide, people were out on the intertidal flat collecting mussels and shells and in the back-flat of the mangrove people were seen digging for mud crabs (*S. serrata*) in burrows and picking shells (*Terebralia sp.*).

**Kichangani** (Fig. 1.) was sampled on the 24th and 25th of February. The mangroves in this site were dominated by *S. alba* in a narrow band at the fringe and *R. mucronata* in the inner part of the mangrove. The width of the intertidal zone was about 200 m. During low tide, water remained in small tidal pools that contained *T. hemprichii* and *H. opuntia*. Near the low-water mark, the puddles also contained a lot of small sea anemones. Close to the mangrove fringe *C. crassa* and other filamentous green alga were more abundant and the seagrass scarce. Inside the mangrove no other vegetation was observed. The subtidal contained dense stands of *E. acoroides* and lesser amounts of *T. hemprichii* covering about 80% of the seafloor. The seagrass was not notable grazed but had a large number of anemones growing on them. Amongst the seagrass many black sea urchins (Family: Diadematidae) were observed during sampling. The substratum close to the mangrove fringe consisted of mud and fine sand. In scattered places close to the fringe the underlying coral rock emerged into platforms covered with a fine layer of sand. The substratum in the low intertidal and subtidal consisted of fine sand and shell sand. This site, in contrast to the others, had large non-vegetated patches between the mangrove fringe and low intertidal. During night transects a lot of juvenile/small fish and shrimp were observed in the mangrove fringe and inside the mangrove during falling tide. Human activity was moderate in the area. There was a footpath through the mangrove and a few fishermen were observed during sampling. This site had notably more shore birds then the others and a large number of carapaces from *Thalamita spp.* were found close to the mangrove fringe.

**MIMP.** This site (Fig. 1.) was only used in the transect sampling of juvenile *S. serrata* in the mangroves and consisted of a narrow stretch (7 m wide) of mangroves close to where the Mafia Island Marine Park (MIMP) has its headquarters. The dominating species in the mangrove was *S. alba* in the fringe and *A. marine* at the shoreline. The site had a back-flat, approximately 10 m wide, between the mangroves and the shoreline. The substrate was muddy with a lot of dead leaves and debris accumulating in puddles at low tide. The Mangrove fringe had a muddy to sandy substrate with some small patches of *Halodule sp.* During night transects many juvenile fish and cuttlefish were observed in the back-flat of the site. Juvenile barracudas, batfish, needlefish, eels and schools of catfish were seen during the falling tide. The site was close to a hotel beach but there seemed to be little human activity in the area.
2.3. Seagrass sampling

In each of the sites (Utende, Kilole and Kichangani) we sampled 4 different habitat-types, with the aim to assess the distribution of juvenile *Scylla serrata* and other mobile epifauna. We chose to sample three seagrass habitats; high intertidal (close to mangrove fringe), low intertidal (closer to the low-tide mark) and subtidal (below the low-tide mark) and one non-vegetated intertidal habitat as a comparison to the intertidal seagrass.

All sites were sampled during the day at low tide to estimate the abundance of species that use the habitat permanently during the tidal cycle, and 5 random samples were taken from each habitat, at each site. The high and low intertidal seagrass (i.e. seagrass in small tidal pools) were sampled by pressing a plastic cylinder (Ø = 0.33 m) into the substratum. Everything inside the cylinder and approx. 10 cm of sediment was dug up and filtered through a 1 mm sieve. Sampling of the non-vegetated intertidal habitat was done in the same way as for high/low intertidal seagrass and the 5 samples were spread out over the whole intertidal flat in small tidal pools that were free of vegetation. The subtidal seagrass habitat was sampled at 2-3 m depth using a 200 µm meshed net-bag connected to a circular metal frame (Ø = 0.4 m). By snorkelling, the frame and net was placed over the seagrass stand and the frame pressed into substratum (Fig. 2.). The frame was lifted a little on one side (trying to minimize the gap as much as possible) and the seagrass stalks inside were cut of and pushed up into the bottom of the net-bag. A small spade was used to dig up the sediment, which was thrown into the bottom of the net-bag. The net-bag was then rapidly lifted out of the water and emptied into buckets.

In all samples, the seagrass was cleared of epiphytes and rinsed in water so that no animals would remain on them. The rhizomes were cut off and the seagrass dried and weigh to get the above-ground dry weight (DW) biomass. The dominant algae (*Halimeda spp.*) were dried separately and weighed. The sample and rinsing water was filtered.
through a 1 mm sieve and everything that remained in the sieve was saved in marked zip-lock bags and stored in a freezer until analysis.

The samples were sorted in the laboratory at MIMP and all epifauna were preserved in 95% ethanol. Animals that were too big to fit into the vials were thoroughly measured and documented. Time limits forced a less thorough sorting in 2 of the 5 sample replicates taken from each habitat in Kilole and Kichangani where only crabs, hermit crabs, fish and mantis shrimp were collected. For remaining animals the sample size at these two sites was therefore changed to 3 instead of 5 replicates. As a result, a total area of 5.76 m$^2$ was sampled for crabs, fish, hermit crabs and mantis shrimp, and a total area of 4.22 m$^2$ was sampled for remaining animals.

![Figure 2. Seagrass sampling in the subtidal](image)

The species classification was done back in Sweden at the Institute for Marine Ecology (Gothenburg University). Species were identified to the lowest possible taxa with the available literature, Vannini and Innocenti 2000 was used for portunid crabs and Richmond 1997 was used for other species. For identification of shrimp, Matz Berggren at Svens-Lovén center for marine science, Kristineberg was consulted. Due to differences in diameter between sampling equipment, all data was standardized to number of animals per square meter. The dominant species and groups of epifauna were tested separately as dependent variables in a 2-factor mixed-model analysis of variance (ANOVA) using habitat (fixed factor) and site (random factor) as independent variables. Prior to analysis, homogeneity of variance was tested for all data using Cochran’s c-test. If variance was not homogenous, the data were subjected to Sqrt(x) transformation. A multiple comparison post-hoc test was done with the Student-Newman-Keuls (SNK) method.

2.4. Mangrove sampling of juvenile S. serrata

To assess the abundance of juvenile mud crabs in the mangrove forest, a pilot study of habitat sampling was initially carried out at Utende, January 28$^{th}$–29$^{th}$. Five samples each were taken during the day from the inner mangrove and mangrove fringe using a plastic cylinder (Ø = 0.43 m) that was pressed down into the mud. Everything, including pneumatophores, within the cylinder was dug up and sieved through 1 mm mesh and subjected to the same analyses as the seagrass samples. With the exception of a few Thalamita spp. at the mangrove fringe, this sampling method did not collect any portunid crabs, and the sampling was not continued at the other sites. Instead transects were employed to sample juvenile mud crabs in the mangroves.
Transect samplings was carried out to determine the abundance of *S. serrata* in 2 habitats (the mangrove fringe and inside the mangrove) and also to see if there were any difference in their abundance between day and night.

Transects were done in the same sites as for the seagrass sampling plus at an additional site close to the marine park headquarters (MIMP; Fig. 1) where high numbers of juvenile *S. serrata* were encountered during test-sampling. At each of the 4 sites, samples were taken during day and night in the 2 habitats (mangrove fringe and mangrove inner) in a 2 x 2 orthogonal design using 2 replicates. The sampling took place just after high tide, during falling tide, with water levels ranging from 0 to 20 cm. The transect line was 20 m long and the area sampled was approximately 80 m² (20 x 4 meter). The line was laid out by walking with the rope in a half-circle to avoid unnecessary disturbance of the area. The sampling was done by walking along the line recording all *S. serrata* that were located within 2 m on each side of the line. The crabs were captured using nets and measured. Crabs under 100 mm were considered to be juveniles (Hill *et al.* 1982)

The number of juvenile *Scylla serrata* per transect were tested as the dependent variable in a 3-factor mixed model analysis of variance (ANOVA) using habitat (fixed factor), day/night (fixed factor) and site (random factor) as independent variables. Prior to analysis homogeneity of variance was tested using Cochran’s c-test. A multiple comparison post-hoc test was done with the Student-Newman-Keuls (SNK) method.

3. **RESULTS**

3.1. **Seagrass sampling**

3.1.1. **Vegetation**

The biomass of narrow bladed seagrass (dominated by *Thalassia hemprichii* with a small percentage of *Halodule sp.* and *Syringodium isoetifolium*) was significantly higher in the intertidal habitats compared to the subtidal habitats at all sites, and the biomass was significantly higher at Utende than at Kilole and Kichangani (Fig. 3a and 4, Appendix II). The broad bladed seagrass *Enhalus acoroides* was only found in the subtidal habitats where it dominated the biomass at two of the sites (Fig. 3b: no statistical test could be carried out on *E. acoroides* because of too many zero-values in the data). The calcium algae *Halimedea spp.* was abundant only at Utende. The highest biomass was found in the subtidal and low intertidal seagrass habitat, resulting in a significant Habitat x Site interaction effect at this site (Fig. 3c, Appendix II).
Figure 3. Mean DW biomass (g) per square meter of a) narrow bladed seagrass (dominated by *Thalassia hemprichii*) b) *Enhalus acoroides* c) *Halimeda sp.* in 4 different sampling habitats (NV = Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani) (NOTE: different scales on the y-axis) Different letters above bars indicate significantly different means at p<0.05 (SNK).

Figure 4. Pooled values from the 3 sites showing mean DW biomass (g) per square meter of narrow bladed seagrass (dominated by *Thalassia hemprichii*) in 4 different sampling habitats (SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal). Different letters above bars indicate significantly different means at p<0.05 (SNK).
3.1.2. Portunid crabs

Seven species of portunid crabs were found in the samples (see appendix I for complete species list). All species were encountered in all of the 4 habitat-types, but different species had higher abundance in different habitats. The abundance were dominated by two small portunid species, *Thalamita chaptali* and *T. Poissonii*. *Thalamita chaptali* was most abundant in high intertidal seagrass (on average 10.9 crabs m$^{-2}$), but the habitat-specific distribution varied between sites and the difference was only significant at Kilole, resulting in a significant Habitat x Site interaction effect (Appendix II, Fig. 5a). In contrast *T. Poissonii* was mainly found in the non-vegetated habitat (on average 8.5 crabs m$^{-2}$), but this pattern was only borderline significant (P=0.071; Appendix II, Fig. 5b).

The remaining species of portunids had too low abundance to be tested statistically in the ANOVA-model (Fig. 5c). Two species, *T. crostneri* and *Portunus iranjae* were only found in subtidal seagrass at Utende. *Portunus granulatus* was only encountered in unvegetated tidal pools (Appendix I). No *S. serrata* was found in any of the samples.

**Figure 5.** Mean number of Portunid crabs (+SE) per square meter of a) *Thalamita chaptali*, b) *Thalamita poissonii*, c) Remaining portunid species, in 4 different sampling habitats (NV= Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani). Different letters above bars indicate significantly different means at p<0.05 (SNK).
3.1.3. Non-portunid crabs

Fourteen taxa of non-portunid crabs were found in the samples (Appendix I). The species found most frequently throughout the samples was *Caecopilumnus hirsutus* (bristle crab). *C. Hirsutus* was only found in seagrass habitats and was most abundant in the low intertidal seagrass (on average 11.6 crabs m\(^{-2}\)). The difference was significant only at Utende and Kichangani, resulting in a significant Habitat x Site interaction effect (Appendix II, Fig. 6a).

The pooled values for the remaining species show that non-portunid crabs can be encountered in all of the 4 habitat-types. Non-portunid crabs were most abundant in the two intertidal seagrass habitats (on average 20.5 crabs m\(^{-2}\)), but the habitat-specific distribution varied between sites and the difference was only significant at Kilole, giving a significant interaction effects between Habitat and Site (Appendix II, fig. 6b). Several species of Xanthid crabs were encountered in subtidal seagrass, but only at Utende (Appendix I). The box crab (*Calappa hepatica*) was the only non-portunid crab that was only found in non-vegetated tidal pools (Appendix I).

![Graph showing the mean number of Non-portunid crabs per square meter in different habitats.](image)

**Figure 6.** Mean number of Non-portunid crabs (+SE) per square meter of a) *Caecopilumnus hirsutus* (bristle crab), b) Remaining Non-portunid species pooled, in 4 different sampling habitats (NV= Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani). Different letters above bars indicate significantly different means at p<0.05 (SNK).
3.1.4. Fish

Thirteen taxa of fish were found in the samples (appendix I). The most abundant species was *Gnatholepis sp.* (eyebar goby) and the samples were dominated by juveniles (average size 18.5 mm). *Gnatholepis sp.* was only found in samples from the intertidal zone (on average 14.0 fish m$^{-2}$), both in seagrass and non-vegetated habitats with no consistent habitat-specific distribution (Fig. 7a, Appendix II).

The remaining *Gobiidae* species showed higher abundances in the non-vegetated intertidal habitat, but the data contained too many zero-values to be tested statistically in the ANOVA-model (Fig. 7b).

The remaining fish species (non-gobiidae species) showed a high abundance in the non-vegetated habitat (on average 4.7 fish m$^{-2}$) but this trend could not be supported statistically (appendix II, fig. 8).

**Figure 7.** Mean number of Gobiidae (Gobies) (+SE) per square meter of a) *Gnatholepis sp.*, b) Remaining gobiidae species pooled, in 4 different habitats (NV= Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani) (NOTE: different scales on the y-axis). Different letters above bars indicate significantly different means at p<0.05 (SNK).
3.1.5. Remaining Crustaceans

Six taxa of hermit crabs were found in the samples (Appendix I). Hermit crabs were only found in the seagrass habitats. The highest numbers were found in the intertidal seagrass habitat (on average 3.9 hermit crabs m$^{-2}$) but the data contained too many zero-values to be tested statistically in the ANOVA-model (Fig. 9a).

Two taxa of mantis shrimp were found in the samples (Appendix I). Mantis shrimp were found in all habitats except high intertidal seagrass (Fig. 9b). No ANOVA could be performed due to low abundance in many samples.

Eight taxa of carid shrimp were found in the samples (Appendix I). Shrimp were only found in the seagrass habitats (on average 9.4 shrimp m$^{-2}$). Due to low abundances in many samples ANOVA could not be performed (Fig. 10).

Amphipods were found in all 4 habitats. The habitat-specific distribution varied between sites, but high abundances could be seen in the low intertidal and subtidal of Utende and in the low intertidal and non-vegetated intertidal of Kichangani (Appendix III, Fig. 11a).

Tanaids were most abundant in the low intertidal seagrass (on average 333.6 tanaids m$^{-2}$), but the habitat specific distribution varied between sites and the difference were only significant at Kichangani, resulting in a significant Habitat x Site interaction effect (Appendix III, Fig. 11b).

Isopods were also most abundant in the low intertidal seagrass (on average 403.6 isopods m$^{-2}$) but this pattern was only significant at Kilole, giving a significant interaction effect between habitat and site (Appendix III, Fig. 12a).

Ostracods were most abundant in the low intertidal seagrass as well (on average 12.4 ostracods m$^{-2}$) but the results were inconsistent between sites and the difference was only significant at Kichangani, resulting in a significant Habitat x Site interaction effect (Appendix III, Fig. 12b). All small crustaceans (e.g. carid shrimp, amphipods, tanaids, isopods and ostracods) showed high abundance in subtidal seagrass, but only at Utende.
**Figure 9.** Mean number of a) Hermit crabs, b) Mantis shrimp, (+SE) per square meter, in 4 different sampling habitats (NV= Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani).

**Figure 10.** Mean number of shrimp (+SE) per square meter in 4 different sampling habitats (NV= Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani).
Figure 11. Mean number of a) Amphipods, b) Tanaids, (+SE) per square meter in 4 different sampling habitats (NV= Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani) (NOTE: different scales on the y-axis). Different letters above bars indicate significantly different means at p<0.05 (SNK).

Figure 12. Mean number of a) Isopods, b) Ostracods, (+SE) per square meter, in 4 different sampling habitats (NV= Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani) (NOTE: different scales on the y-axis). Different letters above bars indicate significantly different means at p<0.05 (SNK).
3.1.6. Mollusca

Bivalves were found in all sample habitats. One important species for artisanal fishery, the pen shell (*Pinna muricata*) was only found in seagrass habitats (on average 7.3 pen shells m$^{-2}$) and was most abundant in the intertidal zone (Fig. 13). This result was supported by observations made during sampling, were *P. muricata* was observed in larger numbers at the intertidal habitats compared to the subtidal, but this observation could not be supported statistically due to high variance (Appendix III).

The remaining species of bivalves were found in all habitats, but significantly higher numbers were found in the low intertidal and subtidal seagrass habitats (on average 38.7 bivalves m$^{-2}$) in comparison with the other habitats, and this pattern was consistent between sites (Appendix III, Fig. 14).

Gastropods were found in all sample habitats, but showed significantly higher abundance in the 3 seagrass habitats (on average 174.5 gastropods m$^{-2}$) in comparison with the unvegetated habitats at all sites (Appendix II, Fig. 15a).

Nudibranchs were only found in the low intertidal and subtidal seagrass habitats and the abundance was significantly higher in the subtidal seagrass habitat (on average 9.4 nudibranchs m$^{-2}$) in comparison with the other habitats at all sites (Appendix III, Fig. 15b).

![Figure 13. Mean numbers of *Pinna muricata* (+SE) per square meter, in 4 different sampling habitats (NV= Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani). Different letters above bars indicate significantly different means at p<0.05 (SNK).](image-url)
Figure 14. Pooled values from the 3 sites showing mean numbers of Bivalves (remaining species pooled) (+SE) per square meter, in 4 different sampling habitats (NV = Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal). Different letters above bars indicate significantly different means at p<0.05 (SNK).

Figure 15. Pooled value from the 3 sites showing mean number of a) Gastropods, b) Nudibranches, (+SE) per square meter in 4 different sampling habitats (NV = Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) (NOTE: different scales on the y-axis). Different letters above bars indicate significantly different means at p<0.05 (SNK).
3.1.7. Ophiuroidea

The highest numbers of ophiuroids were found in the low or high intertidal seagrass habitats (on average 70.5 ophiuroids m\(^{-2}\)) giving a significant interaction effect between Habitat and Site (Appendix III, Fig. 16). This result was supported by observations done during sampling, where more ophiuroids were observed in the intertidal compared to the subtidal.

![Figure 16. Mean number of Ophiuroids (+SE) per square meter in 4 different sampling habitats (NV = Non-vegetated intertidal, SHI = Seagrass high intertidal, SLI = Seagrass low intertidal, SS = seagrass subtidal) at 3 different sites (Utende, Kilole and Kichangani) Different letters above bars indicate significantly different means at p<0.05 (SNK).](image)

3.2. Mangrove sampling

3.2.1. Pilot study in Utende

The most abundant species during the day-sampling at two mangrove habitats (Inner mangrove and fringe) at Utende were the grapsid crab *Pachygrapsus minutus*, small ocypodid crabs and one small unidentified brachiuran crab (Appendix I). *P. minutus* was the only crab in abundant numbers that were exclusively found in the mangrove sampling. Higher abundances and diversity of crabs were found at the mangrove fringe compared to the inner mangrove (Appendix I). No portunid species except for low abundances of *Thalamita spp.* in the mangrove fringe were found in these samples.

3.2.2. Transect sampling of juvenile *S. serrata*

The results from the transect sampling of juvenile *Scylla serrata* showed a significant difference in their abundance between day and night, inner mangrove and the fringe, and between sites, resulting in a significant 3-way interaction effect (F= 158.8, df = 3,14, P = 0.001). No *S. serrata* were found during the day-transects in any of the sites, this data has therefore been excluded from the graph (Fig. 17). An average of 2.9 crabs were found per transect at night. Significantly higher numbers of juvenile *S. serrata* were found in the inner mangrove (on average 5.7 crabs per transect) compared to the mangrove fringe (on average 0.6 crabs per transect) in 3 of the 4 sites (in Kichangani, only one adult *S. serrata*
were found during night transect in the mangrove fringe; Fig. 17). A significantly higher number of crabs were found at the MIMP site compared to the other 3 sites (significance not shown in the graph).

A higher number of small juvenile *S. serrata* were found in the inner mangrove compared to the fringe (Fig. 18). The mean size of *S. serrata* found in the inner mangrove and mangrove fringe was 32 mm and 68 mm carapace width (CW) respectively. The smallest crab collected was 4 mm (Fig. 19).

![Figure 17](image1.png)

**Figure 17.** Mean number of juvenile *S. serrata* (+SE) per transect collected at night in 2 different habitats (MI = Mangrove inner, MF = Mangrove fringe) at 4 different sites (Utende, Kilole, Kichangani and MIMP). Different letters above bars indicate significantly different means at p<0.05 (SNK).

![Figure 18](image2.png)

**Figure 18.** Pooled numbers of *S. serrata* found during 9 night transects in a predefined set of size-classes (CW in mm). (MI = mangrove inner, MF = Mangrove fringe). Crabs < 100mm are considered as being juveniles.
4. DISCUSSION

4.1. Nursery habitat for juvenile mud crabs

Juvenile *Scylla serrata* were only found in the mangrove habitat, and only at night. As far as we know from literature, this is the first time that the nursery habitat for young, newly settled *S. serrata* has been identified. The nursery habitat has never been described in East Africa before and only larger juveniles have been found on a tidal flat in Australia (Hill et al. 1982). The smallest crab found during the study was 4 mm CW. This is the approximate size of a newly settled and metamorphosed *S. serrata* (Holme et al. 2006), and the smallest crab ever recorded in the wild at the coast of East Africa. This knowledge is important because it provides an argument to the importance of protecting the mangrove back-flats and fringe, which are often a target for exploitation. This knowledge also makes it possible to collect juveniles with little effort for grow-out aquaculture.

The nursery habitat for *S. serrata* is not a nursery in conventional sense. The crabs only seem to use it at night. As far as we know from literature, this behavior has not been observed in juvenile mud crabs before. It is possible that the crabs migrate up from subtidal habitats and into the mangrove with the rising tide at night and accumulate here. It could be to feed (Hill et al. 1984) within the mangrove when they are not seen by visual predators on land, like birds and when they are not exposed to the heat from the sun. This migration into the mangrove could also be to avoid predators in the subtidal at night, like nocturnal predatory fish (many species of fish and cuttlefish were observed in the mangrove when the water was still 20-40 cm deep). The young juvenile crabs (average CW 32 mm) seemed to stay in the inner mangrove at night, even when the tide had reseeded completely, as they were found moving about in the small tidal pools that were created at low tide. However, no juvenile crabs were found in the pools the following morning, or at the mangrove fringe despite extensive sampling under leaves and roots and in the sediment. This result is not consistent with a study in Australia where larger juvenile *S. serrata* (20 to 99 mm CW) were found in the mangrove zone during the day at low tide, under rocks and taproots (Hill et al. 1982). In Kenya juvenile *S. serrata* (15-100 mm CW) were found in the mangrove fringe also during the day (pers. com. D. Mirera). Studies on another species of the same genus (*Scylla paramamosain*) also showed that newly metamorphosed juveniles could be found in the mangrove fringe during the day (Walton ME et al. 2006). The transient behavior of juvenile mud crabs found in the present study may be an adaptation to local physical or biological conditions. It is possible that this area gets too hot during the day and that the juveniles migrate back out with the next high tide that comes in before dawn. This

![Figure 19. Juvenile *S. serrata* (4 mm CW) found during night at MIMP (Mangrove inner).](image)
behavior could be related to the fact that small juveniles are not able to dig burrows that can protect them against dehydration and bird predation during the day. In a study on Mafia Island in 2002 the smallest crab collected from a burrow was 70 mm CW (Barnes et al. 2002). In the present study, larger burrows were not examined during sampling but it is possible that larger juveniles could have been present in burrows during the day.

If the juvenile crabs migrate out during the day, how come we could not detect them in our samples from the intertidal and subtidal? It is possible that the area that we sampled was too small. There are extensive areas covered with seagrass inside Chole bay and the total area that we sampled for crabs in the intertidal and subtidal was only 5.76 m$^2$, which is not much compared to the total area available for them. The back-flat and fringe that were sampled was only about 10 m wide, but the intertidal flat could be as wide as 400 m, and the subtidal comprised an even larger area. This means that the crabs accumulate in a smaller area if they migrate into the mangroves at night, which makes it easier to detect them here compared to when they are spread out on the intertidal flat. More samples and possible also deeper ones (including the *Thalassodendron* seagrass meadows) could have been necessary to detect them.

That the crabs were not detected in any of the samples from the intertidal and subtidal seagrass habitats does not mean that these areas of seagrass are unimportant as nurseries for the juvenile *S. serrata*. It might just means that the crabs are not limited by the amount of seagrass and that they are therefore scattered over a larger area. Seagrass could still be an important nursery habitat that stands for the highest production of the adults in the area (Dahlgrean CP 2006) and it has been seen that the mud crab do feed in seagrass areas adjacent to the mangroves (Demopoulos et al. 2008).

Higher abundances of juvenile mud crabs were found in the inner mangrove compared to the fringe. This means that the inner mangrove back-flats in particular are important to protect against exploitation. Crabs found in the inner mangrove also seemed to be smaller than the crabs in the fringe (32 and 68 mm CW respectively; fig. 18). It could be that the larger crabs avoid the more shallow parts and puddles that were created at low tide in the inner mangrove. Possibly because they are more exposed here or because they find more prey to feed on amongst the tap roots of the fringe, were the water still was about 10-20 cm deep during transect-sampling. When the tide had reseeded completely inside the mangrove no larger crabs (> 60 mm CW) were observed here and this supports the theory that subadults migrate into the intertidal zone to feed at high tide and retreat during low tide (Hill et al. 1982). The smaller juveniles on the other hand are not as exposed in the puddles at low tide and it might be favorable to them to remain inside the mangroves at low tide where they are protected from the predators (e.g. fish, cuttlefish) observed where the water level was still around 20 to 40 cm.

There was a great spatial variation in the abundance of crabs between the different sites, with significantly more at the MIMP site. This is hard to explain and could be due to many factors. One explanation could be effects of the spring and neap tide (i.e. higher settlement of crab larvae and movement of juveniles during the stronger tidal currents at spring tide), since the low abundance of crabs at Kichangani was sampled at neap tide. However, this spatial difference appear not to be an effect of the tides since large amounts of *S. serrata* were found (the size of 5-14 mm) at MIMP during the same 2-day period. At MIMP juvenile *S. serrata* were found continuously throughout the study even though the numbers varied from one day to another. This might be due to a higher larval supply and the strong currents at this site. The factors which influence the difference in abundance between sites needs to be investigated more in order to find the optimal spots and the best time for collection of crabs for grow-out aquaculture.
4.2. Implications for Aquaculture

These results have important implications for aquaculture of mud crabs and the collection of seed crabs. The present study demonstrates that up to 30 juvenile crabs (4-45 mm CW; mean size 32.0 mm CW) could be collected by two people at the mangrove back-flat in approximately one hour. This number is almost 10 times as high as the cpue (catch per unit effort) of adult crabs (3.79 crabs h⁻²; mean size 124.7 mm CW) collected at the mangrove fringe of Utende (Barnes et al. 2002). This means that it would be more effective to collect juvenile crabs instead of subadults for aquaculture.

Moreover, a concurrent field study of predation mortality in juvenile mud crabs suggests that using small juvenile mud crabs as seed-crabs in aquaculture may be more sustainable. This tethering study conducted at the same time and locations as the present study at the mangrove fringe and in the subtidal seagrass showed that the predation mortality of juvenile *S. serrata* increased as the size of the crabs decreased, from below detection for crabs > 72 mm CW up to above 70% for crabs below 12 mm CW (Fig. 20; from Palmqvist 2009). Even though tethering-studies may not provide absolute estimates of predation mortality, due to for example alterations in the crab’s natural behavior, it can give good data on the relative predation rates on for example different size-classes of crabs (Aronson et al. 2001). According to the tethering results, the natural mortality from predation is 8 to 16 times higher for juveniles in the 6-24 mm size range compared to the 37-87 mm size range. The present crab-fattening in East Africa use seed-crabs of 120-140 mm CW (Mahika et al. 2005), suggesting that the natural mortality of the seed crabs are > 10 times lower than the predation mortality of the small juvenile crabs found in the mangrove back-flats in the present study. The high predation mortality for the smallest size classes indicated in the tethering study suggests that natural mortality may be higher than the mortality in grow-out farms. The collection of this size for grow-out farms would therefore minimize the impact on the natural population of mud crabs in the area, and have a much larger potential to be sustainable than the present crab-fattening activities.

It will be important to do follow-up studies for a better understanding of the factors that control variations in the abundance of juvenile mud crabs (e.g. larval recruitment) in the area and furthermore to get a better estimate on the population size of mud crabs around the Island. This understanding is critical for the success of these grow-out farms, since the fishermen needs to benefit from the collection of juveniles instead of adult crabs.

![Figure 20. Predation mortality in % per 24 hours (+SE) in 4 different size-classes (A = 72-87, B = 37-62, C = 11-24, D = 6-12 mm CW) Different letters above bars indicate significantly different means at p<0.05 (SNK) (Palmqvist 2009).](image-url)
4.3. Intertidal seagrass community

Despite the fact that no juvenile *Scylla serrata* were found during the seagrass sampling, a rich faunal community were found in these intertidal habitats at low tide. The abundance of mobile epibenthic species is poorly studied in these areas at low tide and most studies focus on the fish community in these seagrass habitats at high tide. A total of 46 taxa of mobile epibenthic animals were found in vegetated and unvegetated tidal pools at low tide, indicating that the intertidal mud flats constitute an important "permanent" habitat for small epibenthos, and a critical habitat for the biodiversity in shallow soft-sediment communities in East Africa. The abundance of animals per square meter in the low intertidal seagrass habitats was more than double that of the subtidal seagrass, even though the diversity was quite similar between the two habitats, suggesting that intertidal seagrass might be a more important habitat than subtidal seagrass for small epibenthic animals. The seagrass habitats of the intertidal seemed to have an important role, displaying an overall higher abundance and diversity of animals in comparison with the unvegetated intertidal. The distribution of animals were not random amongst the sampling habitats, but appeared to be affected by both biological and physical factors.

The presence of seagrass appears increase the diversity of many animal groups in the intertidal zone. The intertidal seagrass had a higher diversity of species compared to the unvegetated intertidal and the total abundance of animals in the seagrass was more than twice that of the unvegetated intertidal (1090 and 470 animals m$^{-2}$ respectively). Consequently, seagrass seem to be important for the production and diversity of many (but not all) animal groups. Some animal groups that clearly seem to benefit from the presence of seagrass were small crustaceans (shrimp, paguroids, isopods, tanaids, ostracods and some species of crab), prosobranchian gastropods, bivalves and ophiuroids. Seagrass protects the animals from direct exposure to the sun and prevent water from evaporating as quickly in these tidal pools at low tide. The seagrass could also work as a protection against predators on land. This could explain the low numbers of *Pinna muricata* found in the unvegetated habitat. These bivalves are sessile, and if they are not covered by seagrass they are more frequently spotted by shorebirds (or humans). Structurally complex habitat like seagrass can also work as a refuge from predation, which might explain why higher abundances of small crustaceans (isopds, tanaids, ostracods and shrimp) were found in the intertidal seagrass compared to the unvegetated intertidal. At the intertidal of Utende, high biomasses of the calcium algae *Halimeda sp.* were found amongst the seagrass. This alga, which looks like a tangled mass, constitutes a complex habitat and could explain the high abundances of some small crustaceans (shrimp, isopods and paguroids) found at this site. Differences in the biomass of algae, such as *Halimeda sp.* might be responsible for some of the spatial variations found between sites. Another benefit of residing in the vegetated intertidal would be that more food is available. Animals that feed on epiphytes would surely benefit from staying in an area with seagrass. This could explain why higher abundances of gastropods were found in seagrass. Furthermore, hydrodynamics of seagrass leads to a higher accumulation of organic material in these tidal pools compared to the unvegetated. Consequently, deposit feeders, such as ostracods, tanaids, isopods, paguroids, some species of bivalves and crabs benefit from inhabiting these habitats. The high supply of organic material amongst the seagrass is also beneficial for passive suspension feeders such as ophiuroids and filter feeders such as *Pinna muricata* and some species of shrimp. Seagrass is also an important settling habitat for juvenile bivalves (Bologna and Heck 2000), which may explain the high abundances found in these habitats.
Intertidal pools without vegetation are also important habitats for mobile epifauna and contained an unexpectedly rich diversity of animals. The highest abundance and diversity of fish were found in these habitats, and many of the fish species were exclusive to this habitat. Gobiid species, such as Gnatholepis sp. were found throughout the intertidal but were most abundant in the unvegetated intertidal and the majority of the animals were juveniles. Other species, found exclusively at the unvegetated intertidal was the burrowing crab Calappa hepatica and the portunid crab Portunus granulatus. Also, the highest abundances of the portunid crab Thalamita poissoni came from samples in the unvegetated habitat. The only small crustacean found in abundant numbers in the unvegetated intertidal was amphipods. The advantage of staying in the intertidal at low tide may be that you better avoid predators, like fish, in the subtidal. However, to reside in the unvegetated habitat means that you are more exposed to predators on land and to the sun. Burrowing crabs such as C. hepatica and burrowing amphipods can escape direct exposure to the sun and it is possible that they prefer to stay in tidal pools without vegetation because the rhizomes from the seagrass make the sediment more difficult to dig in. During sampling of the unvegetated habitat in Kichangani, T. poissoni was observed lying buried just under the surface of the sandy sediment. The colour of the crab closely resembled that of the sediment, making it hard to detect even when it was not buried. Adults of the fish species Gnatholepis sp. prefer to live in sandy areas (Richmond 1997) and it might be that the juveniles prefer a similar habitat, avoiding the seagrass habitats. The juveniles are also quite transparent and well camouflaged against the sand in these unvegetated tidal pools, which might explain how they escape predation by birds. The reason that a lower abundance of fish were found in the vegetated intertidal could be that they are disfavoured by some other factor in these habitats, for example predation by crabs or juvenile predatory fish like moray eels, which were observed during sampling.

The physical stress of the high intertidal seems to affect the abundance and diversity of animals in a negative way. The abundance of animals in the high intertidal seagrass was > 6 times lower than the abundance found in the low intertidal seagrass. The high intertidal is exposed during low tide for a longer period of time than the low intertidal. This means that animals here need to be able to cope with higher temperatures, higher salinities and the risk of dehydration (during sampling, a water temperature of 42°C was measured in a pool situated high up on the tidal flat). Certain taxa, including gastropods, some species of burrowing crabs and hermit crabs were found in higher abundance in the high intertidal seagrass compared to the low intertidal seagrass. Gastropods and hermit crabs have a protective shell that reduces the risk of dehydration. The portunid crab T. chaptali and one unidentified ocypod crab were abundant in samples from the high intertidal. These species can burrow in the sediment, which could explain how they can survive in this habitat. Another reasons behind the high abundance of certain taxa might be that these animals are euryhaline and adapted to living in fluctuating salinities. If the animal is able to cope under conditions like this, they benefit from not having to compete for space and food in the same way as in the low intertidal. The abundance of ophiuroids and small crustaceans (amphipods, isopods, tanaids, ostracods and shrimp) decline as you move from low to high intertidal. These animals lack a protective shell and might be more vulnerable to high water temperatures, fluctuating salinities and dehydration. The abundance of bivalves were also lower in the high intertidal compared to the low intertidal seagrass. Despite the fact that the mussels are able to close their shell and survive during times of exposure at low tide, many of them are sessile or have a restricted capability to move. This means that they might not survive in the high intertidal for a longer period of time without water, for example during spring low tide. We did not identify the mussels down to species level, but burrowing
species of mussels, that are able to escape direct sun exposure, might survive better in these high intertidal habitats. It is also possible that bivalves and other animals in the high intertidal are subjected to a higher predation pressure from birds compared to animals in the low intertidal.

The highest diversity of species and the highest abundance of animals per square meter were found in the low intertidal seagrass. The abundance of most animals groups was more than twice as high in the low intertidal seagrass compared to samples from the subtidal seagrass. Animal groups with noticeably higher abundance in this habitat were small crustaceans (amphipods, isopods, tanaids and ostracod), Pinna muricata, remaining bivalves and ophiuroids. The reason behind this high diversity and abundance could be that the low intertidal seagrass has the most optimal conditions for the majority of animals. Animals that reside in these habitats escape predation by fish in the subtidal and they are subjected to less physical stress and bird predation compared to animals that live high up on the intertidal. The seagrass protects them against exposure to the sun and can work as a refuge from predation. Furthermore, the low intertidal is not exposed during low tide for as long as the high intertidal and when the tide comes in, the current brings new food particles into these habitats. This inflow of food during high tide may be particularly important for ophiuroids that are passive suspension feeders. Ophiuroids and the pen shell (Pinna muricata) were found in abundant numbers in seagrass from the low intertidal but were almost absent from the subtidal. Consequently, there seem to be some factor that prevents them from surviving in the subtidal. Large schools of fish were observed during sampling of the subtidal and it is possible that the low abundance is a result from a high predation pressure by fish in these areas. This could also explain the low abundances of small crustaceans found in seagrass samples from the subtidal. Although seagrass in the subtidal might be an important settling habitat for juvenile bivalves, it is possible that many bivalves are eaten before they reach adult size.

Only a few species seem to benefit from residing in subtidal seagrass. Animal groups that were found in higher abundances in the subtidal were nudibranches, and some groups of small crustaceans. Nudibranches are sensitive to dehydration, which makes them less adapted to living on the intertidal flat. However, since many species contain toxins they might be able to avoid predation in the subtidal. Smaller crustaceans such as shrimp may find a refuge from predation amongst the seagrass and calcium algae in the subtidal.

The sampling technique of the subtidal failed to include larger fish species, and this technique might not be optimal since animals may have escaped when the frame was tilted. A better way of doing this sampling could have been to use a suction sampler. More replicates, and a larger area of the cylinder-sampler would also have been preferable to get a better estimate and a more representative picture of the difference in taxa and abundance of animals between the sampling habitats. This might also have reduced the spatial differences between sites.

Only a small number of comparable studies in seagrass environment have been performed in East Africa (de Boer and Prins 2002, Eklöf 2005). The results from the present study showed that Thalassia hemprichii was the dominating seagrass species in the intertidal and Enhalus acoroides in the subtidal. The biomass of T. hemprichii in the low intertidal seagrass was similar to the biomass found in a study by Eklöf et al. on Zanzibar in 2005 (approx. 80 g m^{-2}), but the biomass of E. acoroides was greater in the present study (approx. 230 g m^{-2} compared to 100 g m^{-2}). Eklöf found higher abundances of animals per square meter in these seagrass habitats compared to the present study, but the results are not
fully comparable due to the use of a smaller mesh-size in the former. However the most abundant taxonomical group of the present study was crustaceans (40 taxa), which corresponds to the results obtained in the Zanzibar study. In the present study, the greatest number of animals per square meter was found in the low intertidal seagrass habitat (appendix I) of Utende. This site was the only one in which high biomasses of *Halimeda sp.* was found in the intertidal, and there have been indications from other studies that this calcium alga may function as a nursery for many species and also as a refuge from predation (Jinendradasa and Ekaratne 2000) which could potentially explain the high abundances of animals in these samples.

Even though the results varies between sites and does not include larger fish species in the subtidal, they still gives a fairly good picture of what animals can be found at the intertidal zone during low tide. The result demonstrates the importance of these habitats for many species of animals and also their importance as nurseries. In addition, these areas could also house species that are important as a food source for many species of fish at high tide, as well as for mud crabs (de Boer and Prins 2002, Demopoulos *et al.* 2008).

4.4. Conclusion

Juvenile *Scylla serrata* were found in the mangrove back-flats or inner mangrove at night during low/reseeding tide, were they could easily be collected by hand or by using nets. These results may facilitate the development of small-scale, grow-out aquacultures of mud crabs in East Africa.

The results from the intertidal seagrass sampling demonstrates a rich faunal community that utilize these habitats at low tide. The highest abundance and diversity of animals were found in the low intertidal seagrass habitat. The results state the importance of these habitats for many species of animals and also their importance as nurseries.

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Appendix

Appendix I. Species list – Seagrass/mangrove sampling. Mean number of animals per square meter in 6 sampling habitats: SS = subtidal seagrass, SLI = seagrass low intertidal, SHI = seagrass high intertidal, NV = non-vegetated intertidal, MF = mangrove fringe, MI = mangrove inner (Picture demonstrating the position of the sampling habitats on the tidal flat).

(n=15 for SHI, SLI, NV and SS, n=5 for MI and MF)

<table>
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<th></th>
<th>SS</th>
<th>SLI</th>
<th>SHI</th>
<th>NV</th>
<th>MF</th>
<th>MI</th>
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<td>1904.2</td>
<td>275.4</td>
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<td>147.7</td>
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<td>30</td>
<td>20</td>
<td>23</td>
<td>11</td>
<td>6</td>
</tr>
</tbody>
</table>

**Crustacea**

**Order: Decapoda**

**Infraorder: Brachiura**

**Family: Portunidae**

*Portunus granulatus* - - - 2.3 - -
*Portunus iranjae* 0.5 - - - - -
*Thalamita bouvieri* 1.1 1.6 - - - -
*Thalamita chaptali* 1.1 0.8 10.9 3.1 1.4 -
*Thalamita crosnieri cf.* 1.1 - - - - -
*Thalamita poissonii* 0.6 2.3 0.8 8.5 2.8 -
*Thalamita prymna* - - - - 1.4 -

**Family: Ocypodidae**

*Macrophthalmus boscii cf.* - - 0.8 - 1.4 -
*Uca sp.* - - - - 1.4 -
*Unidentified ocypod crab cf.* - 11.6 13.2 0.8 13.8 -

**Family: Calappidae**

*Calappa hepatica* - - - 3.9 - -
Appendix I (continued)

<table>
<thead>
<tr>
<th>Family: Grapsidae</th>
<th>SS</th>
<th>SLI</th>
<th>SHI</th>
<th>NV</th>
<th>MF</th>
<th>MI</th>
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<tr>
<td><em>Pachygrapsus minutus</em> cf.</td>
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<td>24.8</td>
<td>9.6</td>
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<tr>
<td>unidentified grapsid crab A</td>
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<td>unidentified grapsid crab B</td>
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<tr>
<td>unidentified grapsid crab C</td>
<td>-</td>
<td>0.8</td>
<td>-</td>
<td>0.8</td>
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**Family: Pilumnidae**

*Caecopilumnus hirsutus* 1.1 11.6 2.3 - - -

**Family: Leucosiidae**

*Ebalia sp.* - 0.8 - - - -

**Family: Parthenopidae**

unidentified parthenopid crab A - 2.3 - - - -
unidentified parthenopid crab B 1.6 1.6 - - - -

**Family: Xanthidae**

unidentified xanthid crab A 4.2 4.7 - - - -
unidentified xanthid crab B 0.5 - - - - -
unidentified xanthid crab C 0.5 - - - - -
unidentified xanthid crab D - - 5.4 4.7 20.7 -

unidentified brachyuran crab A - - - 3.9 77.2 2.8
unidentified brachyuran crab B - - - 0.8 - -

**Infraorder: Anomura**

**Superfamily: Paguroidea**

*Clibanarius donai* cf. - - 0.8 - - -
unidentified paguroid A - 2.3 - - - -
unidentified paguroid B - 0.8 - - - -
unidentified paguroid C 0.5 - - - - -
unidentified paguroid D - - 0.8 - - -
unidentified paguroid E - - 0.8 - - -

**Infraorder: Caridea**

**Family: Alpheidae**

*Alpheus lobidens* 2.1 3.1 - - - -
*Alpheus longecarinatus* - 7.0 - - - -
*Alpheopsis equalis* 1.1 - - - - -

**Family: Hippolytidae**

*Hippolytidae sp.* - - - - - 1.4

**Family: Palaemonidae**

*Leander tenuicornis* - 0.8 - - - -
*Periclimenes andamanensis* 1.6 - - - - -

**Family: Processidae**

*Nikoides danae* 2.1 8.5 0.8 - - -

unidentified Thalassinid - - 1.3 - - -
## Appendix I (continued)

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>SLI</th>
<th>SHI</th>
<th>NV</th>
<th>MF</th>
<th>MI</th>
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<tr>
<td><strong>Order: Stomatopoda</strong></td>
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<td><strong>Family: Pseudosquillidae</strong></td>
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<td><em>Pseudosquilla ciliata</em></td>
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<td><strong>Family: Squillidae</strong></td>
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<tr>
<td><em>Squillidae spp.</em></td>
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<tr>
<td><strong>Order: Amphipoda</strong></td>
<td>344.2</td>
<td>821.4</td>
<td>72.9</td>
<td>298.1</td>
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<td><strong>Order: Isopoda</strong></td>
<td>153.7</td>
<td>460.8</td>
<td>5.3</td>
<td>4.2</td>
<td>-</td>
<td>-</td>
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<tr>
<td><strong>Order: Tanaidacea</strong></td>
<td>132.8</td>
<td>353.1</td>
<td>27.5</td>
<td>1.1</td>
<td>-</td>
<td>-</td>
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<tr>
<td><strong>Class: Ostracoda</strong></td>
<td>5.6</td>
<td>12.4</td>
<td>-</td>
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<td>-</td>
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</tbody>
</table>

**Chordata**

|                |      |      |      |      |     |     |
| **Order: Perciformes** |    |      |      |      |     |     |
| **Family: Gobiidae** |    |      |      |      |     |     |
| *Gnatholepis sp.* | -    | 12.4 | 11.6 | 17.8 | 1.4 | -   |
| Unidentified juvenile Gobiid A | - | - | - | - | 1.4 | - |
| Unidentified juvenile Gobiid B | - | 0.8 | 85.3 | - | - | - |
| Unidentified juvenile Gobiid C | - | - | - | 16.3 | - | - |
| **Family: Microdesmidae** |    |      |      |      |     |     |
| *Ptereleotris helenae cf LF* | - | - | - | 1.6 | - | - |
| unidentified perciform fish A | - | - | - | - | - | 2.8 |
| unidentified perciform fish B | - | - | - | 0.8 | - | - |
| unidentified perciform fish C | 0.5 | - | - | 2.3 | - | - |
| unidentified perciform fish D | - | 0.8 | - | - | - | - |
| unidentified perciform fish E | - | - | - | 0.8 | - | - |
| unidentified perciform fish F | - | - | - | 4.7 | - | - |

|                |      |      |      |      |     |     |
| **Order: Scorpaeniformes** |    |      |      |      |     |     |
| **Family: Scorpaenidae** |    |      |      |      |     |     |
| unidentified juvenile scorpionfish | - | 1.6 | - | - | - | - |
| **Order: Tetraodontiformes** |    |      |      |      |     |     |
| **Family: Tetraodontidae** |    |      |      |      |     |     |
| unidentified juvenile pufferfish | - | 0.8 | - | - | - | - |

**Mollusca**

|                |      |      |      |      |     |     |
| **Class: Gastropoda** |    |      |      |      |     |     |
| Nudibranchia spp. | 10.8 | 3.2 | - | - | - | - |
| gastropoda spp. | 27.4 | 29.6 | 42.4 | 2.1 | - | - |
| **Class: Bivalvia** |    |      |      |      |     |     |
| *Pinna muricata* | 0.7  | 12.7 | 8.5 | - | - | - |
| Bivalvia spp. | 31.7 | 54.7 | 10.6 | 4.2 | - | - |

**Echinodermata**

|                |      |      |      |      |     |     |
| **Class: Ophiuroidea** |    |      |      |      |     |     |
| *Ophiuroidea* | 3.6  | 77.2 | 58.1 | - | - | - |
Appendix II. Factorial analysis of variance – Seagrass sampling. Dominant species and groups of epifauna tested separately as dependant variables in a 2-factor mixed-model ANOVA using habitat (fixed factor) and site (random factor) as independent variables. (df = 3,2,6,47)

<table>
<thead>
<tr>
<th>Variables</th>
<th>Habitat</th>
<th>Site</th>
<th>Habitat*Site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
</tr>
<tr>
<td>Portunid crabs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Thalamita chaptali</em></td>
<td>1.72</td>
<td>0.261</td>
<td>2.41</td>
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<td><em>Thalamita poissonii</em></td>
<td>2.51</td>
<td>0.071</td>
<td>1.81</td>
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<tr>
<td>Non-portunid crabs</td>
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<tr>
<td><em>Caecopilumnus hirsutus</em></td>
<td>6.34</td>
<td>0.001</td>
<td>3.68</td>
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<tr>
<td>Remaining crabs</td>
<td>1.49</td>
<td>0.230</td>
<td>0.58</td>
</tr>
<tr>
<td>Fish</td>
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<td></td>
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<tr>
<td><em>Gnatholepis sp.</em></td>
<td>3.00</td>
<td>0.040</td>
<td>2.03</td>
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<tr>
<td>Remaining fish</td>
<td>2.30</td>
<td>0.090</td>
<td>2.79</td>
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</tbody>
</table>

* sqrt(sqrt(x))-transformed to meet the assumption of homogenous variance.

Appendix III. Factorial analysis of variance - Seagrass sampling. Dominant species and groups of epifauna tested separately as dependant variables in a 2-factor mixed-model ANOVA using habitat (fixed factor) and site (random factor) as independent variables. (df = 3,2,6,32)

<table>
<thead>
<tr>
<th>Variables</th>
<th>Habitat</th>
<th>Site</th>
<th>Habitat*Site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
</tr>
<tr>
<td>Bivalvia</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Pinna muricata</em></td>
<td>1.59</td>
<td>0.211</td>
<td>0.96</td>
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<tr>
<td>Remaining bivalve</td>
<td>7.08</td>
<td>0.0009</td>
<td>8.35</td>
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<tr>
<td>Ophiuroidea</td>
<td>38.99</td>
<td>&lt;0.0001</td>
<td>5.46</td>
</tr>
<tr>
<td>Nudibranchia</td>
<td>4.92</td>
<td>0.006</td>
<td>0.84</td>
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<tr>
<td>Gastropoda</td>
<td>5.01</td>
<td>0.006</td>
<td>5.72</td>
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<tr>
<td>Amphipoda</td>
<td>9.24</td>
<td>0.0002</td>
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<td>Isopoda</td>
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<td>Tanaida</td>
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<tr>
<td><em>Halimeda spp.</em></td>
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</tbody>
</table>

sqrt(x)-transformed, *sqrt(sqrt(x))-transformed to meet the assumption of homogenous variance.
REFERENCES


