

**Capture-based mud crab (*Scylla serrata*)
aquaculture and artisanal fishery in East Africa
– Practical and ecological perspectives**

Linnaeus University Dissertations

No 159/2014

CAPTURE-BASED MUD CRAB (*SCYLLA
SERRATA*) AQUACULTURE AND
ARTISANAL FISHERY IN EAST AFRICA
– PRACTICAL AND ECOLOGICAL
PERSPECTIVES

DAVID OERSTED MIRERA

LINNAEUS UNIVERSITY PRESS

Capture-based mud crab (*Scylla serrata*) aquaculture and artisanal fishery in East Africa – Practical and ecological perspectives

Doctoral dissertation, Department of Biology and Environmental Science, Linnaeus University, Kalmar, Sweden, 2013

ISBN: 978-91-87427-70-1

Published by: Linnaeus University Press, S-351 95 Växjö

Printed by: Elanders Sverige AB, 2013

Abstract

David Oersted, Mirera (2014). *Capture-based mud crab (Scylla serrata) aquaculture and artisanal fishery in East Africa – Practical and ecological perspective*. Linnaeus University Dissertations No 159/2013, ISBN: 978-91-87427-70-1. Written in English.

Mud crab *Scylla serrata* is a crustacean that spends most of its life cycle in the mangrove environment throughout its range. Fishery and aquaculture of this crab are significant economic activities in coastal areas in the tropics and sub-tropics because of the meat quality and nutritional value. However there is a significant shortage of information on the ecology, fishery and aquaculture of these crabs in sub-Saharan Africa. This impacts the development of a sustainable aquaculture and fishery for the benefit of coastal communities. The present study analyses various aspects of mud crab ecology, fishery, aquaculture and social economics in East Africa using multidisciplinary approaches. The results are given in seven papers based on field and laboratory studies.

The study established for the first time that high intertidal mangrove back-flats constitute a key habitat for the earliest instars of *S. serrata* (4–30 mm CW). It also showed that diurnal tidal migration behaviour occurs in small juveniles that migrate to sub-tidal habitats during the day, possibly due to variable predation risks. Monthly sampling of juveniles in Kenya and Tanzania indicated continuous recruitment throughout the year. The large numbers of juvenile crabs along mangrove fringes indicate that these habitats could serve as sites suitable for collection of juvenile crabs for aquaculture. However, these areas must also be managed and protected to support the recruitment to the wild crab populations.

An assessment of the crab fishery indicated that artisanal crab fishers possess significant traditional knowledge mainly inherited from their parents that enabled them to exploit the resource. Such knowledge could be useful for the development of the aquaculture and in management of the fishery. Mud crab fishing was found to be a male dominated activity, and fishers on foot practiced fishing in burrows at spring low tides. Interviews indicated that the average size of marketable crabs has declined over the years and a weak management system was observed with most fishers operating without a license. Due to the knowledge required regarding the local conditions, fishers are unable to shift to new areas. Furthermore fishers could not fish at neap tides. Such limitations provide a “natural closure” of the fishery. Also foot fishers cover fairly limited distances in their daily operations, an aspect that can be utilized to effect site-specific management for the fishery if necessary.

Laboratory and field experiments indicated that cannibalistic interactions are heavily influenced both by size differences of crabs and the availability of shelter but no significant effect was found for different stocking densities. Such information is of direct importance for crab farmers in East Africa, where seed from the wild are of multiple sizes and there is a need to grade juvenile crabs and provide shelter at stocking to ensure maximum survival. Experimental studies in earthen pond and mangrove pen cultures indicated high mortality rates. Comparing growth in earthen pond and mangrove pen systems indicated that growth rates were generally high in both systems, but significantly lower in pen systems without shelter, suggesting that shelter may have a stronger effect on growth than has been previously thought.

Similar to artisanal mud crab fishery, an assessment of small-scale mud crab farming by organized community groups in Kenya indicated low level of women participation. A good knowledge of the market existed among the mud crab farming groups where hotels and exporters offered the highest prices. However there is a need for national policies to be directed to support small-scale aquaculture development by ensuring training and capacity

building for women, operation and management of groups, data management and provision of user rights for communities working in the mangrove environment.

Market analyses showed that the common market size of crabs in East Africa ranged between 500-1000 g and are thus larger than in Southeast Asia where the average size is reported at 300 g. Prices for mud crabs were over 50 % lower in Tanzania than in other East African countries and most of the profit was earned by middlemen and exporters. Cost revenue analysis showed that it would be more profitable to farm smaller commercial crabs, and develop a market for 300 g crabs to increase the profitability of crab farming in East Africa. Also, the same analyses found that farming large crabs in individual cages, which is the dominant culture form in East Africa today, had very low profitability due to high labor costs and low growth rates. Using a step-wise function of natural growth it was shown that growth rates of *S. serrata* cultured in cages was 40 % of the growth rates obtained in experimental pond and pen cultures, which were similar to natural growth. Therefore the good performance of grow-out cultures of juvenile mud crabs in earthen ponds and mangrove pens showed a potential to develop into a profitable and sustainable intervention. However, more work is needed to improve survival in culture systems and address the identified limitations of crab seeds and feed to enable development of sustainable mud crab aquaculture in East Africa.

Key words: mud crab, ecology, fishery, aquaculture, livelihood, sustainability

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ABBREVIATIONS

ACDI/VOCA: Agricultural Cooperative Development International/Volunteers in Overseas Cooperative Assistance
ANOVA: Analysis of variance
CW: Carapace Width
CPUE: Catch per unit effort
CWT: Coded wire tags
FAO: Food and Agricultural Organization of the United Nations
GPS: Global Positioning System
ICW: Internal Carapace Width
IFS: International Foundation for Science
KFS: Kenya Forest Service
KMFRI: Kenya Marine and Fisheries Research Institute
MASMA: Marine Science for Management
MIMP: Mafia Island Marine Park
NEM: Northeast monsoon
OCG: Organized community group
PVC: Polyvinyl chloride
ROI: Return on Investment
SEA: Southeast Asia
SEAFDEC: Southeast Asia Fisheries Development Center
SEM: Southeast monsoon
TAFIRI: Tanzania Fisheries Research Institute
UNDESA: United Nations Department of Economic and Social Affairs
USD: United States Dollar
VBGF: von Bertalanffy growth function
WIOMSA: Western Indian Ocean Marine Science Association
WIO: Western Indian Ocean

DEDICATION

To my wife Jackleen and our children Jacob, Jeremiah and Esther

ABSTRACT

Mud crab *Scylla serrata* is a crustacean that spends most of its life cycle in the mangrove environment throughout its range. Fishery and aquaculture of this crab are significant economic activities in coastal areas in the tropics and sub-tropics because of the meat quality and nutritional value. However there is a significant shortage of information on the ecology, fishery and aquaculture of these crabs in Sub-Saharan Africa. This impacts the development of a sustainable aquaculture and fishery for the benefit of coastal communities. The present study analyses various aspects of mud crab ecology, fishery, aquaculture and social economics in East Africa using multidisciplinary approaches. The results are given in seven papers based on field and laboratory studies.

The study established for the first time that high intertidal mangrove back-flats constitute a key habitat for the earliest instars of *S. serrata* (4 -30 mm CW). It also showed that diurnal tidal migration behaviour occurs in small juveniles that migrate to sub-tidal habitats during the day, possibly due to variable predation risks. Monthly sampling of juveniles in Kenya and Tanzania indicated continuous recruitment throughout the year. The large numbers of juvenile crabs along mangrove fringes indicate that these habitats could serve as sites suitable for collection of juvenile crabs for aquaculture. However, these areas must also be managed and protected to support the recruitment to the wild crab populations.

An assessment of the crab fishery indicated that artisanal crab fishers possess significant traditional knowledge mainly inherited from their parents that enabled them to exploit the resource. Such knowledge could be useful for the development of the aquaculture and in management of the fishery. Mud crab fishing was found to be a male dominated activity, and fishers on foot practiced fishing in burrows at spring low tides. Interviews indicated that the average size of marketable crabs has declined over the years and a weak management system was observed with most fishers operating without a license. Due to the knowledge required regarding the local conditions, fishers are unable to shift to new areas. Furthermore, fishers could not fish at neap tides. Such limitations provide a “natural closure” of the fishery. Also foot fishers cover fairly limited distances in their daily operations, an aspect that can be utilized to effect site-specific management for the fishery if necessary.

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Similar to artisanal mud crab fishery, an assessment of small-scale mud crab farming by organized community groups in Kenya indicated low level of women participation. A good knowledge of the market existed among the crab farming groups where hotels and exporters offered the highest prices. However there is a need for national policies to be directed to support small-scale aquaculture development by ensuring training and capacity building for women, operation and management of groups, data management and provision of user rights for communities working in the mangrove environment.

Market analyses showed that the common market size of crabs in East Africa ranged between 500-1000 g and are thus larger than in Southeast Asia where the average size is reported at 300 g. Prices for mud crabs were over 50 % lower in Tanzania than in other East African countries and most of the profit was earned by middlemen and exporters. Cost revenue analysis showed that it would be more profitable to farm smaller commercial crabs, and develop a market for 300 g crabs to increase profitability of crab farming in East Africa. Also, the same analyses found that farming large crabs in individual cages, which is the dominant culture form in East Africa today, had low profitability due to high labour costs and low growth rates. Using a step-wise function of natural growth it was shown that growth rates of *S. serrata* cultured in cages was 40 % of the growth rates obtained in experimental pond and pen cultures, which were similar to natural growth. Therefore the good performance of grow-out cultures of juvenile mud crabs in earthen ponds and mangrove pens showed a potential to develop into a profitable and sustainable intervention. However, more work is needed to improve survival in culture systems and address the identified limitations of crab seeds and feed to enable development of sustainable mud crab aquaculture in East Africa.

Key words: mud crab, ecology, fishery, aquaculture, livelihood, sustainability

LIST OF PAPERS

The thesis is based on the following papers, referred to by the Roman numbers:

- Paper I: Moksnes P-O, Mirera DO, Eriander L, Palmqvist K, Mahudi HM, Björkvik E, Nyqvist D. (*Manuscript*). Ecology of juvenile mud crab (*Scylla serrata*) in East Africa.
- Paper II: Moksnes P-O, Mirera DO, Björkvik E, Hamad MI, Mahudi HM, Nyqvist D, Narriman Jiddawi N, M Troell. (*Accepted*). Step-wise function of natural growth for *Scylla serrata* in East Africa: A valuable tool for assessing growth of mud crabs in aquacultures
- Paper III: Mirera, O. D., Moksnes, P-O. 2013. Cannibalistic Interactions of juvenile mud crabs (*Scylla serrata*): The effect of shelter and crab size, *African Journal of Marine Science*. 35: 545-553
- Paper IV: Mirera, O. D., Moksnes, P-O. (*Submitted*). Comparative performance of wild juvenile mud crab (*Scylla serrata*) in different culture systems: net cages, mangrove pens and earthen ponds
- Paper V: Mirera, O. D, Ochiewo J, Munyi F, Muriuki T. 2013. Heredity or tradiional knowledge: Fishing tactics and dynamics of artisanal mangrove crab (*Scylla serrata*) fishery. *Ocean & Coastal Management*. 84: 119-129
- Paper VI: Mirera, O. D, Ochiewo J, Munyi, F. (*Manuscript*). Social-economic implications of small-scale mud crab (*Scylla serrata*) aquaculture: The case of organized community groups along the Kenyan coast
- Paper VII: Moksnes P-O, Mirera D. O, Lokina R, Ochiewo J, Mahudi HM, Narriman N, Hamad M. I, Troell M. (*Manuscript*). Economic and environmental performance of small-scale aquaculture of mud crab *Scylla serrata* in East Africa

1.0 INTRODUCTION

1.1 Background

The world human population continues to increase steadily and is projected to reach about 9.6 billion in 2050 with Sub-Saharan Africa being expected to have faster population growth compared to other regions (UNDESA, 2013). Globally, there are about 1.4 billion people living in poverty (less than USD 1.25/day) of which Sub-Saharan Africa contributes 28 % (UNDESA, 2009). Poverty is multifaceted and includes lack of income, resources to ensure sustainable livelihoods, hunger, malnutrition, health problems, lack of access to education, lack of housing, unsafe environment and social discrimination.

The global increase in population and change in eating habits has increased the global annual per-capita fish consumption¹ from on average 9.9 kg in the 1960s to the current estimates of 18.6 kg (FAO, 2012, 2013). Due to increased demand and need to overcome poverty, many of the world's major fisheries are either fully fished, overexploited or have collapsed (FAO, 2012; Worm and Branch, 2012). Over the last half century many ecosystems supporting fisheries have been degraded by humans more rapidly than any other time in history. Capture fisheries has plateaued at 94 million according to the Millennium Ecosystem Assessment (FAO, 2010e). Especially capture fisheries in tropical countries are on the declining trend due to challenges associated to overfishing and climate change (Cheung et al. 2010; Worm and Branch 2012). Hence, aquaculture is one important way of increasing the production of fish and shellfish and thereby contributing to job creation and provision of protein.

With over 600 species of aquatic animals and plants under culture worldwide, the contribution of aquaculture to total fishery products has steadily increased over the years. Its contribution to global food fisheries output increased from 9 % in 1980 to 47 % in 2010 (FAO, 2012). Global farmed fish production was 59.9 million tons in 2010 increasing by 7.5 % from 2009 (55.7 million tons). Overall aquaculture production is expected to contribute about 120-130 million tons of fish

¹ Consumption is measured by per capita availability of fish and shellfish, including shell weight.

by 2020. The larger portion of this production will meet the demand for food in developing countries as well as employ about seven million people, mostly in developing countries (FAO, 2003; Rana et al., 2009; FAO, 2012).

Whereas aquaculture production is increasing globally, there are large regional differences. In 2010 significant food fish aquaculture production took place in Asia (53.3 million tons, representing 89 % of world production) and Europe (2.5 million tons, 4.2 %) while Sub-Saharan Africa contributed with only 0.6 % of the global output (FAO, 2012). Therefore unlike many Asian countries, Sub-Saharan Africa has a limited history in aquaculture, which still remains largely undeveloped (Brummett and Williams, 2000; FAO, 2012). The future role of aquaculture in Africa is uncertain. Currently more focus is on finfish production in freshwater systems whereas mariculture of shellfish remains underdeveloped (Bryceson, 2002; Rönnbäck et al. 2002; Mirera and Ngugi, 2009; Troell et al, 2011; Ndanga et al., 2013).

The industrial or commercial aquaculture in the coastal zones in Southeast Asia (SEA) have in some cases resulted in ecological and environmental consequences, for example in the form of habitat/ecosystem loss, excessive harvesting of wild seed and or spawners, bycatch (catching of un-intended juveniles which are thrown away), spread of diseases and pollution (Primavera, 2006; Naylor et al 2010). Due to the destructive nature of industrial or commercial aquaculture (Baconguis et al., 1990), development of community based small-scale mangrove friendly aquaculture was advocated as a livelihood alternative for the local poor (Primavera, 2000; Trino and Rodriguez, 2002). Therefore to develop coastal aquaculture in East Africa, lessons learnt from SEA are essential.

As mariculture development in the Western Indian Ocean countries still is slow (Troell et al. 2011), there is a need for investments in research and extension to ensure development of aquaculture in order to improve income and the availability of food for the coastal poor communities. However, at the same time the integrity of the environment must be maintained (Ronnback et al., 2002; Mirera, 2009; Mirera and Ngugi, 2009). In this context there is a conflict between the current aquaculture methods often employed in Sub-Saharan Africa and the traditional capture fisheries, as current aquacultures to a large extent is based on collecting seed stock and feed from the wild (de Boer and Longamane, 1996; Mgaya et al., 1999; Carle'n and Olafsson, 2002; Sallema, 2004; Mirera, 2011b).

The mud crab, also called mangrove crab (genus *Scylla*), is among the most extensively consumed and farmed marine shellfish globally, being second to shrimp/prawn. Mud crabs are common in mud flats of littoral zones including supralittoral, intertidal and subtidal zones in and close to mangrove forests throughout the Indo-Pacific (Macnae 1968; Keenan et al., 1998). These portunid crabs are exploited both commercially and for subsistence by small to moderate scale fisheries. They constitute a valuable component of artisanal fisheries in most countries of tropical Indo-Pacific (Le Vay, 2001; Barnes et al., 2002; Fondo, 2006; Ochiewo, 2006; Richmond et al., 2006; Mirera 2011b). Through the crab fishery, coastal communities have an important source of food and income (Arriola 1940; Macintosh et al. 1993; Overton et al. 1997; Le Vay et al. 2001; Overton and Macintosh 2002). Despite its significance in East Africa as an artisanal fishery, there is limited information on the abundance and population distribution of this species, as well as the current exploitation techniques (Barnes et al., 2002; Richmond et al., 2006; Mirera, 2011b).

Mud crab culture has been promoted globally to counter the declining capture fisheries and to meet the increasing market demand. Culturing the crabs has been done successfully in SEA where crabs fetches high price in local and international markets (Cowan, 1983; Nghia et al., 2007; Shelley, 2008; Petersen et al., 2011; Bondad-Reantaso et al., 2012). Considerable effort has been undertaken in SEA over the last decades to develop the required technology for mud crab aquaculture (Brick, 1974; Angell, 1992; Heasman and Fielder, 1983; Angell, 1992; Keenan and Blackshaw, 1999; Anon., 2001; Anon., 2005; Wang et al., 2005; Shelley, 2008; Primavera et al., 2010; Quintio and Estepa, 2011).

To meet the increased tourist and export demand and provide an income for the local community, while conserving the critical mangrove ecosystem, small-scale mud crab aquaculture has attracted some attention in the Western Indian Ocean region over the last two decades (Mwaluma, 2002; ACDI/VOCA, 2005; Mirera, 2009; Mirera and Mtile, 2009). However, unlike some parts of SEA the culture in the Western Indian Ocean is wholly dependent on wild caught seeds. Capture of wild juveniles and young adults, if not well managed, may impact on wild stock recruitment and consequently (wild) fisheries production. This may be the risk if crab aquaculture expands in the WIO region as specific information on habitat utilization by juvenile crabs, as well as population dynamics and fishing trends, are

limited. This thesis explores different trends in mud crab fisheries, capture-based aquaculture interventions and ecological as well as socio-economic aspects of mud crab fisheries and aquaculture in Sub-Saharan East Africa.

1.2 Mud crab (*Scylla serrata*) ecology

Mangroves function as a nursery and feeding habitat for juveniles of many commercial fish and shellfish species (Robertson and Duke 1990; Chong et al. 1996; Vance et al. 1996; Ronnback et al. 1999; Huxham et al. 2004; Mirera et al., 2010). It has been estimated that 1 ha of mangrove has the potential to generate 1.0–11.8 tons of fish catch per year, figures that are much higher than those for other coastal ecosystems like coral reefs (Ronnback 2001; Alcalá, 1988). Mud crab populations are typically associated with mangroves globally and are at times used as indicators for mangrove habitat condition (Hill et al., 1982; Walton et al., 2006b). Four species of mud crabs are recognized globally (*S. serrata*, *S. paramamosain*, *S. tranquebarica* and *S. olivacea*), but only one species (*S. serrata*) has been identified in East Africa (Keenan et al. 1998, Fratini and Vannini, 2002). Most of the lifecycle of the mud crab is associated with mangroves and juvenile crabs are abundant in estuaries and mangrove swamps (Muthiga, 1986; Overton et al., 1997; Onyango, 2002; Walton et al., 2006a). Crabs also utilize intertidal and sub-tidal sheltered soft sediment habitats (Hill et al., 1982; Keenan et al., 1998).

In Australia, larger juvenile *S. serrata* (30–80 mm spine-to-spine carapace width; CW) reside in the mangrove zone in small burrows, whereas sub-adult crabs (81–119 mm CW) have been observed to migrate into the intertidal areas at high tides and retreat with the outflowing water at low tides (Hill et al., 1982). Adult stages of all mud crab species (>120 mm CW) are considered to be more sub-tidal but some stay in burrows within the mangrove and rarely move to intertidal areas at high tides (Hill et al., 1982; Nandi and Dev-Roy, 1991; Kalk, 1995; Le vay, 2001; Barnes et al., 2002; Walton et al., 2006a). Mud crabs are active during incoming tides, feeding omnivorously and opportunistically in the mangrove ecosystem. Thus the abundance of mud crabs may be impacted by degradation of the mangrove forests and associated ecosystems (Kosuge, 2001).

Studies on *S. paramamosain* in southern Vietnam indicate that crabs start utilizing mangrove habitat at instar 1 (5 mm CW) living among pneumatophores and intertidal mudflats (Walton et al., 2006a) whereas for *S. serrata* little information is

available about the preferred habitat of the earliest juvenile stages (4-20 mm CW) globally (Webley et al., 2009), including also Sub-Saharan Africa. In order to address the governance challenges related to culturing of mud crabs, it is important to investigate the factors influencing occurrence and selection of habitat during different juvenile phases. These questions forms part of the current study.

Information regarding the factors influencing the preferred habitats by juvenile crabs is of increasing importance since the developing mud crab aquaculture in East Africa, as in other parts of the world, is based on wild seed collection (Rodriguez et al., 2007, Mirera, 2011b; Dumas et al., 2012). Expansion of crab aquaculture is likely to target all size fractions of the crab population (juveniles, sub-adults and brooders) and affect the traditional capture fishery as well as the sustainability of the aquaculture itself. Currently collection of juvenile crabs for aquaculture may be difficult to manage since abundance of crabs as well as collection methods and gears are poorly understood in the region. Furthermore there are limited examples of well-managed crab fisheries to learn from (Pillans et al., 2005; Shelley, 2008). The present research is carried out in a region where there is no official statistics on the mud crab fishery, and much less on juvenile (less than 100 mm CW) collection for aquaculture. The research provides information on the occurrence and abundance of crabs in mangrove areas as a potential for capture based aquaculture development and management.

In addition, there is limited information about the natural growth of mud crabs. In Vietnam, natural growth in juvenile and adult *S. paramamosain* was estimated using mark-recapture techniques and described using a von Bertalanffy growth function - VBGF (Le Vay et al., 2007). However, no growth functions are available for other species of *Scylla*. The growth in adult *S. serrata* in South Africa was also described using mark-recapture techniques (Hill, 1975), but no growth rates of wild juvenile *S. serrata* have been published. The lack of a description of growth in *S. serrata* poses a limitation for management of fished populations since the generation time or age of the commercial sizes are not known. It also impedes assessment of different culture systems, and production and cost-revenue estimates in aquacultures of *S. serrata*, particularly in East Africa where culture is in its infancy and different methods are presently being assessed. One aim of this thesis is to provide information that can be applicable in estimating natural growth in mud crabs. Furthermore, there is lack of information on natural mortality of juvenile and adult crabs in the region.

1.3 Mud crab fisheries

Mud crabs being associated to mangrove ecosystems form an important source of food and income for local communities (Keenan et al., 1998; Keenan, 1999; Le Vay, 2001; Bonine et al., 2008). However, although a number of communities along the East African coast are involved in mud crab fisheries, there is limited and/or poorly collected data to provide information on catch rates, trends in fisheries etc. (Barnes et al., 2002; Richmond et al., 2006; Mirera, 2011b). Obviously it is extremely difficult to manage a fishery without good understanding about catches, fishing methods, fishing pressure and population dynamics (Hay et al., 2005; Glazachev and Perfilova, 2008; Maynou et al., 2011). Lack of such vital information makes any attempt to develop a sustainable capture based mud crab aquaculture highly uncertain. The heavy dependence on wild seeds requires consideration of both the fishing sector as well as the aquaculture sector for being able to assess the overall sustainability of crab production. Indeed Le Vay, (2001) asserts that as long as culture of mud crabs is dependent on wild caught seed, the requirements for sustainable development of crab culture and management of fisheries will remain closely interlinked. Walton et al. (2006b) also observed that supply of seed stock from the wild varied over time due to seasonality and thus the need for a well managed fishery. This thesis provides baseline information on various aspects related to structure of artisanal capture fisheries and recruitment dynamics of juvenile mud crab and population assessments. This understanding enables improvement of policy and regulations related to the management of the fishery and small-scale aquaculture in the region.

Globally, artisanal mud crab (*Scylla spp.*) fishers use several techniques (tools) for catching the crabs, which have changed over time (Bonine et al., 2008). The methods for capture are generally similar throughout the tropics but the techniques may differ somewhat from one region to another depending on habitat complexity and traditions of fishers (Perrine, 1978; Le Vay et al., 2001; Ochiewo, 2006; Bonine et al., 2008). The dominant tools include; baited crab pots, baited traps, hooked metal rods, baited lines attached to a pole, scoop nets, head lights/torches with scoop nets, gill/seine nets, intertidal collection by hand and baited lift nets (Hill et al., 1982; Overton et al., 1997; Le Vay et al., 2001; Barnes et al., 2002; Walton et al., 2006; Leбата et al., 2007; Bonine et al., 2008).

In East Africa burrow fishing is a common technique of collecting market size (above 500 g) crabs for sale and sub-adult (100-500 g) crabs for cage and pen culture (Barnes et al., 2002; ACIDI/VOCA, 2005; Mahika et al., 2005; Richmond et al., 2006; Mirera, 2009; Mirera, 2011b). This fishing technique requires considerable experience and beginners only damage the crabs and thus make them useless for the market (Mirera and Mtile, 2009; Nirmale et al., 2012). Dumas et al., (2012) observed that fishers frequently check burrows along usual trails inside their respective fishing territories and collect individuals found on or buried in the sediment along the trails. However, there is limited information on local knowledge required by artisanal mud crab fishers in East Africa to be successful in the fishery. Some of these information gaps are addressed in the thesis.

Studies performed already three decades ago indicated the importance of crustacean fishery, being the most profitable fishery along the East African coast with some level of under-exploitation (Mutyagera, 1981; Muthiga, 1986). Population studies of mud crabs in Mafia Island (islands of Utende, Juani and Chole) and Mozambique (Quirimba and Ibo) by Barnes et al. (2002) indicated a crab fishery that, at that time was only lightly exploited with potential for improved income generation if sustainably managed. However, in the last decade, site or region specific decline in catches have been observed in different studies along the East Africa coast (Mahika et al., 2005; Fondo, 2006; Richmond et al., 2006). Thus the thesis undertakes to provide information on the skill and knowledge required by artisanal mud crab fishers and how such knowledge can be used in aquaculture and management of the fishery.

1.4 Mud crab (*S. serrata*) aquaculture

Global overview

World marine aquaculture contributed about 30.3 % of the total aquaculture production in 2011 of which only 3.8 % comprised of marine crustaceans (FAO, 2012). Mud crabs contributed only about 0.2 million tons. Most (89 %) of the production originates from China and SEA (Shelley, 2008; FAO, 2012). High dependency on wild seed is a major problem that continuous expansion of mud crab aquaculture is facing. However this issue has in the recent decade been addressed through development of hatcheries (*S. serrata*) in Southeast Asia and China (Quinitio et al., 2011; Rodriguez et al., 2001; Quinitio and Parado-Estepa, 2008). Availability of juveniles from hatcheries reduces competition with wild fishery, increase mud crab production per area, facilitates planning for production by farmers and reduces the size difference of the seed stock as opposed to when seeds are collected from the wild (Shelley, 2008). However, hatcheries have high initial investment costs in addition to having sensitive technological requirements. This implies that hatchery produced seeds are likely to be more expensive than wild collected seeds. Hence small-scale mud crab farming will to some extent depend on wild crabs seeds until such time that investment policies in East Africa will be prioritised for marine hatchery development.

Cannibalism, moulting, salinity and temperature fluctuations and feed are the main factors that affect survival in mud crab culture. Also indirectly, shelter and stocking density influence cannibalism and hence survival (Trino et al. 1999a; Ruscoe et al. 2004; Holme et al. 2007; Mann et al. 2007; Mirera 2009; Rodriguez et al. 2007). Aggression and cannibalism are ranked as main behavioural causes of low survival in semi-intensive and intensive culture systems and still remain a challenge (Quinitio et al. 2001; Williams and Primavera 2001; Allan and Fielder 2003; Paterson et al. 2007; Shelley and Lovatelli, 2011; Quinitio and Estepa, 2011). However, provision of shelter to cultured crabs in different culture systems (ponds tanks and net cages), improves survival and various types of shelter have been used in experiments to test their effectiveness in providing protection when crabs are kept in captivity in SEA - i.e. seaweeds (*Gracilariopsis*), bamboo shelters, brick or shells and nets (Trino et al., 1999a; Rodriguez et al., 2007; Ut et al., 2007a).

Studies of stocking density in mud crab farming have indicated that gross income increases with increasing densities when cannibalism is reduced to improve survival. Crab densities in aquaculture productions have been evaluated at 0.5 to 3.0 crabs/m² for crab sizes between 20 and 60 mm CW in pond and pen culture systems (Trino et al., 1999a, 2001; Trino and Rodriguez, 2002; Christensen et al., 2004; Primavera et al., 2010). Survival ranged between 35 – 98 %, with highest survival in lowest crab density. Feed experiments have shown that formulated pellets or flesh (such as mussel or fish biomass) do not affect survival or growth significantly (Trino et al., 2001; Mann et al., 2007; Primavera et al., 2010).

Mud crab culture is carried out in a number of different ways throughout the tropics, ranging from extensive (low density, less feeds, less controlled culture systems) to intensive (high density, more feeds, controlled environment), monoculture (culture of one species) to polyculture (cultured with one more or several other species). The farming methods also vary i.e. mangrove pens, aquaculture ponds (earthen or concrete) for grow-out or cages (individual or shared) for fattening. Each of these crab culture methods may to some variable degree be suitable for small-scale or large industrial scale. Techniques have been developed to meet specific local circumstances and the potentials and needs of small-scale crab farmers. The different techniques are well described in a number of manuals, workshop reports, proceedings and scientific papers (Heasman and Fielder, 1983; Angell, 1992; Keenan and Blackshaw, 1999; Trino et al., 1999b; Trino and Rodriguez, 2002; Mirera, 2009). The key farming approaches for crab production can be summarised as; grow-out, fattening and soft-shell crab (Shelley and Lovatelli, 2011; Pandiarajan et al., 2013).

Grow-out crab culture: An operation that involves raising of young seed crabs (5-43 mm ICW) to marketable sizes of 300-500 g or above over an extended culture period. It encompasses use of different methods and systems with minimal variations between regions (Angell, 1992; Fortes, 1999; Keenan, 1999; Trino and Rodriguez, 2002; Thach, 2003; Mirera, 2009; Primavera et al., 2010).

Mangrove pens are commonly used in small-scale crab culture. They have been developed as farming systems that utilize habitat preference of juvenile and adult mud crabs. Pens are designed to retain crabs within a specific area of mangrove so that they can be fed and monitored for growth. This grow-out culture system has been considered to be mangrove friendly (low impacts on mangroves) and the

constructions are well documented (Baliao et al., 1999; Genodepa, 1999; Trino and Rodriguez, 2002; Primavera et al., 2010). To facilitate management, harvesting and sampling and at the same time limit degradation of mangrove forest since pens are usually small i.e. up to 200 m² (Genodepa, 1999; Trino and Rodriguez, 2002; Primavera et al., 2010). Crab growth in mangrove pens is relatively high while survival is quite varied in most studies and hence rated as average (Mwaluma, 2002; Trino and Rodriguez, 2002; Mirera, 2009; Primavera et al., 2010).

Small-scale mud crab farming in Asia is also performed in small earthen ponds ranging between 0.05- 0.5 ha under monoculture in extensive (low investment) culture systems (Dat, 1999; Fortes, 1999). In large-scale grow-out cultures in Asia, earthen ponds with sizes ranging from one to tens of hectares earlier used for culture of shrimp, have been converted to crab cultures (Dat, 1999; Trino et al., 1999a & b; Shelley and Lovatelli, 2011). This is often carried out in areas where shrimp farms have been affected by disease or degraded due to overproduction (Marichamy and Rajapackiam, 1996; Pandiarajan et al., 2013). In some areas, larger ponds have been redesigned to enable different culture techniques for crabs through sub-division and farmers are then able to utilize a single pond for different stages of the production cycle (Baliao et al., 1999; Anon, 2007).

Crab fattening: The term refers to the process whereby recently moulted crabs with low meat content (often called “empty crabs”), identified at harvest (either from the wild or from farm stock), are held and fed for a short period until they are full of meat and ready for market (Shelley and Lovatelli, 2011). In SEA they are harvested prior to moult to decrease mortality (Keenan, 2003). Structures that are currently used for mud crab fattening include; floating cages, drive-in cages or fixed cages, ponds or tanks. Its often estimated that a crab fattening cycle will take from 14 to 60 days since the process depends on the degree of “fullness” of the crab at the start of the fattening regime. The initial size of the crabs at the start of the fattening is of importance (the larger the crab, the longer it will take to fatten), as well as the temperature and feed provided (Anil and Suseelan, 2001). Crab fattening can be done in small-scale to large-scale operations and is considered to have relatively low operating costs, high survival and a fast turnover of stock, making it economically attractive if enough “empty” crabs are available. In fattening systems, crabs are fed 7–10 % of their total body weight per day with trash fish or molluscs. Compared to grow-out culture system, fattening in SEA has relatively higher survival due to the individual stocking in cages and short culture periods or low density stocking in

ponds and pens in addition to the short culture period whereas the situation in East Africa is slightly different – see below (Anil and Suseelan, 2001; Mirera, 2009; Shelley and Lovatelli, 2011).

Production of soft shell crabs: Crabs have a soft exoskeleton directly after moult. The soft crabs are considered a delicacy and has attracted a strong market and high prices, for example in many Asian countries. Production of soft shell crabs is usually performed in large scale industrial systems where crabs are held individually in containers (or “cells”) made of PVC to mitigate cannibalism, facilitate inspection and provide controlled conditions for growth (Quinitio and Lwin, 2009). In these systems, small crabs (80–120 g) are held in isolation for a few weeks until they moult, at which point they are either chilled or frozen before their new outer shell can harden (Shelley and Lovatelli, 2011). Sophisticated systems have been built with a variety of technological features incorporated into them to minimize labour and maximize production. For out-door culture systems floating platforms have been constructed to hold several plastic boxes which can be slid on PVC pipe with a polyethylene rope to facilitated inspection and feeding (Quinitio and Lwin, 2009). In in-door systems, cameras linked to a computer system have been developed to regularly scan crabs in cells. Where two “crabs” in a scan means the crab has moulted, leaving an empty shell and a soft-shell crab that needs to be harvested. The cage systems also include a sophisticated water recirculation system. Crabs in these systems are obtained both from wild harvest or farms. Currently, no local market in East Africa exists for soft shell crabs. However, as there is a high demand in Asia this may initiate production in the region.

Crab farming in East Africa

Marine aquaculture is still at its infancy in East Africa (Bryceson, 2002; Ronnback et al., 2002; Troell et al., 2011). For along time, coastal aquaculture has been dominated by seaweed farming and few intensive shrimp farms (Mshigeni, 1985; UNEP, 1998). However, recently a number of other aquaculture species have been introduced and are now being cultured along the coast with variable level of success, i.e. mud crabs, oyster, milkfish, mullets and rabbitfish (Mwaluma, 2002; Rice and Savoie, 2005; Rice et al., 2006; Mirera, 2009; Mirera and Ngugi, 2009).

Mud crab (*S. serrata*) farming was introduced along the East Africa coast in late 90’s mainly as a strategy to conserve mangrove forests while at the same time offer

alternative livelihoods for local. Thus, simple pens and cages used for keeping crabs in the mangrove forests was aimed for providing the coastal communities with motivation to participate in mangrove conservation and management. Farming of crabs was, and still is, mainly a small scale activity and was initially spearheaded by non-governmental organizations (NGOs), research institutions and universities. This type of aquaculture was offered to communities that previously had been involved in mangrove conservation efforts by government ministries, local authorities and conservation/livelihood NGOs. The private sector have not been involved to any larger extent.

Development of crab farming along the East Africa coast has been slowed down by a number of factors including limited knowledge of rearing techniques (crab behaviour in captivity at all stages), poor extension services, high mortalities, access to seed, etc. Whereas hatchery production of juveniles of *S. serrata*, significantly improved seed supply for crab farming in SEA and China, no hatchery facilities are in operation in Sub-Saharan Africa (Mirera, 2011b).

Crab mortality is likely to be lower in cultures relying on seeds from hatcheries compared to farms where farmers use seeds with variable sizes from the wild. Studies on other portunid crabs and other crustaceans indicate that highest rates of cannibalism occur when predating crabs are large enough to kill prey crabs in intermoult with hard exoskeletons and in the absence of shelter refuge (Moksnes et al. 1997, 1998; Marshall et al. 2005). However, there is limited information in the literature on the range of sizes that can be stocked together in culture systems with minimal cannibalistic losses.

In natural populations of portunid crabs, shelter have shown to reduce mortalities related to cannibalism (Moksnes et al., 1997, 1998). However, there is limited information to what extent such shelters can be effective among crabs of varied size ranges in pond and pen culture systems in East Africa. Therefore more research is needed since mud crab farming is at an initial stage and the technology needs to be adopted locally.

Crab culture in East Africa is today dependent on feeds like fish offal, gastropods or kitchen remains. However, with such products there is potentially a competition with human consumers and domesticated animals. To be able to expand the aquaculture of mud crabs in East Africa conflicts with other resource users need to

be considered (Rodriguez et al., 2003; Mirera, 2009), and there is a need to find alternative feeds.

Farming techniques in East Africa and current issues

Small-scale crab farming in East Africa uses simple techniques and materials accessible locally. Initially mangrove pen culture systems were assessed, but with limited success (Mwaluma, 2002, 2003). Later small-scale cage (floating or drive-in) culture systems were promoted by NGOs and reserach institutions (ACDI/VOCA, 2005; Mirera, 2009, 2011). Due to low investment costs, preference has been the use of drive-in or floating cage culture system (i.e. individual cages with lids built of mangrove sticks or bamboo) as opposed to pens (Mirera, 2009). In these cultures, locally referred to as "crab fattening" cultures, the cages are placed in the intertidal in the mangrove forest without cutting any trees, and are stocked with subadult crabs (ca 150-300 g) collected from the wild. These crabs are farmed through several moults (many months) until they reach 500-1000 g and obtain a high market price (ACDI-VOCA 2005, Mahika et al. 2005, Shipton and Hecht, 2007).

However, recent studies indicate that the mud crab cage cultures may not be the best method for a profitable and sustainable aquaculture in East Africa. Cost-revenue analyses in Tanzania indicated that profitability is low (ACDI-VOCA 2005), whereas the profit-margin appear to be higher in Kenya (Mirera 2009). These studies did not include the cost of labour and it is therefore unclear how this activity compares to other livelihood options. Moreover, experimental assessment of these culture systems (Mirera, 2009; Mirera and Mtile 2009) indicate that growth and survival may be low. However, it has been difficult to comparison with cultures in SEA since different sizes of seed crabs and different growth periods have been used in different studies. Grow-out cultures of small juvenile mud crabs have not been attempted in East Africa, and neither has culture of crabs in ponds (Ronnback et al., 2002) even though such techniques are well developed in SEA where faster growth has been observed in ponds compared to other methods (Keenan, 1999; Mirera and Samoilys, 2008).

Crab farming in East Africa face a number of challenges to become a sustainable livelihood alternative for coastal communities. In all culture systems, the survival rate is relatively low compared to reported survival rates in SEA. This has been

associated with cannibalism, theft, poor recovery and escape (Mwaluma, 2002; Mirera, 2009; Mirera and Mtile, 2009). The quality of crabs has been observed to be low due to loss of chelipeds and presence of a higher portion of empty (less meat) crabs. The results are low growth rates and this affects market prices. Other aspects that need attention include development of appropriate feeds for crab to maximise growth and minimize the ecological impacts and well as possible competition associated with use of live/wild caught feeds or feed/food resources. Participatory research that involves experts working with the farmers is a way to upgrade the skills of the farmers. Through such collaboration, innovations as well as ideas from other parts of the world could be tried locally in East Africa (Molnar, 1987; Lionberger and Gwin, 1991).

1.5 Socio-economic aspects and sustainability of mud crab aquaculture

Globally, small-scale aquaculture is suggested to be fundamental for the livelihood, welfare and food security of some of the poorest communities in developing countries (Brummett and Williams, 2000). Thus, aquaculture stimulates economic development by providing much needed job opportunities and may also provide valuable food to local communities (Khan and Alam, 1992; Bene, 2005; FAO, 2013). However, with the exception of seaweed cultures even though with its challenges, marine aquaculture has not been realised in Africa and generally the start of aquaculture has been very slow (Brummett and Williams, 2000; FAO, 2012). Past development initiatives in East Africa have failed to take off or achieve sustainability (Mirera, 2011b; Troell et al., 2011). The reasons may be lack of a history in aquaculture, political and socio-economic constraints and limited technology, as opposed to East and South East Asia where all these conditions have been in place and have led to dramatic development with growth figures of 5 to 10 % per year for the last decades (Jiang, 2010).

Small-scale community based mud crab aquaculture is a potential livelihood option in East Africa although more work is needed in research at all levels (Mwaluma, 2002; ACDI/VOCA, 2005; Mirera and Samoilys, 2008; Mirera, 2009). Research may also include aspects of local community social dynamics in order to better understand the type, magnitude and extent of drivers for aquaculture development as well as what social factors may prevent or facilitate development.

The expansion of crab farming industry in SEA has during the last decade mainly depended entirely on wild seed (juvenile crab). This has in some regions led to overexploitation and shortage of wild juvenile crabs, which then limited growth of crab aquaculture (Keenan, 1999; Fortes, 1999; Allan and Fielder 2003). The unstable wild seed supply in Vietnam, in the 90s resulted in unstable stocking and stocking of more than one species. Different species have different growth and behavioural traits that impact growth and survival (Le Vay 2001; Walton et al., 2006b; Petersen et al., 2011). To date, wild seeds are still used in many Asian countries even where hatcheries have been developed (Quinitio et al., 2001; Quinitio, pers com).

Small-scale crab farms use, in addition to fish waste, various low valued fish and molluscs as feed, which are easily collected in the intertidal zone (Hutabarat, 1997; Mann et al., 1997; Marasigan, 1997; Baliao et al., 1999; Fielder, 2004; Quinitio, 2004; Rodriguez et al., 2007; Mirera, 2009). Household leftovers and agriculture farm wastes are also used to reduce operational costs (Mann and Paterson, 2003; Quinitio, 2004; Mirera and Samoily, 2008; Mirera, 2011b). In SEA formulated feeds have been developed for crab farming and use of pellet feeds could bring many advantages such as minimized dependence on availability (and competition) of fresh feeds. However, storage and quality of formulated feeds may have issues that need to be solved (Catacutan, 2002). In East Africa, development of formulated feeds is minimal or not existing at all due to technological constraints and costs. The use of fish as crab feeds in East Africa may lead to increase in price for fish since there may be a market for this fish for human consumption and/or to feed domesticated animals (Rana et al., 2009). Also, other wastes from human food production may have a market as feed for chicken and pigs.

Despite all the challenges related to seed and feed supply, crab culture has been demonstrated to be profitable in different culture systems, stocking densities and harvesting regimes in SEA (Trino et al., 1999a; Trino et al., 2001; Trino and Rodriguez, 2002; Rodriguez et al., 2003; Primavera et al., 2010). The best documented profitable crab grow-out cultures have been either earthen pond or pen culture systems. However, most of the studies addressing profitability of mud crab farming have not included the full costs for construction or maintenance and labour, and the ability and willingness of communities to invest in mud crab aquaculture. These costs and aspects need to be taken into consideration when assessing if mud crab aquaculture could become an economically sustainable livelihood.

1.6 Scope of the thesis

This thesis is based on research which was carried out between 2009 and 2013. It focuses on mud crab (*Scylla serrata*) as a natural resource that spends most of its life cycle in the mangrove forest. The fishery and aquaculture of this crab are significant livelihood activities in coastal areas in the tropics and sub-tropics. However, the size of mud crabs caught in the wild in East Africa has over the years declined while demand has increased locally and internationally. Due to the increasing demand, mud crabs are traded globally and increasingly becoming an important

economic activity that involves many levels of actors within the socio-economic spectrum. However, there is a significant shortage of information on the ecology, fishery and aquaculture of these crabs in Sub-Saharan Africa. This lack of knowledge hampers a sustainable development of crab aquaculture and fishery benefiting coastal communities.

Small-scale aquaculture has been introduced in East Africa with the aim to provide coastal communities with an additional livelihood and simultaneously supporting mangrove conservation activities. Mud crab aquaculture initiatives have previously used sub-adult crabs (more than 150 g or 90 mm CW) fished from the wild in short culture periods of 3-4 months mainly in "drive-in" (bottom fixed) or floating cages and experimentally in pens. In the long run, use of sub-adult crabs from the wild may impact negatively on the recruitment into the capture fishery. To attain sustainability while practicing capture-based small-scale crab aquaculture in East Africa; this thesis has looked into various aspects of mud crab ecology, fishery, aquaculture and socio-economics in East Africa using multidisciplinary approaches. The results are given in seven papers based on field and laboratory studies.

The overall objective of the thesis is to aid in development of a sustainable, small-scale grow-out aquaculture of mud crab *Scylla serrata*, as a livelihood for coastal communities in East Africa. This was achieved through the following specific objectives: (1) Identify mud crab nursery habitats, seasonal and spatio-temporal/tidal distribution of different life-stages, and determine appropriate methods to obtain small juvenile "seed-crabs" for grow-out aquaculture. (2) Develop a model for natural growth for mud crabs in East Africa that could be used to evaluate and compare growth in different culture systems, and estimate growth-cycles in cost-revenue analyses. (3) Assess how size-differences, density, and shelter affect cannibalistic behaviour, survival and growth to develop optimal culture conditions in cultures. (4) Assess applicability of low-technology methods for grow-out aquaculture of mud crab for coastal communities in East Africa. (5) Establish the technology requirement by traditional artisanal mud crab fishers, resource exploitation levels and management implications for a sustainable fishery. (6) Understand the social and economic dynamism in organised community groups undertaking mud crab culture and policy requirements for a sustainable aquaculture. (7) Compare economic and ecological sustainability of different mud crab culture methods in an East Africa setting.

The thesis is based on seven scientific papers (**Figure 1**). **Paper I** provides information on the diurnal, tidal and seasonal occurrence and abundance of juvenile crabs within the mangrove ecosystem. It also provides details on habitat utilization by juvenile crabs. **Paper II** provides information on a model that could be used to

estimate natural growth in mud crab. **Paper III** explores the different methods through which cannibalism can be reduced in mud crab farming while **Paper IV** evaluates the impact of different culture systems and methods in mud crab farming in net cages, earthen ponds and mangrove pens. **Paper V** discusses the dynamics of artisanal mud crab fishers, fishing knowledge, tactics and aspects of migration. **Paper VI** evaluates the social and economic dynamics of OCGs involved in crab farming. **Paper VII** provides an analysis of the profitability and sustainability of mud crab aquaculture in East Africa. The links of the main topics covered in the thesis and associated papers are detailed in **Figure 1**.

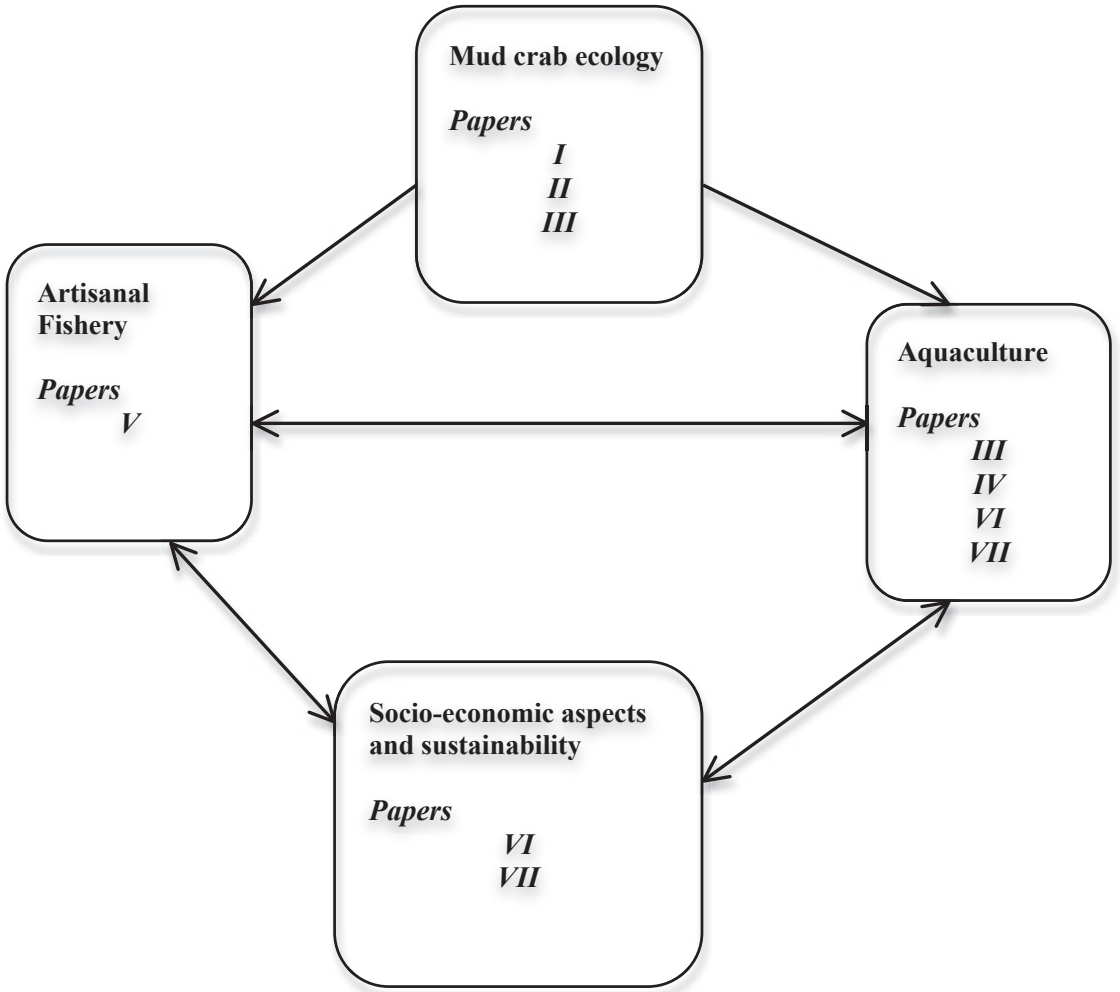


Figure 1: An overview of the links of topics covered in the thesis and papers contributing to each topic. The arrows indicate connections between the different topics of study

2.0 MATERIALS AND METHODS

2.1 Study area

The studies looked into various aspects of mud crab ecology, behaviour, culture, fishery, socio-economics and sustainability at different sites along the East Africa coast. Most of the studies were carried out in Kenya stretching from Gazi Bay in the South to Ungwana bay in the north (Gazi Bay, Mtwapa, Kilifi and Mida Creeks and Marereni) and Tanzania around Mafia Island. A smaller field study was carried out on Inhaca Island in Mozambique, and data on market and prices of mud crabs was also collected from Dar es Salaam and Zanzibar in Tanzania and from Maputo in Mozambique.

The East Africa coast experiences tropical climate influenced by the monsoon winds in two distinct periods; Northeast monsoon (NEM- Kaskazi) and Southeast monsoon (SEM- Kusi) where, kaskazi and kusi are the local kiswahili names for the respective seasons. NEM blows from September to February and brings hot and calm weather while SEM blows from March to August and is characterised by strong winds, cool temperatures and rough sea. Rainy seasons occur between the monsoon periods with long rains occurring from March to July while short rains from October to December. Mean rainfall ranges from 508 mm to 1150 mm per year. Highest average wind speed is recorded between 9.3 - 9.8 knots and the speed increase during the morning and drops during the nights. Annual mean water temperature ranges between 28 and 32 °C (McClanahan, 1988; Linden and Lundin, 1996).

Laboratory experiments were carried out to assess the behavioural characteristics of juvenile crabs and interactions among conspecifics at the Kenya Marine and Fisheries Research Institute (KMFRI) **Paper III**. Mud crab culture experiments in net cages, mangrove pens and earthen ponds was done at Mtwapa Creek-north coast, at Kwetu training center's demonstration farm and at Makongeni, baraka community farm, Gazi Bay in the south (**Paper IV**). A combination of studies in various regions (Kenya and Tanzania) was used to estimate natural growth for mud crabs in East Africa. This included short-term laboratory studies at the Kenya Marine and Fisheries Research Institute (KMFRI) and Institute of Marine Science (IMS), Zanzibar, Tanzania; pond and mark-recapture studies at Mafia Island,

Tanzania and mud crab studies at the Kwetu training centre, Kenya. Also, more data was obtained from published work in South Africa (Hill, 1975; **Paper II**). Field ecological studies were carried out in the north coast of Kenya (Mtwapa, Mida and Kilifi Creeks) in Tanzania (Mafia Island) and in Mozambique (Inhaca Island) to assess habitat utilization, occurrence, predation mortality, population and dispersal of juvenile mud crab *Scylla serrata* (**Paper I**). Field and experimental surveys were carried out in the north and south coast of Kenya to establish the fishing dynamics of artisanal fisheries and the role of organized community groups in improving livelihoods through crab aquaculture (**Paper V and VI**). To assess sustainability, field studies were carried out along the coast of Kenya and Tanzania-Mafia island and Tanga and published data in Kenya was also used (Mirera, 2009; **Paper VII**).

2.2 Mud crab ecology

Habitat utilization and occurrence of juvenile mud crabs

There is no documented information in East Africa on the habitat utilization and occurrence of juvenile mud crabs within the different marine habitats. In fact, the settlement and important nursery habitats of young juveniles (< 30 mm CW) have not been described anywhere for *S. serrata* (Webley et al. 2009). Therefore to address this gap, field studies were carried out to assess juvenile crab distribution and abundance in different mangrove habitats in Kenya and Tanzania at different tidal and spatial scales (**Paper I**). Sampling was done in four sites in Mafia Island, Tanzania (MIMP, Utende, Kilole and Kichangani) and in two sites in Kenya (Mtwapa and Mida Creeks). Sampling was done both day and night using drop traps and line transects along the inner mangroves, mangrove fringes, back-flats and mangrove intertidal flat-boundaries (boundary separating mangrove forest and open tidal back-flats) and tidal creeks. In addition, sampling of intertidal and sub tidal seagrass beds was carried out using diving.

The transects measured approximately 20 m long and were searched 2 meters on each side giving an area of 80 m². Sampling took place at different tidal (high and low tide) and diurnal (day and night) times. In addition, monthly samples were carried at one site on Mafia Island, and at two sites in Mtwapa Creek in Kenya for one year. Crabs were collected using either small scoop nets or picked by hand at low tide and measured for carapace width (CW) to enable size classification. Transects were randomly replicated in the sites diurnally for different tidal cycles and care was taken to ensure replicates were separated by not less than 50 m from each other. For the purpose of this study, day represent tides receding between 7 am and 6 pm and night 7 pm to 6 am. In addition, in Kenya local fishers were engaged to collect juvenile crabs for stocking community aquaculture ponds and catch per unit effort (CPUE) was calculated based on time taken and number of crabs obtained.

Predation mortality on juvenile mud crabs

Natural mortality is highly prevalent in juvenile portunid crabs even though little information exists for mud crabs (Heck and Coen, 1995; Moksnes, 2002; Moksnes and Heck, 2006). Thus knowing how predation mortality changes during development of juvenile mud crab is essential to help understand how the loss of crabs in aquaculture compares with natural mortality rates. To assess how natural mortality change with the size of juvenile crabs, a tethering experiment was carried out in three sites at Mafia Island, Tanzania (Utende, Kilole and Kichangani) to test the effect of crab size and habitat using methods developed by Heck and Thoman (1981). The crabs used ranged between 6 and 87 mm CW and were subdivided into different size classes. Mangrove fringe and subtidal seagrass were used as the habitats in these experiments. Crabs used in the experiment were collected from Mafia Island Marine Park (MIMP) at night during receding tides. The crabs were attached to a monofilament nylon line or stainless steel wire with Super Glue (cyanoacrylate) at the top of the carapace (**Paper I**). Each crab was then tied onto a long line (4 m) while creating space to avoid interaction and the line was attached onto the ground. The experiments were initiated during the day and monitored for 24 hours for any predation. At the end of the experiment predation was only recorded if a broken piece of carapace remained on the line or if the line was cut for smaller size classes while unclear losses were excluded.

Dispersal and population dynamics

To understand a fishery, dispersal behaviour and population dynamics are key features to be investigated. Such information is lacking for mud crab fisheries along the East African coast. A combination of techniques using the mark-recapture principle was used to assess dispersal and population in East Africa (Le Vay et al., 2007; Bonine et al., 2008). The study was done in 2 creeks in Kenya (Mtwapa and Mida). Crabs (70-185 mm ICW) were collected by fishers using baited box traps. They were measured and tagged with buttons using Supper Glue according to Bonine et al. (2008), released at one central point and recapture rate monitored over two months period. Awareness was created to fishers to report any tagged crabs caught and site of collection during their daily fishing activities. In addition, fishers were engaged to carry out experimental collections after every two weeks.

In all the studies, Schnabel's census-method was used to estimate population size with mark and recapture data (Schnabel 1938): $N = \Sigma(C*M) / \Sigma m$ Where N is the population estimate, C number of individuals caught in sample t, M number of individuals in the population marked before sample t and m number of recaptures in sample t. The method makes the following assumptions: (1) the population is closed hence population size (N) is constant during the whole study period. (2) all individuals in the population have the same chance of being caught. (3) the probability of being caught is not affected by the marking, and (4) there is no loss of tags between two samples and all recaptured individuals are reported (Seber 1973).

Natural growth

Assessment of individual growth in mud crabs is key for assessing population growth for effective management of fished populations as well as aiding in estimation of growth periods in aquaculture and hence farm revenue estimates. Growth in mud crabs as in all crustaceans, involves a rapid growth in external size after moult (moult increment), when the exoskeleton is shed, and a longer period between moults (intermoult period), when growth of muscle tissue occur to fill the new shell. To develop a model of natural growth in East African mud crab, data of moult increment and intermoult period were obtained from different sources; laboratory, pond and cage studies and mark-recapture studies data in Kenya, Tanzania and published data from South Africa (Hill, 1975). To estimate natural growth in mud crabs, the functional relationships between pre-moult size (CW) and proportional growth increment at moult and intermoult period were assessed with linear and non-linear functions using least square estimates and assessing random distribution of residuals to determine the best fit. Segmented growth of *Scylla serrata* was estimated using the function between pre-moult size and proportional increment at growth to determine the post-moult size, and the function between pre-moult size and intermoult period to determine the time to the next moult. The growth of mud crabs was modelled in a stepwise procedure from 4 mm CW until a carapace width of approximately 240 mm CW (maximum size of *S. serrata*; FAO 2013). The growth curve was then transformed into growth in biomass using the functional relationships between carapace width and wet weight of crabs, which was fitted to a von Bertalanffy growth function using non-linear least-square methods (Paper II).

2.3 Mud crab fisheries

Fishing tactics and catch trends

A study to assess fishing tactics and use of traditional knowledge by artisanal crab fishers was conducted in the north coast of Kenya stretching from Mtwapa Creek to Marereni in Ungwana Bay. This provided information about social and fishing challenges that could possibly impact (positively or negatively) crab seed availability to aquaculture farms. Complementary approaches (catch data, experimental and fisher-based surveys) were used to investigate how fishing tactics of artisanal mud crab fishers could influence exploitation or management of the fishery. Primary data was obtained from surveys of artisanal mud crab fishers, through direct observation, and semi-structured and key informant interviews. To obtain information on movement of crab fishers (e.g. route complexity, distance covered, fishing time) fishers were provided with a Garmin GPS that tracked their movements. Also fishers were engaged to fish in familiar and unfamiliar sites to compare their migration and skill requirement in the fishery (**Paper V**). A socio-economic survey was also carried out to help understand the dynamics of the fishery. Fisher based surveys were conducted in Mtwapa, Kilifi and Mida Creeks and Marereni in Kenya. Data was obtained through direct observation, semi-structured interviews and key informant interviews.

2.4 Small-scale mud crab aquaculture

Mud crab culture was introduced in East Africa only about a decade ago (Mirera, 2011b). Hence the methods for culturing crabs are not well developed. Specifically, the methods and techniques to farm (wild caught) young juvenile crabs in low-tech, small-scale farms in East Africa is missing, and the aim of these studies was therefore to assess available methods from SEA, to identify those suitable for maximizing survival and growth using locally available materials in East Africa.

Laboratory study of cannibalism-effect of crab size and shelter

Cannibalism among mud crabs is a behavioural trait that is not well understood but comprise a major challenge to mud crab farming under different culture systems. A

laboratory experiment was conducted to compare techniques for reducing cannibalism related mortalities in mud crab culture. Four size classes of juvenile crab (A: 21–30 mm, B: 31–40 mm, C: 41–50 mm and D: 51–70 mm ICW) were tested in all possible combinations using four different substrata with varying degree of shelter (seaweed, plastic strings, bamboo tubes and open sand substratum) in 48 h trials (Paper III). A density of four crabs per tank was used in all treatments (either four of the same size class (control) or one predator crab of a larger size class and three smaller prey crabs).

Cage study of cannibalism- effect of density, size and shelter

In transferring the laboratory experiment to the field, a three-factor experiment was conducted to determine the effect of shelter, size grading, and stocking density on survival and growth in net cages (1 x 1 x 1.5 m) installed in earthen ponds (300 m²) at Kwetu training centre for 7 days. Bamboo tubes were used to provide shelter at a density of 4 pieces/m². Crabs of size 20 – 50 and 20 – 80 mm CW) were stocked at densities of 4 and 8 crabs/m² (Paper IV).

Pond and pen cultures – effect of shelter on growth and survival

To assess the effect of shelter and culture system on growth and survival of small juvenile mud crabs in different grow-out cultures, experiments were conducted in mangrove pens and earthen ponds at Kwetu training centre and Makongeni, Baraka conservation group. Four mangrove pens measuring 5 x 10 m (50 m²) and heights of 2.0 m were constructed according to technologies developed in SEA (Trino and Rodriguez, 2002; Primavera et al., 2010) in the mangrove forest. Four community earthen ponds measuring 10 x 10 m and 1 m deep were hired from the community for use during this experiment. Stocking in the ponds and cages was done at 2 crabs/m² and the culture period was between 60 and 90 days and bamboo tubes were used to provide shelter in all sheltered experiments in the different culture systems (Paper IV).

Socio-economic aspects

Organized Community Groups (OCGs) have been used as an entry point for small-scale mud crab culture in East Africa. A study was conducted to understand the social, cultural, economic and policy implications of small-scale mud crab farming along the Kenyan coast as key drivers for crab aquaculture. Four OCGs with previous experience in mud crab culture were involved, i.e. Dabaso, Ihaleni, Majaoni (both from north coast) and Makongeni (from south coast). Focused group discussions were used to collect primary information from the OCGs that were supplemented with key informant interviews as detailed in Bunce et al. (2000) and de la Torre-Castro et al. (2007). Focus group discussions were used with open-ended questions to prompt participants into free discussions on mud crab culture issues. Members who participated in the focus group discussions were randomly selected in a group meeting to avoid bias in representation. The number of participants in a focus group discussion ranged between 5 and 10 and two focus group discussions were conducted per group. Key-informant interviews were also conducted for each of the OCG, involving knowledgeable people in the society who command some respect and could be taken as spokes persons of the community (Paper VI).

To assess markets and prices available to mud crab farmers in East Africa, informal interview were carried out with crab fishers, crab fattening farmers, middlemen, exporters, market salesmen and hotels in Mombasa and Malindi area in Kenya, in Dar es Salaam, Mafia and Zanzibar in Tanzania, and in Maputo in Mozambique (Paper VII)

Sustainability issues of mud crab farming in East Africa

To compare profit margins of pond and cage farming of mud crabs in Kenya and Tanzania, cost-revenue analyses were carried out estimating the total cost to produce 450 market size crabs (i.e. 500 g each) with the two culture methods. Data for pond culture estimates was obtained from pond experiments in Mafia Island, Tanzania and Mtwapa Creek, Kenya while cage-farming data was obtained from published experimental work on drive-in cages in Kenya (Mirera, 2009). Pond farming estimates were based on farming 0.5 to 2.0 g juvenile crabs in 15 x15 m earthen ponds for 9 months. In cage farming, the estimates were based on consecutive 3-

month culture periods, growing 300 g seed crabs in 200 individual compartments. Growth in the cultures were simulated using the model of natural growth in *S. serrata* (Paper II). Survival rates in both culture systems was assumed to be 90 % month⁻¹, which is higher than presently obtained in these systems in East Africa (Mirera 2009, Paper IV). Realistic estimates of all costs, including initial construction costs of the culture facilities and all labour costs in Kenya and Tanzania were used to enable mud crab farming to be comparable to other alternative sources of income (Paper VII).

To establish the profitable and sustainable production scale of small-scale mud crabs in East Africa, analysis were made using the cost-revenue assessment model explained above for profitability in different pond size ranging from 50 – 500 m² (Paper VII). Also considered in this assessment was the availability of wild collected seed-crabs and local feed sources and possible effects on the ecological functioning of the mangrove environment. To assess how feed and seed may become limitation factors when scaling up, a grow-out pond farm at Mafia Island in Tanzania was used since information on feed and seed resources were readily available (Nyqvist 2011, Hamad 2012). The scale assessment was made at two price-scenarios, USD 2.5 and 5.0, representing the high end of crab prices offered by hotels at Mafia Island and in Dar es Salaam, respectively.

An assessment was also made to establish the size requirement for market size crabs in East Africa and how that differs from SEA. The resources required and sustainability aspects of producing different sizes of crabs as per the market needs using the established growth model was evaluated (Paper II; VII). To assess how cost changes with crab size at harvest, the total number of seed crabs and the total amount of feed required was estimated (using a feeding-rate of 10 % of the biomass of crabs per day), and the total cost of seed crabs, feed and theft prevention (employing a night guard one month before the crabs reach 300 g and thereafter) to produce 100 kg of mud crabs harvested at either 300, 500, 700 or 1000 g body weight. Seed crabs of 15 mm CW, an average mortality of 10 % per month, and a 10 x10 m pond for all size-classes was used.

3.0 Results and Discussion

3.1 Mud crab ecology

Habitat utilization and occurrence of juvenile mud crabs

Intertidal mangrove flats, i.e. the open tidal flats in the mangrove system, are ecologically harsh ecosystems due to lack of shelter habitats, adverse physical conditions like desiccation, high temperatures, high or very low salinity levels and at times hard substrate (Walton et al., 2006a). Despite the adverse conditions, these ecosystems serve as valuable nursery grounds for fish and shellfish due to the fact that they offer food generated mainly through a detritus based food web and large predatory fish cannot easily access these sites mainly due to shallow waters often and the protection offered by mangrove stands (Hill et al., 1982; Ronnback, 2001; Huxham et al., 2004; Mirera et al., 2010). In the current study, intertidal mangrove fringes, back-flats and intertidal mangrove boundary zones were identified as primary nursery habitats for juvenile mud crabs both in Kenya and Tanzania (Mafia Island) where newly settled mud crabs (4-30 mm CW) were found in large numbers (**Paper I**). This is the first description of the nursery habitat of young juveniles of *S. serrata*.

At Mafia Island (Tanzania), young juveniles (4-30 mm CW) were found to aggregate in mangrove back-flats and fringes at night during low tides in small tidal pools in high numbers (up to 50 crabs/100 m² in some areas). Sampling of the same habitats during the day revealed very low numbers. Mark and recapture studies demonstrated that most young juveniles left the nursery habitats during the day for subtidal habitats, but returned in high numbers the following night with the rising tides. Extensive sampling of subtidal seagrass habitats during the day did not collect any juvenile mud crabs indicating that other subtidal habitats were used during the day, or that their abundance was too low to be collected with this method. Larger juveniles (40-100 mm CW) were collected at night in tidal creeks and along the mangrove fringes during receding tides at densities of up to 5-crabs/100 m² and were probably residing in mangrove burrows during the day. No juveniles were captured during the day presumably because they dispersed into subtidal habitats until the following night. However, in Kenya juvenile crabs (10-50

mm CW) occurred both during the day and at night though at lower abundances (up to 7-crabs/100 m²). At low tide they were found in shallow burrows at the zone separating the mangrove forest and the start of the open intertidal flat in the soft mud, where they could be retrieved by hand with minimal effort (Paper I; Figure 2). They also occurred on the surface of the mud under loose mangrove detritus, decaying leaves or pieces of mangrove wood and at times in areas colonised by gastropods (*Terebralia palustris*) on the seaward side of intertidal mangrove fringe (Figure 3). The results from both Kenya and Tanzania are of significance for the mud crab fisheries and aquaculture in East Africa since the nursery habitat of small juvenile *Scylla serrata* has never been described in literature for this region or elsewhere (Webley et al., 2009).

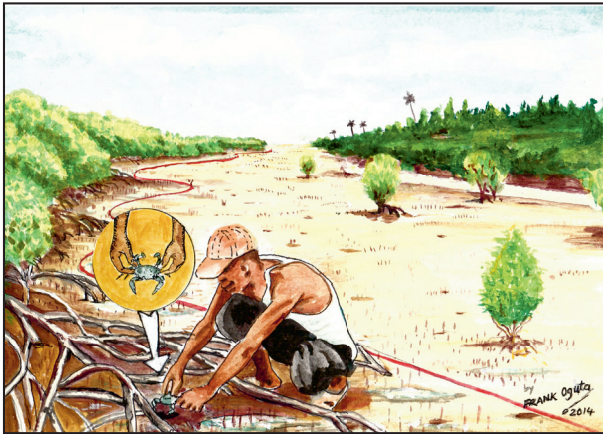


Figure 2: Picture showing the intertidal mangrove boundary zone landwards (indicated by red line) where juvenile mud crabs were collected at low tides and at receding tides in Mtwapa Creek, Kenya (Picture drawn by Francis Oguta)

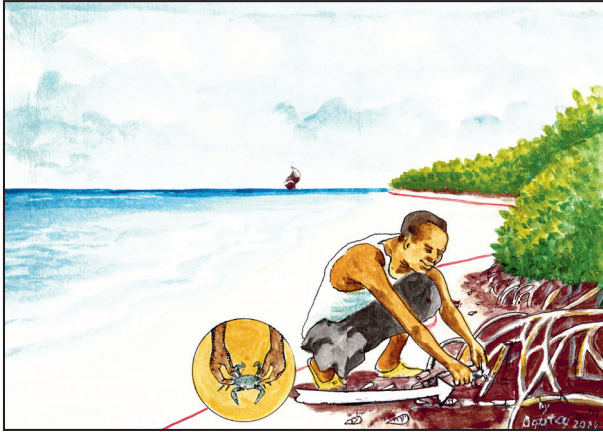


Figure 3: Picture showing the intertidal mangrove boundary zone seawards (indicated by red line) where juvenile mud crabs are collected at low tides and at receding tides in Mida Creek, Kenya (Picture drawn by Francis Oguta)

The results from monthly sampling of small juvenile mud crabs from Tanzania and Kenya demonstrated that *S. serrata* in this region spawn and recruit in all seasons, as juveniles <30 mm CW were collected during all months of the year. The abundance of the smallest juveniles (< 20 mm CW) collected on Mafia Island indicated seasonality in juvenile recruitment with higher abundance of small juveniles (<10 mm CW) from May to October. Although the data was only from one site during 2009, subsequent extensive sampling in 2010 showed the same seasonal pattern. The period of higher recruitment on Mafia Island coincided with the SE monsoon when the prevailing wind change from north to southwest, indicating that the seasonal recruitment may also be a result of changes in larval supply (Paper I). Thus no clear seasonality in recruitment of juvenile mud crab juveniles, which, is consistent with a continuous spawning period in mud crab reported from Kenya (Onyango 2002) and the northeast coast of South Africa (Robertson and Kruger, 1994).

Size specific predation mortality

Predation mortality is listed as one of the factors leading to low survival in portunid crabs in the wild and is highly prevalent in juvenile crabs before they pass the predation bottleneck (Heck and Coen, 1995; Moksnes and Heck, 2006). The

present study showed that relative estimates of predation mortality decreased strongly with the size of the crab, with over 60 % loss in 24 hrs on the smallest size class (6-12 mm CW) and with no detectable loss of prey crabs greater than 70 mm CW. Although these rates may overestimate the natural mortality rates, they demonstrate that predation mortality in juvenile mud crabs decrease exponentially with size, consistent with studies in other portunid crabs (Pile et al., 1996; Moksnes et al., 1998). The results are also in line with the cannibalistic finding in this study that tended to decrease with size of prey crabs (Paper III). This suggests that predation can cause a bottleneck (Moksnes et al. 1998; Smith and Herrnkind 1992) in the population in early juvenile stages of *S. serrata*. Consequently, the size when the behaviour of juvenile *S. serrata* change from using tidal pools to subtidal habitats at night as observed in Mafia Island, Tanzania, coincide with the sizes that received a strong size refuge from predation.

Habitat complexity has been observed to decrease relative predation mortality (Herrnkind and Butler, 1986; Fernandez et al., 1993; Moksnes et al., 1998). However, in the current study, no significant difference could be found between the two habitats, the mangrove fringe and the subtidal seagrass. Structural complexity was relatively higher in the subtidal seagrass, which had a mix of several species of seagrass and algae with different morphology that created a complex canopy that covered almost 100 % of the bottom. Whereas the mangrove fringe habitat in Mafia island, Tanzania was dominated by pneumatophores of *Sonneratia alba*, and occasional patches of *Halodule sp.* and filamentous algae (*Chaetomorpha crassa*). The lack of a positive effect of habitat complexity in the present study may be due to the fact that the mangrove fringe was only accessible to aquatic predators during high tide conditions, providing a temporal refuge from predators. Temporal avoidance of predators may also be the ultimate factor behind the nocturnal tidal migration of young juvenile mud crabs to intertidal mangrove back-flats, observed on Mafia Island and Mtwapa Creek in Kenya.

These results indicate that collecting the crabs at the smallest size possible would minimize the negative impact of seed-crab collection on local crab populations depending on the method of collection used (i.e. by avoiding methods that generate by-catch). If the mortality rate of small crabs in the culture systems is lower than the natural mortality, grow-out farming could increase the overall production of crabs in an area by removing young crabs from the environment during a period when natural mortality is high.

Natural growth

The use of a step-wise growth function method, though not used previously to describe growth in crabs, has the advantage of taking into account the discrete, segmented growth observed in crustaceans as it was found to provide a better description of growth in spiny lobster than traditional size at age models adopted for fish species (Ehrhardt, 2008). However, the challenge of the method is to obtain good data to describe the growth variables, in particular for assessing the intermoult period, which is notoriously difficult to measure in the field.

The results from the present study showed that proportional increment of carapace width at moult was fairly constant around 20 % similar to observation by Mirera and Mtile (2009). However, the current study observed a weak decreasing trend in CW increment with size of the crab. Intermoult period increased exponentially with age from around 7 days in young juvenile crabs to over 3 months for adult crabs. This growth pattern is consistent with studies of other portunid crabs and crustaceans where growth per moult decreases, and the length of the intermoult period increases with age (Millikin and Williams, 1984, Ehrhardt 2008). The modelled segmented growth function resulted in a sigmoid growth pattern in carapace width, with an exponential growth in juvenile mud crabs slowing in adult crabs towards an asymptote, whereas growth pattern in biomass was exponential also in crabs weighing over 1 kg (**Paper II**).

The modelled growth appears to be consistent with other reports of growth in *S. serrata*. The estimated intermoult period for 3rd instar crabs (6.9 days) is similar to growth rates measured in laboratory hatched *S. serrata* in northern Australia at similar temperatures and salinities (5.5 - 7.6 days; Ruscoe et al., 2004). The results of the model suggests that *S. serrata* will reach 300 g and sexual maturity approximately 9.9 months after settlement, and a commercial size of 500 g after 12.4 months. The growth model allowed a comparison of growth rates in different culture systems from the literature and indicated that growth in cages in East Africa was below estimated natural growth, while growth in ponds was similar to natural growth even though growth in ponds in East Africa was lower than that observed in SEA for the same species (**Paper II**). In **Paper IV**, juvenile mud crabs kept in replicate pen and pond systems with shelter and surplus of food grew from on average 7 to 43 g (in pen cultures) and from 23 to 74 g (in pond cultures) in 64 and 67 days, respectively. The presented growth function estimates that 62 and 69 days

are needed for the same growth, respectively, only 7 to 8 % difference from the measured growth.

Mud crab dispersal and populations

Studies carried out in Mtwapa and Mida Creeks in Northern Kenya tagged 396 crabs ranging between 50 and 160 mm ICW. The results indicated that 60 % of all recaptured crabs had moved less than 1 km and half of those had only moved 0.5 km from the release point. Less than 20 % of all the recaptured crabs moved more than 2 km (maximum distance being 2.5 km) **Figure 4**. This implies that crabs only covered short distances i.e., less than 1 km from release locations. Similarly, in Mafia Island, Tanzania, juveniles and adult crabs (20 – 140 mm ICW) showed limited dispersal distances with 75 % of the recaptured crabs remaining within the area of release and less than 5 % moving more than 2 km (Björkvik 2010). The findings are inline with Hill, (1994) who observed that due to the sedentary nature of *S. serrata* with the exception of female crabs during spawning, movement is minimal.

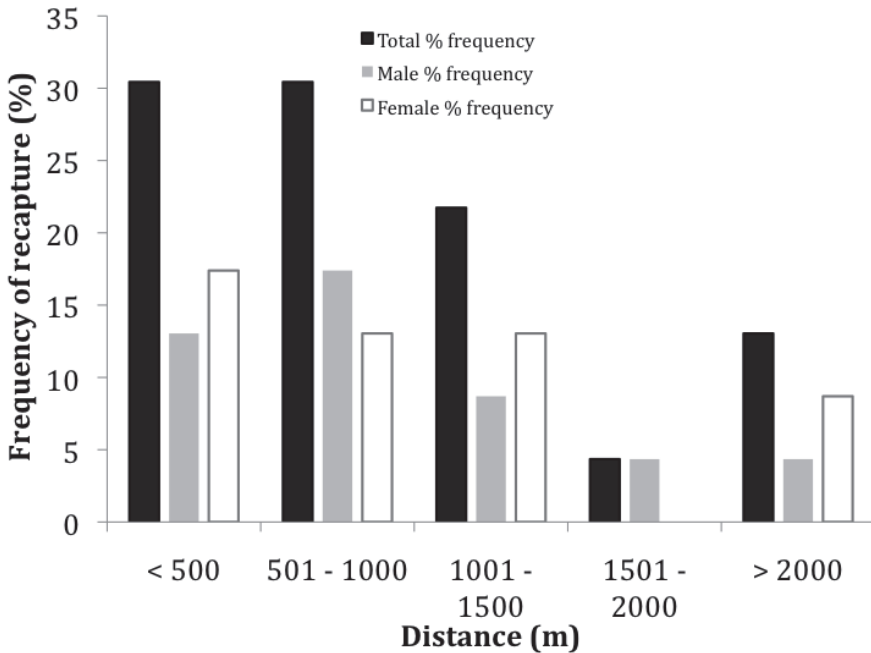


Figure 4: Dispersal distances of all mud crabs and different sexes as percentage frequency of recaptures in Mtwapa and Mida Creeks, northern, Kenya

In a study by Le Vay et al. (2007), some crabs of *Scylla spp.* were observed to cover longer dispersal distances (12.3 km) an aspect that may be associated with the longer period under which his studies were conducted and the larger number of crabs tagged. However, the current results may not rule out the fact that mud crabs could move larger distances since some of the crabs might have been recaptured far away and were not reported or some crabs may have lost their tags and could not be identified. Lack of chelipeds was observed to limit dispersal of mud crabs leading to movement of less than 0.2 m in 24 hours. However the results did not show any clear dispersal distances between sexes as established by Hyland et al., (1984; **Figure 4**).

All tagged crabs (n = 396) had a sex ratio of 1:1.02 (male to females respectively). The ratio did not vary significantly by site (Mtwapa Creek: 0.99:1, Mida Creek: 1.1: 1 respectively). No female was captured with eggs during the study period.

Due to the limitation of the tagging method (button and glue which could be lost after moult and therefore a short time was available for tagging and monitoring the experiment) used in the study, only 270 crabs were tagged in Mtwapa and 126 in Mida Creeks. An average of 17 % and 7 % were recaptured in Mtwapa and Mida respectively. These recapture rates were higher than those recorded by Pillans et al., (2005), an aspect that could be associated to the small size of the creek and the level of exploitation. Similarly, in Mafia Island (Tanzania), a total of 525 crabs were tagged and 4 % were recaptured (Björkvik 2010). Population estimation using Schnabel's census method (Schnabel, 1938) indicated that 1,855 crabs existed in Mtwapa (5 km area) and 1,714 in Mida Creeks (4 km area). While in Mafia Island, Tanzania a similar study estimated 16,000 crabs in 11 km area. These populations estimates indicate that there is a likelihood of higher fishing pressure in the creeks or there are risks of localised overfishing that may be caused by the fishing strategies of the artisanal fishers which may require specific site management (Mirera, et al., 2013). However, more studies are needed to ascertain this observation.

3.2 Mud crab fisheries

Fishing and fishing methods

The minimum and maximum sizes of adult mud crabs landed by artisanal fishers in the north coast of Kenya in the current study (0.25-0.9 kg; **Paper V**) appeared to have declined compared to observations made 2-3 decades ago on the south coast of Kenya where sizes varied between 0.5 -1.5 kg (Muthiga, 1986; Onyango, 2002). This may be taken as an early sign of overexploitation. Considering the growing dependency of the fishery for provision of aquaculture seed and increasing demand for market size crabs (Barnes et al., 2002; Mirera, 2011b), the resource maybe constrained i.e. crab fishers may make more trips to meet the growing demand leading to high exploitation levels. No management of the crab fishery is in place at present and measures should be taken to ensure that the stock is not overused.

The choice of a fishing area and method of fishing for mud crab fishers depends on the target crabs being fished in addition to skill and equipment required. More than 60 % of the fishers fish for adult mud crabs in burrows within the mangrove at low tide using traditional hooks and sticks. Other fishermen use baited traps, scoop nets or seine nets along the seaward mangrove fringe and channels. Almost all crab fishers practice fishing by foot with limited use of equipment and a wide local knowledge of fishing area as observed in other fisheries (Jones et al., 2008; Ochiwo et al., 2010). The study established that fishing is never random; it follows specific patterns mainly depending on the knowledge of the fisher on preferred mud crab areas where the harvest is likely to be high or hereditary burrows (Dumas et al., 2012; **Paper V**).

Artisanal crab fishing in Kenya, mainly occur during the day (early morning) rather than in mid afternoon or evening. Fishing is also influenced by tidal regimes irrespective of the fishing technique applied, a fact supported in the literature (Moser et al., 2005). Fishers preferred to fish during low spring tides and return at high spring tides. Only limited fishing takes place during neap tides (*locally called maji mavu*) since crabs found in burrows at neap tide are in the moulting period or

have just moulted and thus currently have no market value locally despite their high demand in Asia (**Paper V**).

The habitats for collection of juvenile crab differed with those of adults as detailed in **Paper I** and to a lesser extent the collection methods however, knowledge requirement was similar. Juvenile crab collection mainly included scooping with nets at receding (falling) tides, hand collection from shallow burrows or collection from under the *Telebralia* shells or mangrove roots.

The similarity level of knowledge and technical skills and equipment used by artisanal mud crab fishers suits them in engaging in the business of supplying aquaculture farmers with crab seeds to stock culture facilities.

3.3 Small-scale mud crab aquaculture

Cannibalistic interactions

a. Shelter

Results obtained in 48 h laboratory experiments indicated that cannibalistic interactions between juvenile mud crabs were strongly influenced by availability of shelter. However, shelter had less influence on controlling cannibalistic rates in the smallest size class (20-30 mm CW). In contrast, cannibalism on larger prey crabs (31-50 mm CW) decreased by over 50 % in the presence of shelters compared to sand substrate (**Paper III**). A set of experiments done in the earthen ponds with net cages over a period of 7 days also showed a strong influence of shelter on survival i.e. shelter decreased cannibalism and mortality by 26 %. In contrast to the results in the lab and cage experiments, there was no significant effect of shelter on the estimates of survival in the pond and pen study (**Paper IV**). This may partly be explained by the possible high initial cannibalistic rates on the smaller crabs (due to the presence of relatively larger crabs), and the size-dependent shelter provided by bamboo-tubes (**Paper III**).

In this study, several types of shelters that are available to local farmers in East Africa (bamboo tubes, macroalgae, plastic ribbons) were found to reduce cannibalism significantly in juvenile mud crabs, similar to earlier studies (Ut et al.

2007a, b). A positive correlation of presence of shelter materials on cannibalism has been found by a number of studies (Moksnes, et al., 1998; Moksnes, 2002; Nystrom et al., 2006). The significance of shelter suggests that care should be taken to provide different types of shelter that provide refuges for different size-classes of crabs to improve survival. Comparisons of survival rates of mud crabs in aquaculture studies with and without shelter from the literature show only a marginal higher survival rates in cultures with various types of shelter compared to studies without any shelter (on average 70 % and 64 % survival, respectively; **Paper IV**). This lack of stronger shelter effect in larger scale studies warrants further investigation. Also availability of shelter was observed to increase growth rate in pen culture systems in the present study (**Paper IV**).

b. Size class

In laboratory experiments, the response of prey crabs to experimental treatments was strongly size-specific. Cannibalism on the smallest size class (20-30 mm ICW) increased 10 fold in the presence of the largest predatory crabs (51-70 mm) compared to control treatments. In control treatments, where the relative size difference was below 50 %, cannibalism was low ($< 2 \% 48 \text{ h}^{-1}$) but increased with increasing size difference between prey and predator to 27 % mortality 48 h^{-1} in the presence of the largest predators, representing a mean size difference of approximately 140 % between prey and predator. In larger prey sizes (31-50 mm ICW), cannibalism did not increase in the presence of larger predators, suggesting that cannibalism affected mainly newly moulted crabs (**Paper III**). The low cannibalism on hard, inter-moult crabs could in part be explained by a smaller mean size difference between prey and predator crabs in these treatments (28 – 70 %) compared to the smallest size class, but also that a larger size difference is required to allow cannibalism on hard crabs for the larger prey crabs.

Using small nursery cages, we assessed how size-class separation affected cannibalistic rates in small juvenile crabs (20-80 mm CW) in short (7 days) experiments. The study found significantly higher losses of crabs in treatments with a large size-ratio (20-80 mm CW) than in treatment with only smaller crabs (20-50 mm CW) on average 42 % and 29 % week^{-1} , respectively (**Paper IV**). The results suggest that separating small and larger juvenile crabs may increase survival with on average 31 % week^{-1} in the nursery cages, a result that is consistent with the laboratory studies (**Paper III**). In portunid crabs, cannibalism between similar sized

crabs in intermoult is minimal and only occurs at relatively low rates on newly moulted, soft and defenceless crabs (Moksnes et al. 1997, 1998). However, above a critical size-difference, cannibalism can affect hard intermoult prey crabs that usually result in many times higher cannibalistic rates (Kurihara et al. 1988; Moksnes et al. 1997; Fernandez 1999; Moksnes 2004a; Marshall et al., 2005). Also the level of cannibalism has been observed to reduce through trimming or removal of chelipeds (Quinitio and Estepa, 2011). Thus there is need to grade juvenile crabs at stocking to improve survival in addition to size grading during the culture period to attain maximum survival

c. Density

The present study did not find a significant effect of crab density on proportional loss of crabs in net cages (on average 33 and 39 % at 2 and 4 crabs m⁻², respectively; **Paper IV**). Lack of a negative effect at the higher density may be associated to a potential effect of density being weakened by the many replicates that were excluded from the analyses because there were holes in the net. It is also possible that the tearing behaviour was enhanced at high densities resulting in a loss of the replicates where density-dependent cannibalism would have been the highest. In mud crabs similar to other portunids, agonistic behaviours increase with density (Moksnes et al. 1997; De Albormoz Nuno, 2003; Moksnes 2004a), and over crowding has been observed to increase cannibalism rate in mud crab culture systems (Baliao et al., 1981). A number of aquaculture studies also have found decreasing survival rates at higher stocking densities of mud crabs (Genodepa 1999; Trino et al. 1999a; Trino and Rodriguez 2002). Using growth models to compare growth and survival in mud crabs from aquaculture studies in the literature we show that shelter may have a stronger effect on growth than has been previously thought, whereas crab density appear to be more important for survival (**Paper IV**).

Effect of culture systems

The study assessed the suitability of small net-cages as nursery culture systems for young juvenile mud crabs, facilitating recovery and size grading of crabs before they are placed in larger grow-out system. Even though we used cage net material of the highest quality available in the local markets (monofilament nylon of approximately 500 µm thread), most of the cages quickly developed holes through which the crabs escaped into the larger pond area (**Paper IV**). It was unclear if the holes were created

by the juvenile crabs inside the cages, or by other wild decapods (e.g. hermit crabs) that were present in the pond. It may also be possible that wild seed crabs, in comparison to hatchery reared crabs used in similar systems in Southeast Asia (Rodriguez et al., 2007), may be more aggressive in the artificial cage environment, and more likely to tear the material. Based on the high number of broken cages resulting in loss of crabs, and the high initial cost of the cages, the use of net-cages as nurseries for small wild-caught seed-crabs (20-80mm ICW) in grow-out aquacultures may not be recommended at this stage for small-scale farms in East Africa.

Assessment of growth and survival in long-term studies (2-4 months) using mangrove pens and earthen ponds showed overall low recovery of crabs (4-26 %) with no significant effect of culture-system on survival while growth rate was generally high in both systems, but significantly lower in pen systems without shelter (**Paper IV**). Mud crab recovery rates found in the earthen ponds and mangrove pens in the present study (equivalent to 41-59 % survival month⁻¹) were similar to previous studies in East Africa, but lower than survival rates found in similar studies in Southeast Asia - on average 73 % survival month⁻¹ (**Table 1**). Since theft and escape from culture systems were unlikely, and feed and physical conditions in the cultures were within acceptable levels, mortality due to cannibalism is the most likely explanation for the high losses in the present study (**Paper IV**). Thus the main reason for the apparent high rates of cannibalism in the pond and pen studies were most likely the large size-ratio of seed crabs used (**Paper III; IV; Table 1**).

Table 1: Comparison of proportional survival and growth rates for different *Scylla* species from different studies. The calculations are made using the final survival recorded in the studies and the culture period. The last column shows the proportional difference in duration between the measured and modelled duration. Four species are included, *Scylla serrata* (Ss), *S. tranquebarica* (St), *S. olivacea* (So), and *S. paramamosain* (Sp) in mono- and mixed crab cultures. Only longer studies (≥ 1 month) carried out in larger culture system have been included in the comparisons.

Reference	Scylla spp.	Country	Culture system	Density (crabs m ⁻²)	Seed size range (mm)	Final Size Ave (g)	Culture period (d)	Prop. survival month ⁻¹	Rel. growth (Model/S study)
Present study	Ss	Kenya	Pens	2	11-63	26	64	0.42	0.93
					6-54	17	78	0.40	0.64
Mirera, 2009	Ss	Kenya	Ponds	2	9-85	74	67/126	0.59	0.93
					4-70	53	70/134	0.54	1.12
Mwaluma, 2002	Ss	Kenya	Pens	2	85	146	90	0.67	0.17
					20-100	-	120	0.51	-
Trino and Rodriguez, 2002	Ss	Philippines	Pens	0.5	51-54	317	160	0.90	1.30
					316	160	0.81	1.29	
Rodriguez et al., 2007	Ss	Philippines	Ponds	3	12	16	30	0.54	2.61
					5	10.5	30	0.37	2.13
					5	13	30	0.70	2.36
Keenan, 1999	Ss	Philippines	Ponds	1.5	-	370	120	0.86	2.09
Trino et al., 2001	Ss	Philippines	Ponds	1	-	-	156	0.86	-
Primavera et al., 2010	Ss	Philippines	Pens	0.8	49-52	181	153	0.75	0.91
					0.5	401	120	0.99	2.21
Trino et al., 1999a	Ss & St	Philippines	Ponds	1.5	35-43	380	120	0.88	2.15
					3	367	120	0.75	2.11
Baliao et al., 1999b	Ss & St	Philippines	Ponds	1	52	210	90	0.91	1.7
Primavera et al., 2010	So	Philippines	Pens	0.8	32-63	88	153	0.75	0.27
Ut et al., 2007b	Sp	Vietnam	Ponds	0.5	29.3-30.3	198	106	0.67	1.83

In contrast to the apparent low survival rates in the pond and pens, growth rates of the crabs after 2-3 month was high, similar to estimated natural growth for East African mud crabs, and similar to many other studies in SEA with different species of mud crabs, although growth in *S. serrata* appear to be higher in SEA (**Paper II, IV**). In the ponds, growth rates was high in treatments with and without shelter (93-112 % of the estimated natural growth), whereas in the pens, growth was only high in treatments with shelter (108 % of natural growth), but significantly lower in treatments without bamboo-tubes (64 % of natural growth). The reason for the strong positive effect of shelter on growth only in mangrove pens may be related to tidal changes of available areas in the pen system that could have resulted in density-dependent interference between crabs that affected feeding and growth negatively. In contrast to the pond cultures, only the channels in the middle of the pen were submerged during low tides in the mangrove pens, at which time most crabs were found to concentrate in the channel. This is supported by a meta-analysis of the literature that showed that crab cultures which provided various types of shelter in the cultures on average had 83 % higher relative growth rates compared to studies that were not using shelter (**Paper IV**).

3.4 Socio-economic aspects and sustainability implications

Social and demographic characteristics

Mud crabs are an important livelihood activity for many households along the coast of Kenya. An average household of crab fishers and crab farmers ranges between 6.7 and 6.8, respectively, hence similar to what has been recorded for other fisheries along the coast of Kenya (Ochiewo et al., 2010; **Paper V**). The crab fishery is men dominated (90.3 %). Also only half of the organised community groups (OCG) undertaking mud crab farming in cages had more than 30 % women representation, which is the minimum threshold according to the current national constitution for Kenya while the others had under-representation. Equally, only one OCG (Makongeni, baraka conservation) had a woman as chairperson and treasurer while all other groups had men in all administrative positions with women existing only as members (**Paper VI**). The study results differ from those of other studies like

northwest New Caledonia where women played a central role in mud crab fishing (Dumas et al., 2012).

Artisanal crab fishery involving market size crabs was practised by fishers aged more than 25 years while those with less years mainly engaged in collection of sub-adults for sale to crab farmers. Most crab fishers in Kenya aged between 23 and 55 years thus differing from finfish fishers whose age composition range between 15 and 45 years (Fulanda et al., 2009). The composition of crab farmers (crab fattening in cages) was similar to that of crab fishers, may be an indication of doubling roles i.e. crab fishers turning into crab farmers. Indeed, based on the technique requirement for crab fishers, they are best suited to participate in crab farming due to the additive effect as opposed to relatively new farmers (**Paper V**). In addition, the crab fishery appeared to have a limited number of entrants, a fact that was associated to the extensive skills required and the difficult mangrove environment. The fact that skills had to be handed down from one generation to another (heredity) and in some cases from close friends through peer learning may limit participation (**Paper V**). Such limitation in entry to the fishery may be constitute a self-regulating mechanism for the fishery (management), but a constraint to aquaculture development i.e. limited workforce to collect required crab seeds for stocking aquaculture production systems.

The study established that 65-74 % of crab fishers along the Kenyan coast had only attained primary school education while 0-5 % attained secondary education depending on region. Similarly, the study showed varied levels of formal education in the OCGs undertaking mud crab aquaculture ranging between 5-80 % for secondary education. Most of the community members participating in mud crab farming having formal education beyond secondary and up to college level were mainly men; women contributed only 1 % while youth (24-40 years) comprised 80 % of the educated population (**Paper VI**). The observed gender disparities in level of education suggests that there is a constraint in access to education for women at the coast of Kenya which may be a major contributor to their marginalization in decision-making (Ndanga et al., 2013). Lack of education and training for women has also been observed in Southeast Asia, where women have over time assumed critical role in aquaculture development (Nash, 1995; Ahmed and Lorica, 2002).

Governance and policy issues

The number of individuals involved in crab farming using cages in OCG in Kenya was observed to decrease overtime, a fact that was associated to the youth who seek other jobs and moved from the villages. In addition there was often conflicts among crab culturists. The high number (23-80 %) of women involved in crab culture was linked to the significant participation of women in aquaculture development. Ndanga et al (2013) established that women have a greater opportunity in aquaculture developed through participation as fish farmers or marketers in central and western Kenya. The decline in number of crab farmers was associated to a number of factors i.e. the length of time taken to realise financial benefits, and thus a diversion to other income activities, the nature of work (tedious and dirty) discouraged others, group conflicts as some, especially men, looked at aquaculture as primarily a female activity or for those who can not for one reason or another go fishing (**Paper VI**). Most importantly, analyses also showed that profitability of crab farming in individual cages are low (**Paper VII**; see discussion below).

Communities (OCG) with less training and experience in mud crab culture faced high mortalities in culture systems (sometimes more than 60 %) and theft leading to loss of hope among group members. Such mortalities were often linked to poor handling, poor construction of culture structures leading to cannibalism or escape, inadequate feeding or feeding at the wrong times. It is therefore important to teach farmers the basic aspects of crab cultivation and supply them with the most recent technologies in aquaculture to maximize survival and growth and improve the financial situation while enhancing social welfare (Jiang, 2010). Also government extension support was indicated as weak in Kenya even though it has been observed to be key in adoption of technologies elsewhere (Lionberger and Gwin, 1991). Therefore in addition to developing appropriate policies for provision of extension services, its important to have simple culture manuals developed in all local languages (and Kiswahili and English) to facilitated adoption of technology especially to farmers (Mirera and Samoilys, 2008).

Consequently, the present investigations have indicated the need to develop policies that will guard small-scale mud crab farmers through provision of un-conditional user rights to operate in the culture areas. Mud crab farmers were initially not received well by the Kenya Forest Service (KFS) that holds the mandate of protecting all the mangrove forests in the country. This became and is still to some

extent a major hindrance to the development of small-scale mud crab farming. However, the situation has improved through the Kenya Forest Act of 2007 that introduced participatory management of the mangrove forests (co-management) where user groups like small-scale mud crab farmers were allowed. The bottleneck to the new strategy is the aspect of user groups being required to make payments (levies) for activities carried out in the mangrove environment. The introduction of such forest user levies are likely to put out small-scale mud crab farmers who have nurtured the technology and give way to rich people who will go commercial to attain profitability, maybe at the expense of the environment and livelihoods of coastal communities (Lewis, 1998; Ahmed and Lorica, 2002; Primavera, 2006).

Also the current study has established that use of earthen ponds may be more profitable to the farmers compared to cage farming (**Paper VII**). However, the initial investment costs for pond cultures are relatively high and hence may not be affordable to local communities along the East Africa coast. Thus such high investment costs and environmental effects of larger production ponds may require initial subsidies or loans, and elaborate clearance/permission that is not likely needed in cage farming.

Economic and sustainability issues

Earthen pond and drive-in cage culture systems differ strongly based on the initial investment costs and amount of labour needed during the culture period. Large initial investment is needed for the construction of ponds, including tools and labour, and the material costs, in particular the net fence around the pond to prevent crabs from escaping. A good constructed earthen pond with good soil can last up to approximately 10 years with minor yearly repairs. The construction costs represented 36-37 % of the total cost per harvest (crop), whereas the costs of daily labour maintaining the culture (on average 2.4 h per day) constituted approximately 41-42 % in Tanzania and Kenya respectively (**Paper VII**). In addition a night watch (guard) close to harvest for 2.5 months (labour) constituted 12 % and seed stock 12 % and 8 % in Kenya and Tanzania, respectively. Trino et al. (2001) found that to produce mud crabs in one hectare, 17.4 % of the total investment costs represented materials and pond repair per crop although construction labour was not factored, cost of crab seed represented 31.6 % and caretaker costs 1.1 %.

In contrast, the cost in cage farming involved only a smaller initial investment to construct the cages, but very high labour costs per growth cycle for maintenance. The labour costs to maintain the crabs in 200 individual cages for three 3-month growth-cycles represented approximately 68 and 69 % of the total cost per harvest in Kenya and Tanzania respectively. Also the need for a night guard during the production cycle to prevent theft of the easily accessible crabs constituted approximately 21 % of the total cost per harvest. However, the total cost per 3-cycle harvest of crabs seeds and cage construction was small (4-6 % in Kenya and Tanzania respectively). In cage culture, high labour cost required is a result of the time taken in feeding individual crabs each day and repairing the cages (in total approximately 8 h per day) an aspect that was also noted by Mirera and Mtile (2009) when comparing cages and pens. Although the labour costs for the guard can be reduced through community awareness campaigns, and by having more people enter into farming, the high cost of daily maintenance does not significantly decrease with the scale of the culture operation (**Paper VII**). Also integration of cage culture (to fatten the lean crabs as used in SEA) and other farming systems like ponds or pens may help reduce the high production cost observed.

Under the current conditions, cost-revenue analyses showed that profit margins were low in both systems, particularly in cage farming that gave negative results at all scales in both countries. Grow-out farming in a 15 x 15 m pond showed a 226 USD profit in Kenya, but a net loss in Tanzania, an aspect that was associated to the difference in market prices where higher prices were offered for crabs in Kenya (almost 2x) compared to Tanzania. The higher prices in Kenya more than compensated for 30 % higher labour costs, and on average 22 % higher cost for material (**Paper VII**). The result showing low profit of mud crab farming in cages differ from analyses of an experimental crab-farming system in Kenya, which showed a high return of capital investment (Mirera, 2009). However, in that analysis the total cost of labour for daily maintenance was not included. However, the present result is consistent with cost-revenue analyses from the Tanga region that also showed a net loss (ACDI/VOCA 2005). In the present analyses of crab fattening, it was assumed that growth rates were 50 % higher, and mortality 50 % lower than what has been obtained in experimental farming in cage cultures (Mirera 2009, Mirera and Mtile 2009, **Paper VII**). Thus, realistic profit margins of cage cultures are even lower than the ones estimated here.

Comparatively, in Southeast Asia, mud crab fattening has been described as a profitable enterprise, but it differs in an important aspect from cage farming operation in East Africa, i.e. crabs are only fattened for a short period of time (<1 month), and are sold prior to moult, to decrease mortality (Keenan, 2003). Mud crab cage farming in East Africa could possibly become profitable if farmers adopted the same strategy, and only fattened large crabs with low meat content for a short period of time. The low growth and survival rates in cage cultures suggest that intertidal cages are in a poor environment for completion of the moulting process. By avoiding moult, growth and survival rates will likely increase in the cages.

A market survey showed that common market size of crabs in East Africa (500-1000 g) was larger than in Southeast Asia (average 300 g). Cost revenue analysis of pond cultures showed that it would be more profitable to farm smaller commercial crabs, and developing a market for 300 g crabs would be one way to increase the profitability of crab farming in East Africa.

In pond based grow-out farms, profitability was observed to increase with size of the pond, e.g. the area of the pond available for crabs increases faster than the cost of the surrounding fence, and the cost of transport and distributing feed increase very little with the size of the pond. Thus, one way of increasing the profit of farms is to increase their sizes. However, analyses showed that increase in size of culture facilities in East Africa are limited by availability of seeds and feeds due to the likelihood of over exploitation and competition with other resource users. Taking these limitations into account, it was estimated that a maximum of 500 commercial crabs (i.e 500 g) per year could be farmed sustainably in an average coastal community in Mafia Island. At this size of a farm, the break-even price for crabs given to farmers is USD 3.4 kg⁻¹, which is obtainable in Kenya and Mozambique today, but difficult in Tanzania (**Paper VII**).

In SEA relatively large earthen ponds (1 ha) have been used in mud crab farming and advances have been made to produce seeds in the hatchery and produce formulated feeds (Trino et al., 1999b; 2001). However, under silvofisheries, profitability is not only based on the cash obtained but it includes value for preservation of the overall mangrove ecosystem services. Thus, depending on mode of cultures, care must be taken when making consideration for expansion of culture facilities in East Africa since they may have negative impacts on the mangrove

environment as observed in SEA (Primavera, 2006). However, if the pond size is maintained at the lowest profitable scale established in this study 133 m² or 500 m² (**Paper VII**), then the integrity of the mangrove environment will be maintained under a silvofisheries approach (Primavera et al., 2000).

CONCLUSION

The study demonstrates that there are strong links between mud crab fisheries and capture-based aquaculture at the community level. For the development of a mangrove friendly and sustainable small-scale mud crab aquaculture in East Africa, the links (nursery habitats, seed, feed, income, market, livelihood, environment) must be well understood and effectively addressed.

The study established for the first time that high intertidal mangrove back-flats and seaward fringes constitute a key habitat for the earliest instars of *S. serrata* (4 -30 mm CW). These habitats are easily accessible by all (men, women, youth and children) for small-scale aquaculture seed collection. However, for sustainability such habitats may need protection from aquaculture development and effective management to avoid over exploitation of seeds, which may hinder recruitment into the capture fisheries. Continuous recruitment of juveniles was observed throughout the year and in substantial numbers to support capture based aquaculture development. However, the relatively low densities of small juvenile crabs will limited a sustainable aquaculture to a small-scale activity. More studies assessing sustainable levels of harvests of juvenile seed crabs are needed.

Continuous recruitment of juveniles was observed throughout the year and in substantial numbers to support capture based aquaculture development. However, estimates of the population of juveniles available was not made.

Mud crab fishers are bestowed with rich traditional and hereditary information on mud crab exploitation and the mangrove environment that could if well understood and nurtured help in management of the capture fisheries. Proper management of the capture fisheries will ensure sustainable seed supply for aquaculture or supply of broodstock for hatchery seed productions once developed like if Southeast Asia.

Stocking of similar sized crabs (less than 50 % difference in carapace width) and provision of shelters improved survival of mud crabs in the laboratory and in different field culture systems. Farmers are advised to sort crabs before stocking so that similar sizes are stocked together to reduce aggression and improve growth and survival. In addition, during the culture period, farmers may employ selective harvesting to remove the bigger crabs rather than waiting for one terminal harvest.

In addition, the shelters used need to be enough in quantity and suitable for providing refuge for all sizes of crabs (juvenile to adult).

Organised community groups (OCGs) are a good entry point for small-scale mud crab aquaculture due to increased community participation in the common resource (mangrove environment and mud crabs). However, a number of challenges may need to be addressed for effective operation of OCGs in small-scale mud crab aquaculture development i.e. developing deliberate policies to ensure training especially for women, and provision of user rights for use of mangrove areas; develop and maintain good market structures/networks (target high end markets); improve profits, transparency in profit sharing to be encouraged in addition to equal participation from community members as stipulated in the OCG constitutions; development of a framework to elucidate where the OCG management is answerable to at the higher level and clear strategies for conflict resolution.

A market analyses showed that the common market size of crabs in East Africa ranged between 500-1000 g and are thus larger than in Southeast Asia where the average size is reported at 300 g. Analyses indicated that culture of 300 g crabs could be more profitable, and more sustainable from a feed perspective, if a market for the same could be established in East Africa.

The profitability of mud crab pond cultured was found to increase with the scale of the operation. However, such increment will require more seeds for stocking the culture facilities, which may not be readily available from the wild, and may thus require development of hatcheries. Further, feed requirement was found to be limiting and thus need to be addressed in for a sustainable mud crab farming. Equally, expansions should be done with caution since small-scale mud crab farming is believed to be mangrove friendly (silvofisheries). Even though the current study has provide benchmarks for pond profitability, more research is needed on how such sizes will impact the ecological integrity of the mangrove environment in relation to provision of ecosystem services.

Cost revenue analysis found that farming large crabs in individual cages over several molts (3-4 months), which is the dominant culture form in East Africa today, had low profitability due to high labour costs and low growth rates. Using a step-wise function of natural growth it was shown that growth rates of *S. serrata* cultured in cages was 40 % of the growth rates obtained in experimental pond and pen cultures, which were similar to natural growth. Growth and profitability of drive-in cage

culture may improve if crabs were only fattened for short period (2-3 weeks) and sold prior to moult, as cage farming is carried out in Southeast Asia. This implies that cage culture could be explored to supplement or add value to other culture systems like mangrove pens and earthen ponds.

The performance of grow-out cultures of small juvenile mud crabs in earthen ponds and mangrove pens showed a potential to develop into a profitable and sustainable intervention. The studies demonstrated that natural predation rates decreased from very high levels on small juveniles to low levels on large juveniles. Using small juveniles as seed crabs would therefore minimize the negative impact of a seed crab fishery on local populations, and if survival rates in the cultured are higher than in the wild, the captured based culture would increase the local production of crabs compared to a fishery of adult crabs. More work is needed to improve the survival in grow-out cultures in East Africa before this could be achieved.

FUTURE PERSPECTIVES

Small-scale mud crab aquaculture in East Africa is in its initial stages, and increased research and training are needed to ensure sustainability in the region. More studies in different areas are required on the available mud crab populations and recruitment trends in the region. One possible way is to carry out awareness campaigns and provide incentives for the artisanal crab fishers to provide information on catches to help monitor stocks. Also middle agents, traders, hoteliers and exporters should provide information. These data could be supplemented by experimental studies possibly by Kenya Marine and Fisheries Research Institute (KMFRI), Tanzania Fisheries Research Institute (TAFIRI) and universities in the region.

More studies should be done in different areas along the East Africa coast to map significant nursery habitats for juvenile mud crabs. Mapping of these areas will facilitate zoning/demarcation by the authorities to direct the collection of seed to the right sites and decide which areas should be protected from such collection. Such information will also help in policy formulation to ensure a sustainable capture-based mud crab aquaculture in the region.

In order to improve the techniques for mud crab cultivation, comprehensive research and training efforts are needed to improve survival and growth. The current survival rates are relatively low compared to the situation in SEA and as a consequence the profitability is low in East Africa. The attempts to improve profitability can build on the results from the present research, e.g. in order to find more effective shelter for different size-classes of juveniles, and development of methods to separate size classes to improve survival and growth in cultures. Such work may involve research institutions like KMFRI (Kenya) and TAFIRI (Tanzania) to develop mariculture demonstration centres where technologies are improved and monitored before being transferred to the community level, such as in SEA by the Southeast Asia Fisheries Development Centre (SEAFDEC). Currently participatory research with communities is being practiced in East Africa. While it has advantages such as in the form of faster transfer of new technologies to the community level and the participation by farmers in development work, it may have a negative impact as too

early transfer of new methods may lead to more failures and a loss of confidence by farmers.

The optimal location and design of different production systems (mangrove pens, earthen ponds and cages) needs to be investigated in the region. Furthermore the crucial role that mangroves play in the life cycle of mud crabs must be considered. Financial profitability of the mud crab culture systems depend intimately with the protection and conservation of the mangrove forests. Unfortunately mangrove friendly aquaculture or silvofisheries as well as seed supply and feed resources currently require a lot of additional research and development. In addition, research into mud crab polyculture (with milkfish or other finfish species) in ponds may be investigated as a way of attaining profitability through diversification of culture systems.

In the long run, it will be necessary to develop demonstration sites where ecosystem approaches to fisheries and aquaculture are applied with respect to mud crab fisheries and aquaculture in the region. This could be the overall sustainability emblem for small-scale capture-based mud crab aquaculture in the region that may be used for marketing crab products from the region globally. However, for a significant expansion of mud crab farming in East Africa to larger scales, the development of mud crab hatcheries will be required in order to secure the supply of crab seeds to the farmers.

ACKNOWLEDGEMENT

This work was made possible through the dedicated help of a number of people and institutions and I am bound to forget some in this acknowledgement. To all this wonderful people and institutions I say thank you. My sincere appreciation goes to my supervisor and colleague Prof. Per-Olav Moksnes and co-supervisor Prof. Max Troell, who did guide through the design, data collection and analysis and critical write up process. You have always been supportive and taken time to discuss my work for which I am very grateful. Indeed it was our brainchild to develop a WIOMSA-MASMA project through which the mud crab research was developed and the PhD work initiated. I also want to thank my other co-supervisor Prof. Olof Linden for your kind attention to my progress, technical advice and support throughout the whole process which is highly appreciated. Without your writing expertise and constant follow-ups this work could not have been achieved. To Dr. Obura, thank you for providing the opportunity for my professional development.

All my co-authors, it has been a pleasure working with you. Thank you all and may God bless you. My local community partners and fishers who worked tirelessly in the research projects deserve special attention. Specific thanks I extend to Dickson Mwamure, Abdhallah Mtile, Juma Mwarandani, Mariam Mwarandani, Khassim Chondo, David Taura, Daniel Shida Charo, Saidi Guyo and Benjamin Karisa. This was a wonderful team of fishers and leaders of community groups; I am fortunate to have had the chance to work with you. To the communities and institutions that offered mariculture sites for the field experiments (Makongeni, baraka conservation, Majaoni youth development and Kwetu Training Centre), I appreciate the support.

Colleagues at Linnaeus University and KMFRI: My colleague Andrew Wamukota – thanks for the wonderful encouragement especially during times of frustrations and for company during the cold winter in Europe. The shared strength made it very successfully. Anna Gustavsson thanks for your hospitality and professional work that ensured all I needed was availed in good time despite your tight schedule. All the administrative staff at Linnaeus University; Ymke, Margaretha, Lena, Anders and all the others; thanks for your support and professionalism. Colleagues at KMFRI, thanks for your team work and support. Without you this thesis could not have been accomplished. Friends, colleagues and students; Mwendwa Mbaluka, Venny Mwainge, Emilly Wafula, Justus Wakili, Johnson Nyamari, Lydia Nyaboke

and Faith Keya, receive my sincere thanks for your untiring support during laboratory and field experiments. Great appreciation is to Francis Oguta for providing drawings that have communicated the required message in the thesis.

Special appreciation is extended to Linnaeus University for the PhD scholarship which was financially supported by the Swedish Center Party. This support is highly appreciated. Furthermore I thank Western Indian Ocean Marine Science Association (WIOMSA) and IFS for the initial research funds. Thanks to my employer, Kenya Marine and Fisheries Research Institute (KMFRI) for the logistical support and permission to undertake the PhD studies.

I finally could like to express my gratitude and love to my parents who made it possible to reach this point. You always supported my interests in education even with the meager resources but more so with prayers and encouragement. My brothers and sisters, I appreciate your support and prayers throughout my study period. Thanks to my late grand father who always provided prayers wherever I visited and my grand mother who did provide money for my secondary education at the age of 80 years, even though you never went to school, you saw the need for my education.

Lastly, my beloved wife Jackleen: Thank you for your prayers, patience, warmth and love; you have been the best supporter in my studies. I owe you a special debt of gratitude for taking care of our three children Jacob, Jeremiah and Esther during the lonely months when I was away in Sweden and times when I was too busy and little around. I cannot imagine a better friend and life-companion. My young children, I love you and hope to be able to give you the support needed in life. Indeed with God all is possible, thanks to my church for the constant prayers.

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PAPER I:

Juvenile ecology of mud crab



Ecology of juvenile mud crab (*Scylla serrata*) in East Africa

Per-Olav Moksnes¹, David Oersted Mirera^{2,3}, Louise Eriander¹, Kajsa Palmqvist¹,
Humphrey Matalu Mahudi⁴, Emma Björkvik¹, Daniel Nyqvist^{1,5}

¹Department of Biology and Environmental Sciences, University of Gothenburg, Box 461, SE-405 30 Göteborg, Sweden

²Kenya Marine and Fisheries Research Institute, Box 81651, Mombasa, Kenya

³Linnaeus University, 391 82 Kalmar, Sweden

⁴Mafia Island Marine Park (MIMP), Tanzania

⁵Department of Marine Resources, Ministry of Livestock and Fisheries, P. O. Box

Abstract. The mud crab *Scylla serrata* is a commercially important species throughout the Indo-Pacific region. In East Africa, there is a growing interest to develop small-scale aquaculture of mud crabs, but progress is prevented by a lack of information of the juvenile ecology of the species. Here we present the results of a series of field studies carried out over 2 years at multiple sites in Tanzania and Kenya to assess the ecology of small juvenile *S. serrata* (<30 mm CW), with the aim to identify the nursery habitats, describe the juvenile recruitment dynamics, and assess how habitat- and size-specific predation affect the behavior and distribution of juvenile crabs.

We show for the first time that high intertidal mangrove back-flats constitute a key habitat for the earliest instars of *S. serrata* (4-30 mm CW), and identify previously undescribed diurnal tidal migration behavior in which small juveniles use the back-flats only at night during ebb tides, and migrate to subtidal habitats during the day, likely in response to variable predation risks. No mud crab megalopae were encountered during two years of extensive sampling of intertidal and subtidal habitats, supporting suggestions that the settlement in *S. serrata* occurs outside estuaries and mangrove areas, which are subsequently colonized by juvenile stages.

A tethering experiment demonstrated a strong size-refuge from predation in juvenile crabs, and field studies showed that larger juveniles start to migrate to subtidal habitats at night when they obtain the size-refuge. Monthly samples of early recruits demonstrated a continuous recruitment in both Kenya and Tanzania, but a clear peak in abundance on Mafia Island that coincided with the SE monsoon, possibly indicating variation in wind-driven larval supply from large coastal populations. The results have important implications for the possible development of a sustainable grow-out aquaculture of *S. serrata* based on collection of small juvenile crabs

Key words: nursery habitat, mangrove, predation, diurnal migration, recruitment, aquaculture

Introduction

Settlement and early juvenile stages are thought to be critical periods in the life cycle of many benthic organisms because of high predation mortality that can substantially alter abundance and distribution of juveniles, and cause a bottleneck in the recruitment (see Gosselin & Qian 1997; Hunt & Scheibling 1997 for review). Nursery habitats may play an important role in mitigating this mortality, and young juveniles of motile benthic organisms are often concentrated in structurally complex microhabitats that are thought to provide refuge from predation (Heck & Orth, 1980; Petersen 1984, Herrnkind & Butler, 1986, Whale & Steneck, 1991, Carr 1994, Eggleston, 1995). Habitat-specific predation rates have been demonstrated for settling postlarvae of several decapod species in the laboratory (Johns & Mann 1987, Dittel et al. 1996, Moksnes et al. 1997, 1998) and for juvenile stages using tethering techniques (Wilson et al. 1987, Barshaw & Able, 1990, Smith and Herrnkind 1992, Fernandez et al. 1993, Moksnes et al. 1998) and is often suggested as the process responsible for the non-random distribution of juveniles. However, habitat selection rather than predation can be the proximate cause, and both postlarvae and young juveniles stages of decapods have been found to actively select habitats that provide refuge from predation and redistribute in response to habitat- and size-specific predations risks, leading to ontogenetic shifts in habitat distribution (Smith & Herrnkind 1992, Eggleston 1995, Moksnes 2002, Moksnes & Heck 2006).

Most studies to date assessing these processes in decapods have been carried out in temperate and subtropical waters. Much less is known for tropical species, in particular species inhabiting soft sediment habitats such as portunid crabs. In tropical oceans, predation rates are generally thought to be higher than in temperate areas, in particular on prey organisms protected by shells (Palmer 1979, Heck & Wilson 1987, Heck & Coen 1995) possibly making size- and habitat-refuges less respectively more important. At present, little is known as there has been a lack of studies assessing these processes in young juvenile stages of tropical decapods.

Mud crabs (*Scylla* spp.) are a commercially important genus of portunid crabs found throughout the Indo-Pacific region (Macnae 1968). Four species of mud crabs are recognized (*S. serrata*, *S. paramamosain*, *S. tranquebarica* and *S. olivacea*), but only one species (*S. serrata*) is found in East Africa (Keenan et al. 1999, Fratini et al. 2010). Adult mud crabs are generally found in estuaries where they build burrows within the mangrove or reside in subtidal habitats (Macnae 1968, Hill 1982). Oviparous females move offshore to spawn (Hill 1994) releasing pelagic larvae that spend 3-4 weeks in the plankton before settling into the benthic habitat (Brick 1974). Mud crabs are fished by artisanal and commercial fishermen throughout their range, and have been successfully farmed throughout Southeast Asia and Southern China for the last 40 years. Because of an increasing demand for mud crabs, the aquaculture industry has expanded rapidly in the last 10 years and reached a global production of 158 000 tons (at value of US\$ 459 millions) in 2011 (FAO 2013).

Considering the economic value of mud crabs surprisingly little is known about their early juvenile ecology. The nursery habitat has only been identified for one species, *S. paramamosain* in Vietnam (Walton et al. 2006), but are presently not known for small juvenile *S. serrata*. Despite considerable sampling of estuarine habitats, the settlement habitat of the megalopae (postlarvae) has never been identified, and small juvenile crabs (i.e. 4-30 mm spine-to-spine carapace width; CW) of *S. serrata* have rarely been found (Webley et al. 2009 and references therein). In northern Australia,

extensive sampling of a *Avicennia marina* mangrove collected high numbers of juveniles 30-60 mm CW, but only a handful of smaller crabs (all >20 mm CW; Hill 1982). The lack of megalopae and small juvenile crabs within mangrove habitats has led to suggestion that the postlarvae settle and metamorphose outside estuaries, where after the benthic juveniles invade mangrove areas (Webley & Connolly 2007). In partial support of these suggestions, laboratory experiments with hatchery reared *S. serrata* found that megalopae did not select between different estuarine habitats, whereas small juveniles selected seagrass over sand and mud habitats (Webley et al. 2009). In East Africa, the ecology of adult *S. serrata* has been extensively studied in South Africa (Hill 1975, 1976, 1978, Robertson & Kruger 1994) and to lesser extent in Kenya, Tanzania and Mozambique (Barnes et al 2002, Onyango 2002). Recent analysis of the genetic diversity in *S. serrata* in the Western Indian Ocean suggest that the mud crabs in East Africa consist of one large metapopulation spreading from Kenya to South Africa (Fratini et al. 2010). Mud crab megalopae and pelagically swimming early juvenile *S. serrata* has been sampled in the plankton at the entrance to a large estuary in South Africa (Forbes & Hay 1988), but as far as we know there exist no information regarding the benthic habitat of small juvenile *S. serrata* in East Africa. Thus, there is a general lack of understanding of the processes that affect the abundance and distribution of young juvenile mud crabs.

Understanding the ecology of juvenile mud crabs in East Africa is of more than merely of academic interest given the growing interest to develop small-scale aquaculture of *S. serrata* as a source of income for coastal communities. Recent studies suggest that the present culture systems growing large crabs in cages are not optimal, and that small-scale grow-out farms stocked small juvenile crabs may be more profitable and sustainable (Moksnes et al. **Paper VII**). However, since hatcheries are not available in rural East Africa, wild seed crabs will have to be used. At present the lack of understanding of the processes that control the abundance and distribution of young juvenile mud crabs may prevent the development of such an aquaculture in East Africa.

Here we present the results of a series of field studies carried out over 2 years at multiple sites in Kenya, Tanzania, and Mozambique to assess the ecology of small juvenile *S. serrata*. The main goals with the studies were (1) to identify the nursery habitats of small juvenile *S. serrata* in tropical East Africa, (2) to assess if predation mortality on juveniles is habitat- or size-specific, and (3) to assess the recruitment dynamics of juveniles over the year.

Material and methods

To obtain a general view of the ecology of juvenile mud crabs in tropical East Africa, field sampling was carried out at multiple sites from the north coast Kenya to southern Mozambique. The main field studies were carried out on Mafia Island of the coast in central Tanzania and in two tidal creeks in Kenya. In addition, a small field survey was carried out on Inhaca Island in southern Mozambique (Fig. 1). The study areas in Kenya and Tanzania are located just south of the equator with a tropical climate and seawater temperature above 25°C on average. The climate of this region is subjected to two distinct monsoon winds, which have marked effects on rainfall, water temperature, prevailing wind and water circulation. The NE monsoon blows from November to March and bring hot and dry weather with light winds, and a weak East

African coastal current (EACC). The rainy season occurs between the two monsoons with extensive rains from May to June. The SE monsoon season blows from June to September and is characterized by strong winds, rough seas and cooler temperatures, and an EACC with strong northward flow along the coast. Tides in the study areas are semidiurnal with average amplitude of approximately 3 m (McClanahan, 1988).

For the purpose of this study we use the definition of Hill (1982) referring to crabs <100 mm spine-to-spine carapace width (CW) as juveniles. In addition we define crabs ≤ 40 mm CW as small juvenile mud crabs, which are the focus of this study.

Field studies Mafia Island, Tanzania

Study area and habitats

Mafia Island is located outside the Rufiji delta of the coast of central Tanzania. The average salinity and temperature in the waters outside of Mafia Island are 34.4 ppt and 27° C, respectively (McClanahan 2000). All field sampling and experiments were carried out along the southeastern coast of the island and in Chole Bay (Fig. 1). This area is included in the Mafia Island Marine Park, which restricts fishing and resource use in certain areas (Francis et al. 2002). Protected from wave energy by islands, this section of the coastline has a more or less continuous belt of mangroves dominated by *Sonneratia alba* along its fringe, and by *Rhizophora mucronata* further in and along tidal creeks. *Aveicennia marina* is also common at the shoreline in many areas. In the more exposed southeastern part, outside of Chole Bay, the mangrove belt is rather narrow (10-100 m wide) and dominated by *S. alba* all the way to the shore in narrow sections, and with a sandy sediment in most areas. Along the western and northern side of the more sheltered Chole Bay, the mangrove forest is more developed and wider (up to 500 m), with a higher dominance *R. mucronata* and with more muddy sediment (Fig. 1).

Outside the mangrove fringe, a 150-400 m wide intertidal flat with a patchy growth of seagrass and algae is found in all parts of the study area. Closest to the fringe the vegetation is dominated by the small seagrass *Halodule sp.* and mats of filamentous green algae, whereas the larger seagrass *Thalassia hemprichii* and the macroalgae *Halimeda opuntia* dominated in lower areas, where they are mainly found in small tidal pools that retain water during low tides. Most of the subtidal area of Chole Bay, and the shallower parts of the southeastern study area contain large seagrass beds, dominated by *T. hemprichii*, *Syringodium isoetifolium* and *Enhalus acoroides* in the shallower part, and by *E. acoroides* and *Thalassodendron ciliatum* in the deeper areas down to approximately 15 m depth. Patches of *H. opuntia* are mixed in with the seagrass in most areas. In the subtidal areas sampled by diving (down to approximately 5-6 m depth MTL) seagrass coverage varied between 40-80%.

Three sets of field sampling were carried out to assess the distribution of juvenile mud crabs in different habitats: (1) day-sampling of intertidal pools and subtidal seagrass habitats using diving, (2) day- and night-sampling of mangrove fringes using transects, and (3) night-sampling of tidal creeks and mangrove fringes using transects. In addition, a monthly sampling program was carried out to assess seasonal variation in juvenile recruitment, a mark-recapture study was performed to assess diurnal migration of juvenile crabs, and a tethering experiment to assess size- and habitat specific mortality.

Field sampling of intertidal pools and subtidal seagrass

To assess if mud crab megalopae and small juveniles use intertidal and subtidal seagrass as settlement and juvenile habitats, extensive sampling using diving were carried out. Three sites, two in Chole Bay (site A and C) and one in the southern area (site E, Fig. 1a) were sampled during the day at low tide at two separate dates from Jan 28 to Feb 25, 2009. At each site, 15 random samples were collected from tidal pools with and without seagrass, at different heights along the intertidal flats using a 0.09 m² plastic cylinder that were pressed into the substratum. All vegetation, animals and the top 10 cm of the sediment was removed and filtered through a 1 mm sieve. In addition, five random samples were taken of subtidal seagrass at 2-3 m depth (MLW) using diving and a 200 µm mesh sampling bag fitted to a 0.13 m² metal frame that was lowered over the seagrass pressed into the sediment. In total, 120 samples were collected, sampling a total area of approximately 11.5 m². All samples were sieved (1 mm), transported on ice, and frozen before being analyzed in the laboratory under stereomicroscope. Portunid crabs were identified following the descriptions given by Vannini and Innocenti (2000).

Field sampling of mangrove fringes and back-flats - day and night

To assess if mangrove fringes constituted an important habitat for small juvenile mud crabs, transect sampling was carried at the same dates and sites as described above. In addition, a fourth site located at the southern opening of Chole Bay (site D; Fig. 1) was included. At each of the sites samples were taken during both day (11.00-16.00) and night (19.00-24.00) in two mangrove habitats: the seaward fringe of *S. alba*, and the mangrove back-flat, i.e. the open area between the shore and the back of the mangrove. At the more sheltered site A and C, *R. mucronata* fringed the back-flats, whereas the other sites were dominated by *S. alba* also in the back-flats.

To be able to sample large areas, transect sampling was carried out. A 20 m rope was randomly placed along the fringe of the mangrove and all *S. serrata* located within 2 m on each side of the line were collected (sampling approximately 80 m² for each transect). The sampling was carefully timed with the tide, occurring during ebbing tides, just after the water had drained the site. Tidal pools and debris were carefully searched for crabs. Burrows were not searched as juvenile mud crabs <20 mm CW have been found not to dig burrows (Walton et al. 2006), and pilot studies failed to find any small juveniles in the burrows along the mangrove fringes or within the mangroves. Crabs were collected by hand or by small nets, identified and measured in the field, and released at the end of the sampling. During night samples, strong headlamps were used. Day and night samples were collected in random order on consecutive days at each site. The two habitats were sampled day and night, at the 4 sites in an 2 x 2 x 4 orthogonal design using 2 replicate transect at all times. The number of juvenile *S. serrata* per transect was tested as the dependent variable in a 3-factor mixed model ANOVA using habitat and time of the day as fixed factors, and site as a random factor. In all analyses, homogeneity of variance was tested using Cochran's c-test prior to the analyses. A multiple comparison post-hoc test was done with the Student-Newman-Keuls (SNK) method.

Field sampling of mangrove fringes, backflats and tidal creeks - size-specific habitat distribution

To assess the habitat specific distribution of different size-classes of juvenile (4-100 mm CW), subadult and adults crabs, a more extensive night-time transect sampling was carried out from February 2 to March 23, 2010 that including also tidal creeks. This sampling included a total of 14 sites, regularly spaced from Utende tidal creek in Chole Bay (site B, Fig. 1) to Changarama tidal creek in the western end of the study area (site E, Fig.1), a distance of approximately 7 km. Three types of mangrove habitats were assessed: seaward fringes, fringes along tidal creeks inside mangrove forests, and back-flats. Sampling was carried out as in the previously described transect study, occurring at night on ebbing tides, but using 20-100 m long transects, depending on the sites, and the targeted size-class of crabs. For the three larger size classes, sampling was carefully timed with the tides, sampling the fringes as the water drained the site (water depth 10-30 cm) and larger juveniles and adult crabs were found to migrate towards the sea with the receding tide at night. For the smallest size-class (<40 mm CW) tidal pools and debris were also searched after the tides had receded. The 14 sites included 4 different tidal creeks, 5 sites with both back-flats and seaward fringes and 5 sites with only seaward fringes. Each site was sampled 6 to 12 times during the 2-month period (a total of 96 transects were sampled). Habitat distribution was assessed in a two factor ANOVA-model using the density of mud crabs (no. 100 m²) as the dependent variable, and habitat and crab size class (<40 mm, 41-75 mm, 76-100, 101-160 mm CW) as fixed independent variables.

Monthly field sampling of juvenile abundance

To assess the seasonal variation in juvenile recruitment, a monthly sampling program was carried out at site d (where the highest abundance of small juvenile crabs was consistently encountered) from February 2009 to February 2010 on Mafia Island. Sampling was always carried on spring tides (when catches appeared to be higher in previous studies), and at night during optimal conditions (as described in the transect study above). One 20 m transects (of approximately 80 m²) were sampled at each time.

Mark-recapture study of juvenile migration

The results from the field studies indicate that small juvenile mud crabs (4-40 mm CW) may perform diurnal migrations to the mangrove back-flats. To better understand this dynamic, a small mark-recapture study was carried out in the August to October 2010. To assess if the same juveniles migrate back to the mangrove back-flats each night, and if the density of small juveniles in the back-flats affect the migration, replicated transect sampling was carried out for 3 and 2 consecutive nights at site d and e respectively, during 3 periods between Aug 24 and Oct 25 (in total 40 transects were collected). During the first two nights (only first night at site e), all juveniles were marked with a small drop of nail polish on the carapace, and by cutting the tip of one of the large carapace spines (i.e. Robertson 1996). Different colors of nail polish were used, and different spines (i.e. left or right) were cut on different nights to separate the dates. All recaptured crabs were released again. The spine-cutting was used as a complement to nail polish since the latter can be lost over time (before molt). Both markings were assumed to disappear with molting. Average

abundance and proportion of recaptured crabs tagged the previous night were estimated from each date and site. To assess if any of the crabs remained during the day, complementary daytime samples were carried out for 3 consecutive days at site d during the first sample period (Aug 24-26).

Tethering experiment of size- and habitat specific predation mortality

To experimentally assess how predation mortality differ between different habitats and size-classes of juvenile crabs, a tethering experiment was carried out in February and March 2009. Four size classes of juvenile crabs (6-12, 12-24, 37-62 and 72-87 mm CW) were assessed in two habitats (seaward mangrove fringe, and subtidal seagrass) in three separate sites (A, C and E; Fig. 1). We assessed seaward mangrove fringes instead of back-flats since the former was present at all sites and used by all size-classes of juvenile mud crabs.

We used tethering techniques similar to those used by Heck & Thoman (1981) and Moksnes et al. (1998). For the three smaller size-classes of crabs, a 15 to 40 cm monofilament line (0.25-0.50 mm in diameter; longer and thicker lines for the larger size-classes) was glued to the carapace of the crab using cyanoacrylate glue. Because the largest size class could cut the monofilament line, a 50 cm long, coated stainless steel wire (0.50 mm in diameter) was used, which was attached to the carapace by tying a wire between the carapace spines. During pilot studies in the laboratory, no crab was able to cut the tethering line. In the field, one crab of each size class was attached to a 4 m transect line with enough space between each crab to inhibit any interaction. The transect line was anchored into the sediment with metal rods. At each site and time, 3 transect lines with 4 tethered crabs per line was left in each of the two habitats for 24 h before they were collected. Crabs were deployed in the mangrove fringe when the habitat was submerged with 10-40 cm of water. The proportion of crabs eaten of each size class per trial constituted a replicate in a study. Occasionally only two mud crabs were used per replicate due to shortage of crabs. The trials were repeated 9 times (3 times at the 3 different sites), which constituted the replicates. In total, 169 crabs were assessed in the tethering experiment.

Loss of a crab was only scored as predation when a broken piece of carapace remained on the line, or when the line was cut. For the largest size-class, exceptions were made when the crabs were observed tearing the wire against the carapace, leaving a characteristic threaded wire on the broken tether. These few cases were excluded from the analyses. Molted crabs were easy to discern from predation since their entire carapace remained on the tether, and were also excluded from analysis. No intact dead crabs were encountered. Proportional relative predation rate [no. of crabs scored as eaten / (no. of crabs tethered - no. of crabs excluded)] served as the dependent variable in a two-factor ANOVA-model with size and habitat (fixed factor) as independent variables.

Tethering techniques have been used to assess relative predation rates in the field in different habitats for several species of decapod crustaceans (Heck & Thoman 1981, Herrnkind & Butler 1986, Wilson et al. 1987, Barshaw & Able 1990b, Moksnes et al. 1998). The technique has been examined for interaction effects between treatment effects and tethering-artifacts effects (Peterson & Black 1994) for different size classes of portunid crabs tethered in different habitats (Pile et al. 1996). In the present study, observations showed that most tethered crabs displayed a 'normal' behavior when placed in the field and started foraging or buried themselves.

Field studies Mida and Mtwapa creek, Kenya

Study area and habitats

The studies were carried out in Mida and Mtwapa creeks along the northern part of the Kenya coast (Fig. 1). Both creeks include large areas of mangrove (525 and 1600 ha respectively; Doute et al., 1981; Kirui et al., 2012). Mida creek is within the Watamu marine park and reserve where fishing is regulated while in Mtwapa creek open access fishery or resource utilization is practised. The creeks are protected from wave energy and have soft silty sediments in most parts. The shores are covered with more or less continuous belt of mangroves dominated by *Rhizophora mucronata* along its fringe and inner mangroves, *Ceriops tagal* along the *R. mucronata* boundary zone landwards and *Avicenia marina* scattered in the intertidal back-flats and the ocean land boundaries. The width of the mangrove belt varies between 10-500 m.

In Mida creek, outside the seaward fringe of the mangrove, a 100-200 m wide intertidal flat exists with a patchy growth of seagrass (*Halodule sp.*) and macroalgae (*Halimeda opuntia*) usually found in small tidal pools.

In the shallow subtidal parts of the creek substantial seagrass beds are found dominated by *E. acoroides*. In contrast, no seagrass is found in Mtwapa creek, which have a very short and steep tidal flat on the seaward side of the mangrove, but 20-150 m wide back-flat behind the main mangrove forest i.e. *R. mucronata*.

Field sampling of Intertidal pools, subtidal seagrass and mangrove fringes in Mida creek

To assess abundance of mud crab megalopa and small juveniles in intertidal and subtidal seagrass habitats in northern Kenya, a field survey of intertidal and subtidal habitats similar to the one performed on Mafia Island was carried out in Mida Creek in February 2009. At two sites, subtidal seagrass and unvegetated intertidal pools were sampled with the same methods used at Mafia Island. Each site was sampled at two different dates with 5 random replicate samples per site and habitat. In total, 30 samples were taken, sampling a total area of approximately 2.6 m².

To assess the abundance of small juvenile mud crabs along mangrove fringes, transect sampling were also carried out using 20 m transects, similar to the methods used in Tanzania. However, because there is no back-flat between the mangrove and shore in Mida Creek, only the mangrove fringes facing the creek were sampled. Moreover, only day-time sampling at low tide were carried out. Two sites were sampled at 3 different dates in February, with replicate transects.

Monthly day and night sampling of juvenile abundance in Mtwapa creek

To assess seasonal variation in juvenile recruitment in northern Kenya, a monthly sampling program was carried out in Mtwapa creek. Similar to the Mafia island study, the sampling occurred monthly during spring-tide conditions, using 20 m transects. However, sampling was carried out at two replicate sites, and at two different times of the day: in the evening after sunset during ebbing tides, just as the water was draining the site (water levels ranging from 0 to 20 cm), and the subsequent morning (after sunrise) during ebbing tides after the water had left the sites. In Mtwapa creek, sampling was carried out only in the back-flat, on the shoreward side of the mangal next to the mangrove fringe (*R. mucronata*). The sediment on the short mud flat on

the seaward side was too soft to allow sampling of the mangrove fringe there. Two replicate samples were used at each time and site. Monthly sampling was carried out from March 2009 to January 2010. The number of small juvenile *S. serrata* (≤ 40 mm CW) per transect was tested as the dependent variable in a 2-factor ANOVA-model using month and time of the day as fixed factors. Because no night-sampling was carried out in the month of January, the data from this month were excluded from the analysis.

Field studies Inhaca Island, Mozambique

Because the diurnal migration behavior in small juvenile mud crabs appeared to differ between Mafia Island and the tidal creek mangrove systems in Kenya, a small additional field study was carried out on Inhaca Island in southern Mozambique (Fig. 1) in February 2010 to assess if the migration behavior was unique to Mafia Island. Day and night sampling using replicated 20 m transects was carried out as described previously at two sites: the larger mangrove located in Saco (site a) at the southeastern part of the island, and at the smaller mangrove located around the tidal creek at Ponta Raza (site b) in the southwestern part of the island (see Paula et al. 2003 for a description of the site). Both mangroves are dominated by *R. mucronata*. Since no back-flats that are regularly inundated are present in these mangroves, sampling was carried out along the seaward mangrove fringes at Saco, and along the fringes of the tidal creek at Ponta Raza.

Results

Field studies, Mafia Island, Tanzania

Field sampling of Intertidal pools and subtidal seagrass

An abundant and species rich assembly of fish and crustaceans were collected from the intertidal flats and subtidal seagrass habitats, including seven species of portunid crabs. However, no *S. serrata* megalopae or juveniles were found in any of the samples. The portunids were dominated numerically by two small species, *Thalamita chaptali* that was most abundant in intertidal pools with seagrass (on average 10.9 crabs m^{-2}) and *T. Poissonii* that was mainly found in the non-vegetated habitat (on average 8.5 crabs m^{-2}). Of the remaining species of portunids, two species, *T. crosnieri* and *Portunus iranjae* were only found in subtidal seagrass and *Portunus granulatus* was only encountered in unvegetated tidal pools (see Karlsson 2009 for a complete description of species collected).

Field sampling of mangrove fringe and back-flats - day and night

The transect sampling of mangrove fringes revealed that small juvenile *S. serrata* aggregate in tidal pools in mangrove back-flats during low tides, but only at night. No juvenile mud crabs were found in any sample during the day, whereas on average 2.9 crabs per transect were found during the night. Moreover, there were large differences in abundance between habitats and sites, resulting in a significant 3-way interaction effect ($F = 158.8$, $df = 3, 14$, $P = 0.001$). Juvenile *S. serrata* had significantly higher abundance and smaller size in the mangrove back-flats (on average 5.7 crabs transect⁻¹, and 32 mm CW, respectively) compared to the mangrove fringe (on average 0.6 crabs transect⁻¹, and 68 mm CW, respectively; Fig. 2; SNK-test at $p < 0.05$). This

difference as driven by a very high abundance of small juveniles at the back-flat at site D (on average 18 crabs transect⁻¹), but as significant also at site C and E (on average 1.9 and 1.5 crabs transect⁻¹ on back-flats, compared to 0.5 crabs transect⁻¹ along sea ward mangrove fringes, respectively). No juvenile *S. serrata* were collected at site A on the northern end of Chole Bay. Importantly, two juveniles collected in the back-flat were only 4 mm CW, suggesting that they were newly metamorphosed first instar mud crabs (Holme et al. 2006).

Field sampling of mangrove fringes, back-flats and tidal creeks - small and large juveniles

Analyses of the three habitat types (mangrove back-flat, creek and fringe) showed a size-specific distribution of crabs resulting in a significant interaction effect between crab size and habitat ($F=3.65$, $df=6,48$ $p=0.0045$). Similar to the study in 2009, small juvenile mud crabs (<40 mm CW) were almost exclusively found in tidal pools after the tide had receded, and mainly high up in the intertidal in the mangrove back-flat, where their abundance was significantly higher than in the other habitats, and significantly more abundant compared to the larger size-classes that were collected with the ebbing tide in the same habitat (SNK-test at $p<0.05$; Fig. 3). For larger juveniles, a shift in habitat use was detected, as the proportion collected from the back-flats decreased, and the proportion in tidal creeks and mangrove fringes increased. The intermediate size class (41-75 mm CW) appeared more abundant in tidal creeks and sea ward fringes, but their density did not differ significantly between habitats or compared to the other size classes. The largest juvenile size class (75-100 mm CW) was significantly more abundant in tidal creeks and mangrove fringes compared to the back-flat habitats, and their density in mangrove fringes was significantly higher than the other juvenile size-classes (SNK-test at $p<0.05$). Subadult and adult crabs (101-160 mm CW) showed a similar distribution as did the larger juveniles (Fig. 3). In comparison to the previous studies on Mafia Island, densities of small juvenile mud crabs were low, and no crabs <10 mm CW were collected, indicating a period of low juvenile recruitment in late February and March.

Monthly field sampling of juvenile abundance

Monthly transect-sampling of mud crabs in the mangrove back-flat at site C showed that the area constituted an important habitat for small juvenile *S. serrata* (≤ 40 mm CW) all year around, with an average abundance and size of 14.8 crabs 100 m⁻², and 17.6 mm CW, respectively. Only 3 juvenile crabs > 40 mm CW were collected in total (all between 40-50 mm CW) indicating that tidal pools in mangrove back-flats at nights are mainly a habitat for small juvenile mud crabs. The results demonstrated that juveniles <20 mm CW were present every month of the year, indicating a continuous recruitment, but with seasonal variation in abundance (Fig. 4a). Densities of the smallest size-class (≤ 10 mm CW) including newly metamorphosed 4 mm CW crabs peaked in the beginning of the rainy season in May, where after densities of small juvenile mud crabs were high until October (20 to 41 crabs 100 m⁻²). Densities of all size-classes dropped in November-December (<3 crabs 100 m⁻²) and then increased until February, where after densities of smaller juveniles decreased during March and April (Fig. 4a). This indication of lower recruitment was also seen in the average size of crabs, which increased from 10 to 26 mm CW from January to March, dropped to 9 mm in May, was constant around 18-19 mm in June to October, and then increased to 23 mm in November and December.

Mark-recapture study of juvenile migration

Recapture rates of small juvenile mud crabs (<40 mm CW) 24 h after release were generally high at all times (on average 18%; range 0-38%). At site D, where crabs were marked and released for two consecutive nights, the abundance and recapture rates of juveniles was consistently high (14.7 ± 1.4 crabs 100 m^{-2} and $21 \pm 0.04\%$; average \pm SE; Fig. 5). Of the crabs that were marked the first night, 10-22% were recaptured also the second night. At site E, the abundance and recapture rates were lower and more variable (on average 5.7 ± 2.4 crabs 100 m^{-2} and $15 \pm 0.09\%$). However, the only occasion when no crabs were recaptured occurred when densities were very low and only 4 crabs were tagged, which could explain the low recapture rate. At other dates, recapture rates were similarly high between the two sites (Fig. 5). During the last sampling occasion at site E, two crabs were collected that had been marked two weeks earlier at the same site, indicating low dispersal along the coast. To assess if the average density of juvenile crabs during the mark-recapture period affected the recapture rates, a linear regression was carried out, which did not find a significant relationship (*Simple linear regression*: $F=1.18$, $df=1,7$, $p=0.31$, $r^2=0.14$; Fig. 5).

At site D we also carried out daytime samples together with the night samples during 3 consecutive days. In contrast to earlier studies, a few juveniles were encountered also during the day, although in low numbers compared to the night samples (on average 2.0 and 17 crabs per transect, respectively; Fig. 6). Of the crabs that were marked the first night, a higher proportion were encountered during the consecutive nights compared to during the days (on average 10% and 1.6% per night, respectively). The sizes of the crabs recaptured during night samples suggested that it was not the same crabs returning the second night. Of the 22 crabs tagged and released the second night, 3 was found the next day. The last night, 7 of crabs that were tagged the second night were recaptured (32%). Based on their sizes, at least 5 of these (23%) were not the same as the ones recaptured during the day (Fig. 6). These results indicate that most of the recaptured crabs did not remain in the back-flat, but migrated to unknown subtidal habitats and returned the next night.

Tethering experiment of predation mortality

Relative predation rates differed significantly between juvenile size-classes, but not between the two habitats (Table 1, Fig. 7). Predation rates were significantly higher on the smallest size class (6-12 mm CW; on average $61\% \text{ 24h}^{-1}$) compared to the larger size classes, and significantly higher on the 13-24 mm size class (on average $22\% \text{ 24h}^{-1}$) compared to the predation rates on the two largest size classes (7 and $0\% \text{ 24h}^{-1}$), which did not differ from each other (SNK-test at $p < 0.05$; Fig. 7).

Field studies Mida and Mtwapa creek, Kenya

Field sampling of Intertidal pools, subtidal seagrass and mangrove fringes in Mida creek

Similarly to the results in Tanzania, the sampling of intertidal flats and subtidal seagrass collected an abundant and species rich assembly of fish and crustaceans, but no *S. serrata* megalopae or juveniles were found in any of the samples.

The transect sampling along the seaward mangrove fringes within the tidal creek revealed that small juvenile mud crabs use these habitats also during the day at low tide, in contrast to what was found on Mafia Island. The average density of small juvenile mud crabs in Mida creek during the day (1.4 crabs per transect) were slightly higher compared to densities collected along seaward *S. alba* fringes on Mafia Island, but 10 times lower compared to densities on mangrove back-flats at night in Tanzania. No crabs ≤ 10 mm CW were collected in Mida creek and the 21-40 mm crabs dominated the collection that had an average size of 29.3 mm CW (Fig. 8), which are larger than the average size found at back-flats on Mafia Island at most times.

Monthly day and night sampling of juvenile abundance in Mtwapa creek

Monthly transect-sampling of small juvenile mud crabs in Mtwapa creek demonstrated that juveniles < 30 mm CW were present every month of the year, indicating a continuous recruitment, similar to the results in Tanzania. However, in contrast to the study in Mafia Island, there was no clear seasonal variation in abundance (Fig. 4a), and the ANOVA found no significant differences in densities between months, nor between day- and night-time samples (on average 2.0 and 1.3 crabs transect⁻¹ on day and night samples, respectively; Table 2, Fig. 9a). Few crabs ≤ 10 mm CW were collected (smallest crab 8 mm CW), and the average size over the sample period was 24.6 mm (Fig. 9b). Thus, in comparison with back-flats in Mafia Island, the juveniles along the mangrove fringes in the Mtwapa creek are larger and have approximately 10 times lower density, and were found both during day and night.

Field studies Inhaca Island, Mozambique

Similar to the results on Mafia Island, no small juvenile mud crabs was found during day sampling at the two small mangals on Inhaca Island, whereas on average 7.0 crabs per transect was found at Saco and 0.5 crabs at Ponta Raza during night time sampling, with an average size 25.8 mm CW (range: 15-37 mm CW). The results indicate a diurnal migration behavior similar to what was found on Mafia Island, Tanzania.

Discussion

This study demonstrates that the mangrove fringes, and in particular the high intertidal flats between the mangrove and the shore (i.e. back-flats) constitute important habitats for small juvenile *S. serrata* in tropical East Africa. On Mafia Island, up to 41 juveniles < 30 mm CW 100 m⁻² could be found on these back-flats at night, and regularly juveniles as small as 4 mm CW were encountered, which is approximately the size of first instar *S. serrata* (Holme et al. 2006). In the tidal creeks in northern Kenya and on Inhaca Island in Mozambique, juveniles < 20 mm CW were also regularly caught in the same type of habitat. As far as we know this is the first time the post-settlement habitat has been identified for *S. serrata* and the results demonstrate a previously undescribed diurnal tidal migration behavior in the smallest juveniles likely related to diurnal variation in predation risk in different habitats. We also show that predation is very high on small juvenile mud crabs, but that larger crabs received a strong size-refuge from predation. Recruitment of small juvenile *S. serrata* was continuous in both Tanzania and Kenya, but on Mafia Island densities

were higher during the rainy season and the SE monsoon, possibly reflecting seasonal variation in larval supply. The results from the study have important implication for the possible development of a sustainable grow-out aquaculture of *S. serrata* based on collection of small juvenile crabs for coastal communities in East Africa.

Size-specific habitat use in juvenile *Scylla serrata*

Settlement habitat

No mud crab megalopae were encountered during two years of extensive sampling of intertidal and shallow subtidal habitats in several regions of East Africa. Although early juvenile stages were found in intertidal mangrove habitats, in contrast to previous studies, first instar crabs were never abundant or dominated the size distribution of small juvenile crabs even during peak recruitment events (e.g., Fig. 2). This pattern is very different from the size-distribution in portunid crabs species where megalopal settlement occur in the juvenile habitat, and abundance is dominated by postlarvae and first instar crabs after settlement events (e.g. Moksnes 2002, Moksnes & Heck 2006).

Taken together, the results suggest that megalopae did not settle and metamorphose in the juvenile habitats. They therefore support the suggestions by Webley & Connolly (2007) that the settlement in *S. serrata* occurs outside estuaries or mangrove areas, which are subsequently colonized by juvenile stages. Small juvenile *S. serrata* are capable swimmers, as demonstrated in a plankton survey at the mouth of an estuary in South Africa where early juveniles mud crabs were regularly caught swimming in the surface (Forbes & Hay 1988). Small juveniles therefore have the capacity to disperse large distances, possibly using selective tidal stream transport to reach the mangrove habitats, which are used by larvae in several portunid species to control their horizontal transport in and out of estuaries (Queiroga & Blanton 2005).

On Mafia Island, the small size of the juveniles collected in the mangroves suggests that at least some megalopae had settled close by, possibly in the deeper areas of Chole Bay (Fig. 1). The fact that we did not collect any megalopae in the subtidal seagrass samples is likely explained by low densities of postlarvae and that they appear not to actively select seagrass at settlement (Webley et al. 2009) in contrast to most other portunid postlarvae (Kenyon et al. 1999, Moksnes 2002, van Montfrans 2003). In the tidal creek systems in Kenya, no juveniles <8 mm CW were collected and the average sizes (25 to 29 mm CW) were 50% larger than on Mafia Island. The larger sizes in Kenya may indicate that the megalopae had settled outside the tidal creek along the coast, and invaded the creeks as juveniles. In comparison to the tidal creeks in Kenya, the fresh water supply to the study area on Mafia in Mafia is low, and the salinity in the mangroves is >30 in all month of the year except during short periods of heavy rain in April and May (H. Mahudi unpubl. data). If lower salinity is used as a cue for settlement in *S. serrata*, it may explain the presence of smaller crabs in the Mafia Island mangroves.

Diurnal tidal migration of small juvenile mud crabs

On Mafia Island, small juvenile mud crabs (<40 mm CW) were found to aggregate at mangrove back flats in small tidal pools at low tide in high numbers, but only at night. During the day, none or very few crabs were found in the same habitats. Because

juvenile mud crabs <20 mm CW appear not to be able to dig burrows (Walton et al. 2006), small juveniles likely do not reside within the mangrove in burrows as do larger mud crabs on Mafia Island and other coastal areas in East Africa (Barnes et al 2002). At site D, where high densities of small juveniles were consistently found at back-flats at night, considerable efforts was spent in attempts to locate small juvenile mud crabs during the day, also within the *S. alba* mangrove (including digging up burrows at low tides), without finding any juveniles. Thus, the most plausible explanation for the lack of juveniles in back-flats and mangroves during the day is that they perform diurnal tidal migrations between the back-flats and unknown habitats in the intertidal mud flats or the subtidal seagrass beds. As far as we know, this type of diurnal tidal migration has not been described previously in juvenile mud crabs.

Interestingly, the results from the mark- and recapture study demonstrated that a large proportion (on average 18%) of the juveniles returned to the same small stretch of the shore (approximately 50 m long) the subsequent nights, indicating that they must have resided in a nearby habitat during the day. The fact that we did not encounter any juvenile mud crabs during sampling of intertidal pools and subtidal seagrass habitats may seem contradictory to this suggestion. However, although considerable effort went into this sampling (120 samples), the total area sampled (approximately 12 m²) is just a fraction of the several hectares of intertidal and subtidal seagrass habitats available outside each 50 m stretch of shore-line in the study area. Considering the relatively low densities also at the back-flat at site D during peak recruitment periods (equivalent of approximately 0.2-0.4 juveniles m⁻²) the chances of encountering the same juveniles spread out over the waste expanses of seagrass is very low.

Importantly, diurnal tidal migration was not found in all of the assessed regions. The small field survey on Inhaca Island indicate that the same migration behavior may be present there, whereas in the two tidal creeks in Kenya, small juveniles were found along the mangrove fringes in similar densities day and night, indicating absence of a diurnal migration. The reason for the diurnal tidal behavior, and for the difference between the different regions are not known. Density-dependent interactions appeared not to influence the behavior as no correlation was found between the densities of juveniles on the back-flats and the proportion that returned on subsequent days. It can be speculated that the small juveniles migrate into the high intertidal mangrove with the rising tide in the evening to feed on the mud flats or to avoid nocturnal predators. As the ebbing tide recede, they remain in the intertidal, aggregating in small tidal pools or burried in the sediment, possibly because the risk of predation is higher in subtidal habitats at night than in the mangrove back-flats. At night, high numbers of larger juvenile mud crabs migrate with the ebbing tide to forage in subtidal habitats (see below). Since juvenile *S. serrata* are highly cannibalistic (Mann et al. 2007, Mirera & Moksnes 2013) and many other predators also are night active, predation risk in the subtidal may be larger at night compared to the day, and larger than in the intertidal during the night. In support of this suggestion, large squids and eels were also regularly seen foraging the tidal flats at night but never during the day. In contrast, predatory birds such as egret and herons, which are abundant on Mafia Island and known to prey on *S. serrata* (Mukherje 1971) were not active during the night. Thus, remaining in tidal pools during low tide at night likely provide a spatio-temporal refuge from predation. In contrast, during the day when birds are active, the predation risk is probably lower in subtidal habitats where the structural complexity of seagrass habitats provide shelter. The results from the tethering experiment support

these suggestions. Even though it did not assess day and night differences, the similar predation rates in the two habitats, in spite of the much higher structural complexity of the subtidal seagrass, suggest that the regular low tide conditions in the mangrove fringe habitat provided a temporal refuges from predation during low tides, and most likely mainly during the night.

In the tidal creeks in Kenya where juveniles were found in the mangrove back-flats at low tide also during the day, the small juvenile *S. serrata* were found buried in the mud, or hiding under debris. Larger individuals were also found to build shallow burrows in the soft mud. In comparison to the sandy sediment of the *S. alba* mangroves that dominated on Mafia Island, the sediment was substantially muddier in the Kenyan tidal creek systems dominated by *R. mucronata*. The different sediment condition and the ability of small juvenile crabs to bury themselves during low tide could possible explain the different migration behaviors in the different regions. Further studies are required to assess these hypotheses.

Predation risk and ontogenetic shift in habitat use

Surveys of larger juvenile *S. serrata* on Mafia Island suggest a shift in habitat use for juvenile *S. serrata* >40 mm CW, which followed the ebbing tides to subtidal habitats during the night. Even though all different size-classes were collected in all habitats, juveniles <40 mm CW were exclusively collected in tidal pools during ebb tides, whereas the larger crabs were collected during ebbing tides along edge of the water. Only smaller individuals of the 41-75 mm CW size class were occasionally found in tidal pools along mangrove fringes during ebb tide. The clear tidal movement of larger juveniles and adult *S. serrata* at night suggest that most crabs were only visiting the intertidal mangroves during high tides, and were using subtidal habitats during low tides. Some of the larger crabs probably resided in burrows within the mangrove during low tides, coming out at night to forage. However, at several sites where the *S. alba* mangrove was narrow and the number of burrows could be assessed, the number of crabs >76 mm CW often greatly exceeded the number of burrows, indicating that a majority of these crabs were using subtidal habitats during low tides. Thus, using the number of burrows to assess densities of mud crabs, as has been done in previously studies of adult mud crabs on Mafia Island (Barnes et al. 2002) risks to underestimate the populations.

Interestingly, the size when the behavior of juvenile *S. serrata* change from using tidal pools to subtidal habitats at night coincide with the sizes that received a strong size refuges from predation. In the tethering experiment, juveniles between 37-62 mm CW had on average 7% predation mortality 24 h^{-1} , which was on average 82% lower than the predation rates on juveniles <24 mm CW. For juveniles >72 mm CW, no predation mortality could be detected. Taken together, these results suggest that decreased predation risk for juveniles >40 mm CW may be the ultimate factor responsible for the change in behavior and habitat use at this size. Such ontogenetic shifts in habitat use driven by habitat- and size-specific predations risks have been suggested for a number of decapods in temperate and subtropical areas (Whale & Steneck 1991, Smith & Herrnkind, 1992; Pile et al. 1996, Moksnes et al. 1998). The present study is first in suggesting that it may be common also in tropical mud crabs.

The shift in habitat use in the present study is consistent with studies of juvenile *S. serrata* in North Australia where only juveniles >40 mm CW were found to migrate

out of the mangroves with the falling tides (Hill 1982). The results are also similar to the habitat use of juvenile *S. paramamosain* in Vietnam, where the smallest juveniles <15 mm CW were only found along seaward fringes of the mangroves, seeking shelter among pneumatophores and in tidal pools during low tide. Larger juveniles (25-85 mm CW) were mainly found in burrows inside the mangrove or migrating to subtidal habitats at low tide, whereas subadult and adult crabs were mainly found in subtidal habitats (Walton et al. 2006). Size-specific predation rates may be responsible also for these shifts in habitat use.

As far as we know this is the first study of size-specific predation in a tropical decapod, and the strong size-refuge from predation in juvenile mud crabs was surprising considering that the number of large teleost fish, shark and rays that crush their prey are thought to be more numerous and more specialized in tropical oceans compared to temperate and subtropical regions (Palmer 1979). Still, in comparison with similar tethering experiments of blue crabs *Callinectes sapidus* in temperate and subtropical USA, overall predation rates on similar size classes were higher, and the size refuge weaker in both the Gulf of Mexico (>80% mortality 24 h⁻¹ for 7-21 mm CW juveniles; Heck et al. 2001) and Chesapeake Bay (77-36% mortality 24 h⁻¹ for 6-62 mm CW juveniles; Pile et al. 1996). This contradicts results from latitudinal tethering studies of different decapod species that have found higher relative predation rates at lower latitudes (Heck & Wilson 1987, Heck & Coen 1995). One possible explanation for higher predation rates on portunids in temperate and subtropical areas may be the shorter recruitment season resulting in a concentration juveniles in nursery areas during a short period of the year, when very high densities can result in very high density-dependent predation and cannibalism (Perkin-Visser et al. 1996, Moksnes et al. 1997, Moksnes 2004). In tropical East Africa, the extended recruitment season and diffuse settlement result in very low densities of small juvenile mud crabs, also when they aggregate in mangrove back-flats during peak recruitment periods (up to 0.41 crabs m⁻²), which are 100-1000 times lower than peak recruitment densities of portunids in subtropical and temperate areas (Pile et al. 1996, Heck et al. 2001, Moksnes 2002). Thus in tropical areas, the low densities of juveniles may provide a refuge from predation, as predators develop preference for other prey. Refuge in low numbers has been suggested for small juvenile portunid crabs in temperate and subtropical areas to explain unexpected low predation rates in unvegetated habitats (Moksnes 2002, Moksnes & Heck 2006).

Juvenile recruitment dynamics

The results from the monthly samples of small juvenile mud crabs from Tanzania and Kenya demonstrated that *S. serrata* in this region spawn and recruit in all seasons, as juveniles <30 mm CW were collected during all months of the year (Fig. 4). Moreover, the abundance of the smallest juveniles (<20 mm CW) collected on Mafia Island indicated a seasonality in juvenile recruitment with a major peak in abundance from May to October, and a smaller peak in January and February. Although this result is based only on data from one site during 2009, subsequent extensive sampling in 2010 showed the same results with very low abundance of small juveniles from mid February and March (no juveniles <10 mm were collected), and high abundance in August to October (Fig. 3 and 5). The peak in abundance of early recruits in May is also in accordance with the local knowledge among mud crab fishermen on Mafia Island of high numbers of small mud crabs occurring during the rainy season. Mud

crab fishermen in Kenya have been observed to hold important traditional knowledge that may be useful in management of fishery resources (Mirera et al. 2013).

The observed continuous juvenile recruitment is consistent with earlier studies in southern Kenya where mud crab females with developed ovaries were observed in all months of the year (Onyango 2002). A continuous spawning and recruitment have also been observed in *S. serrata* from the Natal region in the northeast coast of South Africa where females with developed ovaries, as well as mud crab megalopae were collected in all months of the year (Robertson & Kruger 1994, Forbes & Hay 1988). These studies also found a peak in spawning and larval recruitment, but in this subtropical area it occurred during the warmer months from November to June. In the more southern, warm temperate populations of *S. serrata* in South Africa, spawning is seasonal occurring only from November to April (Du Plessis 1971, Hill 1975).

Like most portunid species living in estuarine waters, female mud crabs are believed to migrate from the coast to offshore areas to spawn. In tropical northern Australia, female *S. serrata* was found to migrate offshore to spawn only during a limited period of the year from September to November (Hill 1994). Such seasonal spawning is believed to occur throughout much of the species range (Heasman et al. 1985, Quinn & Kojis 1987) with spawning occurring during the warmer month in most areas (Robertson & Kruger 1994). In the more estuarine mud crab species *S. paramamosain*, small juvenile crabs were collected all year, but their abundance peaked in the beginning of the dry season when salinities increased from 1 to >5 (Walton et al. 2006).

On Mafia Island, the abundance of early recruits (<10 mm CW) peaked in May and was from high until October (Fig. 4). Considering the size range of small juveniles in May, and assuming a larval duration period of 3-4 weeks in *S. serrata*, the larvae resulting in these crabs should have hatched from the beginning of March to September. If the peak in recruitment was caused by a seasonality in mating and spawning of *S. serrata* in this area it would have occurred during the colder part of the year, which is opposite to what have been found for this species in other areas of its distribution (i.e. Robertson & Kruger 1994).

Interestingly, this spawning period coincide with the beginning of the rainy season and the SE monsoon, when the wind direction change from north to southwest and the East African Coastal Current is stronger (Richmond 2011). An alternative or complementary explanation to the seasonal spawning could therefore be that the juvenile recruitment on Mafia Island is affected by a seasonal variation in larval supply from the coastal mainland. The largest mangrove forests in East Africa (covering 530 km²) is located in the Rufiji Delta, approximately 40 km southwest of Mafia Island (Taylor et al. 2003), which has large populations of mud crabs (Mirera 2011). During the SE monsoon when northward currents are stronger and SW winds are common and in this area (Richmond 2011), the transportation of mud crab larvae from the Rufiji Delta and the large mangrove forest around Kilwa in southern Tanzania to Mafia Island may be favored, resulting in higher juvenile recruitment.

In contrast to Mafia Island, no seasonality was seen in the abundance of small juvenile mud crabs from the tidal creek system in Kenya, which correlated poorly in time with the juvenile abundance on Mafia Island. This result indicate that the source populations providing larvae to Mtwapa creek have a less pronounced spawning season, and/or that it is less influenced by variation in larval supply compared to Mafia Island.

Implication for small-scale aquaculture of mud crabs

The results from the present study have important implications for a possible development of sustainable aquaculture of *S. serrata* for coastal communities in East Africa. In the last decade, various NGOs in East Africa have promoted aquaculture of large juvenile *S. serrata* (80-110 mm CW) collected from the wild and farmed in individual cage-system until they reach market size (approximately 140 mm CW; Shipton & Hetch 2007, Mirera 2011). Mortality in these culture systems is high and range between 15-22% month⁻¹ (on average 19% month⁻¹; Mirera 2009, Mirera & Mtile 2009). Since a traditional fishery of adult mud crabs exist in most coastal communities in East Africa, and an aquaculture based on collection of wild "seed crabs" may compete with the fishery, it is important that the aquaculture increase the production of the resource instead of the opposite. In practice this means that the mortality in the aquaculture has to be lower than the natural mortality of the crabs.

Obtaining estimates of natural mortality is notoriously difficult, but for *S. serrata* there exist some unique data. Based on changes in abundance of a *S. serrata* population enclosed in an estuary in South Africa over a 3 year period, Hill (1975) estimated the mortality rate of a population consisting of large juvenile and adult crabs (90-150 mm CW) to 41% year⁻¹ (equivalent to 4.3% month⁻¹). This estimate of natural mortality is in a same range as for adult blue crabs in the USA (5.8% month⁻¹) based on extensive mark-recapture studies (Hewitt 2008), and is supported by the present tethering study where mortality was below detection in 24 h tests for juveniles >76 mm CW. These estimates suggest that the mortality rate of mud crabs in cage culture systems in East Africa is many times higher than the natural mortality affecting wild crabs. If these estimates are correct, this aquaculture is in fact decreasing the production mud crabs in the system; after a growth cycle of 6 month the difference in survival is equivalent of a production loss of 64%. Thus, until mortality rates below 4% month⁻¹ are obtained in the cultures, a better management approach of this resource would be to fish the crabs when they reach commercial size.

The tethering study showed that predation mortality increased exponentially with decreasing size of the crabs, indicating a predation bottleneck for the small juvenile crabs, similarly to what has been found for several decapod species (e.g., Wahle & Steneck 1991, Smith & Herrnkind 1992, Pile et al. 1996, Moksnes et al. 1998). This result indicates that it may be more sustainable and productive to collect seed crabs at a very small size before most of this predation mortality has occurred, since the impact of the seed crab fishery on the local population mud crabs would then be minimized. If mortality in the culture could be kept below the natural mortality of small juvenile crabs, the total production of crabs in the system would increase. The predation rates obtained through tethering experiments do not represent absolute rates, but may provide an accurate relative estimate of differences in predation rate between e.g. crab sizes. Assuming that the mortality rate of 4.3% month⁻¹ represent the natural predation rate on the largest size class and the proportional relation is the same as in the tethering experiment, the 'natural' predation rate on the smallest size class (6-12 mm CW) would be approximately 65% month⁻¹. A similar estimate of the natural mortality (52% mortality month⁻¹) was obtained by monitoring a cohort of small juvenile *S. serrata* (5-14 mm CW) for a month using mark-recapture techniques on Mafia Island (Nyqvist 2011), suggesting that the tethering estimates are in the correct range. In South East Asia, small-scale, grow-out aquacultures of *S. serrata* using

small juvenile seed crabs (12-50 mm CW) in pond- or pen-cultures are obtaining mortality rates $<10\%$ month⁻¹ (Baliao et al. 1999, Trino et al 1999, Trino & Rodrigues 2002). Hence, grow-out cultures based on collection of small juveniles crabs have the potential to increase the production of mud crabs and be much more sustainable than culture based on collection on large juvenile crabs.

The present study identified that small juvenile mud crabs aggregate in mangrove back-flats at night (Mafia, Inhaca Island) or during both day and night (Kenya) where they can be easily picked at low tide by hand with no by-catch and minimal impact on the environment. In the tidal creek systems in Kenya, 3-18 crabs person⁻¹ h⁻¹ can be collected throughout the year, and in Mafia Island 15-33 crabs person⁻¹ h⁻¹ can be collected during high recruitment season in May-October at the best sites. Thus, grow-out cultures based on collection of small juvenile seed crabs may constitute a way to develop sustainable small-scale aquaculture of *S. serrata* for coastal communities in East Africa.

Acknowledgement

We thank the Western Indian Ocean Marine Science Association (WIOMSA), Marine Science for Management (MASMA) for funding this research through a MASMA-grant to the project entitled '*Small-scale, community-based, grow-out aquacultures of mud crabs S. serrata as a sustainable livelihood in East Africa.*

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Table 1. *Tethering experiment- Mafia Island.* Two factor ANOVA model testing the proportional relative predation rate of juvenile mud crabs *S. serrata* (square root-transformed) as a function of habitat (mangrove fringe and subtidal seagrass) and prey size class (6-12, 12-24, 37-62 and 72-87 mm CW).

Source of variation	df	SS	F	P
Habitat (A)	1	1.31	0.21	0.652
Crab size (B)	3	301	15.8	0.0001
A x B	3	4.39	0.23	0.875
Residual	52	331		

Table 2. *Juvenile recruitment - Mtwapa Creek.* Two factor ANOVA model testing the number of small juvenile *S serrata* (≤ 40 mm CW) per transect as a function of time of the day (night and day) and month (March to December).

Source of variation	df	SS	F	P
Time of day (A)	1	10.2	2.96	0.090
Month (B)	9	25.6	0.83	0.596
A x B	9	15.9	0.51	0.860
Residual	60	207		

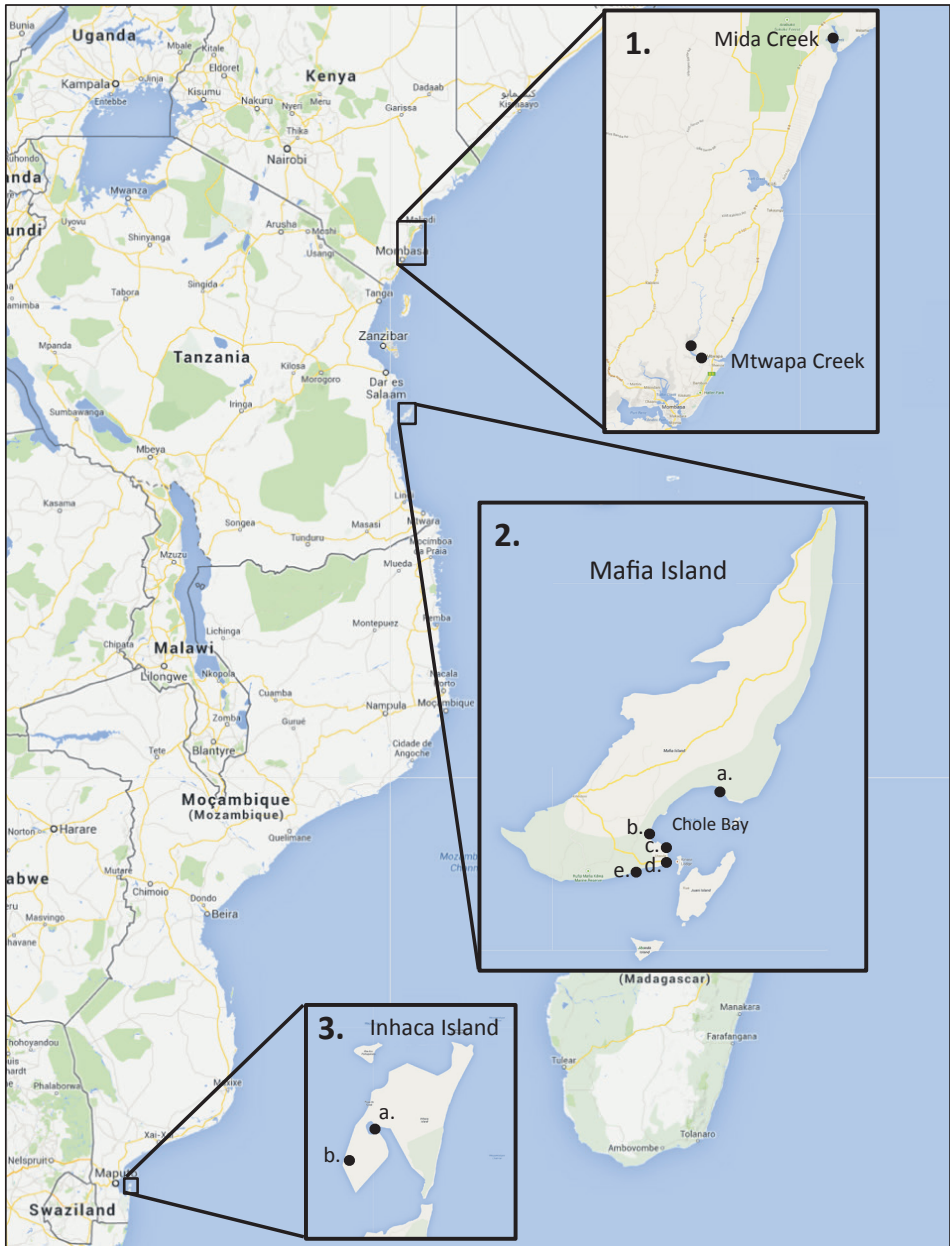


Figure 1. Map of East Africa showing the 3 study regions (1) Mtwapa and Mida Creek north of Mombasa in Kenya, (2) five field sites on Mafia Island, Tanzania and (3) two field site on Inhaca Island in southern Mozambique.

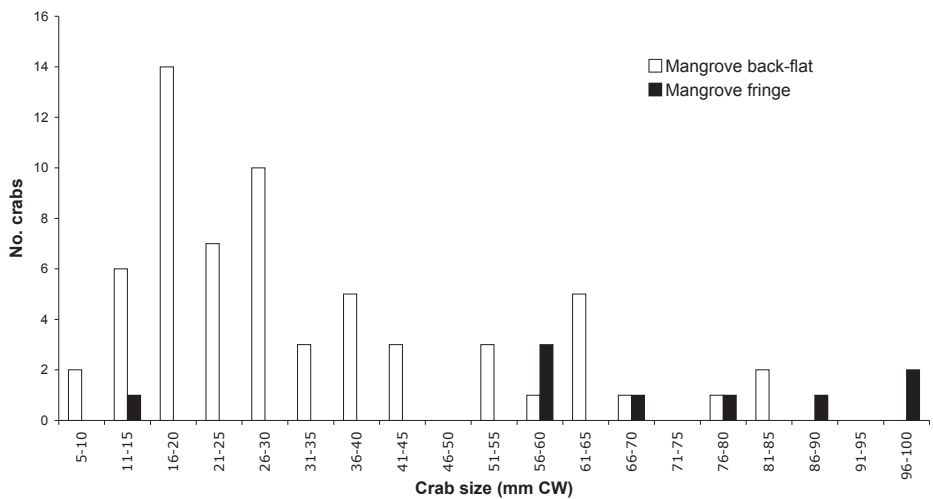


Figure 2. Size-distribution of juvenile *S. serrata* collected during night transects (3 nights per habitat) from mangrove back-flats and fringes at 3 sites on Mafia Island, Tanzania.

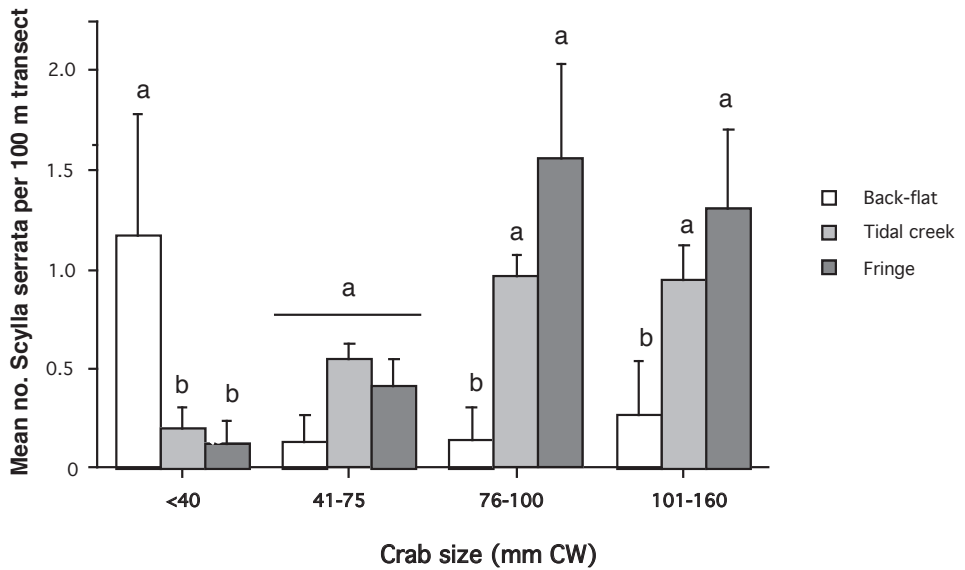


Figure 3. Mean number of juvenile mud crabs 100 m^{-2} (+SE) separated into 3 size-classes of juveniles (≤ 40 mm, 41-75 mm and 76-100 mm CW), and subadult and adult crabs (100-160 mm CW) in three different types of mangrove habitats (back-flats, tidal creeks inside mangroves, and seaward mangrove fringes). Different letters above bars indicate significantly different means between habitats within each size-class (SNK-test at $p < 0.05$).

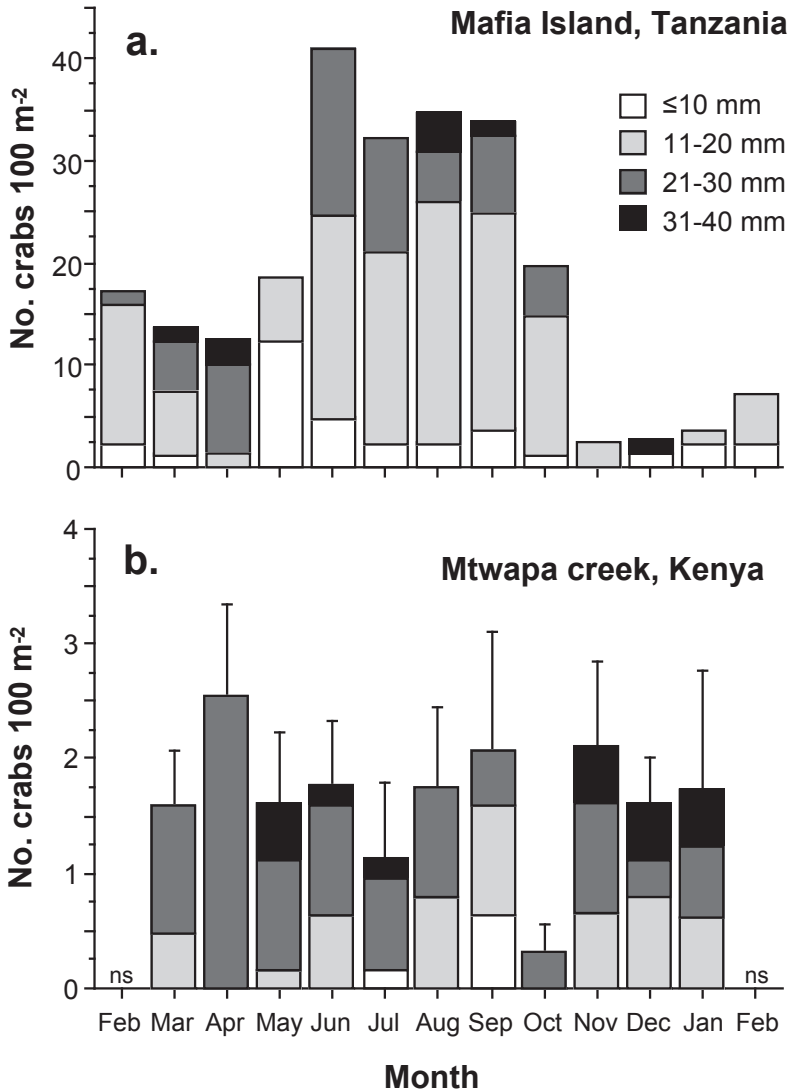


Figure 4. Seasonal variation in juvenile recruitment of *S. serrata* in Tanzania and Kenya from February 2009 to February 2010. (a) Number of small juvenile mud crabs 100 m⁻² collected once a month at a mangrove back-flat on Mafia Island separated into 4 size-classes. (b) Mean number of small juvenile mud crabs 100 m⁻² (+SE) collected with replicate transects during day and night samples from two sites in Mtwapa creek in Kenya. The month of February was not sampled in Mtwapa creek.

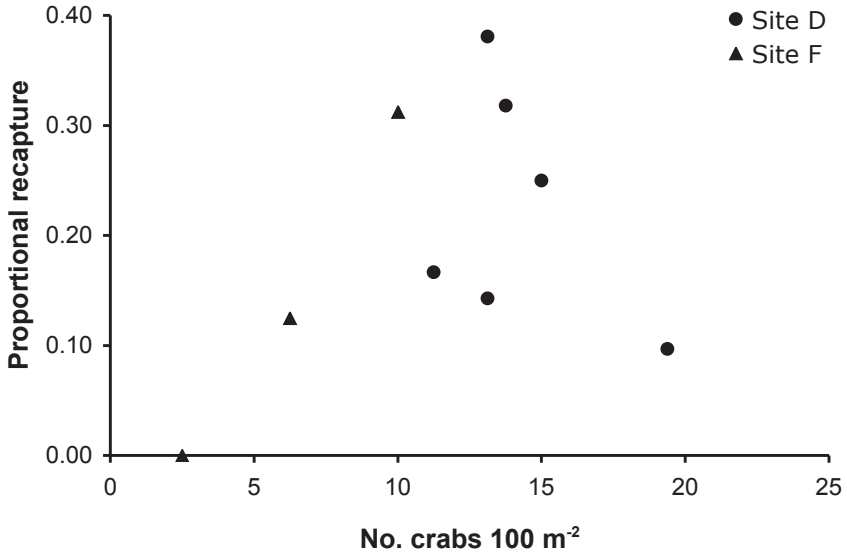


Figure 5. Proportional recapture rate of small juvenile *S. serrata* (≤ 40 mm CW) 24 h after release in mangrove back-flats at two sites at Mafia Island from August to October 2010, in relation to the average density of small juveniles at the time of mark and recapture. No significant relationship was found (*Simple linear regression*: $F=1.18$, $df=1,7$, $p=0.31$, $r^2=0.14$).

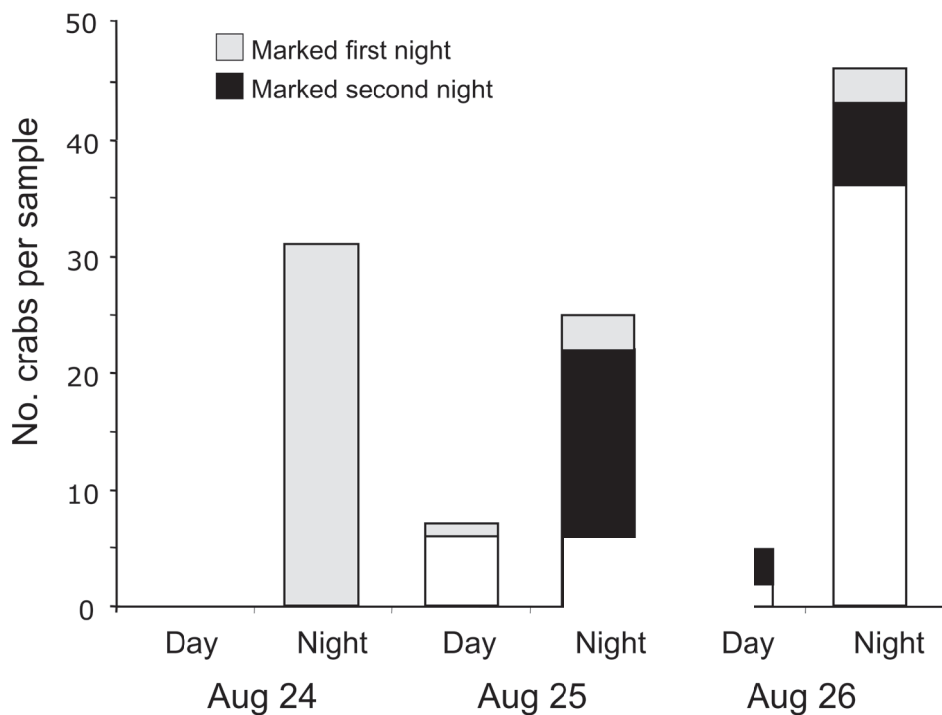


Fig 6. Total number of small juvenile *S. serrata* (4.5-31 mm CW) collected at site d during day and night transect samples on August 24-26, 2010. The legend depicts crabs that were marked during the first two nights and how they were recaptured during consecutive days.

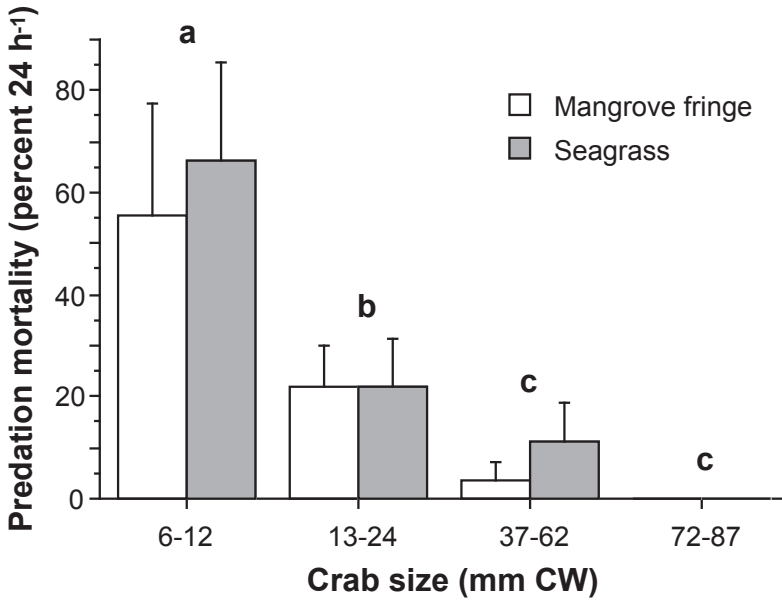


Fig 7. Mean percent relative predation rates (+SE) on 4 size classes of juvenile *Scylla serrata* (6-12 , 13-24, 37-62, and 72-87 mm CW) tethered in two different habitats (seaward mangrove fringe and subtidal seagrass) for 24 h at Mafia Island, Tanzania. Different letters above bars indicate significantly different means between habitats within each size-class (SNK-test at $p < 0.05$).

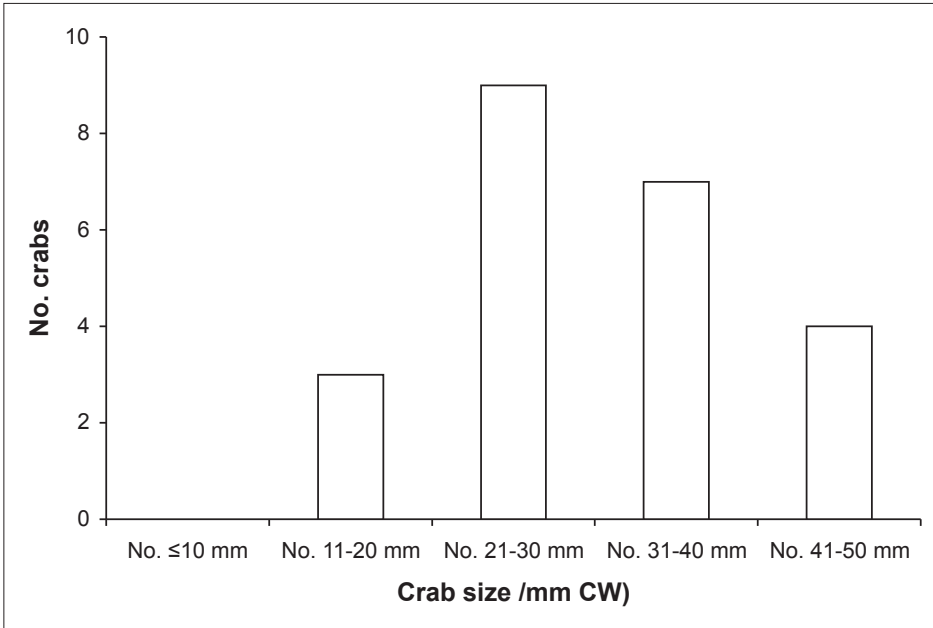


Figure 8. Size-distribution of juvenile *S. serrata* collected during day transects from seaward mangrove fringes at 2 sites in Mida creek, Kenya.

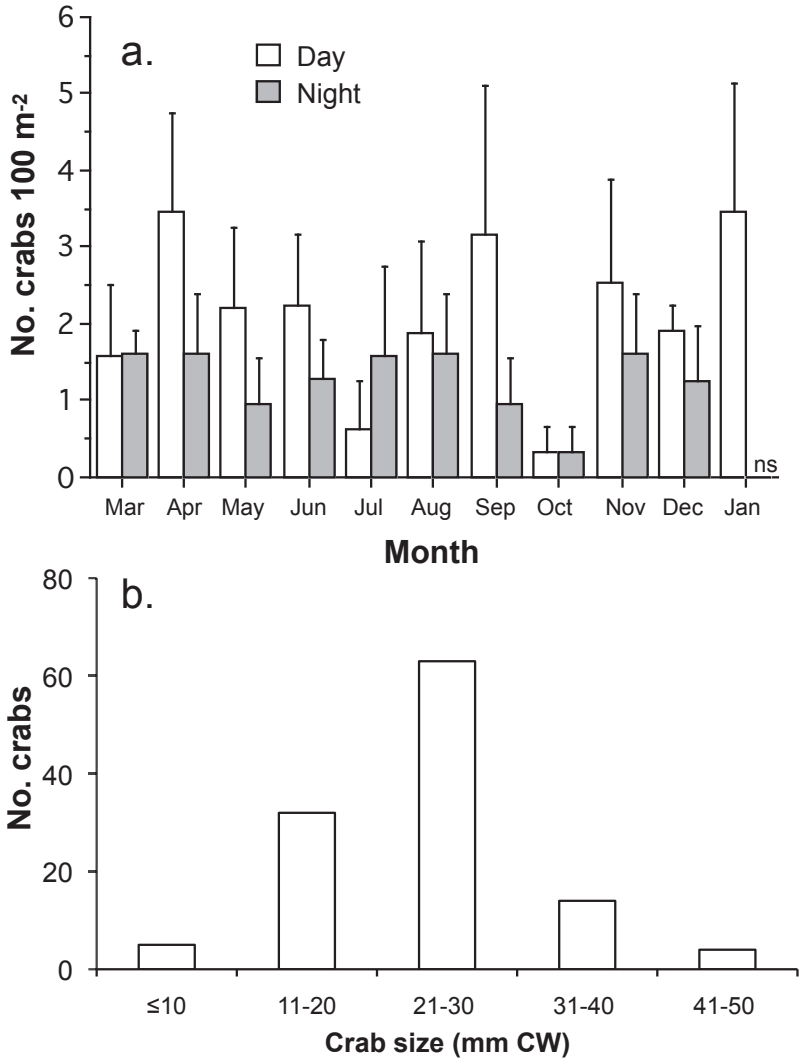


Figure 9. (a) Mean number of small juvenile *S. serrata* 100 m⁻² (+SE) collected with replicate transects during day and night samples from two sites in Mtwapa creek in Kenya. 'ns' denote 'not sampled'. (b) Size-distribution of juvenile *S. serrata* from the same samples.

II

PAPER II:

Natural growth in mud crabs



Step-wise function of natural growth for *Scylla serrata* in East Africa: A valuable tool for assessing growth of mud crabs in aquacultures

Per-Olav Moksnes^{a,1}, David Oersted Mirera^{b,c}, Emma Björkvik^a, Muumin Iddi Hamad^{d,2},
Humphrey Matalu Mahudi^e, Daniel Nyqvist^{a,3}, Narriman Jiddawi^d, and Max Troell^f

^aDepartment of Biology and Environmental Sciences, University of Gothenburg, Box 461, SE-405 30 Göteborg, Sweden

^bKenya Marine and Fisheries Research Institute, Box 81651, Mombasa, Kenya

^cLinnaeus University, 391 82 Kalmar, Sweden

^dInstitute of Marine Sciences, Zanzibar, University of Dar es Salaam, Tanzania

^eMafia Island Marine Park, Box 74, Mafia Island, Tanzania

^fBeier Institute and Stockholm Resilience Centre, Stockholm University, Sweden

¹Corresponding author:

Phone: +46 31 7862710, Fax: +46 31 7862727, E-mail: per.moksnes@bioenv.gu.se

Present address:

²Department of Marine Resources, Ministry of Livestock and Fisheries, P. O. Box 774, Zanzibar-Tanzania

³Department of Biology, Karlstad University, S-651 88 Karlstad, Sweden

Running title: *Growth of Scylla serrata in East Africa*

Keywords: Mud crab, Molt increment, Intermolt period, Segmented growth, Aquaculture

Abstract. We describe natural growth in juvenile and adult mud crabs *Scylla serrata* from East Africa using a step-wise growth function based on data on intermolt periods and growth at molt from field mark-recapture, pond and laboratory studies. The results showed that proportional increment of carapace width (CW) at molt was fairly constant around 20%, whereas the intermolt period increased exponentially from around 7 days in young juvenile crabs to over 3 months for adult crabs. The modeled step-wise growth function suggests that *S. serrata* in East Africa will reach 300 g and sexual maturity approximately 9.9 months after settlement, and a commercial size of 500 g after 12.4 months.

Using the new growth function to estimate the proportional difference between modeled and obtained growth of mud crabs from aquaculture studies we show that growth rates of *S. serrata* cultured in cage systems, which are dominant in East Africa, was <40% of the estimated natural growth and growth obtained in pond systems. The analysis also indicated that growth rates of *S. serrata* in South East Asia was over 50% higher compared to similar culture systems in East Africa, and that different species of mud crabs had large differences in growth rates. More studies employing growth functions of mud crabs in aquacultures are encouraged to increase our understanding of the processes behind these differences.

1. Introduction

Understanding about growth of commercial aquatic species is fundamental for determining age at maturity and at recruitment into the fishery, for cohort identification, lifespan and generation time, which in turn are key variables for a successful management of the species. For example, in stock assessment, age and growth form the basis for yield per recruit estimation, and age-length keys are used in sequential population analyses and definition of management bench-marks (Ehrhardt 2008). For aquaculture, understanding growth is critical for planning and projecting growth cycles, estimating costs and revenues of farms and comparing growth rates and production between different aquaculture system designs.

However, determining age and growth in crustaceans are complicated because growth occurs through shedding of the exoskeleton in a process called molting. Estimating growth is therefore noticeably difficult because no hard parts are available for age determination such as otholites or scales, which are commonly used for age determination in finfish (Green et al. 2009). Moreover, in contrast to fish species that grow continuously towards an asymptotic size, growth in crustaceans is the product of two distinct but discrete biological processes: (1) rapid growth in external size after molt (molt increment) when the exoskeleton is shed, and (2) a longer period between molts (intermolt period), when growth of muscle tissue occur, filling out the new shell. During molt, crustaceans absorb water, which can constitute as much as 80-90% of the total body weight after the molt (Du Plessis 1971), which then slowly is being replaced by muscle tissue during the intermolt period. Thus, both external size and body weight have limitations as variables of growth in crustaceans. In many crustaceans, growth per molt decreases with age, whereas the length of the intermolt period increases with age, particularly after maturity resulting in complex growth patterns (Ehrhardt 2008). Thus, crustacean growth is characterized by discrete, segmented growth that may or may not be modeled by standard size at age models adopted for fish species (e.g. von Bertalanffy growth function, VBGF). For example, in spiny lobster *Panulirus argus*, stepwise growth functions based on field estimates of growth per molt and intermolt period resulted in growth curves that were qualitatively different from von Bertalanffy-type functions estimated for the species from indirect ageing procedures (Ehrhardt 2008).

Mud crabs (*Scylla* spp.) are a commercially important genus of portunid crabs found throughout the Indo-Pacific region (Macnae 1968). Four species of mud crabs are recognized (*S. serrata*, *S. paramamosain*, *S. tranquebarica* and *S. olivacea*), but only one species (*S. serrata*) is found in East Africa (Keenan et al. 1998, Fratini et al. 2010). Mud crabs generate high prices on domestic and international markets, and are fished by artisanal and commercial fishermen throughout their range. They survive and grow well in captivity and they have for the last 40 years been successfully farmed throughout Southeast Asia and Southern China. Because of an increasing demand for mud crabs, an aquaculture industry has expanded rapidly in the last 10 years. In 2011 global production reached 158 000 tons (at value of US\$ 459 millions), with most of the production taking place in China (FAO 2013).

Considering the economic value of mud crabs surprisingly little is known about their natural growth. In Vietnam, natural growth in juvenile and adult *Scylla paramamosain* was estimated using mark-recapture techniques and described with a VBGF (Le Vay et al. 2007). However, no growth functions are available for other species of *Scylla*. The growth in adult *S. serrata* in South Africa has also been

described using mark-recapture techniques (Hill 1975), but no growth rates of wild juvenile *S. serrata* have been published. The lack of a description of growth in *S. serrata* poses a limitation for management of fished populations since the generation time or age of the commercial sizes are not known. It also impedes assessment of different culture systems, and production and cost-revenue estimates in aquacultures of *S. serrata*, particularly in East Africa where aquaculture of mud crabs is in its infancy and different methods are presently being assessed. In the last decades various NGOs have promoted aquaculture of mud crabs in cages as the culture method where large juvenile crabs (200-300 g crabs) are farmed through several molts (many months) in individual "drive-in" cages placed in intertidal zone within mangroves (Shipton & Hetch 2007, Mirera 2011). Recent studies of this culture method indicate that growth rates may be low in these cages (Mirera 2009, Mtile & Mirera 2009), but it has been difficult to compare with growth rates in other studies. Although various estimates of growth rates in *S. serrata* from aquacultures are available (e.g. Keenan, 1999, Ut et al. 2007), they are difficult to compare without a growth function since different sizes of seed crabs and different growth periods have been used in different studies.

The aim of this study was to describe natural growth in *Scylla serrata* from East Africa using a step-wise growth function based on data on intermolt periods and growth increment at molt from field mark-recapture studies, as well as pond and laboratory studies. A second aim was to use the growth function to compare growth in mud crabs from aquaculture studies in the literature and assess differences between methods, regions and species.

2. Materials and methods

Because different techniques are needed for different growth variables in different size-classes of crabs, a combination of different methods and studies from several regions were used to obtain data of growth increment at molt and intermolt period for juvenile and adult *Scylla serrata* in East Africa. To obtain growth estimates in juvenile crabs <30 mm spine-to-spine carapace width (CW), growth was estimated in short term laboratory and cage studies to avoid injuries/mortalities that could be caused through the use of internal tags in small individuals. For larger crabs, mark-recapture techniques were used. Additional data was collected of carapace width and wet weight from crabs of different sizes to enable transformation of modeled growth in CW to biomass. Table 1 summarizes the methods and growing conditions in the studies used to obtain data for the different growth variables. Because juvenile crabs are difficult to differentiate between sexes, while data of adult crabs was too limited to allow a separation of male and female crabs, growth estimates were made for mixed sexes.

2.1 Laboratory and pond studies

Data for estimates of growth increment at molt and intermolt period for small juvenile mud crabs (4-40 mm CW) were obtained from laboratory and pond studies. A laboratory study was carried out at the Institute of Marine Science, Zanzibar, Tanzania, where juvenile crabs were individually kept in tanks for 6 weeks and monitored daily to obtain individual estimates of growth (Table 1; see Hamad 2012 for details).

In a pond study carried out at Mafia Island, cohorts of newly settled mud crabs (5-14 mm CW) were kept in small cages (bottom area 1 m²; 1 mm mesh) at 10 crabs per

age for 1 month and monitored weekly for growth (Table 1, see Nyqvist 2011 for details), and average intermolt period per cohort and size-class was estimated. In addition, data of individual growth increment at molt was also collected when possible. All juveniles used in the two studies were collected from Mafia Island, Tanzania.

Additional data on growth increment at molt were obtained from a laboratory study of interactions between juvenile mud crabs carried out at Kenya Marine and Fishery Research Institute (KMFRI), Mombasa, Kenya (Table 1, see Mirera and Moksnes 2013 for details). To obtain additional data to assess functional relationships between carapace width and wet weight of crabs, data of juvenile and adult crabs that were collected for aquaculture studies in Mafia Island, Tanzania (H. Mahudi *unpubl. data*) and Mombasa Kenya (Mirera 2009, Mirera & Mtile 2009) were used (Table 1).

2.2 Mark-recapture studies

Data for estimating growth in larger mud crabs were obtained from a mark-recapture study carried out at Mafia Island, Tanzania where 525 juvenile and adult crabs (20-140 mm CW) were tagged with sequentially coded micro-wire tags (CWT-tags; Northwest Marine Technology inc.). The CWT-tags were injected into the base of the third walking leg using a handheld single shot injector. Recaptured individuals were identified using a hand held magnetic detector (Northwest Marine Technology inc.; see Björkvik, 2010 for details). Earlier studies of CWT-tags have shown negligible effects on crabs growth and survival (Van Montfrans et al. 1986, Ut et al. 2007). The crabs were tagged in February and March 2010, and recapture collections were carried out weekly for the first 2 months, and thereafter every 3 months for a total of 11 months. A total of 26 tagged mud crabs were recaptured (5.0% recapture rate), most of them during the first 2 months of release. Eleven of the recaptured crabs had molted at least once while at large, allowing estimates of growth (Table 1 and 2).

To obtain growth data also for larger mud crabs (>100 mm CW), which were not obtained in the Mafia Island study, we used published results from a recapture study carried out in two estuaries along the eastern coast of South Africa where estimates of growth in larger mud crabs were obtained (100-152 mm CW; Table 1 in Hill 1975). This was done on the basis that genetic diversity in *S. serrata* in the Western Indian Ocean suggest that the mud crabs in East Africa consist of one large metapopulation spreading from Kenya to South Africa (Fratini et al. 2010), indicating that there should be no genetic obstacles of including data from South Africa. Although winter temperatures are lower in eastern South Africa than in Kenya (Table 1), growth rates of adult *S. serrata* from South Africa appear to be comparable to rates obtain in aquacultures from tropical areas (Hill 1975). To assess if the data from South Africa could be combined with data from the other areas, we carried out analyses with and without South African data and compared the results.

Intermolt periods were estimated following the Munro's (1974) procedure, which assumes that at the time of tagging, individuals of the same size are randomly distributed throughout their molting periods and that 50% should have molted when half of the intermolt period elapsed (see Ehrhardt 2008 for details). For individuals that had molted twice since release (based on an increase in carapace width of approximately 2 times the average molt increment), 50% of the time at large was used as the intermolt period for the intermediate size based on the same assumption.

2.3 Analyses of growth functions and segmented growth

The functional relationships between premolt size (CW) and proportional growth increment at molt and intermolt period were assessed with linear and non-linear functions using least square estimates and assessing random distribution of residuals to determine the best fit. Segmented growth of *Scylla serrata* was then estimated using the function between premolt size and proportional increment at growth to estimate the postmolt size, and the function between premolt size and intermolt period to estimate the time to the next molt, etc. Starting with a premolt size of 4 mm CW (first benthic instar stage; Holme et al. 2006) the growth of mud crabs was modeled in this stepwise procedure until a carapace width of approximately 240 mm CW (around maximum size of *S. serrata*; FAO 2013). This growth curve was finally transformed into growth in biomass using the functional relationships between carapace width and wet weight of crabs. This step-wise procedure generates segmented growth trends that take into consideration the average dynamics of growth for the selected species. Variability on the segmented growth can be studied by including the standard error of the functions in the stepwise procedure or conversely, using the variance of the growth parameters estimated (Ehrhardt 2008).

3. Results

Initial application of the mark-recapture data from South Africa (SA-data) showed an improved fit to the best curves with only minor effects on the estimated growth rates. Including the SA-data in the analysis of carapace width vs proportional increment at molt, increased the r^2 -value of the regression from 0.02 to 0.13, but had little effect on the estimated size at different molts with (<5% difference at all sizes) compared to the analysis when the data was not included. In the analysis of carapace width vs intermolt period, the SA-data also improved the fit to the best curve ($r^2=0.99$), particularly for lower values that showed a more random distribution of residuals. The effect of including the SA-data on estimated intermolt period was small for crabs <100 mm CW (<7% difference), but increased slightly for larger crabs up to a 17% longer estimate of the intermolt period for 150 mm CW crabs compared to the analysis when only data from Kenya and Tanzania was used. Based on these results it was decided to include the SA-data in the analyses.

Proportional increment of carapace width at molt in juvenile and adult *S. serrata* varied between 15% and 32%, and showed a slight decreasing trend from on average 23% in small juvenile crabs to 19% in large adult crabs. No discontinuity in proportional growth increment was seen around the size at maturity (120-140 mm CW; Robertson, 1996) and the functional relationship between the size of the premolt crab (CW) and the proportional molt increment was described with a linear function ($y = -0.0003x + 0.231$; $r^2 = 0.13$; $n = 93$; Fig. 1).

The estimates of intermolt period increased from about 7 days in small juvenile crabs (10 mm CW) to 105 days in large adult crabs (130 mm CW) and the functional relationship between the size of the premolt crab (CW) and the intermolt period was best described with a polynomial function ($y = 0.0053x^2 + 0.028x + 6.35$; $r^2 = 0.99$; $n = 14$; Fig. 2).

These functional relationships were used to model the discrete segmented growth in carapace width of *S. serrata* from 4 mm CW to 240 mm CW, which indicated a

sigmoid growth pattern with an exponential growth in juvenile mud crabs slowing in adult crabs towards an asymptote (Fig. 3).

The relationship between carapace width and wet-weight in mud crabs was best described with an exponential function ($y = 0.0001x^{3.114}$; $r^2 = 0.99$; $n = 900$; Fig. 4). Using this relationship, the segmented growth in biomass of *S. serrata* was modeled. The growth pattern over time was exponential for small juvenile crabs, which slowed toward a linear growth for adult crabs, possibly approaching an upper asymptote (Fig. 5a). The proportional growth increment in biomass per molt was close to a 100% for small juvenile crabs, decreasing non-linearly with age to around 55% for large adult crabs (Fig. 5b).

Fitting the modeled growth curve in carapace width to a von Bertalanffy growth function (VGBF) (Brey, 1999):

$$L_t = L_{inf} * (1 - e^{-K*(t-t_0)}) \quad (1)$$

graphically solving t_0 (-0.019) and using iterative non-linear least-square methods to solve K (0.57) and L_{inf} (310 mm CW) showed a relatively good fit ($r^2=0.89$), although the VGBF did not capture the sigmoid nature of the growth curve for juvenile crabs, resulting in an overestimation of the size of small juvenile crabs, and a slight underestimation of the size of sub-adult crabs (Fig. 6a). Plotting the data as biomass showed a slightly better fit between the modeled growth curve and the VGBF (Fig. 6b).

4. Discussion

4.1. Challenges in using a step-wise growth function

In the present study we describe for the first time natural growth in juvenile and adult *Scylla serrata* in East Africa using a step-wise growth function based on data on intermolt periods and growth increment at molt. This method, which has previously not been used to describe growth in crabs, has the advantage of taking into account the discrete, segmented growth of crustaceans, and was recently found to provide a better description of growth in spiny lobster than traditional size at age models adopted for fish species (Ehrhardt 2008). However, the challenge of the method is to obtain good data to describe the growth variables, in particular for assessing the intermolt period, which is notoriously difficult to measure in the field. In the present study we combined data from different types of studies and from different regions of East Africa. This approach allowed us to obtain estimates of intermolt periods and growth increment at molt of crabs ranging from 5 to 150 mm CW, even though it also introduced some uncertainties and limitations.

We used short-term (3 to 6 weeks) laboratory and cage studies to obtain growth estimates in juvenile crabs that were too small to mark with internal tags. Whereas laboratory studies of individually reared crabs have the advantage of providing exact estimates of intermolt periods, they may generate growth rates that differ from those in wild crabs. To minimize the risk in the present study, efforts were made to maintain optimal growing conditions by feeding crabs in excess and keeping temperature and salinities similar to those in the field (Table 1). Overall, mortality in these studies was <10%.

Mark-recapture data have the advantage of providing estimates of growth in the natural environment, but requires large set of data to generate estimates of intermolt

period. Such estimates are also dependent on assumptions of random distribution of the intermolt stage in the catch (Munro 1974), which introduces some level of uncertainty in the estimates. In the present study, the two mark-recapture studies only generated a total of 6 estimates of intermolt period. To obtain growth data on crabs >100 mm CW, we included data from South Africa (Hill 1975), which has substantially lower winter temperature than Tanzania and Kenya where the other data was collected (Table 1). Since low temperature may lower the growth rate, it is possible that including the data from South Africa may have resulted in a growth function that underestimate the growth rate for crabs in Kenya and Tanzania, particularly for adult crabs. However, analyses showed that data from South Africa fitted the other data well. In comparison with the field data of adult crabs from South Africa, the growth function based only on data from Kenya and Tanzania overestimated the growth increment at molt with only 5% and underestimated the intermolt period with 14%. Taken together, the total period to grow from 4 to 150 mm CW only increased with 10% when including the data from South Africa in the growth function. Based on this analysis, growth rates in adult mud crabs from the more subtropical estuaries of South Africa appear to be similar to estimates of growth rates in tropical East Africa, which is consistent with earlier comparisons (Hill 1975). Thus, combining data from different parts of East Africa appear to have had only minor effects on the estimated results.

Another potential limitation in this study is that the data was not separated for sexes, due to the limited amount of data for adult crabs. This has likely not affected the growth estimates in juvenile crabs since morphology of male and female mud crabs are essentially the same up to about 100 mm CW (Shelley & Lovatelli 2011). However, as crabs reach maturity at 120-140 mm CW (Robertson, 1996), the "crusher" chela of males increases in size from constituting approximately 20% of the body weight in juvenile crabs to approximately 50% of the body weight in large males (Heasman 1980). Since this change in morphology does not occur in females, a 200 mm CW male can weigh up to 80% more than a female crab of the same carapace width (Shelley & Lovatelli 2011). Thus, the presented growth function of biomass is likely an overestimation for adult female crabs and an underestimation for males.

Taken together, the presented growth function should be seen as a first attempt to describe natural growth in juvenile and adult *S. serrata* in East Africa. The model is restricted by a limited amount of data, in particular regarding estimates of intermolt period. It is supported by relatively good data for juvenile crabs, but is only based on data of adult crabs up to 150 mm CW; hence, estimates for larger crabs should be done with care, in particular regarding estimates of biomass. As more data becomes available for growth rates and carapace width-biomass relationship in adult male and female crabs, the growth functions could be improved to provide better estimates of natural growth in mud crabs from different regions of East Africa.

4.1. Natural growth in East African Scylla serrata

The results from the present study showed that proportional increment of carapace width at molt was fairly constant around 20%, with a weak decreasing trend with size, whereas the intermolt period increased exponentially with age from around 7 days in young juvenile crabs to over 3 months for adult crabs. This growth pattern is consistent with studies of other portunid crabs and crustaceans where growth per molt decreases, and the length of the intermolt period increases with age (Millikin and Williams 1984, Ehrhardt 2008). The modeled segmented growth function resulted in a

sigmoid growth pattern in carapace width, with an exponential growth in juvenile mud crabs slowing in adult crabs towards an asymptote, whereas growth pattern in biomass was exponential also in crabs weighing over 1 kg.

The modeled growth appears to be consistent with other reports of growth in *S. serrata*. The estimated intermolt period for 3rd instar crabs (6.9 d) is similar to growth rates measured in laboratory hatched *S. serrata* in northern Australia at similar temperatures and salinities (5.5-7.6 d; Ruscoe et al. 2004). In a recent aquaculture study in Kenya, juvenile mud crabs kept in replicate pen and pond systems with shelter and surplus of food grew from on average 7 to 43 g (in pen cultures) and from 23 to 74 g (in pond cultures) in 64 and 67 days, respectively (Mirera & Moksnes **Paper IV**). The presented growth function estimates that 62 and 69 days are needed for the same growth, respectively, only 7 to 8% different from the measured growth. The model also predict fairly well the growth of one of the tagged crabs from this study, which grew from 34 mm to 125 mm over a 216 d period (Table 2; this data was not used in the study). This growth is only 18% faster than the growth estimated with the models, which also suggest that the crab had molted 6 times during the 7 month period.

The von Bertalanffy growth function is probably the most common growth function used in fisheries biology, but only occasionally used in aquaculture studies (Hopins, 1992). Fitting the modeled growth in carapace width to a VBGF showed a relatively good fit, although the model did not fully capture the sigmoid growth pattern in small juvenile *S. serrata* (Fig. 6a). This resulted in up to 80% overestimation of the size of juvenile crabs <30 mm CW at a given age, but <10% deviation between the VBGF and the segmented growth function in larger sizes. In a similar study of spiny lobsters of the Florida coast in the USA, Ehrhardt (2008) found that VBGF based on indirect ageing procedures differed significantly from growth curves generated by segmented growth functions based on mark-recapture data, and may therefore not be suited to describe growth in the species. For *S. serrata* from East Africa, the presented VBGF appears to provide a good estimate of growth in mud crabs >30 mm CW (>4 g). However for estimate of growth in smaller mud crabs, a different growth function is recommended.

As far as we know, this is the first description of natural growth in juvenile and adult *S. serrata*, which provides significant results for management of mud crab fisheries and aquaculture in East Africa. The models suggests that newly settled 4 mm CW *S. serrata* will reach 300 g and sexual maturity (approximately 120 mm CW) after 9.9 months, and commercial sizes of 500 g and 1000 g after 12.4 and 17.3 months, respectively. This information is critical for cohort identification and estimating generation time, population growth and other key variables for a successful management of exploited mud crab populations. Growth functions are yet not commonly used to assess growth in mud crab aquacultures (see Christensen et al. 2004 for an exception), but could constitute a valuable tool in culture of mud crabs, e.g. for estimating growth cycles, production, optimal size for harvest, and to evaluate the growth rate in the culture, particular in East Africa that has limited experience of mud crab aquaculture. For example, in aquacultures using seed crabs of 10 g, it will take 7.3, 9.8 and 14.6 months to have a harvest of crabs with an average size of 300, 500 and 1000 g, respectively, if similar growth rates are obtained in the farm as the

one found in the present study. If instead seed crabs of 100 g are used, the equivalent predicted growth cycles are 3.6, 6.1 and 10.9 months.

Since this is the first growth function of *S. serrata* it is difficult to compare the results to other studies and regions. The only other published growth function in mud crabs that we are aware of is of *S. paramamosain* in Vietnam, where natural growth was estimated using mark-recapture data that was fitted to a VBGF (Le Vay et al. 2007). This species has a smaller maximum size (approximately 150 mm CW), but, according to the study, a substantially faster juvenile growth rate than *S. serrata* ($k=2.39$; Fig. 6c). The lack of other field based growth functions make it difficult to assess if this species-specific difference in growth rate is general.

4.2 Comparing growth in mud crab aquaculture

There are a number of estimates of growth in mud crabs in the literature from aquaculture studies. However, it is difficult to compare these values since different initial sizes and growth periods have been used, and the growth rate has usually only been estimated using two points in time, giving little information of the shape of the growth curve. In most aquaculture studies, growth is estimated as absolute growth rates per day (AGR):

$$\text{AGR} = (S_T - S_0) / T \quad (2)$$

where S_T =final size, S_0 =Initial size and T =growth period, and usually presented as a standardized "grams per day". However AGR can only be compared between studies if growth during the period is linear, or if the initial sizes of crabs and the length of the studies are the same. Since growth in most animals is non-linear, typically following an asymptotic sigmoid curve, estimates of growth rates will strongly depend on between which two points in time growth is measured (Hopins 1992). It is therefore difficult to compare absolute growth rates between studies that have used different initial sizes or growth periods, a fact that is not always observed in the literature of mud crab aquaculture. In *S. serrata*, AGR of carapace width and weight show different non-linear relationships with the initial size of the crab (Fig. 7ab), complicating comparisons between studies.

In many aquaculture studies, growth is also estimated as relative growth rate per day (RGR):

$$\text{RGR} = ((S_T - S_0) / S_0) / T \quad (3)$$

or as instantaneous growth rate, often called specific growth rate (SGR), typically presented as % growth per day:

$$\text{SGR} = ((\ln(S_T) - \ln(S_0)) / T) * 100 \quad (4)$$

Although these measures are less sensitive to different initial sizes and the growth period, respectively, they are only applicable for exponential growth relationships (Hopins, 1992), and clearly not suitable for growth in adult crabs approaching an upper asymptote. In *S. serrata*, both RGR and SGR show non-linear relationships with the initial size of the crab, decreasing sharply in larger crabs (Fig. 7cf).

One way to address the problem of comparing studies with different initial sizes and growth periods is to use a growth function (e.g. VBGF) to estimate the required time to grow from the initial to the final size, and compare this value with the growth period of the study, to estimate the proportional difference ($T_{\text{VBGF}} / T_{\text{study}}$). This "proportion of modeled growth" has the advantage of compensating for differences in initial sizes and growth periods. Importantly, even if the model is incorrect it compensates all data in the same way, providing a relative value that can be compared between studies. In Table 3, measures of growth rates in mud crabs from aquaculture

studies have been compiled, and the *proportion of modeled growth* has been estimated using the VBGF of *S. serrata* in East Africa. The table shows a large variation between studies and species within the 3 standard measures for growth rate (70-1000 times difference for AGR, RGR and SGR), and that these values are strongly correlated to the initial size of the crabs in the growth studies (Fig. 8), demonstrating the problem of using these measures for comparisons when the initial size and growth period differs. In contrast, the *proportion of modeled growth* shows a relatively small difference between studies (16% to 239% of the growth rates estimated by the VBGF for *S. serrata*), and identifies the outliers from the exponential curves in Fig. 8 (e.g. the low values from some cage studies in Kenya; Table 3). The variation in the *proportion of modeled growth* likely represents "real" differences in growth due to the growing conditions and species-specific differences.

Comparing the growth rates in *S. serrata* from aquaculture studies within East Africa, growth in experimental pond and pen cultures in Kenya are close to the modeled growth (86-99%; Table 3) suggesting that growth in those studies were similar to natural growth. In contrast, mud crabs in "drive-in" cage systems in Kenya (Mirera, 2009, Mtile & Mirera 2009) appear to grow substantially slower (on average 39% of the modeled growth). The reason for the lower growth rate in the cage systems are presently not known, but efforts should be made to assess if the growing conditions could be improved before this culture system is further promoted to local communities in East Africa.

Interestingly, *S. serrata* in different aquaculture systems in the Philippines show considerably higher growth rates than for the same species in East Africa (on average 145% of the modeled growth; Table 3). The reason behind this apparent difference is unclear but warrant further investigation. Recent studies have shown that the *S. serrata* from East Africa consist of a unique metapopulation that is genetically distinct from populations in Australia and other areas of the Indo-Pacific region (Fratini et al. 2010). If the regional difference in growth rate, indicated in the present study, is genetically determined it could have important consequences for the development of the aquaculture of mud crabs in East Africa. Consistent with the comparison of field based growth functions, the growth rates of *S. paramamosain* from aquaculture studies in Southeast Asia was on average 167% of the modeled growth for *S. serrata*, suggesting that *S. paramamosain* has the fastest growth rate of all mud crab species. The growth rates of *S. tranquebarica* and *S. olivacea* in cultures with mono- or mixed species of crabs were on average 124% of the modeled growth for *S. serrata*, but showed a large variation in relative growth rates between similar systems (Table 3) indicating that more studies are needed to assess the species-specific growth rates for these mud crabs. This first comparative analysis of growth in mud crabs indicates large differences between regions and species, with potential important consequences for productivity of mud crab aquaculture. More studies of natural growth and growth functions of mud crabs are encouraged for other species and region to increase our understanding of the processes behind these apparent differences.

Acknowledgements

The authors wish to express their thanks to the staff of Mafia Island Marine Park, Kenya Marine and Fisheries Research Institute and the Institute of Marine Sciences, Zanzibar for providing excellent facilities and support. We also would like to thank Prof. Per Jonsson for help with statistical analyses. Funding was provided through a

MASMA-grant from the Western Indian Ocean Marine Science Association (WIOMSA), and through Minor Field Studies stipends from the Swedish International Development Cooperation Agency (Sida).

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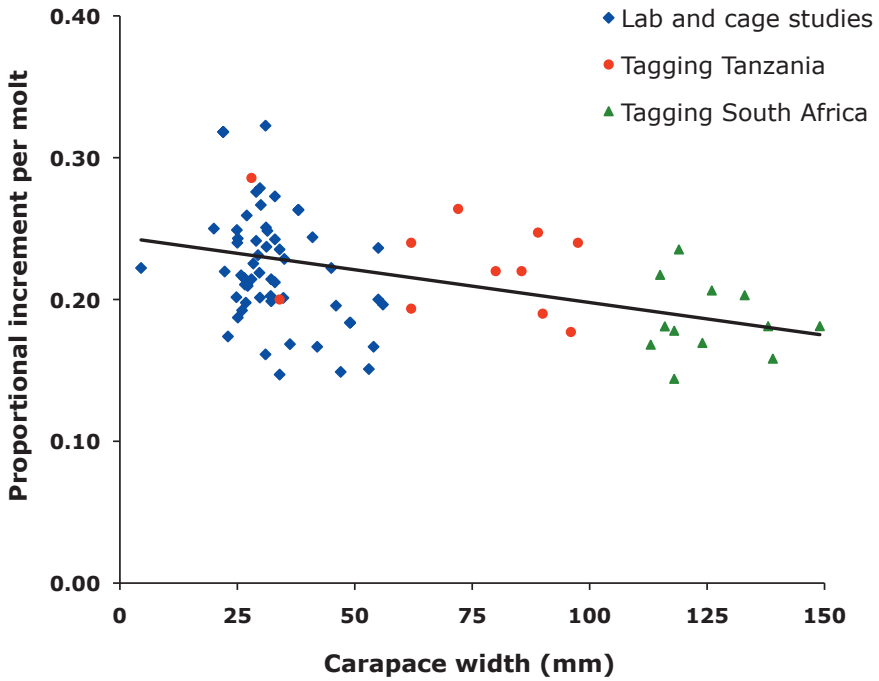


Fig. 1. *Scylla serrata* - proportional growth increment at molt. Linear relationship between the premolt carapace width and the proportional growth increment at molt (pre-molt size/postmolt size) of mud crabs from laboratory and cage studies in Tanzania and Kenya, and from mark-recapture studies from Mafia Island Tanzania and South Africa ($y = -0.0003x + 0.231$; $r^2 = 0.13$; $n = 93$).

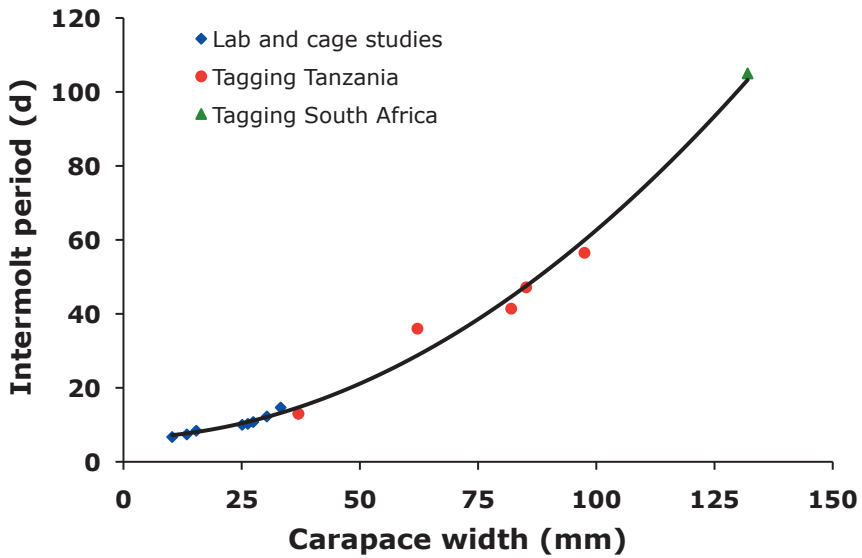


Fig. 2. *Scylla serrata* - intermolt period. Non-linear relationship between the carapace width of premolt mud crabs and the intermolt period (days) of mud crabs from pond and laboratory studies in Tanzania and Kenya, and from mark-recapture studies from Mafia Island Tanzania and South Africa ($y = 0.0053x^2 + 0.028x + 6.35$; $r^2 = 0.99$; $n=14$).

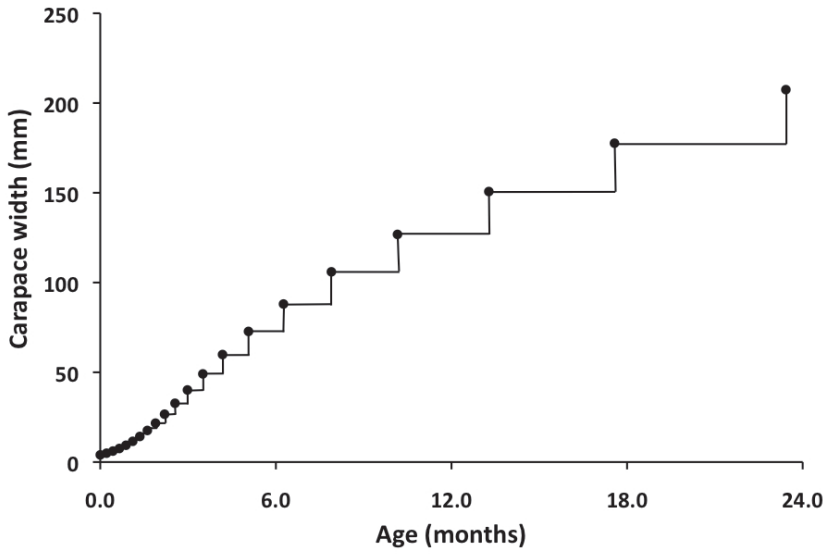


Fig. 3. Modeled segmented growth of carapace width (mm) in *Scylla serrata* as a function of time.

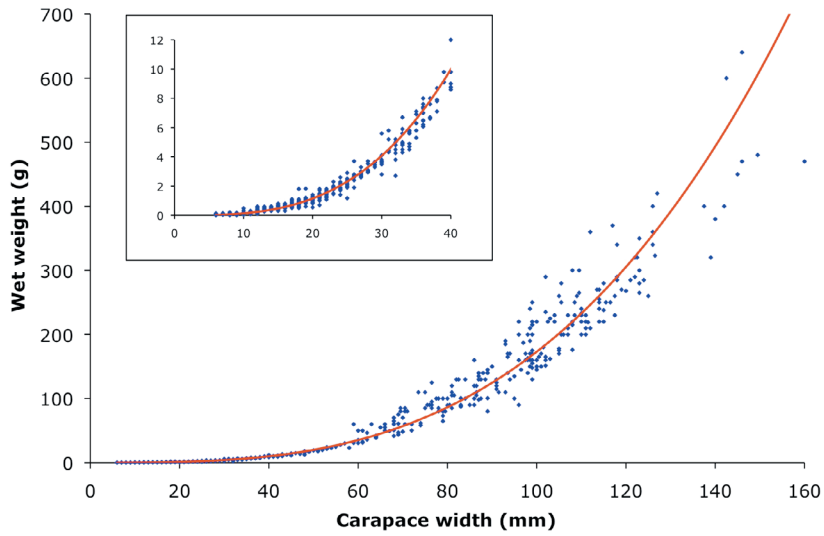


Fig. 4. *Scylla serrata* - carapace width-wet weight function. Exponential relationship between the carapace width (mm) and wet weight of mud crabs from Tanzania and Kenya ($y = 0.0001x^{3.114}$; $r^2 = 0.99$; $n = 900$).

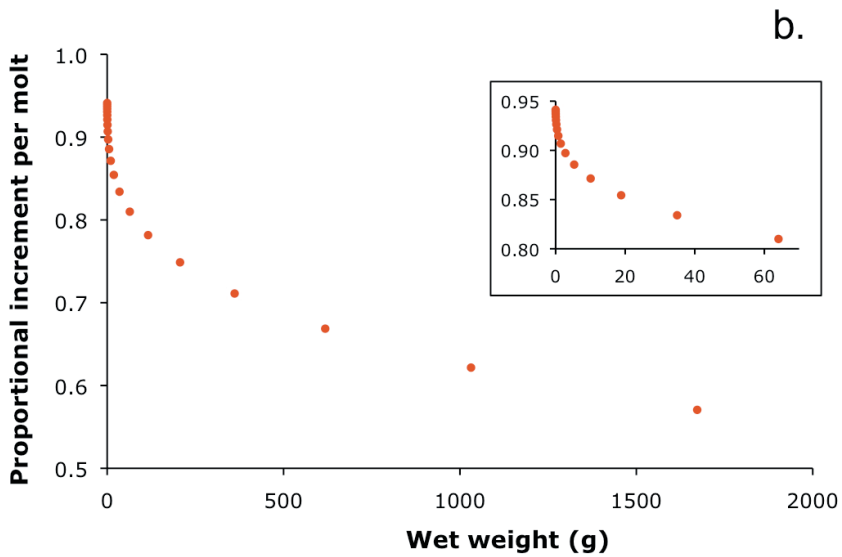
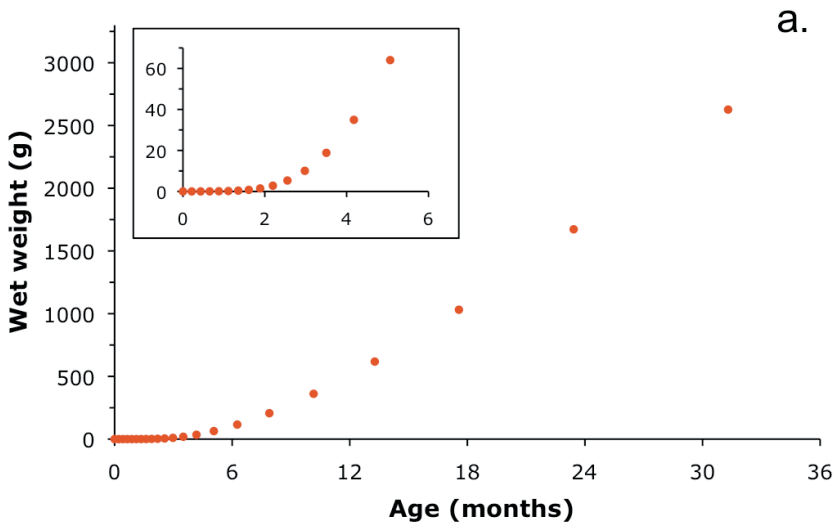


Fig. 5a. Modeled segmented growth of biomass (g wet weight) in *Scylla serrata* as a function of time, and (b) proportional increment in biomass per molt as a function of biomass.

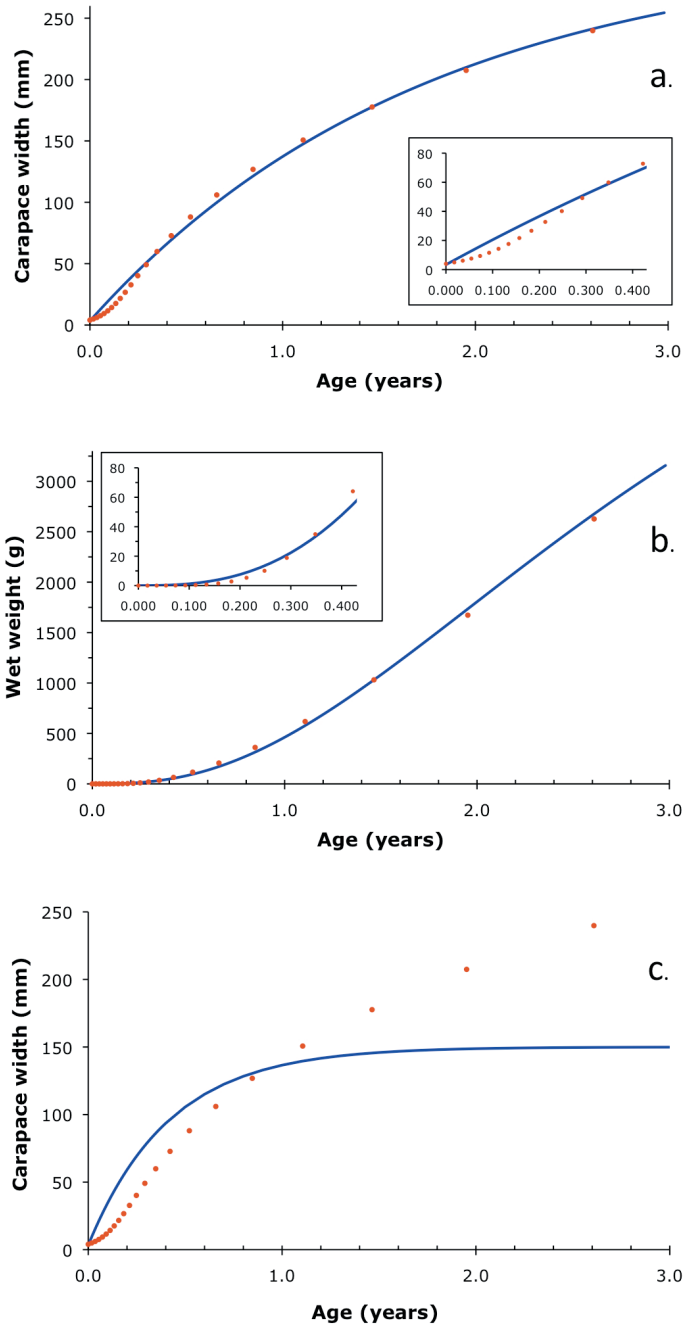


Fig. 6. Modeled segmented growth of *Scylla serrata* (dots) and a fitted von Bertalanffy growth function ($L_t = L_{inf} * (1 - e^{-K*(t-t_0)})$; $L_{inf} = 310$ mm; $t_0 = 0.019$; $K = 0.57$; $r^2 = 0.89$; line) as a function of time for (a) carapace width and (b) biomass. (c) von Bertalanffy growth function of carapace width for *S. paramamosain* in Vietnam ($L_{inf} = 150$ mm; $t_0 = -0.0095$; $K = 2.39$; line; Le Vay et al. 2007) and modeled segmented growth in carapace width of *S. serrata* (dots).

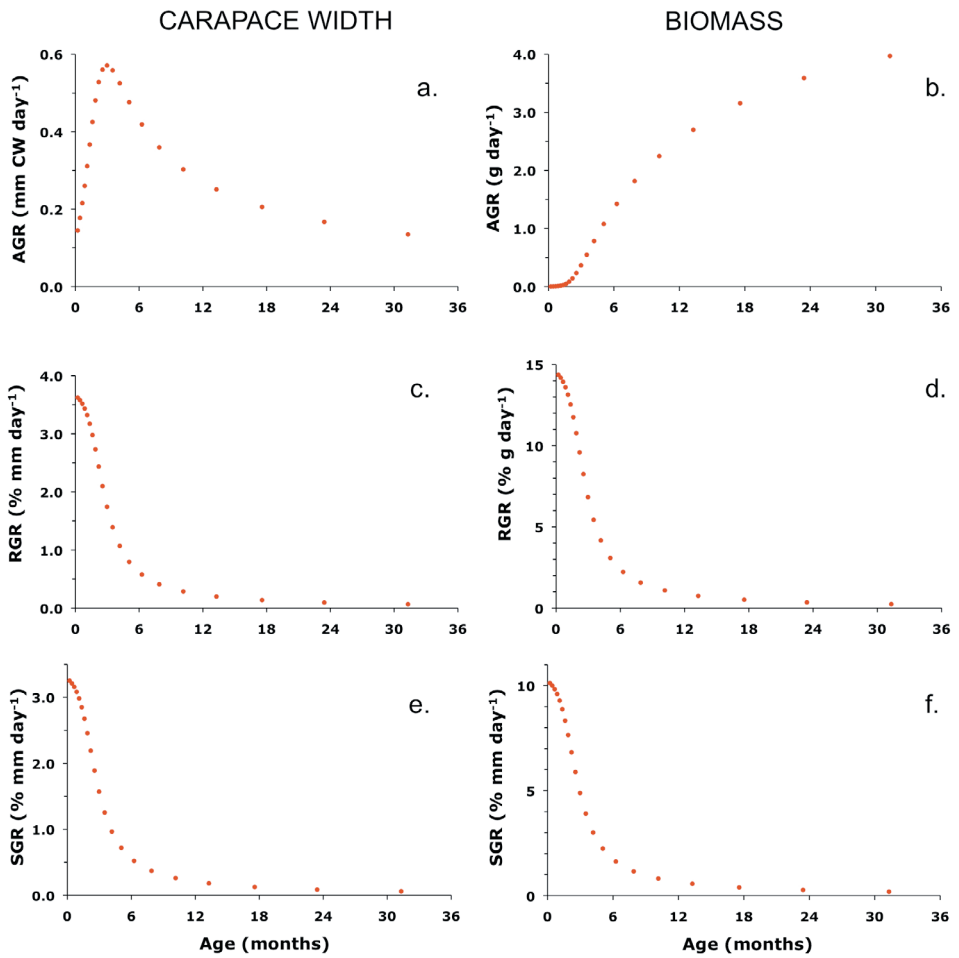


Fig. 7. Growth rates of carapace width and biomass in *Scylla serrata* during each intermolt stage as a function of age. (a-b) Absolute growth rate (AGR) per day, (c-d) relative growth rate (RGR) per day, and (e-f) instantaneous growth rate (i.e. specific growth rate; SGR) per day (see text for equations).

Table 1. Summary of the studies used to obtain data for estimates of growth increment at molt (GI), intermolt period (IP) and carapace width - biomass relationship (CB) in juvenile and adult *Scylla serrata* from East Africa. The number and size of crabs refers to the initial number and sizes of crabs in the growth study, or the number and size range of recaptured crabs that had molted since release. The data on carapace width - biomass relationship is mainly based on measurement of field-collected crabs used in aquaculture studies.

Location	Type of study	No. crabs	Size mm CW	Duration (days)	Temp (°C)	Salinity	Data collected	Reference
Zanzibar*, Tanzania	Lab, 10 L tanks	16	18-25	40	25-30	34-36	GI, IP	Hamad 2012
Mombasa, Kenya	Lab, 10 L tanks	34	22-56	20-30	27-28	32	GI	Mirera & Moksnes Paper IV
Mafia Island, Tanzania	Pond, 1 m ² cages	30	5-14	30	28-32	30-36	GI, IP	Nyqvist 2011
Mafia Island, Tanzania	Mark-recapture	11	28-96	13-216	26-30	30-34	GI, IP	Björkvik 2010
Port Alfred, South Africa	Mark-recapture	20	100-152	23-414	12-28	10-38	GI, IP	Hill 1975
Mafia Island, Tanzania	Field collection	683	6-102	-	28-30	34	CB	Mahudi <i>unpubl.</i>
Mombasa, Kenya	Field collection	217	59-160	-	28-30	25-34	CB	Mirera 2009, Mirera & Mtile 2009

* The laboratory study was carried out on Zanzibar, but the crabs were collected on Mafia Island, Tanzania.

Table 2. Mark-recapture study 2010 on Mafia Island, Tanzania. Summary of recaptured crabs that exhibited growth between time of tagging and recapture.

Date Tagged	Date Captured	Time at large (days)	Tagged size (mm)	Recapture size (mm)	Estimated no. molts
4 Feb	1 Mar	26	28	36	1
5 Feb	5 Jun	120	77	116	2
6 Feb	17 Mar	40	62	74	1
6 Feb	10 Sep	216	34	125	6
16 Feb	5 Mar	18	89	111	1
16Feb	20 Mar	33	96	113	1
18 Feb	11 Jun	113	87	135	2
2 Mar	16 Mar	14	31	44	2
8 Mar	20 Mar	13	72	91	1
22 Mar	12 Jun	82	82	115	2
24 Mar	13 Jun	81	72	106	2

Table 3. Comparison of different measures of growth rates from aquaculture studies, i.e. absolute growth rate (AGR; g per day), relative growth rate (RGR, % per day), specific growth rate (SGR; %/d) and modeled growth using VBGF of *Scylla serrata* in East Africa presented in this paper. All estimates are based on the average initial and final weights (Start W and End W) presented in the studies. The last columns show the modeled duration of growing from the listed initial to the final weight, and the proportional difference in duration between the measured and modeled duration. Four species are included, *Scylla serrata* (Ss), *S. tranquebarica* (St), *S. olivacea* (So), and *S. paramamosain* (Sp) in mono- and mixed crab cultures. The studies were carried out in earthen pond cultures, pen cultures, cage cultures and in laboratory tanks. * denotes experimental studies.

Species	Country	Type of study	Start W (g)	End W (g)	T (days)	AGR (g/d)	RGR (%/d)	SGR (%/d)	T _{VBGF} (days)	Prop. diff T _{VBGF} /T _{Study}	Reference
Ss	Kenya	Pond*	15	63	68	0.70	4.6	2.08	67	0.99	Mirera & Moksnes Paper IV
Ss	Kenya	Pen*	6.1	34	71	0.39	6.5	2.42	61	0.86	Mirera & Moksnes Paper IV
Ss	Kenya	Cage*	259	337	91	0.85	0.3	0.29	33	0.37	Mirera 2009
Ss	Kenya	Cage*	165	266	122	0.82	0.5	0.39	51	0.42	Mirera & Mtile 2009
Ss	Australia	Lab*	0.02	0.21	18	0.01	58.9	13.64	13	0.74	Ruscoe et al. 2004
Ss	Taiwan	Lab*	0.05	1.05	63	0.02	35.0	4.98	26	0.42	Sheen and Wu 1999
Ss	Taiwan	Lab*	0.09	0.83	84	0.01	10.4	2.71	20	0.24	Sheen 2000
Ss	Philippines	Cage*	0.25	4.4	30	0.14	55.2	9.57	41	1.36	Rodriguez et al. 2007
Ss	Philippines	Pond*	0.25	13.3	30	0.43	173.9	13.28	71	2.39	Rodriguez et al. 2007
Ss	Philippines	Pond	14	215	131	1.53	11.0	2.09	171	1.31	Fielder 2003
Ss	Philippines	Pen*	22	319	159	1.86	8.7	1.69	203	1.27	Trino & Rodriguez 2002
Ss	Philippines	Pond*	25	194	90	1.87	7.4	2.27	138	1.53	Agbayani et al. 1990
Ss	Philippines	Pen*	40	200	146	1.09	2.7	1.10	119	0.82	Genodepa 1999
Ss, St	Philippines	Pond*	9.2	391	122	3.12	34.2	3.08	261	2.14	Trino et al. 1999
So, St	Malaysia	Pen	100	300	158	1.26	1.3	0.69	109	0.69	Wei Say & Ikwanuddi 1999
So, St	Malaysia	Pond	250	400	30	4.92	2.0	1.55	62	2.04	Keenan 1999
So	Vietnam	Pond*	8.7	223	130	1.65	19.1	2.50	190	1.47	Christensen et al. (2004)
So	Philippines	Pond*	46	167	125	0.97	2.1	1.03	94	0.75	Fortes 1999
Sp	Indonesia	Cage	315	425	21	5.15	1.6	1.41	43	2.01	Keenan 1999
Sp	Vietnam	Pond*	4.7	198	106	1.82	38.8	3.53	193	1.83	Ut et al. 2007
Sp	Vietnam	Pond*	8.7	234	130	1.73	19.9	2.53	196	1.51	Christensen et al. (2004)
Sp	Vietnam	Pond	63	350	122	2.36	3.8	1.42	161	1.33	Johnston & Keenan 1999

PAPER III:

Cannibalism in Juvenile crabs



Cannibalistic interactions of juvenile mud crabs *Scylla serrata*: the effect of shelter and crab size

OD Mirera^{1,2*} and P-O Moksnes³

¹ Kenya Marine and Fisheries Research Institute (KMFRI), PO Box 81651, Mombasa, Kenya

² Linnaeus University, School of Natural Sciences, Box 391 82, Kalmar, Sweden

³ University of Gothenburg, Department of Biology and Environmental Sciences, Box 461, 40530 Göteborg, Sweden

* Corresponding author, e-mail: dimirera@yahoo.com

In the culture of mud crab *Scylla serrata*, cannibalism is often the greatest cause of mortality. A laboratory study was conducted to compare the influence of size class differences and shelter on cannibalism and limb loss in juvenile mud crabs (20–70 mm internal carapace width; ICW). Four size classes of juvenile crab (A: 21–30 mm, B: 31–40 mm, C: 41–50 mm and D: 51–70 mm ICW) were tested in all possible combinations using four different substrata with varying degree of shelter (seaweed, plastic strings, bamboo tubes and open sand substratum) in 48 h trials. Results suggest that cannibalistic interactions are heavily influenced both by size differences of crabs and the availability of shelter. Cannibalism on the smallest size class (20–30 mm ICW) increased about 10 times in the presence of the largest crab (51–70 mm ICW) compared with treatment with only same-size crabs (control treatment). Shelter provided little refuge for the smallest crabs, whereas cannibalism in larger size classes decreased by >50% in all the shelters compared with the sand substratum. The findings suggest that both size-grading and provision of shelter could minimise cannibalism in the culture of mud crabs.

Keywords: cannibalism, mortality, size combination, size grading, substrata

Introduction

The culture of mud crabs *Scylla serrata* is commercially developed in South-East Asia (Keenan 1999, Agbayani 2001) and has been a focus over the past decade in the Western Indian Ocean (WIO) region (Mwaluma 2002, Rönnbäck et al. 2002, Mirera 2009, 2011). Aquaculture expansion in South-East Asia has been documented to have caused a decline in wild seed supply that has impacted both culture and capture fisheries (Keenan 1999). Research on the development of seed production has achieved significant progress in South-East Asia in recent years (Quinitio et al. 2001, Allan and Fielder 2003, Quinitio et al. 2007, Quinitio and Estepa 2011). However, no effort has been made in the WIO region to produce seed in hatcheries because farming is mainly small-scale. Therefore, the assumption is that there are sufficient numbers of seed crabs in the wild to meet the growing industry. However, this assumption may not hold for long because of overexploitation of the resource by artisanal fishers using traditional capture methods such as hook sticks, pots, traps and seine-nets, as in South-East Asia (Motoh 1983, Angell 1992, Kosuge 2001).

Currently, artisanal fishers in the WIO can meet the demand from tourist hotels, private homes and export markets, which is growing rapidly (Barnes et al. 2002, ACDI-VOCA 2005, Richmond et al. 2006, Mirera 2009, 2011). However, being unregulated, the fishery is vulnerable and there are indications of a significant decrease

in wild populations (Francis and Bryceson 2001). Such a decline will have direct negative impacts on recruitment and seed availability and the behaviour of the industry in the region, as observed in other parts of the world (Takeuchi 2001, Hamasaki et al. 2002).

Because of limited knowledge on the availability of juvenile mud crabs from the wild and their behaviour in culture conditions, most culture initiatives in the WIO grow small subadults to market size over short periods. In South-East Asia, lean crabs which have reached market size are cultured to gain weight in a process referred to as 'fattening'. In the WIO, crab culture is small scale and is mainly carried out in individual cages to minimise cannibalism and aggression (fighting). However, survival is low and growth slow in such culture systems (Mirera 2009, 2011). Recent initiatives have therefore been taken to develop small-scale, grow-out systems in ponds and pens, where small juvenile crabs are farmed for longer to attain market size, similar to the system used in South-East Asia (Mwaluma 2002, Mirera 2009, Mirera and Mtile 2009, Mirera 2011).

Globally, the factors affecting survival in crab culture are cannibalism, moulting, salinity and temperature fluctuations, feed, shelter and stocking density (Trino et al. 1999, Ruscoe et al. 2004, Holme et al. 2007, Mann et al. 2007, Rodriguez et al. 2007, Mirera 2009, Quinitio and Estepa 2011). Some of these mortality-associated

factors have been addressed in South-East Asia and survival is currently between 50% and 70% per growth cycle in various culture systems (pens, cages and ponds). However, aggression and cannibalism, which are ranked as the main causes of low survival in semi-intensive and intensive culture systems, still remain a challenge (Quinito et al. 2001, Williams and Primavera 2001, Allan and Fielder 2003, Mann and Paterson 2003, Paterson et al. 2007). Research in South-East Asia has used hatchery-produced seed crabs that are of similar size at stocking, which reduces cannibalism (Parkes et al. 2011). However, there is little information on how the interactions between different size classes of crabs in culture systems influence cannibalism. Information on different size-class interactions is essential to improve culture success in the WIO, where seed supply is from the wild and there are many size classes being stocked (Mirera 2009, Mirera and Mtile 2009). Cannibalism of juvenile portunid crabs is at its greatest when the cannibalising crabs are large enough to kill other crabs in intermoult with hard exoskeletons (Moksnes et al. 1997, 1998, Marshall et al. 2005). To avoid high rates of cannibalism in crab aquaculture, therefore, it is critical to ensure that the sizes of crabs are kept similar in pens and ponds to preclude this type of cannibalism.

The aim of the present study was to investigate how size-class differences affect cannibalism rates of juvenile mud crabs and how cannibalism is influenced by the availability of shelter. The information will hopefully guide farmers on possible size-class combinations to stock and on suitable shelters to use at the farms.

Material and methods

A series of laboratory experiments was carried out at the Kenya Marine and Fisheries Research Institute (KMFRI), Mombasa, Kenya, to assess the interactive effect of size difference and shelter on cannibalism in juvenile mud crabs. As the primary aim was to assess cannibalism on intermoult crabs, we used short experimental trials (48 h) to minimise moulting, and high densities of crabs (75 crabs m⁻²) to enhance cannibalistic interactions between the crabs.

Experimental set-up

Local fishers were hired to collect juvenile crabs from the nearby mangrove intertidal flat during low spring tides. Crab collection took approximately 3 h and transportation to the laboratory another hour. Sorting was done in the field, hard-shelled healthy crabs (active and with intact appendages) being packed in plastic buckets with clean, wet sand, covered with mangrove leaves and transported to the laboratory. At the laboratory the juveniles were sorted according to size class (see below), placed in 50-litre aquaria with sand at a density of approximately 30 crabs m⁻² and acclimatised for at least 24 h before use in the experiment. Crabs were fed sardine during acclimatisation. Although communal acclimatisation may introduce superior/inferior behavioural traits in crabs (Bergman and Moore 2005, Parkes et al. 2011, Beattie et al. 2012), the effect should be the same in all treatments because the acclimatisation was standard for all size classes. Crabs were measured (internal carapace width, ICW, and carapace

length, CL) at the start of the experiment, each combination of measurements enabling identification of individual crabs at the end of trials that included the effects of moulting. Only healthy crabs (active and feeding) with intact appendages were used in the experiments.

The tests were carried out in small, circular, static tanks (bottom area 0.03 m²; 10 litres) with 20 mm of sieved (1 000 µm) beach sand, filled with natural surface seawater from Tudor Creek, Mombasa, Kenya. Tanks were covered with black polythene sheeting to minimise disturbance. The tanks were provided with mild aeration throughout the experimental period. Water was maintained at room temperature (27–28 °C) and at an average salinity of 32 (SD 1.20). The tanks were arranged in a fully randomised design on vertical metal racks in two parallel rows on one side of the room. The trials were conducted for 48 h (day and night) and the experiment spread over a period of two months.

Treatments

In all experimental treatments, four crabs per tank were assessed (equivalent to ~75 crabs m⁻²), either four crabs of the same size class (control treatment) or one of a larger size class (referred to as the 'predator crab') and three smaller crabs of the same size class (referred to as 'prey crabs'). We used several prey crabs in each tank to increase the chances of detecting differences in the rates of cannibalism between treatments. Cannibalistic interactions between four size classes of juvenile mud crabs (A: 21–30 mm, B: 31–40 mm, C: 41–50 mm, D: 51–70 mm ICW) were tested in all possible combinations in four types of shelter treatments: seaweed (*Eucheuma denticulatum*), plastic strings (bundles of string locally known as 'kakabans'), bamboo tubes, and sand substratum without any extra shelter (all treatments had sand on the bottom of the container). The number of size combinations tested differed between different size classes: the smallest size class (A) was assessed in four size combinations, including the control treatment with the same size (AA) and three treatments with one larger predator crab (AB, AC, AD); the second size class was assessed in three size combinations (BB, BC, BD); the third in two (CC, CD); and the largest size class (D) only with crabs of the same size (DD, i.e. control treatment). In total, 40 different treatment combinations were assessed with five replicates for each treatment. A total of 800 crabs was used in the experiments.

Substrata were selected based on their potential to provide shelter from cannibalism and on their availability to crab farmers. Red algae (*Eucheuma denticulatum*) for the experiment were obtained from community farms along the southern coast of Kenya. Four branches 200–300 mm long with a total weight of 250 g were used for the shelter. The shelter made of plastic strings was cut from sacks into pieces 400 mm long, with about 200 strings tied at the centre in a bundle. The bottom ends of the seaweeds and plastic strings were buried in the sand. Dried bamboo tubes were cut into pieces 105 mm long and with 40 mm internal diameter and three pieces were placed horizontally on the bottom of each tank.

At the start of each trial, the predator crab (if present) was placed in experimental tanks 30 min before introducing prey crabs. The larger crabs were used only once as predators

but could be used as prey crabs in their respective size classes after undergoing an additional acclimatisation for at least 24 h. During the 48 h trials, crabs were monitored daily and any mortality or moulting was noted. At the end of each experimental run, all shelters were carefully removed to avoid loss of the experimental specimens. Water and sand were sieved through a 500 µm sieve to retrieve crabs, moult shells, broken shells and crab remains. Morphometric measurements (ICW, CL) were taken for whole moult shells and live crabs were checked for cannibalistic scars (broken carapace), moulting and loss of appendages. Simultaneously, the presence of dead and uneaten crabs, live crabs, moulted crabs and moult, shells as well as evidence of damaged crabs, were noted.

Statistical analyses

All data were tested for homoscedasticity with Cochran's C-test (Sokal and Rohlf 1981) and, if found to be heteroscedastic, were square-root transformed before the ANOVA was performed. All data for the percentage of cannibalised crabs were square-root transformed to homogenise the variance. *A posteriori* multiple comparisons were carried out with the Student Newman Keuls (SNK) procedure.

To test for the effects of shelter and crab size differences on cannibalistic interactions, a series of ANOVAs was carried out. As the experimental design was not orthogonal, the effect of prey size and predator size was tested in separate sets of two-way ANOVA. In all analyses, the percentage of cannibalised crabs (the percentage of prey eaten) and the percentage limb loss of prey crabs (the percentage of surviving crabs missing one or more appendages) were tested as dependent variables. Limb loss of predator crabs was negligible and not included in the analyses. To assess the combined effect (shelter and size), we also analysed the total percentage of crabs cannibalised or missing a limb. The percentage of crabs found dead and uneaten, and the percentage of prey crabs that moulted, were also analysed as dependent variables to establish whether factors other than cannibalism affected survival, and if moult rate was being influenced by experimental treatments.

The overall effects of predator presence and shelter were tested in a two-factor ANOVA model using predator treatments (control, predator size classes B–D) and shelter treatments (4 levels) as fixed independent variables. Each prey size class (size classes A–C) was also tested in three separate series of analyses using the same two-factor ANOVA model. The overall effect of prey size (size classes A–D) was tested in a one-factor ANOVA model using all data. To assess cannibalistic interactions only within crab size classes, prey size and shelter were analysed as independent variables using only data from the control treatments, in a separate series of analyses.

Results

Experimental conditions

All crabs used in the experiment were accounted for at the end of each trial. In five of the predator treatment combinations (4.1% of the treatments), the predator was dead at the end of the trials, so those data were excluded from

the analyses because the predatory aspect was lost in the treatment. In 7.5% of the predator treatment combinations, the predator crab had moulted and these data were included in the analyses because there was predation in some of the trials. In total, 3.8% of the prey crabs were found dead and uneaten at the end of the trials; their individual data were not used in the analysis. The reason for the mortality was unclear, but it did not differ significantly ($p > 0.05$) between treatments in any analyses (Tables 1 and 2) and should not have affected the cannibalism results. On average, 4.3% of the prey crabs had moulted at the end of the trial. The percentage of prey crabs that moulted did not differ significantly ($p > 0.05$) between predator treatments. However, the percentage of prey crabs that moulted was significantly higher in sand substratum than in the other substrata when analysing data from all experimental units (Table 1, Figure 1). The substratum pattern in moult crabs was indicated for each prey size class, although the difference was not significant when analysing the data separately by size class (Table 2). A similar result was found when analysing the control data separately, where the moult rate was significantly higher in sand than in the bamboo treatment (Table 2, SNK-test $p < 0.05$).

Cannibalistic interaction

Overall, cannibalistic interactions increased with predator size, decreased with prey size and were fewer in the substrata that provided shelter. However, the effect of predator presence and shelter differed between prey size classes.

In all, 51 individual crabs were cannibalised, giving an equivalent of 7.5% cannibalism in 48 h for all predatory treatment combinations. When testing the overall effect of predator crab and shelter treatments, the percentage of cannibalised crabs was significantly higher in the sand substratum (on average 15% loss 48 h⁻¹) than in all substrata combined (3–8% loss 48 h⁻¹) in all predator treatments (Table 1, Figure 1). Cannibalism appeared to increase with predator size, from an average of 5% in control treatments to 13% in the presence of predator size class D, but this trend was not significant (Table 1). There was also a trend of decreased cannibalism with increased prey size, from 11% at prey size A to 5% at prey size C, but no significant effect of prey size was found (one-factor ANOVA; $df = 3,191$; $F = 1.46$; $p = 0.22$).

The percentage of surviving crabs missing one or more limbs followed a pattern similar to that of cannibalism. However, predator treatments had a greater effect than shelter treatments on limb loss. The percentage limb loss increased significantly from an average of 3% in control treatments to 12% in the presence of the larger predator size classes (Table 1, Figure 1), although it was not significantly affected by shelter. Total negative interactions (i.e. the sum of prey crabs cannibalised or missing a limb) showed a significant effect of both shelter and predatory treatment. Sand substratum had a significantly greater degree of negative interaction than the three shelters used. Also, predator size class D had a significantly greater percentage of limb loss than the control treatments (Table 1; SNK-test at $p < 0.05$).

Analyses of each prey size separately demonstrated that cannibalism on the smallest prey crabs was more

Table 1: Two-factor ANOVA model of square-root transformed data (for all prey sizes) testing: the percentage of cannibalised prey crabs 48 h⁻¹; the percentage of live prey crabs missing one or more limbs; the total number of negative interactions (i.e. the sum of prey crabs cannibalised or missing a limb); the percentage of moulting prey crabs; and the percentage of prey crabs found dead and uneaten (mortality), as a function of predator and substratum treatment

Source of variation	df	Cannibalism		Limb loss		Total negative interactions		Moult		Mortality	
		SS	F	SS	F	SS	F	SS	F	SS	F
Predator	3	1.11	1.81 (ns)	0.30	3.38*	2.91	3.31*	0.00	0.13 (ns)	0.07	2.03 (ns)
Shelter	3	1.85	3.00*	0.09	1.00 (ns)	3.26	3.70*	0.14	3.95**	0.02	0.47 (ns)
Predator × Shelter	9	1.09	0.80 (ns)	0.18	0.67 (ns)	1.94	0.74 (ns)	0.07	0.62 (ns)	0.09	0.92 (ns)

* $p < 0.05$; ** $p < 0.01$; (ns) $p > 0.05$

Table 2: Two-factor ANOVA models of square-root transformed data testing: the percentage of cannibalised prey crabs 48 h⁻¹; the percentage of live prey crabs missing one or more limbs; the percentage of moulted prey crabs; and the percentage of prey crabs found dead and uneaten (mortality), as a function of predator treatment (control, predator size B, C and D) and habitat treatment (sand alone, seaweed, plastic strings and bamboo tubes), for prey size class A (21–30 mm ICW), B (31–40 mm ICW) and C (41–50 mm ICW), and for control treatments without predator crabs

Source of variation	df	Cannibalism		Limb loss		Moult		Mortality		
		SS	F	SS	F	SS	F	SS	F	
<i>Prey size A</i>										
Predator	3	3.29	4.46**	0.17	1.48 (ns)	0.013	0.27 (ns)	0.07	2.59 (ns)	
Shelter	3	0.09	0.12 (ns)	0.06	0.56 (ns)	0.11	2.11 (ns)	0.06	2.11 (ns)	
Predator × Shelter	9	2.60	1.17 (ns)	0.32	0.92 (ns)	0.054	0.36 (ns)	0.06	0.76 (ns)	
<i>Prey size B</i>										
Predator	2	0.15	0.40 (ns)	0.06	1.15 (ns)	0.00	0.08 (ns)	0.03	1.37 (ns)	
Shelter	3	1.04	1.90 (ns)	0.01	0.09 (ns)	0.05	1.34 (ns)	0.02	0.50 (ns)	
Predator × Shelter	6	0.74	0.67 (ns)	0.01	0.35 (ns)	0.05	0.62 (ns)	0.07	1.01 (ns)	
<i>Prey size C</i>										
Predator	1	0.05	0.41 (ns)	0.10	3.81 (ns)	0.01	4.08 (ns ¹)	0.03	2.47 (ns)	
Shelter	3	2.08	5.66**	0.06	0.76 (ns)	0.01	1.36 (ns ¹)	0.03	1.14 (ns)	
Predator × Shelter	3	0.13	0.38 (ns)	0.15	1.91 (ns)	0.01	1.36 (ns ¹)	0.03	1.14 (ns)	
<i>Control</i>										
Prey size	3	0.30	0.84 (ns)	0.02	0.91 (ns)	0.00	0.11 (ns)	0.00	0.22 (ns)	
Shelter	3	1.56	4.44**	0.01	0.41 (ns)	0.07	3.19*	0.01	0.38 (ns)	
Predator × Shelter	9	1.33	1.26 (ns)	0.10	1.26 (ns)	0.04	0.66 (ns)	0.16	1.41 (ns)	

* $p < 0.05$; ** $p < 0.01$; (ns) $p > 0.05$

¹ Data heteroscedastic despite transformation

influenced by the size of larger predatory crabs, whereas cannibalism on the larger prey crabs was more affected by the shelter available (Figure 2). Cannibalism on size class A was heavily affected by predatory treatment and increased significantly from 2% in control treatments to 27% in the presence of predator size class D (Table 2, Figure 2). In contrast, cannibalism on size class A was not significantly influenced by the type of shelter, although there was a trend of more cannibalism in sand than where bamboo shelter was available. The percentage of size class A missing a limb appeared to increase from 1% in control treatments to 14% in the presence of predator size class D, but no statistical difference could be detected (Table 2).

Cannibalism of size class B was less affected by the presence of larger predatory crabs (cannibalism and limb loss varied between 4% and 9%, and 4% and 11%, respectively). There was a trend of greater cannibalism in the sand treatment (13%) relative to bamboos, where there was no cannibalism (Figure 2). However, no significant effects

were found on either cannibalism or limb loss (Table 2). Cannibalism of size class C was significantly greater in the sand treatment (20%) than in the shelter treatment (0–2%), whereas no significant effect of predator treatment was found (Table 2, Figure 2). In contrast, limb loss appeared to increase from 3% in the control treatment to 12% in the predator treatments, a difference that was borderline significant ($p = 0.056$), whereas no clear effect of shelter was observed (Table 2).

Analyses of data from control treatments (same size class of crabs) showed significantly more cannibalism in the sand substratum (on average 11%) than on other substrata (0–3%). Although no significant effect of prey size was found (Table 2), a trend of less cannibalism in the smallest size class (on average 1.8%) than in the larger size class (5–8%) was observed. This difference was most apparent in sand where cannibalism in the control treatments was zero for size class A, but 20% for the larger size classes (Table 2, Figure 3).

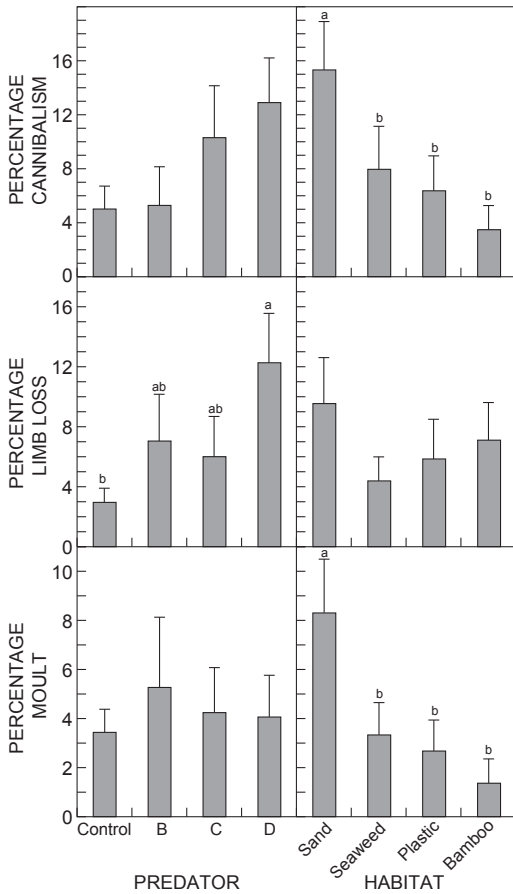


Figure 1: Mean percentage cannibalism, limb loss and moult of prey crabs 48 h⁻¹ as a function of predator treatment (control, predator size B: 31–40 mm, predator size C: 41–50 mm, predator size D: 51–70 mm ICW) and shelter type (no shelter, seaweed, plastic strings and bamboo tubes), pooled across all prey treatments (sand was the substratum in all habitat treatments). Letters above bars indicate significantly different means at $p < 0.05$ for the SNK-test. Error bars denote SE

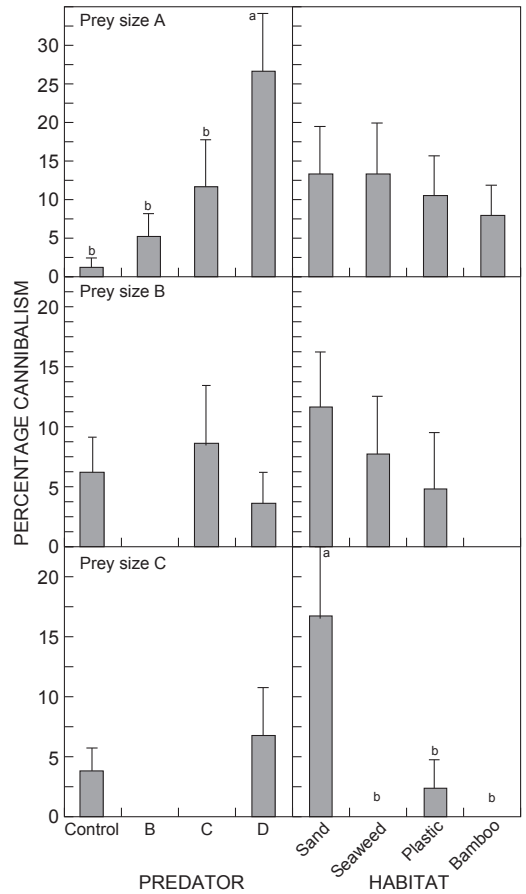


Figure 2: Mean percentage cannibalism of prey crabs 48 h⁻¹ as a function of predator treatment (control, predator size B: 31–40 mm, predator size C: 41–50 mm, predator size D: 51–70 mm ICW) and shelter type (no shelter, seaweed, plastic strings and bamboo tubes), for three prey size classes (A: 21–20 mm, B: 31–40 mm, C: 41–50 mm ICW). Letters above bars indicate significantly different means at $p < 0.05$ for the SNK-test. Error bars denote SE

Discussion

In grow-out aquaculture of portunid crabs, cannibalism often constitutes the biggest cause of mortality, resulting in loss of up to 90% (Rodriguez et al. 2001, Allan and Fielder 2003, Mirera 2009, Shelley and Lovatelli 2011). Two approaches to decrease the rates of cannibalism in culture have recently been suggested: (1) to size-grade the crabs (e.g. nursery culture methods with regular sorting to separate small crabs from larger ones and hence decrease predation on smaller crabs [Marshall et al. 2005, Rodriguez et al.

2005, Parkes et al. 2011]); and (2) to provide structurally complex habitats that provide shelter for cannibalism for smaller prey crabs and moulting crabs (Marshall et al. 2005, Mann et al. 2007, Ut et al. 2007, Parkes et al. 2011, Beattie et al. 2012).

Results from the present study suggest that cannibalistic interactions between juvenile mud crabs are strongly influenced by both the difference in size between the crabs and the availability of shelter. However, the response of prey crabs to experimental treatments was very size-specific. Cannibalism on the smallest size class (20–30 mm ICW) increased 10-fold in the presence of the largest predatory

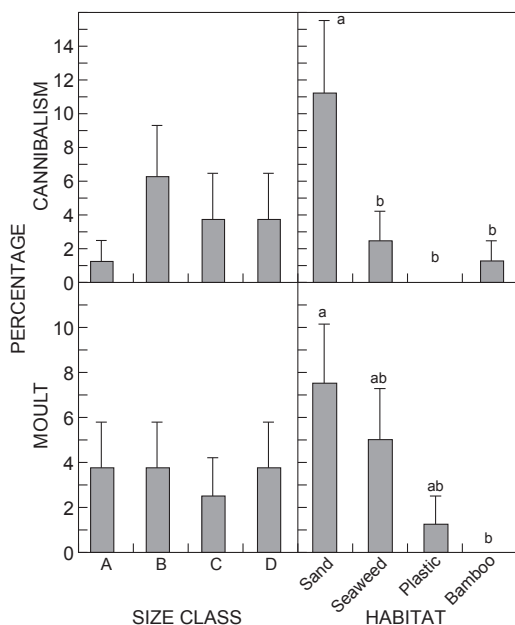


Figure 3: Mean percentage cannibalism and mean percentage moult within each prey size class 48 h^{-1} as a function of crab size treatment (A: 21–30 mm, B: 31–40 mm, C: 41–50 mm, D: 51–70 mm ICW) and shelter type (no shelter, seaweed, plastic strings and bamboo tubes). Letters above bars indicate significantly different means at $p < 0.05$ for the SNK-test. Error bars denote SE.

crabs (51–70 mm ICW) relative to the control treatments. Shelter had less influence on controlling cannibalism in that size class. In contrast, cannibalism on larger prey crabs (31–50 mm ICW) was less influenced by the presence of larger predators but decreased by >50% in the presence of shelters rather than a simple sand substratum. The results suggest that size-grading and shelter could both be important in minimising cannibalism in grow-out aquaculture but that size-grading is particularly important for smaller crabs, whereas shelter is more important for the larger size classes.

Effects of crab size

In brachyuran crabs, the relative difference in size between predator and prey crabs is important in influencing the rates of cannibalism. When crabs are of similar size, cannibalism on intermoult crabs is minimal, although it is greater in newly moulted, soft, defenceless crabs. However, above a critical size difference, cannibalism can affect hard intermoult prey crabs, usually resulting in rates of cannibalism that are much greater (Kurihara et al. 1988, Moksnes et al. 1997, Fernández 1999, Moksnes 2004). To address this situation, size-grading is practised in nursery culture of mud crabs to increase the survival rates of juveniles (Cerezo 2001, Rodríguez et al. 2005, Mann et al. 2007). Therefore, culture

of mud crabs needs to aim to separate crabs of different sizes prior to stocking as well as during culture, to preclude cannibalism on hard intermoult crabs.

In the present study, the effect of relative size differences on cannibalism was demonstrated in the smallest prey size class (20–30 mm ICW). In control treatments, where the relative size difference between prey and predator was <50%, cannibalism was low (<2% 48 h^{-1}), but it increased with increasing size difference to 27% mortality 48 h^{-1} in the presence of the largest predators, in which there was a mean size difference of ~140%. High rates of cannibalism on smaller crabs by larger ones (40–50 mm ICW) suggested that hard shelled (intermoult) crabs of the smallest size class (A: 20–30 mm ICW) were preyed upon at a mean size difference of 80% between prey and predator. The findings suggest that the critical size difference between prey and predator is between 50% and 80% for that prey size, and that juvenile mud crabs 20–30 mm ICW have to be separated from crabs >40 mm ICW to decrease cannibalism.

In larger prey sizes (31–50 mm ICW), the rates of cannibalism did not increase in the presence of larger predators, suggesting that cannibalism was mainly of newly moulted crabs. This is consistent with the findings of Rodríguez et al. (2007) on the preference of farmers in South-East Asia for crab >43 mm ICW to ensure faster growth and reduced mortality. The low rate of cannibalism on hard, intermoult crabs could in part be explained by the smaller mean size difference between prey and predator crabs in these treatments (28–70%) compared with that in the smallest size class, but also that a greater size difference is required to allow cannibalism on hard crabs by the larger prey crabs. Although the presence of larger predatory crabs did not increase the rates of cannibalism for the 31–50 mm ICW prey size class, the percentage limb loss did increase by an average of four times in treatments with the largest predator size relative to the control treatments. The findings therefore support the belief that agonistic interactions may be manifest in limb loss where size differences are small (Parkes et al. 2011, Quinitio and Estepa 2011). This implies that size-grading crabs between 31 and 70 mm ICW may have only small effects on cannibalism and survival, but it could decrease the number of incidents of limb loss that impact crab quality.

Effects of habitat

In natural populations of brachyuran crabs, cannibalism between juvenile size classes is thought to be a major cause of mortality for small juvenile stages that often aggregate in structurally complex shelters such as seagrass and mussel beds, where predation rates by larger predators are minimised (Fernández et al. 1993, Moksnes et al. 1998, Moksnes and Heck 2006). Providing shelter for juvenile mud crabs at aquaculture farms may therefore have strongly positive effects on their survival. This suggestion has received support in the present study because cannibalism, both within and between size classes, was less for the three shelter treatments (i.e. seaweeds, plastic strings and bamboo tubes) than for the sand substratum without shelter. Although cannibalism did not differ statistically

between shelter type, a trend of less cannibalism was observed where bamboo tubes were used as shelter. This was possibly because bamboo provides greater protection on the seabed than plastic strings or seaweed, which provide more shelter within the water column. The tubes may also provide the larger prey sizes of crabs with more effective refuge from cannibalism from predator crabs, as indicated by the lack of cannibalism where bamboo shelters were used for prey size classes B and C (Figure 2). The positive effects of appropriate shelter are consistent with the findings of Ut et al. (2007), who used clam shells and bricks as shelter to increase the survival of juvenile *Scylla paramamosain* relative to crabs on a simple sand substratum. However, in the present study, the effect of shelter differed between prey sizes.

Cannibalism was on average eight times greater on the sand substratum than where any of the three shelter types were used in the control experiments. This difference was strongly influenced by the larger size classes of crabs, which suffered high rates of cannibalism where there was no shelter (on average 20%), whereas there was zero cannibalism for the smallest size class. The size-specific shelter effect was observed also in the predator treatments, cannibalism being greater with no shelter than where shelter was provided, although this was significant only in the largest prey class (D). Cannibalism on the smallest prey size (A) was similar in all shelter treatments. This result is not consistent with other studies on portunid crabs, however, where the survival of young juvenile stages was many times higher in structurally complex habitats relative to sand or mud habitats (Pile et al. 1996, Moksnes et al. 1997, 1998). The present study used small experimental containers and high densities of crabs (75 crabs m⁻²) to enhance agonistic interactions and hence to determine measurable cannibalism rates within a short period. Although this approach provides comparable relative rates of cannibalism, as well as estimates by size of absolute refuge from cannibalism on intermoult crabs, it may decrease part of the refuge value of shelters and provide greater interactions for bigger crabs because of the limited space. This may be because prey and moult crabs were always within a detectable distance of larger predators in the small experimental containers, so the concealment function of the shelter that is provided in a bigger environment with lower crab densities might have been lost.

The results from the present study may therefore reflect mainly the absolute habitat refuge of the shelter material used, where the prey crab is relatively inaccessible to the predators. This may explain why the bamboo-tube shelter appeared on average to provide a better refuge than the others, as discussed above. The lack of shelter refuge for the smallest size classes should be interpreted with caution, however, because the shelters may provide greater refuge from cannibalism in nature and at lower crab densities in aquaculture systems. However, despite this potential artefact that may have decreased the differences in the efficacy of the shelters provided, cannibalism did decrease and survival increased by an average of 60% in the three shelter types relative to the tests with no shelter. This effect of shelter is consistent with previous studies on juvenile

portunid crabs carried out in aquaculture systems in which an increase in survival of ~50% is common when shelters are provided (Mann and Paterson 2003, Marshall et al. 2005, Mann et al. 2007, Ut et al. 2007).

The densities of the crabs used in the experiments were higher than the stocking densities normally used in grow-out pond culture of mud crabs using wild crabs between 40 and 80 mm ICW (Mann et al. 2007, Rodriguez et al. 2007), but similar to the densities used in nursery cultures where mud crab megalopae are grown to ~25 mm ICW (Rodriguez et al. 2001). Although our resulting absolute rates should not be compared with the mortality rates at farms with lower stocking densities, they do provide relative rates of cannibalism to be compared between shelter types, and also provide estimates of absolute refuge by size from cannibalism.

The moulting rate of juvenile crabs was also affected by the presence of shelter, being greater in the no-shelter tests than where shelter was provided in both control and predatory treatments. This result was unexpected and not consistent with other studies of portunid crabs that show greater rates of moult in habitats that provide shelter from predators relative to suboptimal substrata such as open sand, where the moult is delayed (Moksnes et al. 1997, 2003). However, the moult pattern observed was likely not a result of cannibalism removing moulting individuals because that should have produced the opposite pattern (see Figure 1).

Implications for the culture of mud crabs

Cannibalism constitutes a major source of mortality in mud crab culture but is poorly understood globally (Allan and Fielder 2003, Mann and Paterson 2003, Mann et al. 2007, Ut et al. 2007, Mirera 2009, Shelley and Lovatelli 2011). Results from the present study suggest that both size-grading and the provision of suitable shelter can decrease the rates of cannibalism in grow-out culture of mud crabs. To avoid high rates of cannibalism on hard intermoult crabs, this study suggests that the relative size difference between crabs reared together should be small, i.e. all animals should be within 20% of each other by width. This is particularly important if small (<30 mm ICW) juvenile seed crabs are used. In South-East Asia, juvenile seed crabs >40 mm ICW are preferred by farmers because they need less time to reach commercial size relative to smaller seed crabs. However, because the natural mortality of juvenile portunid crabs is many times higher in small, newly settled crabs than in larger ones (Pile et al. 1996, Moksnes et al. 1998) and is often density-dependent (Moksnes et al. 1997, Moksnes 2004), the impact on the fished population will be minimised and aquaculture more sustainable if the smallest juvenile crabs available are used. To avoid exceeding the critical size difference at which cannibalism starts, it is important to stock each culture with crabs of similar size. However, because of the great differences in the growth rates of individual crabs (Mann et al. 2007) and the heavy dependence on a wild supply, continuous size-grading of crabs would likely still be required during their culture. According to the results presented here, size-grading would also decrease limb loss, which has

negative effects on growth, as well as the quality of the crabs and their market value when one or both chelipeds are lost (Juanes and Smith 1995, Paterson et al. 2007, Mirera and Mtile 2009). Continuous loss of chelipeds even from juvenile crabs leads to a disproportionate cheliped to body size ratio that will impact the market value in terms of wet weight.

Rates of cannibalism could be reduced further by providing shelters that reduce the encounter rates of crabs in addition to providing shelter to small or moulting crabs. The results here suggest that shelter is particularly important in reducing cannibalism in the more aggressive larger size classes of mud crabs. In this study and in others (e.g. Ut et al. 2007), several types of shelter reduced cannibalism notably, suggesting that farmers could use several locally-available substrata as shelter for the crabs, including seaweeds (*Gracilariopsis*) and bamboo (Trino et al. 1999). In the present study, the commercial red alga *Eucheuma denticulatum*, which is easily obtained from local seaweed farms, reduced cannibalism by ~50% relative to that which occurred where there was no shelter. However, there is a need first to establish whether that species can flourish in the brackish water ponds used for mud crab aquaculture, in similar manner to other seaweed species such as *Gracilariopsis* spp. and *Caulerpa* spp. (Trino et al. 1999, Putra et al. 2013). If so, the alga itself might produce extra income for the farmers of mud crabs.

Acknowledgements — This research was funded by the Western Indian Ocean Marine Science Association (WIOMSA), Marine Science for Management (MASMA), through a project entitled 'Small-scale, community-based, grow-out aquacultures of mud crabs *Scylla serrata* as a sustainable livelihood in East Africa'. We thank the Kenya Marine and Fisheries Research Institute (KMFRI), where the laboratory work was done, and Linnaeus University, Sweden, for the PhD scholarship and provision of library services in the writing-up process of the manuscript. We also thank the internship students at KMFRI, Venny Mwaiye and Emily Wafula, and laboratory technicians Justus Wakili and Mwendwa Mbaruka, for their support, as well as the artisanal crab fishers who provided the juvenile crabs for the experiment (Abdullah Mtile and Dickson Mwamure).

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PAPER IV:

Cage, earthen pond and mangrove pen culture



Comparative performance of wild juvenile *Scylla serrata* in different culture systems in East Africa: Effect of shelter, crab size and stocking density

David Oersted Mirera^{1,2} and Per-Olav Moksnes³

¹Kenya Marine and Fisheries Research Institute (KMFRI), P.O. Box 81651, Mombasa, Kenya

²Linnaeus University, Box 391 82, Kalmar, Sweden

³Gothenburg University, Department of Biology and Environmental Sciences, Box 461, 405 30 Göteborg, Sweden

Email: dimirera@yahoo.com, dimirera@kmfri.co.ke, david.oersted.mirera@lnu.se

Abstract

Grow-out aquaculture of mud crabs *Scylla serrata* is well developed in Southeast Asia, but in its infancy in East Africa where the culture is dependent on wild seed crabs. We assessed 3 different culture systems and techniques to enhance survival and growth in small-scale aquaculture of mud crabs in Kenya.

Using small nursery cages, we assessed how availability of shelter, stocking-density and size-class separation affected cannibalistic rates in small juvenile mud crabs (20-80 mm internal carapace width) in short (7 days) experiments. The results suggest that shelter and size-class separation decreased cannibalism and mortality with 26% and 31%, respectively, whereas no significant effect was found for different stocking-densities.

Comparing growth and survival in long-term studies (2-4 months) of earthen pond and mangrove pen systems, treatments with and without shelter yielded low overall recovery of crabs (4-26%) indicating very high mortality rates, however, no significant effect of shelter or culture-system on survival was observed. In contrast growth rate was general high in both systems, but significantly lower in pen systems without shelter.

The results indicate that cannibalism is the largest source of mortality in the culture systems, but the use of shelter and size grading of crabs can improve survival significantly. In contrast to the low survival rates, growth rates was high and comparable to natural growth in both pond and pen cultures when shelter was provided. Using growth models to compare growth and survival in mud crabs from aquaculture studies in the literature we show that shelter may have a stronger effect on growth than has been previously thought, whereas crab density appear to be more important for survival. Improving survival in grow-out culture systems is a challenge that remains to be solved for small-scale mud crab culture to be viable in East Africa.

Key words: mud crab, net cages, ponds, pens, shelter, density, survival, growth

Introduction

Mud crab *Scylla serrata* (*S. serrata*) is sought as an important source of food throughout the Indo-Pacific region because of its taste, texture and nutritive value (Cowan, 1983; Cholik and Hanafi, 1992; Keenan et al., 1998; Trino and Rodriguez, 2002). Over the years, it has been exploited by artisanal fisher's walking on foot in the East Africa region to supply local tourist hotels and for export (Barnes et al., 2002; Mirera, 2011b). Interest was developed to culture mud crabs *S. serrata* along the East Africa coast in late 90s (Mirera, 2011b). Initial culture interventions only targeted adult and sub-adult crabs for fattening/culture in cages and pens (Mwaluma, 2002; Mirera, 2009) while current approaches have opted to explore grow-out culture of juveniles in ponds and pens (Moksnes et al., 2012), a technology that is new in East Africa but well developed in Southeast Asia (SEA; Trino et al., 1999a & b; Rodriguez et al., 2007; Primavera et al., 2010).

Hatchery production of *S. serrata* has been significantly developed in SEA but is limited or none existent in sub-Saharan Africa (Quinitio et al., 2011; Rodriguez et al., 2001; Quinitio and Parado-Estepa, 2008; Mirera, 2011b). Therefore culturists depend on wild caught juveniles whose growth, survival and general behaviour is not well understood under nursery and grow-out conditions. This aspect is a major constraint in development of mud crab culture in sub-Saharan Africa.

A number of studies have been carried out in SEA on the different culture methods for juvenile *Scylla spp* using wild and hatchery produced seeds (Trino et al., 1999a & b; Trino and Rodriguez, 2002; Rodriguez et al., 2007; Ut et al., 2007a & b; Primavera et al., 2010). However, more recently, emphasis is on hatchery bred *Scylla spp*. Comparisons of the quality of hatchery produced and wild collected *S. paramamosain* showed faster growth for hatchery bred seeds when grown separately but both attained similar growth when mixed in the culture systems (Ut et al., 2007b). This implies that while hatchery bred *S. serrata* results from SEA may give a broader picture of the behaviour of wild caught juveniles in culture conditions, there is need for modesty in application of similar results in sub-Saharan Africa where the aquaculture seed source is only from the wild and hence different crab populations may be in existence with varied environmental adaptations. To infer to this observation, a model developed to compare natural growth of *S. serrata* in East Africa using different studies showed a relatively slower growth compared to growth obtained in SEA (Moksnes et al., **Paper II**).

Studies indicate that farmers in SEA prefer relatively bigger (30 – 50 mm internal carapace width -ICW) hatchery bred *S. serrata* because of their faster growth to reach market size (Rodriguez et al., 2007). While most experimental studies in SEA have used similar size class of crabs in different culture systems and promoted selective harvesting as a strategy for size grading to eliminate bigger crabs (Baliao et al., 1999a; Primavera et al., 2010), little is documented on the limit on size classes that can be stocked together when dealing with wild seed where size variability is high. In addition limited information exists on the behaviour and performance of wild seed crabs cultured in net cages and ponds. Consequently, varied shelter habitats have been shown to play an important role in reducing cannibalism in juvenile *Scylla spp*. cultured in ponds and net cages (Christensen et al., 2004; Rodriguez at al., 2007; Mirera and Moksnes, 2013). However few or no shelter experiments have focused on

pen culture studies and even those done for earthen ponds have mainly used seaweeds and palm leaves with hatchery produced seed crabs.

The objective of this paper was to explore and assess the suitability of different mud crab culture methods (net cages, pens and ponds) using small juvenile seed crabs collected from the wild. Under the different methods, the influence of shelter, crab size and density on survival and growth was evaluated to provide recommendations to farmers engaged in wild based-mud crab aquaculture in East Africa.

Materials and methods

Net cage and pen experiments were carried at Mtwapa creek using Kwetu training centre's mariculture demonstration site. Earthen pond experiments were carried out at Kwetu training centre and Gazi bay using Makongeni's Baraka conservation group pond facilities (Figure, 1). Artisanal mud crab fishers in each site were employed to collect seed crabs less than 85 mm ICW for the experiments. The fishers were compensated at 0.27 USD/crab. The crabs were collected during the day at low spring tides on the intertidal mangrove mudflats. At the experimental sites, crabs were cleaned off mud, acclimatized in plastic basins (10L capacity) with 25-28° C of clean seawater. Crabs were checked for quality and only active crabs in intermolt with intact appendages were used in the study. The crabs were graded into different sizes and distributed in net cages, pens and ponds according to the experimental protocols for each trial. During stocking, initial body weight (BW g) and internal carapace width (ICW mm) were measured using a digital weighing balance and vernier calipers respectively. Local fish traders (known as *mama karanga* in kiswahili) were engaged to supply fish oval for feed and compensation was made at an individual rate of 6 USD/week. During the experimental period, water quality parameters (Temperature, dissolved oxygen and salinity) were taken regularly in the culture systems using HANNA multi-parameter meter.

Experiment 1: Assessment of shelter, size and density in net cages

To assess various factors affecting the survival of juvenile crabs in pond and pen aquacultures, a three-factor experiment was conducted to determine the effect of shelter (presence or absence of bamboo tubes), stocking density of crabs (4 and 8 crabs/m²) and size ratio of crabs (20-50 and 20-80 mm ICW) on survival in wild juvenile crabs. The experiment tested the effect of culturing juvenile mud crabs in net cages placed in earthen ponds for a period of 7 days. Wild collected juvenile crabs with an ICW ranging between 20 and 80 mm and body weight 0.2 -60 g were used in the experiments.

The study was conducted in 18 units of 1m² (1.0 x 1.0 x 1.5 m; w x l x h) net cages with flat-bottomed base and 1 mm mesh installed in 300m² earthen ponds at the Kwetu Training Centre in Mombasa, Kenya. Cages were held in place by tying them onto stakes of mangrove poles on the upper edge. They were held in the required shape by stretching the base corners and tying them to the same poles under the water to ensure cages rested on the pond bottom. Inner side of the cages, about 20 cm from the upper edge were fitted with plastic sheets to prevent crabs from escaping according to details by Rodriguez et al. (2007). The entire pond was fenced with a thin mesh netting material to prevent wild crabs entering the pond from outside. Shelter habitat was constructed by cutting mature bamboo into standard tubes of 105 mm length and 40 mm internal diameter. A series of four pieces were sewn onto the bottom of the cage to form a density of 4 pieces/m². This habitat provided the best shelter from cannibalism in a recent laboratory study (Mirera & Moksnes 2013). About one meter above the edge of the cages, a roof build of woven coconut leaves were built to provide a cover shade for the entire cage area. A timber walkway was constructed to cover the cage length for easy accessibility at feeding and sampling.

The 6 different treatments (2 habitats x 2 densities x 2 size-classes) were randomly allocated to the 18 cages with 3 replicates for each 7-day trial. The experiment was

repeated 6 times giving a total of 18 replicates for each treatment. Surviving crabs with intact appendages were randomly used in consecutive trials.

At the end of each trial, cages were lifted out of the water, checked for damage and all crabs were retrieved, counted, measured and checked for moult and appendage loss. Any dead crabs and moult shells were checked for signs of cannibalism. Proportional survival of crabs per 7-day period was estimated for each replicate. Before the net trial, net cages were cleaned and any damages or tears were repaired. In all cages, crabs were fed by distributing chopped fish oval once a day in excess.

Data analysis

The effect of shelter, density and crab size on crab survival was tested in a three-way fixed factor ANOVA model using shelter, density and size-range of crabs as independent variables and the proportional loss of crabs as the dependent variable. All data were tested for homoscedasticity with Cochran's C test (Sokal & Rohlf 1981). *A posteriori* multiple comparisons were carried out with Student-Newman Keuls (SNK) procedure.

Experiment 2: Growth and survival in mangrove pens and earthen ponds

The experiment was designed to compare the performance of earthen ponds and mangrove pens in culture of mud crabs, and to test for influence of shelter/substrate on growth and survival of crabs. Each culture system (pond and pen) had four replicates and two of the replicates in each system were provided with bamboo tubes. The tubes were scattered randomly inside each of the replicates including the channels for the pens to give a density of 2 pieces/m². To prevent tubes from floating, mud was placed at the centre to enable them remain and absorb water for stability at the bottom. Tubes had an average internal diameter of 31 mm and length 300 mm. Feeding was done once daily with fish oval at 10% of body weight for the entire experimental period (60-90 days) preferably at high tides for the mangrove pens.

a. Mangrove pens

The mangrove pens were constructed at Mtwapa creek (Kwetu Training Centre) within the mangrove forest in areas that received daily tidal floods. The site had clay-sand mixture with relatively compact and stable mud, easy for crabs to burrow. The selected site had history of *S. serrata* burrows indicating preference by crabs. Common mangrove species in this area were *Cerriops tagal* and *Rhizophora mucronata* at a ratio of 3:2 (Abuodha and Kairo, 2001).

Four rectangular pens were constructed following the techniques developed in SEA with an enclosure net (2mm mesh size) fixed with poles and the upper inner side sewn round with a polythene sheeting about 80 m width (Trino and Rodriguez, 2002; Primavera et al., 2010). They measured 5 x 10 m (50 m²) and an effective height of 2.0 m. A canal that covered 20% of the pen area and measuring 0.5 m width and 0.5 m deep was dug inside the pen to hold water at low tide. Before stocking, all epibenthic macrofauna found within the pen area were removed. Pens were stocked with crabs at a density of 2 crabs/m² with sizes ranging between 6 and 63 mm ICW and 0.03 to 55 g wet weight as detailed in Table 1. The experimental period varied between 61 and 89 days in different replicates.

b. Earthen ponds

The Kwetu training centre and makongeni community ponds used for the experiment were constructed in open intertidal areas behind the mangrove forest. They were flooded frequently during high spring tides and were designed to allow free tidal flooding through screened overflow waste pipes as detailed by Mirera (2011a). All the four ponds measured 10 x 10 m (100 m²) and 1 m deep. Modifications were introduced to the ponds to allow mud crab culture as detailed by Trino et al. (1999a). This ensured that a netting fence (2 mm mesh size) with a plastic sheet and bamboo framework were in place to prevent crabs from escaping. Crabs were stocked at a density of 2 crabs/m² with sizes ranging between 4 - 85 mm ICW and wet weight 0.01 -121 g and a culture period ranging between 66 – 74 days (Table 1).

c. Sampling and harvest

Sampling in pen and pond was done using baited box traps as detailed by Walton et al., (2006), using 30-40 minutes between deployment and retrieval. Ten traps were deployed twice in each replicate, and all crabs retrieved were used as a representative sample to estimate growth and proportional catch rate. The milkfish (*Chanos chanos*) from community farms was used as bait. Sampling was scheduled to take place at 30 days interval although due to logistical issues, the frequency ranged between 20 and 40 days. Sampling in ponds was done in the mornings since it did not depend on tides while pen sampling took place during high tides. Parameters measured during sampling were BW (g) and ICW (mm).

At the end of the experiment, after 2-3 months, all the crabs were retrieved from the pens at high tide using baited box traps. In ponds, recovery estimates were made using baited traps but experiments continued for extra 90 days before the pond was emptied and searched for crabs.

d. Statistical analysis

To assess if the baited box traps provided a good estimate of the total abundance and survival of crabs in the cultures we estimated the proportional catch rate per month ($e^{\ln(\text{total number of crabs caught} / \text{no. of seed crabs} / \text{no. months})}$) as an index of survival after about 2 month experimental period when the pen-cultures were terminated. This value was compared to proportional survival rate per month ($e^{\ln(\text{total number of crabs recovered} / \text{no. of seed crabs} / \text{no. months})}$) based on the total number of crabs recovered when the pen and pond cultured were emptied and searched for all remaining crabs after about 2 and 4 months, respectively (see Table 1 for details). The proportional catch and survival rate per month, and the absolute growth rate (g WW per day) were tested as dependent variables in a fixed two-factor ANOVA model using culture system (pond and pen) and shelter (bamboo tubes and no shelter) as independent variables.

Due to logistic constraints and availability of seed crabs, the average size of the seed crabs and, to a lesser degree, the duration of the experiment varied between trials and treatments (Table 1). Similar to most animals, growth in mud crabs is non-linear, and biomass increases exponentially over time (Moksnes et al. **Paper II**). It is therefore problematic to compare growth rate between studies using different initial sizes of crabs or different growing period, also if standardizing growth measures such as absolute, relative or instantaneous growth rates are used (Hopins 1992, Moksnes et al. **Paper II**). To address this issue in the present study, we carried out a complementary analysis of growth using an index of relative growth that compared the obtained

growth rates in each replicate with the estimated growth obtained from a von Bertalanffy growth function of growth in East African mud crabs.

$$(1) L_t = 310 * (1 - e^{-0.57 * (t - 0.019)})$$

Where L_t is the size (carapace width) at time (t) since settlement (Moksnes et al. **Paper II**). The model is based on empirical data on increment at moult and intermoult period of different sizes of juvenile crabs obtained through field mark-recapture, pond and laboratory studies. We estimated the proportion of natural growth achieved in each trial by dividing the measured growth rate with the modeled growth rate to obtain a relative rate that was tested as the dependent variable in the two-factor ANOVA model.

Results

Experiment 1: Net cage experiments

The temperature in the ponds where net cages were installed ranged between 29.7 – 30.1 °C for the whole experimental period. Salinity varied between 28.0 -29.9 during the course of the experiment while pH averaged at 7.3.

In the middle of the study, small tears were found in several cages, likely caused by larger crabs creating holes in the net through which the crabs could escape. Although these holes were mended, new ones reappeared in many cages towards the end of the study. To avoid confounding mortality rates of crabs with crabs escaping from the cages, all trials with holes in the net were excluded from the data. In total, 33% of the 144 trials were excluded (28% and 38% of the cages with and without shelter, respectively).

The mean and maximum initial size of crabs was significantly larger in the treatments with larger size range of crabs (on average 41.3 and 62.3 mm CW, respectively) compared to treatments with only smaller crabs (on average 33.3 and 41.6 mm CW, respectively). Mean size of crabs did not differ significantly between the other treatments, indicating that the size-range treatment was applied as intended (Table 2).

The three-way ANOVA showed that proportional loss of crabs was significantly higher in treatments without shelter compared to treatments provided with bamboo-tubes (on average 42% and 31% loss week⁻¹, respectively) and significantly higher in treatments with a large size-ratio than in treatment with only smaller crabs (on average 42% and 29% week⁻¹, respectively), but was not significantly affected by the density of crabs (on average 33 and 39% loss at density 4 and 8 crabs cage⁻¹, respectively; Figure 2; Table 2).

Experiment 2: Mangrove pen and pond experiments

The range of water quality parameters in earthen ponds and mangrove pens was similar (Table 1). They were within acceptable levels for different culture systems (Boyd, 1990; Cholik and Hanafi, 1992; Rodriguez et al., 2007).

Catches of crabs by baited box traps varied little between culture systems and decreased over time. Approximately one month after stocking (1st sampling) the catch was on average 22% and 23% of the total number of crabs stocked in ponds and pens respectively. After approximately 2-3 months when the pen-cultures were terminated, the catch was on average 14% and 17% of the seed crabs in ponds and pens, respectively. Standardizing the catches into proportional catch per month as an index of survival per month, the proportional catch rate appeared higher in the pen treatments (41% month⁻¹) than in the pond treatments (30-32% month⁻¹), but no significant differences were found between culture systems or shelter treatments (Table 3, Figure 3a).

The recovery of crabs in the pen cultures ranged between 8 and 26 % over the 61 to 89 day culture period. Standardizing the recovery rate to proportional recovery per month showed the same average recovery rate (41% per month) in treatments with and without shelter (Table 3; Figure 3b). In the pond systems all crabs were put back in the pond after the last sample with the traps and the cultures were continued for an additional two months before they were drained and all surviving crabs recovered. Recovery of crabs was low and ranged between 3.5 and 17% over the 126 to 134 days

period, equivalent to an average recovery rate of 59% and 54% per month in treatments with and without shelter, respectively. Comparing the recovery rate per month between the pond and pen treatments showed no significant differences between culture systems or shelter treatments (Table 3, Figure 3b).

Absolute growth rate varied between treatments and appeared higher in ponds (0.71 g day^{-1}) than in pen systems (0.40 g day^{-1}), and higher in treatments with shelter (0.66 g day^{-1}) than those without (0.45 g day^{-1}), but no significant differences were found (Table 4, Figure 4a). However, because absolute growth rate is positively correlated with the initial size of crabs (Moksnes et al. **Paper II**), this difference in estimated growth may be an effect of differences of size of seed-crabs, which was substantially larger in pond than in pen cultures (on average 15.3 and 6.1 g, respectively), and also larger in treatments with and without shelter (on average 15.0 and 6.3 g, respectively). In contrast, the index of relative growth (observed growth/modeled growth) is not affected by differences in initial size or length of the growth period. The two-factor ANOVA showed a significant interaction effect between culture type and shelter caused by significantly lower relative growth rate in the pen culture without shelter (64%) compared to the other treatments, which were similar to the modeled natural growth (95-114%), and did not differ significantly (Table 4, Figure 4b).

Discussion

Net cage experiments

In grow-out aquaculture of mud crabs, cannibalism often constitutes the largest cause of mortality, resulting in up to 90 % loss (Allan and Fielder 2003; Mann et al. 2007; Ut et al. 2007a; Shelley and Lovatelli 2011). Using small nursery cages, we assessed how availability of shelter, stocking-density and size-class separation affected cannibalistic rates in small juvenile crabs (20-80 mm CW) in short (7 days) experiments. The results suggest that both shelter and size-class separation decreased cannibalism and mortality with 26% and 31%, respectively, whereas no significant effect was found of stocking-density.

The proportional loss of crabs was significantly higher in treatments without shelter compared to treatments provided with bamboo-tubes, irrespective of density and size-treatment (on average 42% and 31% loss week⁻¹, respectively), suggesting that shelter reduced cannibalism and mortality by on average 26% in the 7 days experiment. This result is consistent with previous laboratory studies of juvenile *S. serrata* in East Africa, in which bamboo tubes and other shelters improved survival with up to 50% in 48 hours experiments compared to open sand (Mirera and Moksnes 2013). The present results are new in demonstrating a positive effect of shelter under more realistic aquaculture conditions. Positive effects of shelter on survival has also been found in *S. serrata* cultured in ponds with bamboo or seaweeds as shelters (Trino et al., 1999a) and *S. paramamosain* where survival for 1st instar crabs reared in cement tanks increased when provided with brick and shell shelters (Ut et al. 2007a).

In natural populations of portunid crabs, cannibalism between juvenile size classes are thought to be a major mortality agent for small juvenile stages that often aggregate in structurally complex shelters such as seagrass and mussel beds that decrease predation rates from larger cannibals (Moksnes et al. 1998; Moksnes and Heck 2006). In the wild, mud crab sub-adults and adults construct burrows in muddy substrate to serve as

shelter for part of their life cycle (Hill et al., 1982; Walton et al., 2006). Therefore, providing shelter for juvenile mud crabs in aquaculture farms may have strong positive effects on survival (but see discussion below).

The present study also found significantly higher losses of crabs in treatments with a large size-ratio (20-80 mm CW) than in treatment with only smaller crabs (20-50 mm CW), irrespective of density and shelter-treatments (on average 42% and 29% week⁻¹, respectively). The results suggest that separating small and larger juvenile crabs may increase survival with on average 31% per week in the nursery cages. This result is consistent with Mirera and Moksnes (2013) who found that cannibalism on the smallest size class (20-30 mm ICW) increased 10 fold in the presence of the largest predatory crabs (51-70 mm) compared to control treatments. In portunid crabs, cannibalism between similarly sized crabs in intermoult is minimal and only occur at relatively low rates on newly moulted, soft and defenceless crabs (Moksnes et al. 1997, 1998). However, above a critical size-difference, cannibalism can affect hard intermoult prey crabs that usually result in many times higher cannibalistic rates (Kurihara et al. 1988; Moksnes et al. 1997; Fernandez 1999; Moksnes 2004a; Marshall et al., 2005). Size grading in mud crabs has been practised in grow-out systems through selective harvesting to reduce cannibalism and promote growth of small crabs (Baliao et al., 1999a). An alternative or complementary treatment to reduce cannibalism in cultures could be through removal or trimming of the chela (pincers) of the juvenile crabs. Quintio and Estepa (2011) observed higher survival in juvenile crabs when chelipeds were autotomized or removed compared to when they were intact.

Studies of other species of portunid crabs have shown that cannibalism among juveniles can be density-dependent, resulting in higher rates of cannibalism at higher densities (Perkins-Visser et al., 1996, Moksnes et al. 1997, Moksnes 2004a). In mud crabs, agonistic behaviors increase with density (De Albornoz Nuno, 2003), and over crowding has been observed to increase cannibalism rate in mud crab culture systems (Baliao et al., 1981). A number of aquaculture studies also have found decreasing survival rates at higher stocking densities of mud crabs (Genodepa 1999; Trino et al. 1999a; Trino and Rodriguez 2002), but others have failed to find significant differences (Rodriguez et al 2007) making generalizations difficult. In Table 5, survival rates from aquaculture studies of mud crabs found in the literature have been standardized to proportional survival rate per month to be able to compare effects of density between studies. Assessing the relationship between seed crab density and the survival rate in the different studies show a significant negative relationship (*Simple linear regression*: $F=6.53$, $df=1,29$, $p=0.016$, $r^2=0.16$; Figure 5a). This meta-analysis provides further support that seed crab density is an important variable affecting survival in mud crabs cultures. However, in the present study density did not significantly affect proportional loss of crabs in net cages (on average 33 and 39% at 2 and 4 crabs m⁻², respectively). It is unclear why we did not find a negative effect at the higher density. It is possible that a potential effect of density was weakened by the fact that many replicates were excluded from the analyses because there were holes in the net. If the crabs in the cages had created the holes, it is possible that this tearing behavior was enhanced at high densities (see discussion of density-dependent aggressive behavior below) resulting in a loss of the replicates where density-dependent cannibalism would have been the highest.

The present study also assessed if small net-cages could be used as a nursery system for young juvenile mud crabs, facilitating recovery and size grading of crabs before they are placed in larger grow-out system. However, although we used cage net material of the highest quality available in the local markets (monofilament nylon of approximately 500 μm thread), most of the cages quickly developed holes through which the crabs could escape into the larger pond area. It was unclear if the holes were created by the juvenile crabs inside the cages, or by other wild decapods (e.g. hermit crabs) that were present in the pond, despite our efforts to remove them. It may also be possible that wild seed crabs, in comparison to hatchery reared crabs used in similar systems in Southeast Asia (Rodriguez et al., 2007), may be more aggressive in the artificial cage environment, and more likely to tear the material. Ut et al. (2007b) observed that wild juveniles of *S. paramamosain* grew slower than hatchery-produced juveniles, in part explained by an apparent lower level of aggression in hatchery-produced juveniles. Based on the high number of broken cages resulting in loss of crabs, and the high initial cost of the cages, the use of net-cages as nurseries for small wild-caught seed-crabs (20-80mm ICW) in grow-out aquacultures may not be recommended at this stage for small-scale farms in East Africa.

Pond and pen experiments

Assessing growth and survival in long-term studies (2-4 months) using two types of grow-out aquaculture systems (pond and pens) with and without shelter yielded slightly different results compared to the cage experiment. Overall recovery of crabs was very low (4-26%) with no significant effect of shelter or culture-system on survival. In contrast growth rate was generally high in both systems, but significantly lower in pen systems without shelter.

Survival

The recovery rates found in the pond and pens of the present study (equivalent to 41-59% survival month⁻¹) were similar to previous studies in East Africa, but lower than survival rates found in similar studies in Southeast Asia (on average 73% survival month⁻¹; Table 5). The reasons for the low recovery rates in the present study are unclear. Theft is considered a large problem for aquacultures of mud crabs in East Africa (Mirera, 2009, 2011b; Moksnes et al. 2012). However, the crabs in the present study was still small at the end of the experiment (30 to 60 g on average) with little or no commercial value making theft an unlikely explanation, in particular since catching the small crabs in ponds and pens is a difficult task without traps. Juvenile mud crabs can move on dry land (*authors observation*), and could possibly escape from the cultures through the net fences. However, no juvenile crabs were ever observed moving above the water line in the cultures, and no holes were found in the fences indicating that this source of crab loss was low. Thus, mortality occurring within the culture systems is likely the main explanation to the high losses. Since the physical conditions in the cultures were within acceptable levels during the culture periods (Table 1), and crabs were fed in excess daily and appeared healthy during collection (indicating that feed was not limiting), mortality due to cannibalism is the most likely explanation. It is important to note that a monthly survival rate of 32% (the lowest recorded in the study) is equivalent to a daily survival rate of approximately 96%. Thus, it is enough that a few crabs are eaten per day to obtain the overall low survival rate.

Based on the results from the cage experiment and laboratory studies of cannibalism in East African mud crabs (Mirera and Moksnes 2013), the main reason for the apparent high rates of cannibalism in the pond and pen studies were most likely the large size-ratio of seed crabs used. Due to difficulties to obtain enough seed-crabs, their sizes varied between approximately 10-70 mm CW in most treatments (Table 1), which probably caused high cannibalistic rates on smaller crabs. This was supported when earlier studies were compared in the region, where lowest survival rates (51% month⁻¹) were recorded when the largest size-ratio of seed crabs were stocked in pen culture (20-100 mm CW; Mwaluma 2002; Table 5). Thus, in aquacultures, care should be taken to keep the size-ratio of seed crabs <50% and separate crabs <30 mm CW from those >50 mm CW (Mirera and Moksnes 2013).

On the other hand, the densities used in the pond and pens (2 crabs m⁻²) were not unusually high in comparisons to other studies (Table 5; Fig. 5a), and were likely not a major reason for the low survival rates. The effect of density-dependent cannibalism should also have decreased as the densities in the cultures decreased, making it less and less important.

In contrast to the results in the cage experiment, we found no significant effect of shelter on the estimates of survival in the pond and pen study. This result may partly be explained by the possible high initial cannibalistic rates on the smaller crabs (due to the presence of larger crabs), and the size-dependent shelter provided by bamboo-tubes. Laboratory studies assessing the cannibalistic interactions between different size-classes of juvenile mud crabs in different habitats have demonstrated that bamboo-tubes provide a very strong refuge from cannibalism from larger crab for juvenile crabs of a size range of approximately 30-50 mm CW, whereas smaller crabs received no significant protection, likely due to the fact that cannibals on smaller crabs could enter the tubes (Mirera & Moksnes 2013). Since a large number of seed crabs used in the pond and pen study were in the range of 4-30 mm CW (Table 1), a large proportion of crabs vulnerable to cannibalism received little refuge from the bamboo-tubes in the beginning of the culture period. That losses of crabs was higher in the beginning of the study is supported by the relatively low proportion of crabs caught in the traps at the first sample after approximately 1 month (equivalent to an average "survival rate" of 16% month⁻¹) in comparison to the catches after 2-3 month (equivalent to an average survival rate 36% month⁻¹). In addition, because the surviving crabs eventually became too large to fit into the tubes, the refuge provided by the bamboo-tubes vanished with time. Thus, in aquacultures, care should be taken to provide different types of shelter that provide refuges for different size-classes of crabs. Although lack of strong shelter effect on survival was surprising when compared to smaller scale experiments demonstrating strong effect (e.g. this study; Mirera & Moksnes 2013; Ut et al. 2007a), it is to some extent consistent with the general results in the literature. Comparisons of survival rates of mud crabs in aquaculture studies with and without shelter from the literature (Table 5) show only a marginal higher survival rates in cultures with various types of shelter compared to studies without any shelter (on average 70% and 64% survival, respectively). The lack of stronger shelter effect in larger scale studies warrants further investigation.

Growth

In contrast to the apparent poor survival rates in the pond and pens, growth rates of the crabs after 2-3 month was high, similar to estimated natural growth for East

African mud crabs, and similar to many other studies in SEA with different species of mud crabs (Table 5), although growth in *S. serrata* appear to be higher in SEA (Moksnes et al., **Paper II**). In the ponds, growth rates was high both in treatments with and without shelter (93-112% of the estimated natural growth), whereas in the pens, growth was only high in treatments with shelter (108% of natural growth), but significantly lower in treatments without bamboo-tubes (64% of natural growth).

The reason for the strong positive effect of shelter on growth only in the pen cultures is not clear, but may be related to tidal changes of available areas in the pen system that may have resulted in density-dependent interference between crabs that affected feeding and growth negatively. In the pen cultures, only the dug channels in the middle of the pen were submerged during low tides, at which time most crabs were found to concentrate in the channel. Since the surface area of the channel only constituted 20% of the whole culture area, the resulting density of crabs in the channel was up to 5x higher during low-tide conditions. In the portunid crab *Carcinus maenas*, growth has been found to decrease after a threshold in conspecific density due to increased agonistic behaviors resulting in mutual interference negatively affecting feeding rates and growth (Moksnes, 2004b). Similar to *C. maenas*, juvenile mud crabs display a strong defence reaction (raising the front of the body and extending the chela) when encountering a conspecific (authors observation), and this aggressive behaviour increases with density (De Albornoz Nuno, 2003). In the pens without shelter, densities of crabs may have passed a threshold at low tides when all crabs concentrated in the channels, resulting in an increase in aggressive behaviours and mutual interference that reduced the time available to feed. In pens with shelter, many crabs likely hid in the bamboo tubes at low tides where they could feed undisturbed and at the same time keeping the density below a possible threshold to trigger agonistic behaviours. In the ponds that were inundated also during low tides, densities of crabs may have been below the possible threshold also in treatments without shelter, preventing mutual interference affecting growth.

This is, as far as we know, the first time that a positive effect of shelter on growth has been found in mud crab (*S. serrata*) grow-out culture systems. The effect of shelter on growth has also been assessed for *S. olivacea* in the Phillipines, where bamboo-shelter resulted in a weak (non-significant) positive effect on growth (Fortes, 1999). However, comparison of the relative growth rate of mud crabs in aquaculture studies from the literature (Table 5) show that studies which provided various types of shelter in the cultures on average had 83% higher relative growth rates (on average 65% higher than modelled growth) compared to studies that were not using shelter (on average 10% lower than modelled growth; Table 5). In contrast, we found no relationship between the relative growth rate and the density of crabs in the cultures (*Simple linear regression*: $F=0.34$, $df=1,27$, $p=0.56$, $r^2=0.01$; Fig. 5b). These meta-analyses using a growth function that allows comparison between studies, indicate that the effect of shelter may be larger on growth than previously thought, providing another argument for the benefits of providing shelter in grow-out aquacultures for mud crabs. However, more research is needed in this line of argument.

Conclusion

The present study provided some important results for the development of small-scale mud crab aquaculture in East Africa. The results support the use of shelters in different culture systems to improve survival and growth. However, more research is

required to assess suitability of different shelter materials for different size ranges of crabs. The results also underscore the significance of size grading at stocking as a strategy of improving survival and growth. Both pond and pen culture systems provided high growth rates (when shelter were provided) that were similar to estimated natural growth rates in East Africa. However, survival rates in these systems are still far too low for this activity to be profitable in East Africa. For example, the growth function of East African mud crabs (Moksnes et al. **Paper II**) suggests that a culture time of approximately 10 months is needed to grow a seed crab of 10 g to a commercial size of 500 g (East Africa market size). With a monthly survival of 59% (the highest survival obtained in this study) only one commercial crab per 200 seed crabs could be harvested (equivalent of 0.5% survival after 10 months). To be able to harvest 10% or 50% of the seed crabs, the survival has to be raised above 79% and 93% month⁻¹, respectively. These higher survival rates are presently obtained in cultures in South East Asia, but not yet in East Africa (Table 5). Thus, improving survival in these culture systems is a challenge that remains to be solved for small-scale mud crab culture in East Africa.

Acknowledgement

The Western Indian Ocean Marine Science Association (WIOMSA), Marine Science for Management (MASMA), funded this research through a project entitled ‘Small-scale, community-based, grow-out aquacultures of mud crabs *S. serrata* as a sustainable livelihood in East Africa. In addition, the International Foundation for Science (IFS) provided more funding for the study. Further, appreciation is to Linnaeus University, Sweden for the PhD scholarship and Kenya Marine and Fisheries Research Institute (KMFRI). We are also grateful for Kwetu training centre and Makongeni, Baraka conservation group who provided experimental sites for this research.

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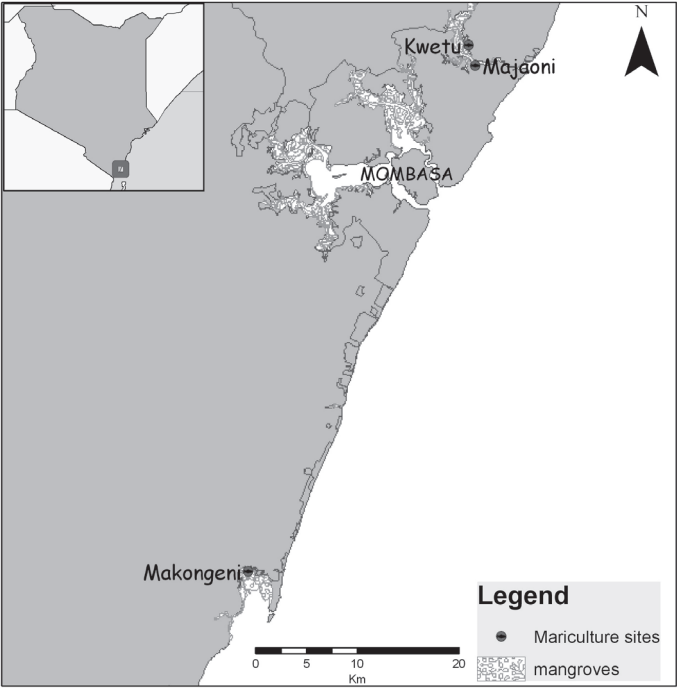


Figure 1: Map of the Kenyan coast. The location of Kwetu Training Centre and Makongeni’s Baraka conservation group’s mariculture sites are illustrated.

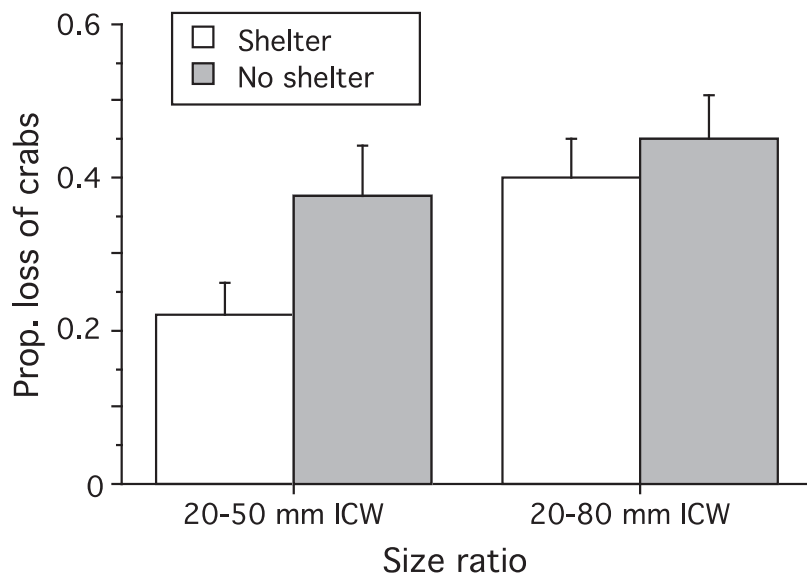


Figure 2: Proportional loss of crabs week⁻¹ (+SE) as a function of shelter and crab size range in net cages installed in earthen ponds

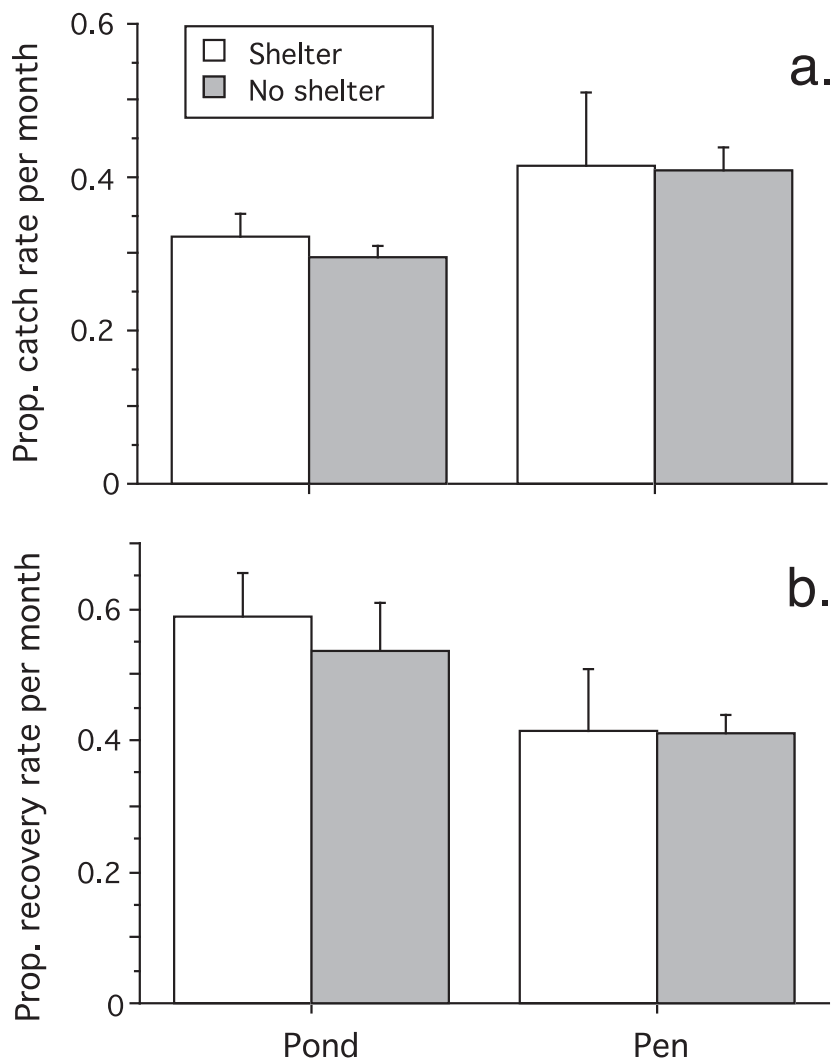


Figure 3: (a) Proportional catch rate per month ($e^{\ln([\text{total number of crabs caught with traps} / \text{no. of seed crabs}] / \text{no. months})}$; +SE) after 2-3 month experiment, and (b) proportional recovery rate per month ($e^{\ln([\text{total number of crabs recovered} / \text{no. of seed crabs}] / \text{no. months})}$) after 3-4 month at the end of the study, as a function of aquaculture type (earthen pond and mangrove pen) and shelter (bamboo-tubes and no shelter).

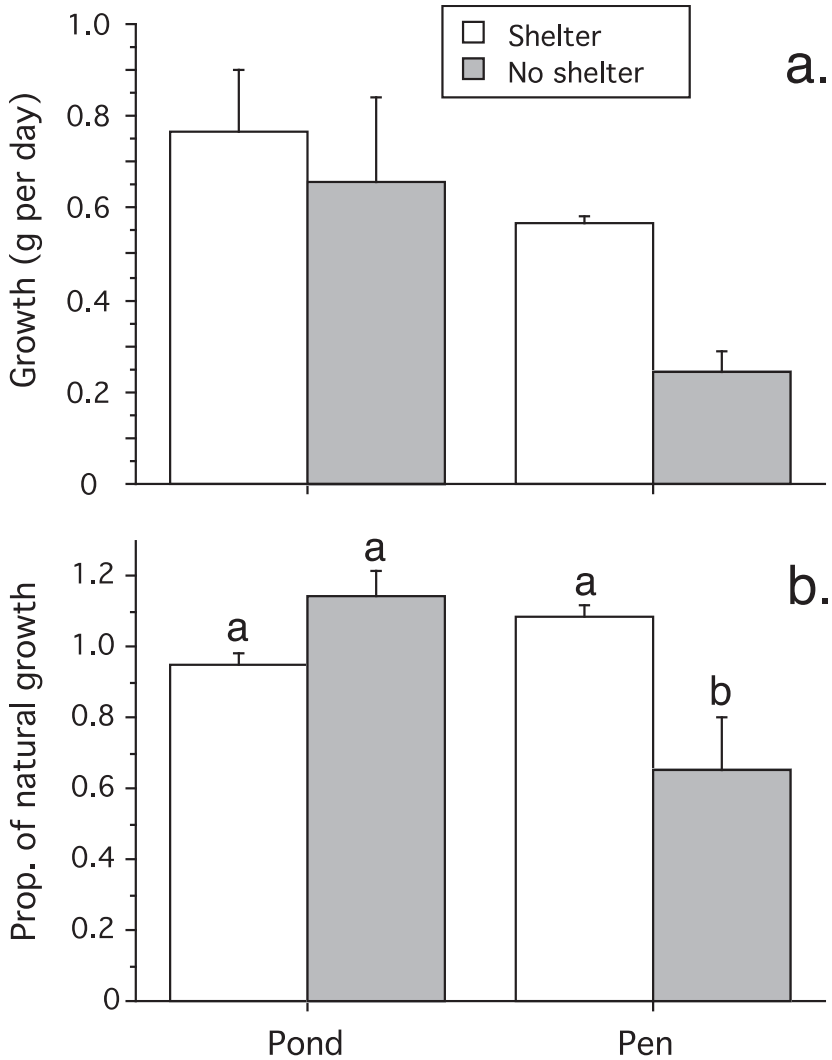


Figure 4: (a) Mean absolute growth rate (g per day; +SE) as a function of culture system (pond and pen) and the presence or absence of shelter (bamboo-tubes). (b) Proportion of estimated natural growth (+SE) obtained in the four culture systems. Different letters denote significantly different means (SNK-test at $P < 0.05$).

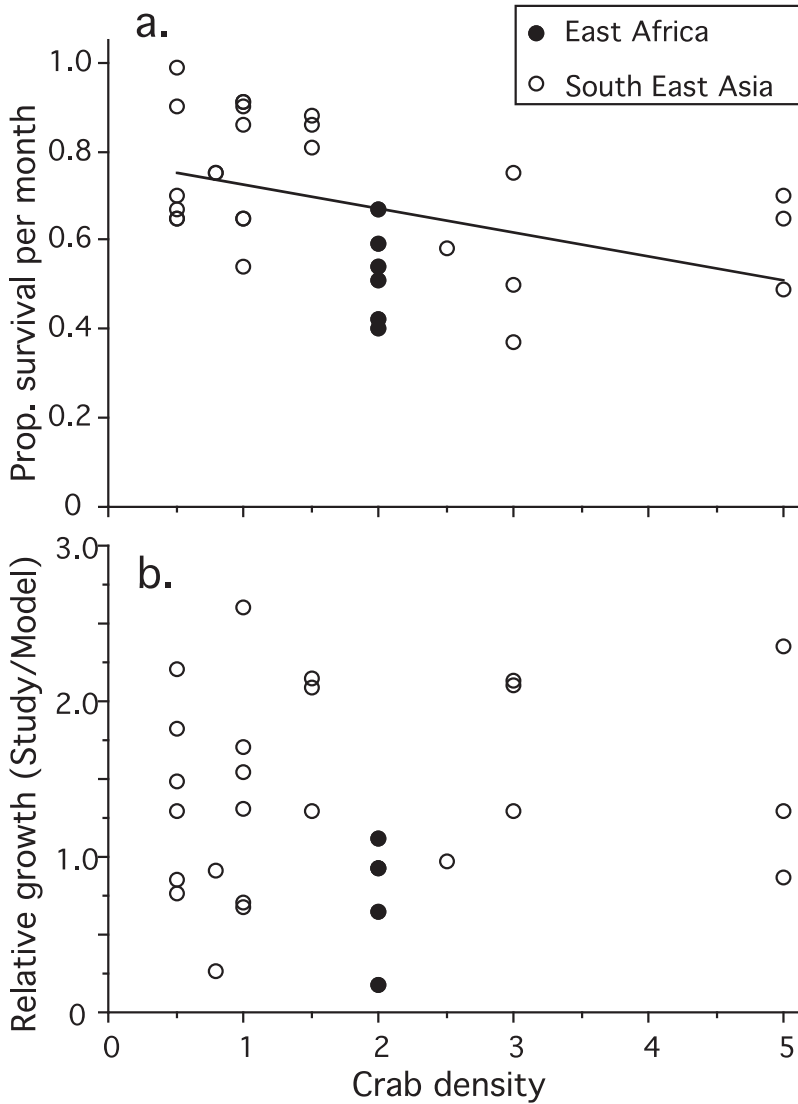


Figure 5: Relationship between stocking density and survival and growth rates in mud crab aquacultures in East Africa and Southeast Asia using data from the literature (see table 5). (a) Linear relationship between seed crab density and the proportional survival rate per month (*Simple linear regression*: $F=6.53$, $df=1,29$, $p=0.016$, $r^2=0.16$). (b) Relationship between crab density and the relative growth rate (growth rate in study/modelled growth rate) in the culture (*Simple linear regression*: $F=0.34$, $df=1,27$, $p=0.56$, $r^2=0.01$).

List of tables

Table 1. Summary showing the experimental replication, sites, culture period, size of crabs at stocking and environmental variables in all the treatments. Stocking density was 2 crabs m⁻² in all treatments.

Treatment	Replication	Site	Size (m ²)	Culture days	Initial size ICW (mm)	Initial weight (g)	Temp. (°C)	Salinity (psu)	Oxygen (mg/l)	pH
Pond + shelter	1	Kwetu	100	67	37±14 (9-73)	11±12 (0.1-72)	30.9 ± 0.8	31.2 ± 2.6	11.1±2.5	8.7±1.2
	2	Makongeni	100	66	43±15 (11-85)	25±25 (0.2-121)	30.8 ± 0.7	31.2 ± 2.6	12.4±2.3	8.6±1.1
	Mean		100	67	40±14.5	18±18.5	30.9 ± 0.1	31.2 ± 0.0	11.8±2.4	8.7±1.2
Pond + no shelter	1	Kwetu	100	66	39±13 (12-70)	10±9 (0.3-48)	31.0 ± 1.1	31.3 ± 2.8	10.6±2.3	8.8±1.1
	2	Makongeni	100	74	21±9 (4-56)	3±7 (0.01-36)	30.9 ± 1.0	30.8 ± 1.9	9.7±1.1	8.7±2.0
	Mean		100	70	30±11	6.5±8	30.9 ± 0.1	31.1 ± 0.4	10.2±1.7	8.8±1.6
Pen + shelter	1	Kwetu	50	67	29±12 (11-63)	7±9 (0.3-50)	29.1 ± 0.9	29.3 ± 0.4	10.7±2.3	7.3±0.1
	2	Kwetu	50	61	29±10 (13-54)	7±9 (0.4-55)	28.8 ± 1.3	29.7 ± 0.3	7.0±2.1	7.8±0.2
	Mean		50	64	29±11	7±9	29.0 ± 0.2	29.5 ± 0.3	8.9±2.2	7.6±0.2
Pen + no shelter	1	Kwetu	50	67	30±12 (13-54)	8±10 (0.4-40)	28.9 ± 1.1	28.6 ± 0.7	7.6±2.3	7.3±0.2
	2	Kwetu	50	89	23±5 (6-30)	2±1 (0.03-5)	29.1 ± 0.1	29.2 ± 0.4	8.3±0.2	7.4±0.2
	Mean		50	78	26.5±8.5	5±5.5	29.0 ± 0.1	28.9 ± 0.4	8.0±1.3	7.4±0.2

All values are means ± SD. The range of initial sizes is given within parenthesis after the mean.

ICW, Internal carapace width; BW, body weight

Table 2. *Cage experiment*. Three-factor ANOVA of the mean size of crabs (mm CW) and proportional loss of crabs week⁻¹, as a function of shelter (bamboo-tubes and no shelter), size range (20-50 mm and 20-80 mm ICW) of crabs and density (4 and 8 crabs per cage). Bold text of p-values indicate <0.05.

Source of variation	df	Mean crab size			Proportional loss of crabs		
		SS	F-value	P-value	SS	F-value	P-value
Shelter (A)	1	3.3	0.15	0.70	0.259	4.07	0.047
Crab size range (B)	1	1430	64.4	0.0001	0.361	5.66	0.020
Crab density (C)	1	19.9	0.89	0.35	0.043	0.67	0.42
A x B	1	19.0	0.85	0.35	0.065	1.01	0.32
A x C	1	9.2	0.41	0.52	0.061	0.96	0.33
B x C	1	0.4	0.02	0.89	0.031	0.05	0.82
A x B x C	1	0.5	0.02	0.88	0.151	2.37	0.13
Residual	80	1776			5.103		

Table 3. *Pen and pond experiment - Survival*. Two-factor ANOVA of the proportional catch rate per month ($e^{\ln([\text{total number of crabs caught with traps} / \text{no. of seed crabs}] / \text{no. months})}$) after 2-3 month experiment, and proportional recovery rate per month ($e^{\ln([\text{total number of crabs covered} / \text{no. of seed crabs}] / \text{no. months})}$) after 3-4 month at the end of the study, as a function of culture type (mangrove pen and earthen pond) and shelter (bamboo-tubes and no shelter).

Source of variation	df	Catch rate			Recovery rate		
		SS	F-value	P-value	SS	F-value	P-value
Culture type (A)	1	0.021	3.782	0.124	0.002	0.16	0.713
Shelter (C)	1	0.001	0.086	0.784	0.046	4.76	0.095
A x B	1	0.000	0.047	0.839	0.001	0.11	0.753
Residual	4	0.022			0.039		

Table 4. *Pen and pond experiment - Growth*. Two-factor ANOVA of the absolute growth rate (g day^{-1}) and proportion of model growth rate (obtained growth/modelled growth) as a function of aquaculture type (mangrove pen and earthen pond) and shelter (bamboo-tubes and no shelter). Bold text of p-values indicate significant difference <0.05 .

Source of variation	df	Absolute growth rate			Prop. model growth		
		SS	F-value	P-value	SS	F-value	P-value
Culture type (A)	1	0.092	3.49	0.135	0.027	1.85	0.246
Shelter (C)	1	0.186	7.03	0.057	0.063	4.24	0.108
A x B	1	0.024	0.91	0.393	0.193	13.0	0.023
Residual	4	0.106			0.059		

Table 5: Comparison of proportional survival and growth rates for different *Scylla* species from different studies. The calculations are made using the final survival recorded in the studies and the culture period. AGR denotes absolute growth rate. The last column shows the proportional difference in duration between the measured and modelled duration. Four species are included, *Scylla serrata* (Ss), *S. tranquebarica* (St), *S. olivacea* (So), and *S. paramamosain* (Sp) in mono- and mixed crab cultures. Only longer studies (≥ 1 month) carried out in larger culture system have been included in the comparisons.

Reference	<i>Scylla</i> spp.	Country	Seed source	Culture system	Area (m ²)	Density (crabs m ⁻²)	Shelter	Seed size range (mm)	Seed size Ave (g)	Final Size Ave (g)	Culture period (d)	Prop. survival month ⁻¹	AGR (g/day)	Rel. growth (Model/Study)
Present study	Ss	Kenya	Wild	Pens	50	2	Bamboo	11-63	3.8	2.6	64	0.42	0.39	0.93
				Ponds	100		None	6-54	2.7	17	78	0.40	0.18	0.64
Mirera, 2009	Ss	Kenya	Wild	Pens	12	2	None	4-70	7.6	53	70/134	0.54	0.64	1.12
				Pens	800		None	85	122.8	146	90	0.67	0.26	0.17
Mwaluma, 2002	Ss	Kenya	Wild	Pens	200	2.5	None	20-100	-	248	147	0.58	1.41	0.97
				Pens	200		None	-	40	190	147	0.49	1.02	0.87
Trino and Rodriguez, 2002	Ss	Philippines	Wild	Pens	200	0.5	None	51-54	19	317	160	0.90	1.86	1.30
				Pens	200		None	1.5	316	160	0.81	1.86	1.29	
Rodriguez et al., 2007	Ss	Philippines	Hatchery	Ponds	200	3	None	12	0.25	10.5	30	0.37	0.34	2.13
				Ponds	200		5	13	30	0.70	0.43	2.36		
Keenan, 1999	Ss	Philippines	wild	Cages	20	3	None	12	0.25	4	30	0.50	0.13	1.30
				Ponds	150		5	4	30	0.65	0.13	1.30		
Trino et al., 2001	Ss	Philippines	wild	Ponds	150	1.5	Seaweed	-	10	370	120	0.86	3.00	2.09
				Ponds	150		1	Seaweed	-	156	0.86	-	-	
Primavera et al., 2010	Ss	Philippines	Wild	Pens	167	0.8	None	49-52	21	181	153	0.75	1.05	0.91
				Ponds	150		0.5	401	120	0.99	3.27	2.21		
Trino et al., 1999a	Ss & St	Philippines	Wild	Ponds	150	1.5	Seaweed	35-43	9	380	120	0.88	3.09	2.15
				Ponds	150		3	367	120	0.75	2.98	2.11		
Baliao et al., 1999b	Ss & St	Philippines	wild	Ponds	5000	1	Bamboo	52	22	210	90	0.91	2.09	1.7
				Ponds	500		0.5	191	125	1.16	0.86			
Fortes, 1999	So	Philippines	Wild	Ponds	500	1	None	-	46	169	125	0.65	0.98	0.76
				Ponds	500		1	156	125	0.88	0.70			
Primavera et al., 2010	So	Philippines	Wild & hatch	Pens	200	0.8	None	32-63	39	88	153	0.75	0.27	0.27
				Ponds	500		0.5	229	130	0.70	1.69	1.48		
Christensen et al., 2004	Sp & So	Vietnam	Wild	Ponds	170	0.5	None	29.3-30.3	4.7	198	106	0.67	1.82	1.83
				Ponds	170		0.5	198	106	0.67	1.82	1.83		

V

PAPER V:

Traditional knowledge and crab fishery





Heredity or traditional knowledge: Fishing tactics and dynamics of artisanal mangrove crab (*Scylla serrata*) fishery



David Oersted Mirera^{a,b,*}, Jacob Ochiewo^a, Fridah Munyi^a, Tabitha Muriuki^a

^a Kenya Marine and Fisheries Research Institute, Box 81651, Mombasa, Kenya

^b Linnaeus University, 391 82 Kalmar, Sweden

ARTICLE INFO

Article history:
Available online

ABSTRACT

Globally, artisanal fisheries are challenged by the combined impacts of overfishing, ecosystem degradation, climate change and lack of management intervention. Little is known of how traditional knowledge/skills held by fishers influence ability to exploit marine resources and whether such information could be incorporated into management practices. Failure to understand fishers' traditional knowledge/skills and behaviour may undermine the success of fisheries management measures. Use of traditional knowledge in exploitation of mangrove crabs (*Scylla serrata*) on local fishing grounds is assessed. The study used complementary approaches (field experiments and fisher-based surveys) to investigate fishing tactics employed by artisanal crab fishers. Also time series data from the ministry of fisheries was used to assess annual trends in production and value of the fishery. Fishers with calibrated GPS fished in different areas and catch per unit effort (CPUE), fishing time, distance and efficiency were assessed. Key informant and semi-structured interviews and direct observation were conducted among mud crab fishers to establish knowledge/skill requirement, fishing tactics and entry into the fishery. The results indicate that mud crab fishing is a male dominated activity. Fishing is done at spring low tide by foot fishers in burrows mainly with rare use of baited traps and lift nets at ankle height water along the intertidal mangrove front boundaries or channels. Fisher's follow specific tracks that are strongly guarded by individual fishers. Fishing for adult crabs showed deeper and further movement in the mangrove forest unlike juvenile crab collection. Fisher's in new areas collected few crabs due to low efficiency compared to well known areas. Entry into the fishery is minimal and skills are inherited from parents or grand parents with limited transfer being obtained from colleagues. The average size of marketable crabs has declined over the years while season and tide have remained major challenges for production and market determination in the fishery. Fisher-based surveys overestimated CPUE and sizes of smallest crabs caught while it underestimated fishing time and distance moved. A weak management system was observed with most fishers operating without a license and lacking a synchronized landing system. Inability of fishers to shift to new areas, "natural closures" and limited distance covered by foot fisher's support site-specific management for the fishery.

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1. Introduction

Mud crabs *Scylla serrata* (mangrove crabs) are associated with mangrove ecosystems (thus name mangrove crab) throughout their range and form an important source of food and income for local communities (Keenan et al., 1998; Keenan, 1999; Le Vay, 2001; Bonine et al., 2008). Increasing demand from both local and global markets has led to overexploitation of wild stocks with resultant

decline in catches and sizes landed (Barnes et al., 2002; Bonine et al., 2008; Mirera, 2011; Dumas et al., 2012). Although several families along the East African coast benefit from mud crab fishing, there is limited and poorly collected catch data (Mirera, 2011) that may be associated with the complexity and dynamics of the exploitation tactics used in the fishery. Studies by Ewel (2008) showed greater differences in crab size over small spatial scales (about 1 km) that could require site-specific management policies. This implies that understanding small-scale mud crab fisher's fishing tactics and obtaining data on ecology and exploitation of the fishery will be essential in addressing management issues (Barnes et al., 2002; Hay et al., 2005; Glazachev and Perfilova, 2008; Maynou et al., 2011).

* Corresponding author. Kenya Marine and Fisheries Research Institute, Box 81651, Mombasa, Kenya. Tel.: +254 722646270.

E-mail addresses: dimirera@yahoo.com, dmirera@kmfri.co.ke, david.oersted.mirera@lnu.se (D.O. Mirera).

Burrow fishing is a common method of crab harvesting and collection of juveniles for aquaculture along the coast of East Africa (Barnes et al., 2002; Mirera, 2011; Moksnes et al., 2012). Large crabs are considered to be more sub-tidal moving from their burrows at high tide to feed in the mangrove forest (Le Vay et al., 2001; Walton et al., 2006). Nirmale et al. (2012) observed that burrow fishing requires a great deal of experience and beginners tend to damage the crabs. While Dumas et al. (2012) observed that fishers frequently check burrows along usual trails inside their respective fishing territories and opportunistically picked crabs lying on the ground or partially buried in the sediment along the trails. Despite that, how fishers identify fishing territories (niche), burrows and what skills are required to retrieve crabs is poorly understood globally.

Considerable progress has been made to understand the biology, recruitment, growth and ecology of *S. serrata* (Le Vay et al., 2001; Walton et al., 2006; Ikhwannuddin et al., 2011). However, little effort has been made to understand the knowledge – “traditional” – used by fishers to exploit the resource and how such information can help to restructure management of the fishery. Traditional knowledge can be summarized as a source of intellectual capital that encompasses the wisdom, knowledge, expertise, skills, beliefs and teachings of local communities that is passed from generation to generation (Soh and Omar, 2012). Local communities use such knowledge to interpret their relationship with the environment and manage natural resources. Therefore fishers’ knowledge is important in supplying information for operational resource management (Jones et al., 2008; Ochievo et al., 2010). Working in India, Nirmale et al. (2012) found a strong relationship between the knowledge owned by mud crab fishers and that published in science but no effort was made to show how such knowledge is gained and how fishers may use it to improve fishing practices. Also no information was provided on how such knowledge could be integrated into contemporary management of the mud crab fishery.

In other small-scale fisheries, entry into a fishery is at the very basic level referred to in literature as seaman (Fulanda et al., 2009). Starter fishers join a fishing unit and become part of the general crew with main duties initially being loading and offloading of fishing gear and catch (Ochievo, 2004; Fulanda et al., 2009; Ochievo et al., 2010). However, no information exists on how mud crab fishers enter the fishery.

The purpose of this study is to analyze the diversity of knowledge required to exploit mud crabs and how such knowledge can be integrated into contemporary management practices. Without a clear understanding of a fishery, policy makers and managers may formulate policies that are not responsive to underlying challenges since management of marine resources is complex and characterized by high levels of uncertainty (Ludwig et al., 1993; Steel et al., 2005).

2. Materials and methods

2.1. Study site

The study was conducted at four sites (Mtwapa, Kilifi and Mida creeks and Marereni) on the northern coast of Kenya where there is ongoing mud crab fishing and farming in the adjacent mangrove forests. The sites were chosen to include both rural and urban settings and different mangrove management regimes. Although mud crab fishing takes place in all the four sites, the extent of the fishing is determined by cultural and economic factors that vary from site to site. Mtwapa creek is located about 25 km north of Mombasa city in an open access fishing area. It is adjacent to the rapidly growing Mtwapa town and it lies between the Nyali–Bamburi–Shanzu tourism site in the south and Kanamai–

Kikambala tourism site in the north. Mtwapa creek is a highly cosmopolitan area that comprises most communities existing in Kenya; however mud crab fishing is practised by Mijikenda (Giriama and Chonyi). Kilifi creek is approximately 70 km from Mombasa and lies in a moderately developing town. Mud crab fishery in the area mainly supplies tourist villas within the town while some is consumed at home. The communities around the creek are mainly Mijikenda (Giriama and Chonyi). Mida creek is located approximately 100 km north of Mombasa City within a marine protected area, the Watamu Marine National Reserve. It is adjacent to the Watamu tourist town, which provides a large market for mud crabs especially during the peak tourism season. The communities around the creek comprise a large proportion of Mijikenda (Giriama) and to a small extent a small proportion of indigenous Wata community. All communities in the creek participate in mud crab fishing. Marereni is located to the north of Malindi town at the Ungwana bay about 150 km north of Mombasa city in a rural setting whose main economic activity is salt production and fishing. Occupants of the area are mainly Mijikenda (Giriama) community (Fig. 1). Only traditional artisanal mud crab fishing methods were used at the study sites.

2.2. Fisher-based surveys

Primary data was collected using a combination of three techniques; semi-structured interviews, direct observation and key informant interviews. Semi-structured interviews were conducted using interview guides/semi-structured questionnaires with open-ended questions. The questions covered a number of parameters including age of the respondent, gender, experience (how long one has been a mud crab fisher), daily landings, size of landings, time spent fishing, distance covered, number of days fished per month, entry into the fishery, fishing methods and landings in different fishing seasons. Respondents were probed to get more details from the answers provided. The respondents were identified using a purposive sampling technique (De La Torre-Castro et al., 2007; Ochievo et al., 2010) where only mud crab fishers were targeted. Key criteria for selection of fishers included number of years the fisherman had been involved in mud crab fishing as a livelihood activity in the respective creek. Since fishers do not land catches at designated landing sites, timing for the interviews was planned to coincide with tides that allowed fishing and respondents were either interviewed at the field or at their respective homesteads. Interviews were conducted in Swahili, which is the national language for Kenya and the language spoken by all the coastal communities. Fishers were interviewed between January 2010 and December 2011.

Key-informant interviews were used to obtain information from opinion leaders (Influential people in the society who have wider knowledge on subject and command the support of many). Interview guides with open-ended questions were used to prompt the key informants to discuss the history and characteristics of the mud crab fishery in their respective areas. Ten key informants were interviewed in total. Snowball method (which involves gathering information by asking an initial informant to suggest other informants) was used to identify key informants at the four sites. The key informants included the most experienced mud crab fishers, leaders of community based mangrove conservation groups (two of these mangrove conservation groups are also engaged in mud crab farming) and mud crab traders who understand the fishery. They provided insights on issues that needed further clarification and helped in the validation of information collected using other research methods.

Data was also obtained through direct observation of the mud crab fishing activities including participation in the field with

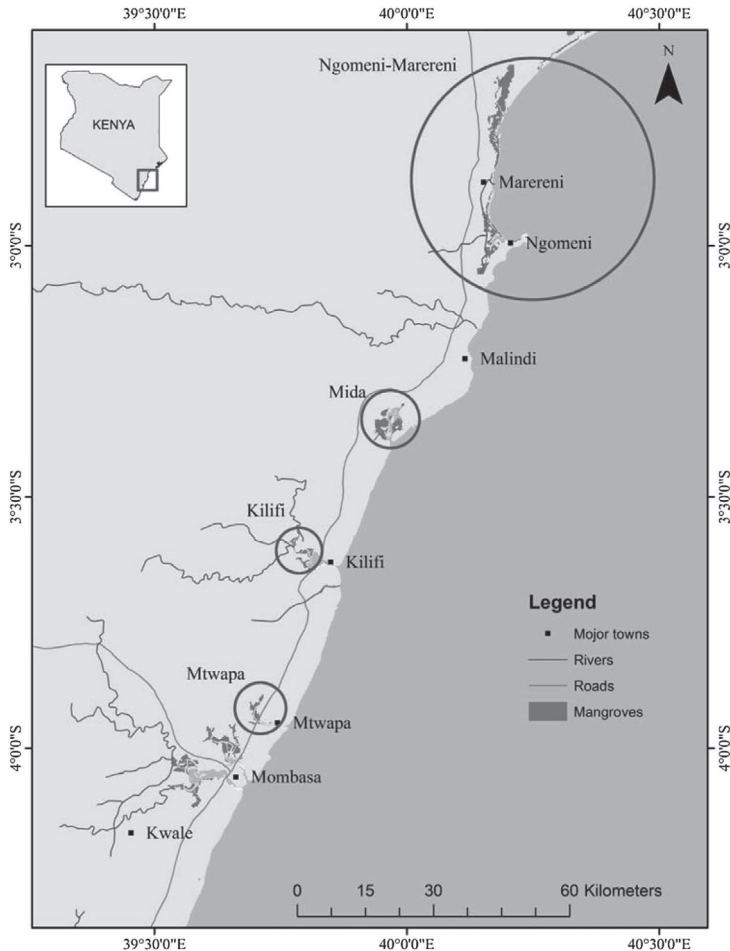


Fig. 1. Map of the coast of Kenya showing the areas covered during the current study.

fishers. The information gathered through direct observation helped to facilitate detailed discussions with the fishers.

2.3. Field based experiments

Sampled study sites were relatively shallow with wider intertidal areas and have relatively gentle gradients. This enabled walking at low tide and collecting crabs over long distances in the mangroves. Most of the area behind the mangrove forest had wide stretches of intertidal sand flats with sections of *Avicennia marina* and *Ceriops tagal*. The middle and forefront mangrove areas had deep mud with extensive root network of *Rhizophora mucronata*, in some areas *Bruguiera gymnorrhiza* and spots of *A. marina*.

To obtain information on movement, time taken, route complexity and distance covered, 3 fishers per site (12 fishers) were provided with a Garmin GPS programmed to take tracks (way points) at 5 min intervals and record distance covered in kilometres

for a period of 10 days in a month as per the preference of the fisher. The Garmin GPS was de-programmed at the end of the fishing activity for each day and way points downloaded into a computer on a daily basis. The tracks were used to estimate time taken, distance covered and movement of the artisanal fishers in the mangrove forest. The mud crabs were bought from fishers, and used to estimate Catch Per Unit Effort (CPUE), size and sex composition. However, CPUE in this study did not take into consideration the aspect of crab abundance per site, which could be a limitation for the study.

To assess the impact of site knowledge on catches, 5 fishers were engaged in one familiar site for 5 consecutive days and then transferred to another site where they had less knowledge for another 5 days. Catch/day was assessed and used to calculate individual mode of catch output. The procedure was repeated for both juvenile (Less than 50 mm Internal carapace width) and adult market size crabs (more than 110 mm Internal carapace width) but

using different fishers each time. When fishers were moved to new sites (unfamiliar sites), artisanal fishers were accompanied by a person from the local community who was not a fisher to help them through the forest in order to minimizing accidents and conflicts with local people.

Time series data from the fisheries department annual statistic database was used to assess trends in production and value of mud crabs over a twenty-year period (1990–2010). However, this data is dependent mainly on what is brought to the market and not what individual fisher's collect.

2.4. Data analysis

Both quantitative and qualitative data have been analysed using descriptive statistics and graphical analysis. Descriptive analysis was undertaken with the help of Statistical Package for Social Scientists (SPSS 13) and Graph Pad Prism 6 programs.

To test the difference between preference of fishing methods and fishing time, a Chi-square statistic was used at $p \leq 0.05$.

CPUE data was tested for normality before analysis. Two-way ANOVA was used to investigate the significance of temporal and seasonal trends on CPUE.

3. Results and discussion

3.1. Beliefs, genealogy and composition

Mud crab fishing is an important livelihood activity for many households on the coast of Kenya. This is particularly so at Mtwapa creek-Mtomondoni, Kilifi creek-Kibokoni, Mida creek-Watamu and Marereni/Gongoni/Fundisa. The characteristics of mud crab fisher communities as observed in the four communities are summarized in Table 1. Household size of mud crab fishers was 6.7 and thus similar to what has been recorded for the sea cucumber fishery along the coast of Kenya (Ochiewo et al., 2010). The fishery is men dominated (90.3%) compared to women (9.7%). Young fishers (<25 years) mainly engaged in collection of juveniles for sale to crab farmers. The study results differ from those of other studies like northwest New Caledonia where women played a central role in mud crab fishing (Dumas et al., 2012). However, women do collect sub-adult crabs during times of food scarcity to meet family needs (Mirera, 2011). The difference in gender involvement in mud crab

fishery may be associated to cultural differences, particularly with respect to beliefs and values.

Mud crab fishers in the current study aged between 23 and 55 years and differed from that of finfish fishers who have been found to age between 15 and 45 years (Fulanda et al., 2009). While the finfish, prawn, lobster, sea cucumber and octopus fisheries attracted a large number of entrants (Ochiewo et al., 2010), the crab fishery appeared to have a limited number of entrants, probably because of the skills required and the difficult mangrove environment. There were cases where mud crab fishing skills had been handed down from one generation to another and cases where close friends through peer learning transferred the skills. At both Mida creek and Marereni north of Malindi town, the mud crab fishers had skills that have been handed down mainly from parents or grand parents. Only a few cases were found where unrelated peers transferred mud crab fishing skills to a young entrant. The observed entry into the mud crab fishery differs from that of other fisheries like sea cucumber and migrant fishing where entry is at a very basic level (seamen) before qualifying as a fisher (Fulanda et al., 2009; Ochiewo et al., 2010).

Peer transfer of mud crab fishing skills occurred only among the youthful mud crab fishers particularly those who are close friends. In this case, an individual who chose to learn how to fish mud crabs followed and keenly studied his friend who was already a mud crab fisher on a fishing mission. The main things to be learnt included identification of a hole that contains a crab using the physical marks that are left by crabs in the surrounding mangrove mud and the capture of a mud crab using traditional fishing sticks (Table 2). Recently, the mud crab fishers have also learned how to tie the claws to avoid breakages that may reduce market value and any injuries that may be caused to and by the crabs (Mirera and Mtile, 2009). At another level, the mud crab fishers were attracted into the fishery by the better prices that were offered by the dealers, especially those who were either selling directly to the tourist hotels or those who were exporting to Kampala and other distant markets.

3.2. Knowledge/skill requirement

Artisanal mud crab fishers recognized that some level of skill, determination, patience and tolerance is required to operate in the fishery (Table 2, Fig. 2). The fishers indicated that the skills required could help increase catches, improve quality of catch (getting crabs with chelipeds intact), avoid wasteful harvesting i.e. just moulted crabs that could easily die, reduce competition from other fishers i.e. going to the fishing ground earlier than others and keeping secrets. Indeed Jones et al. (2008) and St Martin (2004) established that fishers' knowledge is a promising supply of information for operational resource management. The ability of crab fishers to get crabs with chelipeds for quality in the current study differs with observation by Barnes et al. (2002) where fishers at Utende, Mafia Island, Tanzania, removed crab chelipeds (Pincers) before extraction from their burrows, which may be an influence of the market requirements or limited skill by the Utende fishers. Knowledge also helps fishers to manage the catch until it is delivered to the market; the crab chelipeds are tied using palm leaves or manila ropes, kept in baskets made of manila or coconut leaves for easy of aeration and movement in muddy environment. Crabs are washed to remove mud, kept in a safe place and sprinkled with ocean water when held at home to prolong length of life. However, most of the fishers are unaware that holding crabs for long periods leads to loss of wet weight which is important for profitability in markets where weight is a key factor (Mirera, 2009).

The knowledge attained by mud crab fishers also enables them at a glance to tell which crab has just moulted, is preparing to moult

Table 1
General and social demographic characteristics of artisanal mud crab fishers in the four study sites in the north coast of Kenya.

Characteristic	Mtwapa creek	Kilifi creek	Mida creek	Marereni	Average
Size of household (no.)	5.1	8.0	6.4	7.2	6.7
Age (years)					
Minimum	23	24	27	23	24.3
Maximum	45	54	50	55	51
Experience (average in years)	18.6	24.8	20.7	25.3	22.3
Education level					
None	21%	25%	27%	35%	27.0%
Primary	74%	71%	70%	65%	70.0%
Secondary	5%	4%	3%	0%	3.0%
Other	0%	0%	0%	0%	0%
Sex					
Male	96%	80%	95%	90%	90.3%
Female	4%	20%	5%	10%	9.7%
Marital status					
Married	94%	95%	98%	88%	93.8%
Never married	6%	5%	2%	12%	6.2%
Other	0%	0%	0%	0%	0%

Table 2
Knowledge and skill requirement for effective operation by artisanal mud crab fisher's operating in mangrove creeks and bays.

General	Specific	Sources
Mud crab behaviour/ecology	-Movement -Moulting -Spawning -Feeding time -Aggression/defense -Movement style -Hole preparation and appearance when in or out	-Practical training by close relatives/father/grand father/brothers/uncle/cousin -General discussions by colleagues in social places -Skills acquired over time
Mud crab characteristics	-Sex identification - Loss of appendages - Ability to stay alive	- Practical training by close relatives/father/grandfather/brothers/uncle/cousin - Own experience developed - Peers at childhood
Market considerations	- Sex preference - Preferred size - Quality preference - Storage and management before sale - Market sources	- Inheritance from father/brother/grand father/uncle/cousin/in-law - Colleagues - Knowledge development over time (experience related)
Other skills	- New hole identification - Identification of new preferred sites - Capture skills - Keeping hole secreted - Suitable fishing time - Suitable fishing season and tides - Handling techniques - Tools required for fishing - Knowledge of the creek and tidal fluctuations	- Inheritance of holes and tools from close relatives/father/brother/uncle/cousin/grandfather/in-law - Knowledge development over time (experience related) - Training by close relatives/father/grand father/brothers/uncle/cousin - Other fishers - Discovery of new crab harvesting sites in the field - Personal observations of crab behaviour - New tools bought and made using resources obtained
Other requirements	- Determination - Patience - Tolerance	- Inherited from parents - Developed from daily experiences - Developed through interaction with colleagues

or is older than the others. This may help in laying grounds for management of the fishery as a sound way of improving people's livelihood and management of resources (Soh and Omar, 2012).

3.3. Fishing methods (strategies) for juvenile and adult crabs

The choice of a fishing area and method of fishing for mud crabs depends on the skill and equipment required. More than 60% of the crab fisher's fish in mangrove burrows using traditional gear and the rest use other methods along the forefront mangrove edge and channels at low tides (Fig. 3). Almost all fishers practice fishing by foot with limited use of equipment (Plate 1). Burrow fishing is a common method and involves extracting crabs from burrows (holes) using hooked/curved sticks (Plate 1c & d; Barnes et al., 2002).

Burrow crab fishers do not use vessels while seine net fishers may at times use dugout canoes to enable them to operate the nets.

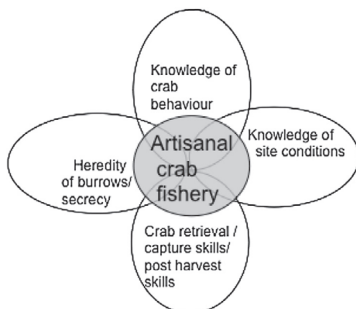


Fig. 2. Key skills/knowledge for entrants into artisanal mud crab fishery in mangroves as foot fishers.

Seine net fishing was dominantly used at Kilifi creek compared to other sites, a fact that was associated to the steep channels occurring in the area. Fishers use simple homemade traditional equipment like hooked sticks, baskets made of coconut leaves (Pakacha), basket traps, seine nets, line and scoop nets and sometimes panga (machete) (Plate 1). The observed gear in the current study has a high similarity with that used by small-scale fishers in other areas (Barnes et al., 2002; Walton et al., 2006; Dumas et al., 2012), implying that with some level modifications to fit local conditions,

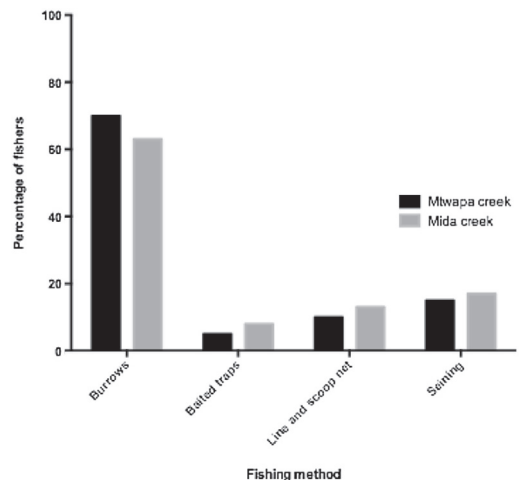


Fig. 3. Preference of fishing methods (adult and juvenile crabs) by artisanal mud crab fisher's in two mangrove creeks in the north coast of Kenya.

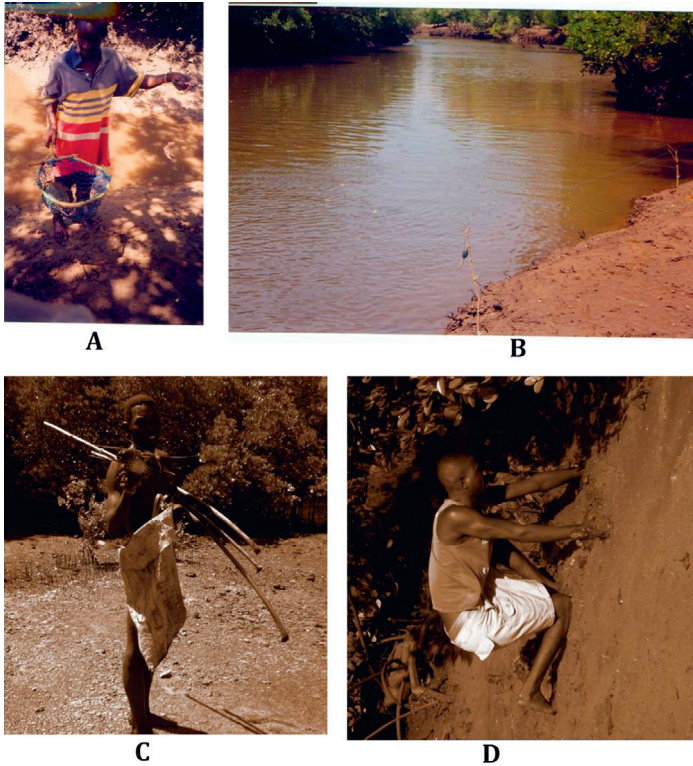


Plate 1. (A). Crab fisher from Marereri using line and scoop net method for catching crabs- photo by Esther (B). Sticks attached to a baited line, placed on the bank of a channel to catch crabs- photo by Esther (C). Crab fisher with hooks sticks used for burrow fishing- photo by Mirera (D). Fisher collecting juvenile mud crabs in the intertidal mangrove boundary burrows at Mtwapa creek- photo by Mirera.

management interventions for mud crab fisheries may be replicated in different regions.

Most crab fishers mainly fish during the day in mangrove burrows by walking on foot through the forest along familiar tracks (Fig. 4). This observation is supported in other studies by Barnes et al. (2002) and Dumas et al., 2012. Fishers using baited traps set them at night and retrieve them at dawn. Most fishers in the two fishing categories work individually to maintain secrecy of fishing areas and burrows. Any fisher spotting the footsteps of another in front will move fast to check specific burrows known to him before turning in another direction to maximize catches. Fishers at times walk on mangrove prop roots to avoid being tracked to secret crab burrows. Ability to track fishers to potential fishing grounds may have significant implication for management of the fishery because of changing catchability (increase in CPUE) due to discovery of new fishing sites thus providing misleading information on abundance of stocks.

The study established that fishing is never random; it follows specific patterns mainly depending on the knowledge of the fisher on preferred mud crab areas where the harvest is likely to be high. In the process, new holes are opportunistically discovered and form part of the territory of the fisher. These observations are supported by findings of Dumas et al. (2012). Since mud crabs don't colonize all sections of the mangrove ecosystem equally, the decision by fisher's to fish in familiar tracks which may be highly preferred by

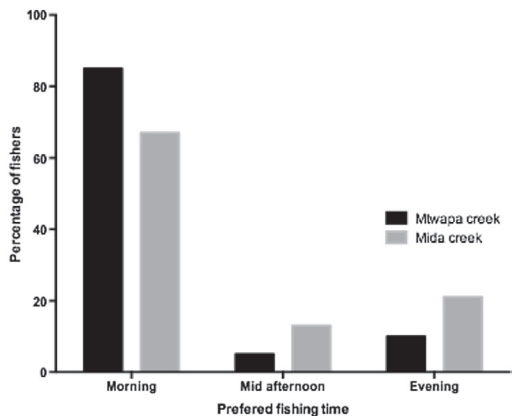


Fig. 4. Preferred fishing time by artisanal mud crab fishers under favourable tidal regime and season (Morning = time between 6am and 11am, Mid afternoon = time between 12 noon and 3pm, Evening = time between 4pm and 7pm).

crabs, may lead to overexploitation of stocks due to hyper-stability in CPUE while stocks are declining because crabs are replenished in burrows during the high tides. Therefore, diversity in potential fishing sites based on fishers' knowledge may require harmonization for effective site-specific management of the fishery.

3.4. Seasonality, migrant fishing and habitat preference

Higher quantities of mud crabs are landed during the southeast monsoon season, which also happens to be the rainy season. Specifically, catches are higher during the months of April to June. This observation is supported by study carried out at the Ramisi River estuary where adult female crabs were caught in large numbers from January to July (Onyango, 2002). Catches are low during the northeast monsoon (October–March) but this is the time when the market price is higher since it's a peak tourism season. Low catches during the northeast monsoon may be associated with movement of large females sub-tidally to spawn (Muthiga, 1986; Onyango, 2002); however, seasonal sex abundance was not covered in the current study for comparison. Seasonality was also observed by Walton et al. (2006) where abundance varied between the different methods employed (torch fishery, scoop net, gill net and burrow fishery). Despite high abundance of mud crabs during the rainy season in the current study, some burrow fisher's preferred not to fish during the rainy season due to difficult to maneuver through the mangrove forest and most crab holes getting covered. Therefore, it is difficult to make use of the usual signs on the mud to track crabs in the mangrove forest.

Mud crab fishing in the current study was influenced by tidal regimes irrespective of the fishing technique applied, a fact supported by Moser et al. (2005) in literature. Most fishers preferred to fish during low spring tides and return at high tides. At low spring adult mud crabs are seined from mangrove forefront at ankle deep waters as observed by Barnes et al. (2002) or retrieved from individual burrows within the mangrove forest. However, some fish adult mud crabs from mangrove channels at high tide using baited traps. Due to tidal influence, there is no extension in time for fishing to recover lost time or meet demand in mud crab fishery. This differs from observation made in other fisheries where fishers may extend fishing time to increase their catches (Ochiewo, 2004).

Limited fishing takes place during neap tides (locally called *maji mavu*). It is believed that at this time most crab burrows are empty because tidal water does not cover the upper zones of the mangrove ecosystem and water is usually deep to allow seining

along the mangrove forefront. However, the burrows are wet enough to host moulting crabs. Also fishers indicated that crabs found in burrows at neap tide are in the moulting period or have just moulted and thus have no market value locally. Therefore, it may be argued to be a natural "closure" for the burrow mud crab fishery. During "natural closure" most fishers engage in fishing for prawns and finfish, or in subsistence farming, or casual jobs. The diversification into other activities during low season along the coast of Kenya (Fulanda et al., 2009; Ochiewo et al., 2010).

More than 90% of the respondents had not participated in fishing new mangrove areas other than their current ones. This implied that migration between creeks/bays by artisanal mud crab fishers was minimal. It was also clear that prior information about a new fishing area was necessary to ensure success: To fish in a new site, the fisher would need specific detail or knowledge that could include; tidal fluctuations, mangrove channels, islands within the mangrove forest, soil characteristics, mangrove species distribution and site gradients. Most fishers were not ready to engage in new fishing sites without local guides. During experimental fishing, fishers at new sites took more days to land the same number of crabs as that landed by the lowest fisher at a familiar site (Fig. 5a and b). While this results are important in explaining the need for knowledge in mud crab fishing, there are limitations on the extent to which the data can be applied due to variations in abundance of crabs in the fished areas (familiar and unfamiliar) hence not comparable using the current research design.

Due to intensity of searching for new burrows, greater effort/energy was used by mud crab fishers in unfamiliar sites. In new sites, fishers will follow footprints of other fishers in addition to opportunistic searching using traditional knowledge according to 85% of the respondents. Fishers indicated that it would take them more than one month to master a new fishing area and be able to increase their catches. The observation was seen to apply to all methods used by artisanal fisher's in the study sites (burrow, hook and line, baited traps and seining). The implication is that artisanal mud crab fishing, lacks the migration aspects experienced in other fisheries (Fulanda et al., 2009; Ochiewo et al., 2010) and, hence, supports site-specific management interventions.

There was high complexity and movement involved in harvesting adult crabs compared to collection of juvenile crabs (Fig. 6a and b). Adult mud crabs were collected within the mangroves from burrows, seined in mangrove forefront at low spring tide and channels at high tide using baited traps. However, juvenile mud

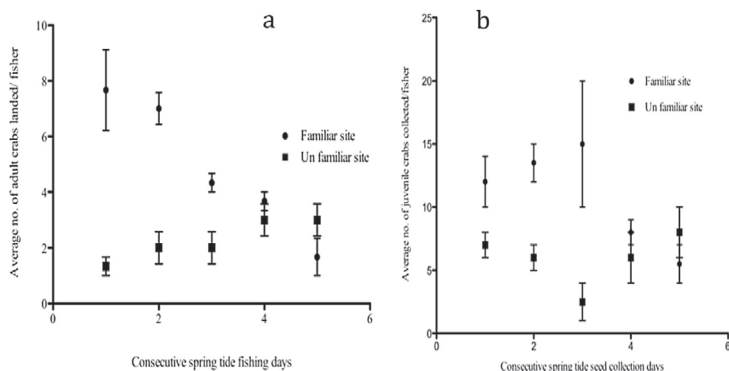


Fig. 5. Average number (\pm SE) of (a) adult (≥ 110 mm ICW) and (b) juvenile (≤ 50 mm ICW) mud crabs landed by artisanal fisher's per day in 5 consecutive fishing days in a familiar fishing site and in a completely new (unfamiliar) site at Mtwapa, Kilifi and Mida creeks. (ICW – Internal Carapace Width).

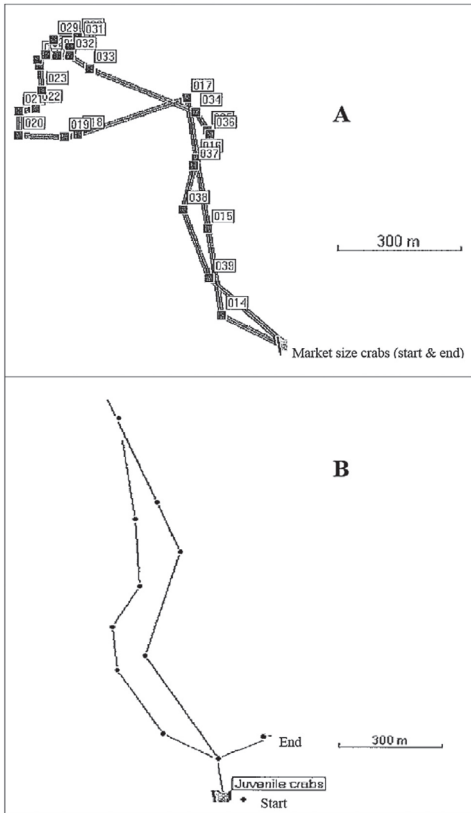


Fig. 6. Tracks taken by artisanal mud crab fisher's in a normal days work (4 h). (a) Collecting adult mud crabs for sale (b) Collecting juvenile crabs for sale in local aquaculture farm.

crabs were partially buried in shallow burrows in intertidal mangrove boundary zones usually at the immediate edge of *R. mucronata* where the intensity of mud was minimal. This may be attributed to the fact that juvenile crabs occur in specific habitats in the mangrove ecosystem while adult crabs occupy different habitats within the same system (Walton et al., 2006; Moksnes et al., 2012). However, the ability to collect juveniles easily compared to adults, thus, creating a risk of overexploitation from aquaculture if no management interventions are put in place (Mirera, 2011).

Also most respondents indicated that different mangrove species attracted mud crabs differently because of varied burrow density although this differed greatly among respondents. Some of the mangrove species that were noted to have influence on mud crab burrow density included; *B. gymnorrhiza*, *Cerriops tagal*, *Sonneratia alba*, *R. mucronata* and *A. marina*. However, there was no clear mangrove species zonation in the study sites.

3.5. Catch dynamics

Overall, there were some similarities and variations though not significant in field experiments and fisher-based surveys in CPUE (0.25–1.43; 0.5–1.7 kg/h), fishing time (3.5–5.0; 2.5–4.5 h/day),

sizes of caught crabs (250–850 g; 400–900 g) and distance moved (3.4–4.5; 2–4 km/day) respectively (Table 3), an observation which has been made in other studies (Dumas et al., 2012). Fisher-based surveys overestimated CPUE and sizes of smallest crabs caught while it underestimated fishing time and distance moved. Over-estimation of minimum size in fisher based surveys than what was actually caught as seen in field based experiments is dangerous for management of stocks because smaller crabs have not reached reproduction stage however, sizes caught are dependent on the target markets. Consequently, minimum and maximum landed sizes in the current study show a huge decline compared to observations made 2–3 decades ago on the south coast of Kenya where sizes varied between 0.5 and 1.5 kg (Muthiga, 1986; Onyango, 2002).

High variability was observed in distance moved by fishers and time used for active fishing per day. However, time spent and frequency of fishing dependent mainly on market demand and tidal regimes at the site while distance dependent on the catches attained and time available. As a result, fewer fishers in different fishing areas in the north coast of Kenya landed more than half of the recorded catch/day. According to Barnes et al. (2002), fisher's could move for long distances to look for crabs, implying that fishing skills, ability to move faster and further in the mangrove forest could contribute to good catches.

Frequency and time spent fishing in the current study was similar to that observed by Rocklin (2006), when comparing two crab-fishing villages in New Caledonia. In addition Barnes et al. (2002) established that a crab fisher at Chole Island in Mafia, Tanzania, could only make two fishing trips/week but the frequency could increase if the demand from tourist hotels was high. The consistency in information obtained through fisher's survey and field experiments concurs with Nirmale et al. (2012) who found similarity in knowledge provided by fishers and that published in scientific literature about mud crabs. Therefore there are indications that in the current study fishermen hold vital traditional/local information and knowledge that may be useful in management of the mud crab fishery as in other fisheries (Jones et al., 2008; Ochiewo et al., 2010).

The fisheries annual statistics trend based on wild catches for Kenya show that mud crab production has progressively increased over time from an average of 70 metric tons to an average of 140 metric tons (Fig. 7a). A drastic increase in production was observed between 1995 and 2000, which levelled out with small variations until 2010. Production and value of the mud crab fishery lagged between 1997 & 98 (Fig. 7a and b). This may be associated to the 1997/1998 El Nino rains that covered the crab burrows with sediments and thus low catches or decline in the number of domestic tourists leading to low demand for the product in the market. Decline in wild production of mud crab fisheries in the year

Table 3
Characteristics of the adult mud crab fishery in small creeks and existing exploitation effort.

Parameter	Response from fishers (interviews)	Field experiment with fishers (burrow fishing)
Maximum CPUE (kg/h)	1.7	1.43
Minimum CPUE (kg/h)	0.5	0.25
Maximum time spent fishing/day (hrs)	4.5	5.0
Minimum time spent fishing/day (hrs)	2.5	3.5
Time spent fishing/month (days)	12	10
Maximum distance covered/day (km)	4	4.5
Minimum distance covered/day (km)	2	3.4
Ratio of sex in your catches (M:F)	Depends on season	1: 1.02
Common size range of caught crabs (g)	400–900	250–850

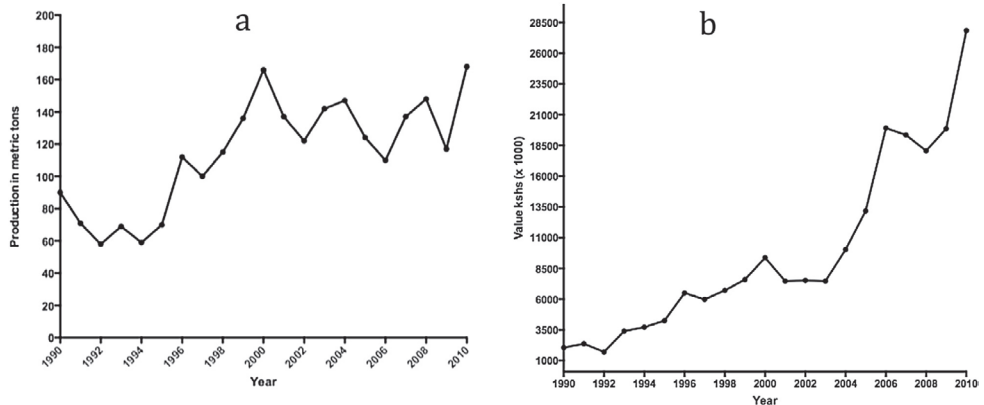


Fig. 7. Annual trend of mud crab fishery (a) production (metric tons) and (b) value (kshs.) for Kenyan coastal waters based on annual statistical database of the ministry of fisheries (1990–2010).

2000 coincided or lead to the introduction of mud crab aquaculture to supply increased demand and large crabs for the market (Mwaluma, 2002; Mirera, 2009; Mirera and Mtile, 2009; Mirera, 2011).

The value of mud crabs in the market has increased from 1990 to 2010 (Fig. 7b). Even with the stagnant production experienced between 2000 and 2010, the value has constantly increased possibly as a result of diversification in market outlets for the product. Such increment in value may trigger entry into the fishery, which may increase fishing effort that may have negative impacts on available stocks. Indeed increased demand from the local tourism industry and export markets has been observed to increase mud crab fishing effort in East Africa (Barnes et al., 2002; Mirera, 2011). Thus the increased production between 1995 and 2000 may have over-exploited large crabs for the market leading to the decline in sizes caught. However, the observed mud crab production statistics may not be reliable due to limitations in compliance to landing procedures, licensing and entry into the fishery.

3.6. Lessons for management

In the last half a decade, a co-management approach was adopted in Kenya to support management of marine fisheries by establishment of Beach Management Units (BMU). BMUs are community-based organizations (CBOs) comprised of fisheries resource users at landing sites. They are given powers through the Regulations issued in a gazette notice in 2007. In liaison with the fisheries department (FiD), they help to implement Fisheries Legislation by controlling activities at landing beaches, elimination of non-legalized fishing gear and promotion of responsible fishing. Despite the fact that BMUs are working well, their mandates have not been fully achieved due to limited capacity to create awareness and provide surveillance. To date, they lack capacity to track down artisanal mud crab fishers since they do not land or operate in designated landing sites. To reach mud crab fishers, therefore, requires extra resources, time and incentives for patrol and awareness creation. It is, therefore, necessary to ensure active involvement of experienced/knowledgeable artisanal mud crab fishers in BMU management structure to facilitate support for the process and help to unlock potential of the fishery through knowledge and information sharing and awareness creation (Steel et al., 2005; Laurens, 2012).

Management of the crab fishery is a mandate of the Fisheries Department under the Fisheries Act CAP 378 of the Laws of Kenya. The Act allows FiD to implement the legislation through issuance of fishing licences, monitoring of landings and compliance with respect to fishing techniques. This implies that all artisanal mud crab fishers need registration on an annual basis and should land catches in designated landing sites. However, currently most fishers operate without a fishing licence nor do they land in designated landing sites, thus crab production estimates are taken at market outlets which tend to under-estimate the fishery potential (Mirera, 2011). The fact is that management of the mud crab fishery is complex since current policies are not responsive to underlying challenges, a fact noted by Ludwig et al. (1993). This may be the reason why managers are not able to effectively implement the legislation for artisanal mud crab fishery in Kenya. Therefore, a modern manager needs to navigate the issues of effective management in the system “Man–Nature–Society” to be able to develop a strategic management matrix (Perfilova and Alizade, 2012).

While residents of coastal areas consume mud crabs locally to a less extent, they are mostly produced for the tourist and export market. Market for mud crabs is readily available in major towns such as Malindi and Mombasa in addition to tourism sites such as Watamu and Diani on the coast of Kenya, especially during the peak tourism season. This has provided an opportunity for investment in production of mud crabs (wild capture and aquaculture) to meet the high demand experienced during the peak tourism season, therefore, creating employment for the coastal fisher population.

Crab fisher's sale the catch to local traders who in turn sale to the second tier of traders often from distant markets such as Malindi or Mombasa. One distinct feature of the market chain is the existence of unwritten arrangements between crab fishers and the first tier of traders/middlemen to prevent traders from distant markets from undercutting local traders. Traders from distant markets can only buy crabs from middlemen. Such an arrangement forms a stronger basis for evaluating profitability of the fishery while providing information to advise policy formulation in relation to management of the emerging fisheries (Ochiewo et al., 2010).

Advancements in communications technology and mobile phone money transfer have further improved transactions in the mud crab market chain. Most mud crab traders from the distant

markets place orders via mobile phone or email and settle transactions through mobile phone money transfer or Western Union in case of export. Crabs are then loaded into public transport ('matatu' or bus or aeroplane), for delivery of the consignment to respective destinations. This implies that mud crab fishery is developing fast through local and export markets and, therefore, there is need for policies to regulate the fishery.

4. Conclusion

Mangrove crabs (mud crabs) are associated with mangrove ecosystems throughout their range and form an important source of food and income for local communities. As mentioned, considerable effort has been made to understand the biology, recruitment, growth and ecology of mangrove crabs. However, little effort has been made to understand the traditional knowledge used by fishers to exploit the resource and how such information can help to restructure management of the fishery. Therefore, the paper serves as a useful reference and encourages active involvement of experienced/knowledgeable artisanal mud crab fishers in co-management. It also highlights that a modern manager must navigate the issues of effective management in the system "Man–Nature–Society" on development of a strategic management matrix.

It is important to tap into the indigenous knowledge that drives mud crab fishery and use it in management of the fishery. It was observed that indigenous knowledge held by artisanal mud crab fishers enable them to identify at a glance a crab that has just moulted or one that is preparing to moult or is older than the others. Such knowledge could be used to ensure sustainable harvesting of crabs, improve catch quality and minimize wasteful harvesting.

Most artisanal fishers are unaware that holding crabs for a long period lead to loss of wet weight, which is an important determinant of price in the market. Therefore awareness programs should be designed to sensitize the fishers of the need to take catches to the market quickly. Also the awareness programs could promote preservation and dissemination of indigenous knowledge on sustainable mud crab harvesting.

The study also established that more than 60% of the crab fisher's fish in mangrove burrows using traditional gear and the rest use other methods along the forefront mangrove edge and channels at low tides. This provides insight into the fishing patterns, which is one of the parameters that should be considered in making fisheries management decisions.

Acknowledgement

Appreciation is to the different donors who funded collection of data that has been used to develop this paper: WIOMSA-MASMA program and IFS. Kenya Marine and Fisheries Research Institute (KMFRRI) and Linnaeus University (Sweden) also provided logistical and technical support for the research and we are grateful for this assistance. Also our special appreciation is to the artisanal fishers, key informants, field guides and all the community members who participated in the research.

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PAPER VI:

Organised community groups in mud crab aquaculture



Social and economic implications of small-scale mud crab (*Scylla serrata*) aquaculture: The case of organized community groups

David Oersted Mirera^{1,2}, Jacob Ochiewo¹ and Fridah Munyi¹

¹*Kenya Marine and Fisheries Research Institute (KMFRI), Box 81651, Mombasa, Kenya*

²*Linnaeus University (LNU), 391 82 Kalmar, Sweden*

Mobile: +254-722646270/ +46737242346

Email: dimirera@yahoo.com, dmirera@kmfri.co.ke, david.oersted.mirera@lnu.se

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Abstract

Small-scale mud crab aquaculture was introduced in East Africa in late 1990s as a mangrove friendly aquaculture to improve the livelihood of coastal communities through organised community groups. The organised community groups approach was a strategy aimed at ensuring benefits to the village and regulating access to the open access resource (land in mangrove forests). Social, structural, policy and economic assessments were conducted at Majaoni, Makongeni, Ihaleni and Dabaso along the Kenyan coast. The paper looks at the social characteristics of the groups, their management systems, contribution of mud crab aquaculture to the livelihoods of local communities and policy issues related to the interventions. There is wider involvement of the mijikenda community who are mostly Muslim (80 %) in mud crab farming however the level of women participation is low. A strong market link exists between the groups and the different market outlets, where hotels and exporters offer the highest prices. Regional price variations existed and may need networking between the groups. The paper concludes that national policies may need to be redirected to support small-scale aquaculture development and ensuring capacity building for women, operation and management of groups, provision of extension services, data management and provision of user rights for communities working in the mangrove environment.

Key words: Aquaculture; community based; mud crab; small-scale; social, policy

Introduction

The future of capture fisheries production in tropical countries is challenged by increasing demand for resources combined with the effects of global climate change thus on the declining trend (Francis and Bryceson, 2001; Cheung et al. 2010; Worm and Branch 2012; Mirera et al., 2013). Indeed most of the tropical countries are socio-economically vulnerable and thus need to develop adaptive strategies to cope with climate change and declining fisheries. Small-scale aquaculture development is one of the adaptations due to its positive contribution to the welfare of communities in developing countries (Ahmed and Lorica, 2002). Globally, small-scale aquacultures are seen to be fundamental for the livelihood, welfare and food security of some of the poorest communities in third world countries (Brummett and Williams, 2000). In addition, it has the ability to act as a buffer for excess labour in the community and turn it into meaningful production (Bene, 2005). However, this has not been achieved in Africa since aquaculture has developed only recently and has so far made only small contribution to economic development and food security (Brummett and Williams, 2000). Whereas, past development initiatives have failed to achieve sustainability due to lack of fish farming culture in addition to political, social and policy constraints, technological progress in aquaculture has been observed to be a powerful method to alleviate poverty, improve financial situations, and enhance social wellbeing in many developing countries (Jiang, 2010).

Mud crab culture was initiated along the coast of Kenya as a small-scale community intervention that could act as a source of food and income to the local communities through the silvofisheries technology (Primavera et al., 2000; Mirera, 2009, 2011b). The intervention could also meet the increased demand from tourism, export and promote conservation of the degrading mangrove ecosystem through the silvofisheries technology (Mwaluma, 2002; Mirera and Mtile, 2009; Mirera, 2009, 2011b). The industry for the production and consumption of aquatic crustaceans is truly globalised, with separation of net producer and net consumer nations requiring significant transboundary movement of live animals (Bondad-Reantaso et al., 2012). Initial culture methods targeted sub-adult crabs of 150-350 g for culture to market size (>0.5 kg) in drive-in (bottom fixed) cages and pens (Mwaluma, 2002; Mirera, 2009, Mirera and Mtile, 2009). However, recently methods are being developed to culture small juveniles in earthen ponds (i.e. grow-out farming), which will attain market size in about 10 months (Mirera, 2011; Mirera and Moksnes **Paper IV**).

Significantly, technological advancement, changes in information and communications and globalization all underscore the need for developing countries to improve food security of low-income people (Pinstrup-Andersen, 1999). Hence, the reason why cereals and crop supply perspectives of food security has currently changed to include products such as fish e.g. the economic stimulus program of the Kenyan government, which was implemented through the ministry of fisheries development from 2009 (Ahmed et al., 1999; Delgado et al., 1999; Ndanga et al., 2013). Consequently, aquaculture is increasingly being recognised as the generator of food and income for households. Although it is not the main source of income, it

makes an important contribution to the income and food of households in rural settings (Ahmed and Lorica, 2002; Shelley, 2008; Mirera and Ngugi, 2009; Ndanga et al., 2013).

There are a lot of similarities between small-scale fisheries and small-scale aquaculture in that both are scattered and unorganised thus making them difficult to monitor. Also, communities carrying out small-scale activities consist of the rural poor who in most cases face social and political marginalization (Pauly, 1997). In addition, they exist in data poor conditions which makes it difficult to capture both socio-economic contributions leading to their under valuation and un-appreciation by policy makers in many countries (Gillet and Lightfoot, 2002; Andrew et al., 2007). In Kenya and other countries of East Africa, the situation is more worrying along the coastline due to the social, policy and cultural constraints that have slowed the pace of mariculture development as opposed to other areas where freshwater aquaculture has progressed (Brummett and Williams, 2000; Mirera and Ngugi, 2009; Mirera, 2011a&b; Mirera et al., 2013; Ndanga et al., 2013). Indeed African mariculture development is small and only reached 779, 433.6 metric tons in 2010, which is about 1.3% of the world aquaculture production (FAO, 2012). Small-scale community based mud crab aquaculture may be a potential livelihood option for coastal communities in East Africa, and has been introduced through several development, research and conservations programs in the region (Mwaluma, 2002; ACDI/VOCA, 2005; Mirera and Samoilys, 2008; Mirera, 2009, 2011b). In order to manage small-scale mud crab aquaculture to contribute to coastal livelihoods, it is necessary to understand the magnitude and extent of their social, structural, policy and economic dynamics since to date such information is missing in East Africa. Thus the study objective is to provide information on the role of organised community groups (OCGs) in mud crab culture, social acceptability and contribution to the livelihood of coastal communities.

In essence, small-scale aquaculture involves production systems operated by smallholding farmers, using locally available feeds and farming organisms that are easy to culture whose seeds are readily available (Mirera and Samoilys, 2008; Mirera and Ngugi, 2009). Investment is in form of land, water and labour and in most cases production is for home consumption however, at times little cash is involved (Brummett and Williams, 2000). For small-scale aquaculture to be effective it requires enabling policies that support acquisition of these basic investment facilities. Indeed, equitable and fairer access to resources utilized for aquaculture is an important policy issue. Thus the study provides information on the policy factors affecting adoption of small-scale mud crab culture and its impact on the poor coastal communities.

Materials and methods

Survey design

The research involved four organized community groups along the Kenyan coast which had some experience in mud crab culture i.e. were involved in mud crab culture or had previously participated in mud crab culture as a livelihood intervention (Figure 1). The community groups selected for the study were: Dabaso, Ihaleni, Majaoni and Makongeni. To assess the

social, cultural, policy and economic dimensions, the groups were drawn from the south (1 group) and north coast (3 groups) of the Kenya coast and had been in operation for different time periods (Table 1).

Sampling design

Semi-structured interviews, focus group discussions (FGD) and key informant interviews were used to collect primary information from the community groups. The semi structured interviews (Bunce et al. 2000; de la Torre-Castro et al. 2007) used interview guides (open-ended questions) that were prepared beforehand to gather information on the social, cultural and economic perspectives of small-scale mud crab farming in addition to challenges, weaknesses and opportunities of the group. Focus group discussions (Bunce et al. 2000; de la Torre-Castro et al. 2007) were used with open-ended questions to prompt participants into free discussions on the mud crab culture issues. This also created room for two-way interactions and exchange of information between the interviewer and the respondent. Members who participated in focus group discussions were randomly selected in a group meeting to avoid bias in representation. Participants in a focus group discussion ranged between 5 and 10 and two focus group discussions were conducted per group. Representation of officials, ordinary members, gender and age was taken into consideration.

Key-informant interviews (Bunce et al. 2000, de la Torre-Castro et al. 2007) were also conducted for the groups. These are knowledgeable people in society who command some respect and could be taken as spokes persons of the community, in addition they had a good understanding of the group activities. Key informants were however, not group members to avoid biased assessment. Snowball method was used to identify key informants in villages where the groups operated. Information provided through this method provided a lot of insight on many issues on attitudes and perceptions of the community towards small-scale mud crab farming and the group itself. The method was used to cross check and validate information collected using focus group discussions.

All focus group discussions were done at or near mud crab culture sites. Thus direct observation was used to assess the cohesiveness of the group and to ascertain existence of activities on the ground.

Data analysis

Since FGDs were mainly used to collect information from the field, data analysis was done descriptively using content analysis whereby the main themes and sub-themes emerging from the field notes were identified and examined. Quantitative and qualitative data were analysed using descriptive statistics and graphics and presented in narratives, tables and graphs. With the help of Graph Pad Prism 6 program graphical data was explored.

Results and discussion

Group dynamics and characteristics

The groups were formed at different time periods ranging from 2 years ago to 12 years ago (Table 1) thus comprising of different levels of experience though with a common goal of attaining a livelihood out of mud crab farming. The entry of new groups into mud crab farming as late as 2 years ago supports the fact that aquaculture development is increasingly being recognised as a source of food and income to rural households or the existence of a desperate need for alternative sources of food and income (Ahmed and Lorica, 2002; Ndanga et al., 2013). Membership is drawn from the wider mijikenda community whose majority are Muslim (80 %). Majaoni youth development had the highest diversity of mijikenda tribes (Table 2).

Dabaso and Ihaleni groups developed as conservation community groups while Majaoni youth development and Makongeni, baraka were self-help groups. Although later, Makongeni, baraka self-help changed its name to attract donor funds. Non-conservation groups were self-initiated to help address common challenges in their communities like unemployment and poverty while conservation groups were spearheaded by local non-governmental organisations (NGOs) to execute funded projects. Researchers and or NGOs introduced small-scale mud crab farming to the groups as a mangrove friendly aquaculture that can promote conservation and improve livelihoods (Primavera, 2006). The respondents elucidated that, because of their existence and influence, active conservation community groups were often targeted for getting involved in the mud crab farming interventions.

Two groups had more than 30% women representation, which is the minimum threshold according to the current national constitution for Kenya while the others had under representation (Table 2). Other than Makongeni, baraka conservation that had a woman as chairperson and treasurer, all other groups had men in all administrative positions with women existing only as members. The study showed varied levels of formal education in the groups: in Majaoni youth development 80 % of the members had attained education above secondary school, 60 % in Dabaso conservation, 5 % in Makongeni, baraka conservation and 20 % for Ihaleni conservation. Most of the community members with formal education beyond secondary and up to college level were men; women contributed only 1 % and youth comprised 80 % of the educated population. The observed gender disparities in level of education suggests that there is a constraint in access to education for women at the coast of Kenya which may be a major contributor to their marginalization in decision-making (Ndanga et al., 2013). Lack of education and training for women has also been observed in Southeast Asia, where women have assumed a critical role in aquaculture development (Nash, 1995; Ahmed and Lorica, 2002).

Membership was observed to decrease overtime and Majaoni youth development had the greatest change compared to the others while Ihaleni and Makongeni, baraka conservation had the least decline (Figure 2). The faster decline in Majaoni was associated to the youthful population that sort for jobs and moved from the village in addition to conflicts among members. Ihaleni was considered to be relatively new in mud crab culture interventions and

thus may have less experience in aspects related to group management and group fall-out. The stability of Makongeni, baraka conservation was linked to the high percentage of women 80 % which is a positive indication of resilience in aquaculture development. The study by Ndanga et al. (2013) established that women have a greater opportunity in aquaculture developed through participation as fish farmers or marketers. The current study associated the decline of membership to a number of factors i.e. the length of time taken to realise financial benefits, and thus diversion to personal activities, the nature of work (tedious and dirty) discouraged others, group conflicts and some especially men looked at it as a female activity or for those who cannot go fishing.

To attain viability, the groups were involved in other activities like milkfish farming, eco-tourism, mangrove nursery establishment and running of mangrove restaurants (Table 2). The groups also engaged in other livelihood activities like; artisanal fishing, peasant agriculture, beekeeping, fish trade, tourism and farm forestry among others. Indeed Ahmed and Lorica (2002) argued that even though aquaculture is being recognised as a generator of income, it is necessarily not the main source of income. Consequently, Bene (2005) found that small-scale aquaculture alone may not be able to lift farmers out of poverty, but can help to sustain livelihoods and prevent households from falling deep into deprivation.

Management, operational structure and capacity

It was clear that the groups lacked capacity to manage the funds transparently, effectively and efficiently, which could lead to poor management of group resources and mistrust among members. By appreciating that these communities consist of the rural poor who face social and political marginalization (Pauly, 1997), it is necessary to develop policy intervention to ensure that training is provided in management.

Results from focus group discussions indicated that groups with less training in mud crab culture experienced high mortalities in their culture systems (sometimes more than 60 %) over a culture period of 3 months, which lead to loss of hope among group members. Specifically the mortalities were linked to poor handling, poor construction of culture structures leading to cannibalism or escape, inadequate feeding or feeding at the wrong times and theft especially in the initial stages. Past aquaculture development initiatives may have failed due lack of a farming culture in Africa (Brummett and Williams, 2000), therefore it is important to empower farmers with the most recent technologies in aquaculture to minimise poverty, improve financial situation and enhance social welfare (Jiang, 2010). Government extension support was indicated as weak in the current study in all groups whereas it has been known to be key in adoption of technologies (Lionberger and Gwin, 1991). In addition to developing appropriate policies for provision of extension services, it is important to have simple culture manuals developed in all local languages (Kiswahili and English) to facilitate adoption of technology especially to the less literate that are significant in the current study (Mirera and Samoilys, 2008).

Community groups operated under a constitution that outlined their operations, terms of

office, elections, meetings, contributions, membership, activities and penalties. Only one group had its constitution written in the local language, Kiswahili, while the other three were in English. Other than Majaoni youth development and Dabaso conservation where most members understood their constitution, members in other groups were not aware of the contents nor was there an understanding of how it is used to run the day to day activities or as a benefit sharing tool. It is thus important for groups to involve all members in collective decision making through understanding the constitution for promotion of unity even though at times collective decisions may be minimized (Katz 1961). Therefore a risk was observed where constitutions could be developed only as tools for registration and not for group management. Coupled with the high illiteracy level among members, this may be a conduit to exploit the weak and poor among the groups by few elites, a fact supported by Kent, (1976) who established that technological knowhow could be used against the less privileged in society (the poor).

Most members were dissatisfied with their democratic rights of electing office bearers despite many years of operations. There exist consistent conflicts associated with election of office bearers that have weakened groups like Majaoni youth development due to selfish interests and desire to remain in office. Additionally, the legal avenue to solve disputes is limited and lacks clear management systems to monitor performance by groups. Whereas the government has provided guidelines on registration and renewal of license, conversely there exist no guidelines to monitor operations. Therefore exists a policy gap which need to be addressed to strengthen the organizational nature of small-scale mud crab farming through OCGs which occur in poor rural areas that face social and political marginalization (Pauly, 1997). Unlike in small-scale fisheries, if well empowered, OCGs will help to capture the economic and social contribution of mud crab farming that may be currently under valued or un-appreciated (Andrew et al., 2007).

Social and cultural aspects

There were variations in experience, skills and understanding of mud crab farming among the different communities. The livelihood contribution of mud crab farming compared to other mariculture related interventions is different between communities. However, all communities showed interest to learn about grow-out farming technology that could involve culture of juvenile crabs in ponds as a new technology in the region (Mirera and Moksnes, **Paper IV**). More than 70 % of the respondents indicated that culture of juvenile crabs in earthen ponds could be more viable. This could therefore supplement crab fattening because the seeds are abundant and labour requirement is low during the culture process but more training was required to equip the farmers with the required skills. This will involve simplification of mariculture technology for adoption by coastal communities that has been a call by most of the communities interested in small-scale mariculture development along the East Africa coast (Mirera and Samoily, 2008).

The respondents concurred that the involvement of women in mud crab farming was initially (about one decade ago) impacted by religious and social norms among the coastal

communities. But due to economic challenges and declining fishery resources the women are slowly being allowed to participate in livelihood interventions related to marine resources like mariculture, a fact that has been underscored by different studies in the region and outside (Nash, 1995; Ahmed and Lorica, 2002; Ndanga et al., 2013).

Negative attitudes from other community members were experienced when mud crab farming was first introduced. There were conspiracies that lead to theft of farmed crabs either a few days after stocking or a few days before harvest. In some instances theft was planned and executed from within the group members especially when harvesting was near, a fact that was associated with lack of effective benefit sharing mechanism and management of group conflicts. Due to the general community involvement and as an awareness creation strategy, it became a challenge to handle theft cases through police arrests since it could lead to social instability. To avert the situation more time was spent in community meetings “*Baraza*” to explain the need for respecting the interventions in addition to putting guards on site. Theft is an act of poverty, food instability and labour redundancy that could all be addressed through small-scale mud crab farming that has the capacity to serve as a buffer for the excess labour in the community (Bene, 2005). Mud crab farming may also produce a series of backward linkages such as hatcheries, nurseries, seed collectors, feed and input deliveries and forward linkages such as harvesting, post-harvest handling and marketing that will absorb community labour and create income for all community members (Lewis et al., 1993, 1996).

In addition, there were also conflicts on usage of culture sites: The fishers feared loss of their fishing routes and grounds. Landowners became jealous of the interventions and claimed ownership of the areas that are managed by the government under the law. This scenario underscores the importance of awareness creation when introducing any small-scale mariculture intervention and the need for appropriate policies to safeguard the interventions. Also it is a challenge for small-scale interventions that may not directly benefit all stakeholders especially when implemented in “free access” areas like the mangrove ecosystems or open sea. Globally, access to resources utilized for aquaculture like water and land (pond) has been a major policy issue and in essence it helps to determine who benefits from aquaculture (Ahmed et al., 1993; Lewis, 1998; Ndanga et al., 2013). Its also evident that in areas where landless and poor people may be holding ponds and sections of water bodies through lease or other arrangements, the rich owners will always exert claims over them once profitability is attained (Lewis, 1998).

Most mud crab farms have been on and off due to lack of financial and expertise support. In addition, farms were initiated as pilots and thus relatively small (holding 50 – 150 crabs at once) in capacity to meet group needs. Due to lack of funds or credit facilities, farms have remained small in 50 % of the groups while communities that had up-scaled their culture (holding 250 – 450 crabs at once) farms are able to meet some basic needs from farm proceeds; thus more expansion appear to be needed for economic sustainability. However, recent analyses show that the economic gains in scaling-up cage farms are limited due to the labour intensive maintenance of the cages (Moksnes et al. **Paper VII**). The issues of limited

credit facilities to facilitated small-scale aquaculture interventions have been highlighted also in Ndanga et al. (2013) for freshwater aquaculture in Kenya. Indeed even though the government of Kenya through the economic stimulus program provided a subsidy for small-scale farmers that was not sufficient and only supported freshwater aquaculture (Anon, 2010; Ndanga et al., 2013). Hence there is a special need for policy direction to make available credit facilities for small-scale farmers to increase production capacity.

It was also observed that exaggerated publicity of profitability is at times made in the media to meet donor demands that have reduced the morale of most group members over time. Other factors associated with temporal closure of farms include; weak management structures of the groups and internal conflicts, seasonality of market, lack of seeds for stocking and repair of culture facilities. In addition, profitability of farming mud crabs in cages over several moults is low (ACDI/VOCA. 2005), particularly when including the high labour requirement (Moksnes et al. **Paper VII**).

Initial mud crab farming interventions were not received well by the Kenya Forest Service (KFS) that holds the mandate of protecting all mangrove forests in the country. Even though most groups were initially involved in mangrove conservation, a lot of resistance was experienced when establishing culture farms due the need for maintaining ecosystem integrity. This continues to be a major drawback to development of small-scale mud crab farming. However, the situation has improved through the Kenya Forest Act of 2007 that introduced participatory management of the mangrove forests (co-management) where user groups like small-scale mud crab farmers were allowed. But the bottleneck to the new strategy is the aspect of user groups making payments for activities carried out in the mangrove environment. The introduction of forest user levies may put out small-scale mud crab farmers who have nurtured the technology over time and give way to the rich who are able to pay levies. This will bring about commercial productions for higher profitability of the few rich but at the expense of the environment and livelihoods of coastal communities (Lewis, 1998; Ahmed and Lorica, 2002; Primavera, 2006).

Economic and livelihood dimension

Out of the four communities along the coast of Kenya, only two have an active mud crab farming activity. However, the communities consider mariculture as a viable alternative livelihood option to fishing households due to declining catch and sizes caught from their traditional fishing grounds (Primavera, 2006; Primavera et al., 2010; Mirera, 2011b; Worm and Branch, 2012; Mirera et al., 2013). Thus crab farming could act as a new way of maximizing the value of crabs in the domestic and export markets, and it is integrated easily because it complements or adds value to the artisanal mud crab fishery (Mirera, 2011b; Bondad-Reantaso et al., 2012). Drive-in cage and floating cages are the main culture systems used in mud crab farming along the Kenyan coast although pond culture has ben introduced experimentally recently (Table 3; **Paper IV**). The systems are constructed using locally available materials, in addition, easily and less expensive to construct. All the culture systems are run in small-scale and extensively by group members

According to the groups, mud crab culture is viewed to have a multi-dimensional approach towards addressing poverty reduction and food security. Other than food supply and income provision to the members, small-scale mud crab culture provides employment and conserves the mangrove environment that has multiple values for the coastal communities. Figure 3 provides a detailed view of the connectivity encompassing the benefits originating from small-scale mud crab culture along the Kenyan coast. It has been established that to reduce vulnerability of coastal artisanal fishing communities and their coastal support ecosystems, alternative livelihoods like small-scale mud crab culture are able to aid in sustaining coastal peoples' income and food supply (Giasuddin and Alam, 1991; Kador, 1991; Primavera et al., 2000, 2010; Primavera, 2006; Mirera, 2009, 2011b).

Communities have developed a market link to supply tourist hotels in addition to other market avenues like middle agents, domestic homes, exporters, group mangrove restaurants and respective households. Prices varied greatly for the different market outlets and among the groups (Table 4). Regional variability in prices offered for mud crabs within the same country has also been observed in other studies mainly being guided by size and accessibility to markets (ACIDI/VOCA, 2005; Richmond et al., 2006; Petersen et al., 2011; Moksnes et al., **Paper VII**), however, current variations may not be associated with size variation since all cultured crabs are of similar sizes and thus other factors may have influenced the price variations. Ndanga et al., (2013) also realised that prices of farmed fish varied between regions and associated it to urbanisation or production capacity. Highest prices were attained when crabs were sold at individual mangrove restaurants but the market was noted to be seasonal and only available at Dabaso conservation group. Hotels and exporters provided second level prices and middlemen and domestic homes offered the lowest prices. Other than Dabaso conservation, all the other groups did not attach any price tag to what was consumed at the respective households. Despite the variations, the prices found in this study were similar to those observed by Moksnes et al. (**Paper VII**) in Kenya for both wild and cultured mud crabs but vary from those recorded by Mirera (2011b) in some aspects like export markets which could be associated to lack of exposure by most groups to the outlet. Subsequently, price variations in mud crabs may be affected by demand and supply and could also be an aspect of societal status based on the market outlets established in the current study and as documented by Mirera (2011b). However, the prices obtained in the current study are similar to what is being offered for farmed crabs in Southeast Asia (Cholik, 1999; Trino et al., 1999). Despite the fact that the price of mud crabs is almost double, that of finfish, which is an incentive for mud crab farming, there is a need to develop policies that will protect farmers from unfair competition for profitability (Mirera and Samoilys, 2008).

Initial mud crab culture interventions involved use of sub-adult and earlier adult crabs that were not market size for culture into the required market sizes i.e. above 500g (Mirera, 2009, 2011b). It was difficult for the farmers to collect these from the wild thus relied on buying from fishers. This approach proved expensive and time wasting due to unavailability of required sizes and thus a constraint to the expansion of crab farming. However, recent interventions where juveniles are cultured in ponds may be a viable approach that could

ensure sustainability because seeds are abundant and accessibility of collection areas is easy in addition to high growth in ponds (Moksnes et al., **Paper I, II; Mirera and Moksnes, Paper IV**). The pond culture system supplemented by cage fattening may help to attain constant supply of the mud crabs to the market. Pond culture has been observed to be viable in culture of small juvenile mud crabs into market size (300-450 g) for a period of 4-6 months in Asia-pacific and viable profits obtained (Trino et al., 1999; Rodriguez, et al., 2001, 2007; Christensen et al., 2004; Petersen et al., 2011). Even though in the current study no cost benefit analysis was done to establish viability of the small-scale mud crab culture because of lack of organized data with the groups nor was data submitted to the fisheries department thus an indication of groups operating in data poor conditions as had also been established by Gillet and Lightfoot (2002). Currently, only Dabaso and Ihaleni conservation groups obtain more than 50 % of their incomes from mud crab farming (Table 5). With the new intervention of pond culture the groups anticipated to gain more from small-scale crab culture compared to other mariculture related activities. However, in the long-term policies and investment approaches need to be developed to ensure hatchery systems are established for constant seed supply and or for restocking wild stocks (Le Vay, et al., 2008; Lebata et al., 2009; Mirera and Samoilys, 2008) to avoid the negative impacts of aquaculture observed elsewhere (Keenan, 1999; Fortes, 1999).

However, in a recent analysis where all the realistic costs were considered in mud crab culture, the cage, pen and pond culture systems had relatively low survival to support profitability (Mirera and Moksnes, **Paper IV**; Moksnes et al, **Paper VII**). A low profit margin was obtained in drive-in cages due to the labour intensive work of daily maintenance of the cultures, but partly also due to low growth rates in these types of farms. Excluding the labour cost, the resulting profit was equivalent to 45 % of the average salary in coastal communities in Kenya, for the hours spent at the farm. In Tanzania where prices for mud crab are lower, the profit was equivalent to only 6 % of the average salary (Moksnes et al. **Paper VII**). Farming small juvenile crabs in ponds show a better profit margin, but high mortality rates in pond and pen farms is a problem that needs to be solved before this method could be profitable (Mirera and Moksnes **Paper IV**, Moksnes et al. **Paper VII**).

Overall, the respondents felt that small-scale mud crab culture has the potential to enable them attain a livelihood since most of the population stays idle the whole day or week at times. In addition, promote management, restoration and conservation of the mangrove forest. They were also categorical that once sustainable benefits are attained membership fluctuation may be minimised. Through the multiplier effect the surrounding communities could also benefit from either produced resources, change in expenditure, established business or improved fish resources or mangrove poles from a well managed mangrove ecosystem (Kairo et al., 2001; Shelley, 2008; Shelley, 2008; Mirera et al., 2010; Mirera, 2011b; Ndanga et al., 2013). Successful establishment of small-scale mud crab culture was also seen as an avenue for other income generating activities like eco-tourism noted in some groups thus providing good market for their products.

Conclusion

The results show that small-scale community based mud crab farming has the potential of improving the welfare of coastal communities, although there is need to improve growth, survival to attain profitability in crabs farms. Community groups spearheading the interventions have realised initial benefits and have a vision of helping their communities out of poverty. Clear market outlets have been established under the organisation capacity of community groups and prices offered for farmers are good but can be improved and harmonised for the different regions by strengthening the networks to provide competitive bargaining power. Even better prices for mud crabs have been attained by communities through establishment of their own restaurants, an aspect that is worth encouraging through appropriate policy structures to attain sustainability. Also through involvement of men, women and youth in the community, redundant labour was well utilised.

Also challenges were evident that may hinder development of small-scale community based aquaculture development under the umbrella of community groups. Whereas the organisational capacity is paramount, transparency and accountability was seen to be weak in most community groups. Therefore policies should be directed towards ensuring that community groups after registration are accountable for their actions, proper conflict resolutions mechanism are in place, the constitution is understood by all and constitutional democracy is promoted within groups. Other policy issues that may need to be addressed include community user rights in the mangrove environment and payment of levy to the Kenya forest service (KFS) by user groups.

Deliberate effort should be made to empower communities with management and technical skills. Most of the groups expressed high levels of illiteracy especially women that hinder aquaculture operations. Indeed even records (data) were poorly kept and in some instances missing which made it difficult to evaluate the economic viability of the interventions. Empowerment of OCGs should also involve ability to follow laid down objectives with minimal drifting towards donor demands as observed in the present study.

In order to build a reliable database and establish trends in small-scale mud crab culture, there is need to make it mandatory for licensed groups to provide data on production to the fisheries department. Further, proper arrangements and policy need to be developed to allow various market outlets keep data on the sources of crabs bought and prices offered to help address issues of farmed crab consumption.

Acknowledgement

The authors are indebted to Western Indian Ocean Marine Science Association (WIOMSA) through the Marine Science for Management (MASMA) that funded part of this work and Kwetu training centre through the Toyota environmental grant program. Special appreciation

is extended to Kenya Marine and Fisheries Research Institute (KMFRI) and Linnaeus University (LNU) for the provision of necessary support to carry out the study and develop the write-up. We also wish to thank colleagues and members of the organised community groups (OCGS) that were involved in this study.

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List of Tables

Table 1. Description of the different community groups in relation to their administrative areas and year of initiation.

Name of Community Group	Village	Location	County	Year of Initiation
Majaoni youth development (<i>Mtwapa creek</i>)	Majaoni	Bamburi	Mombasa	2003
Ihaleni conservation (<i>Kilifi creek</i>)	Ihaleni	Mavueni, Takaungu	Kilifi	2011
Makongeni, Baraka conservation (<i>Gazi bay</i>)	Makongeni	Kinondo	Kwale	2004
Dabaso mangrove conservation (<i>Mida creek</i>)	Dabaso	Watamu	Kilifi	2000

Table 2. Dynamics of the community groups involved in small-scale mud crab culture along the coast of Kenya and type of intervention for income generation

Name of Community Group	Community Integration	Percentage of Women	Percentage of Men	Group Interventions Generating Funds
Majaoni youth development	Kauma Chonyi Giriama Digo	23%	77%	Milkfish farming Mangrove nursery
Ihaleni conservation	Giriama Kauma	35%	65%	Mud crab and milkfish farming
Makongeni, baraka conservation	Digo Duruma	80%	20%	Milkfish and mud crab farming
Dabaso mangrove conservation	Giriama Watha	43%	57%	Mud crab farming Mangrove restaurant Eco-tourism

Table 3: Mud crab culture systems and methods used by the community groups operating at the Kenyan coast.

Name of Community Group	Systems	Methods
Majaoni youth development	Drive-in cages and ponds	Extensive
Ihaleni conservation	Drive-in, floating cages and ponds	Extensive
Makongeni, baraka conservation	Drive-in, floating cages and ponds	Extensive
Dabaso mangrove conservation	Drive-in and floating cages	Extensive

Table 4. Market outlets and price (USD) offered for farmed crabs in the different study sites along the coast of Kenya.

Name Community Group	Middle agents	Hotels	Domestic homes	Exporters	Subsistence consumption	Owned restaurant
Majaoni youth development	2.4-2.9	2.9-4.1	1.8-2.4	3.5-5.9	not costed	-
Ihaleni conservation	1.8-3.5	3.3-4.1	-	-	not costed	-
Makongeni, baraka conservation	2.4-4.1	4.5-5.3	-	-	not costed	-
Dabaso mangrove conservation	-	4.7-5.9	-	-	3.5-4.7	9.4-11.8

*1USD = 85 Kshs

Table 5. Percentage of income derived from mud crab culture compared to other mariculture related activities for each community group

Name of Community Group	Mud crab	Milkfish/ prawns	Fingerlings (milkfish)	Eco-tourism	Seedlings (mangrove)
Majaoni youth development	5%	60%	-	-	35%
Ihaleni conservation	51%	49%	-	-	5%
Makongeni, baraka conservation	7%	55%	38%	-	-
Dabaso mangrove conservation	70%	-	-	30%	-

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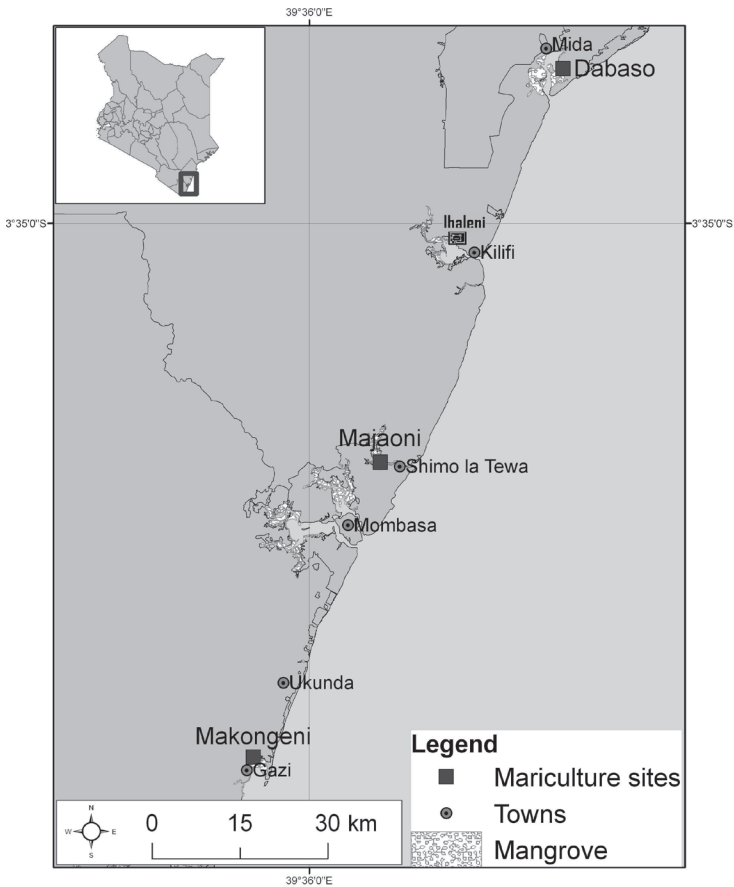


Figure 1: Map with details of the different community groups undertaking small-scale mud crab aquaculture along the coast of Kenya.

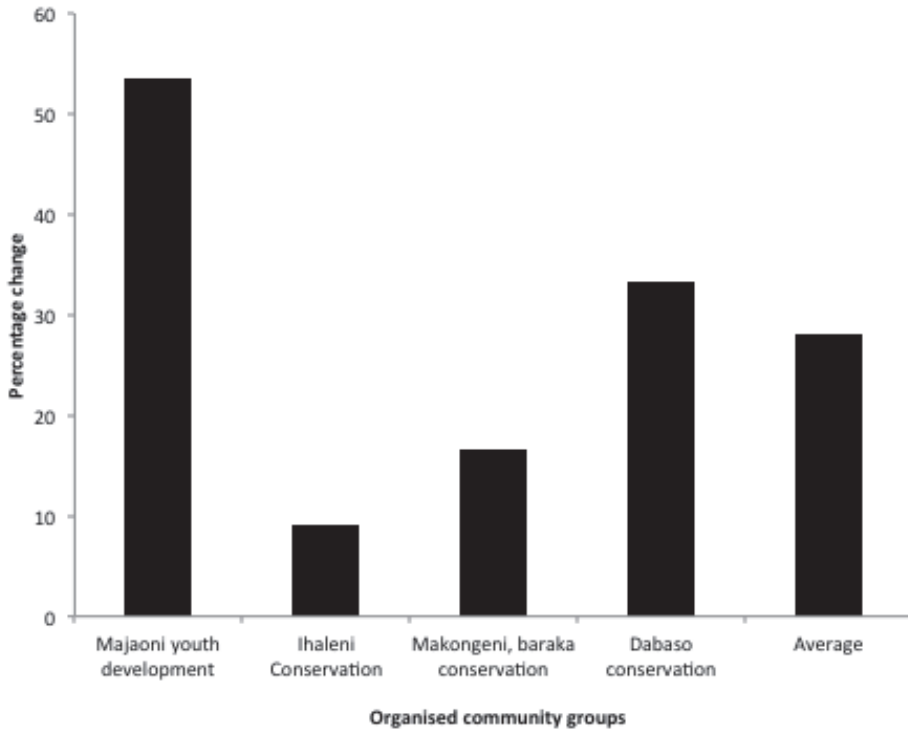


Figure 2: Percentage change in membership number among the different organised community groups assessed from initiation to current (2013).

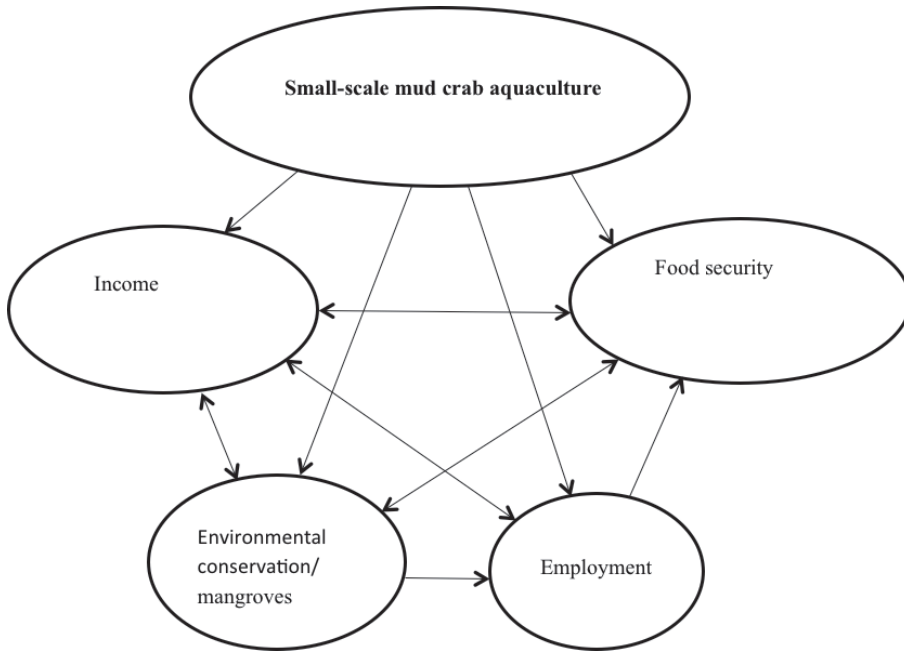


Figure 3: Framework for small-scale mud crab aquaculture showing linkages to the socio-economic welfare of coastal communities in Kenya as elucidated by the community groups. The size of the circles shows the significance attached to the different socio-economic pillars

PAPER VII:

Sustainability of small-scale mud crab aquaculture



Economic and environmental performance of small-scale aquaculture of mud crab *Scylla serrata* in East Africa

Per-Olav Moksnes¹, David Mirera², Razack Lokina³, Jacob Ochiewo², Humphrey Mahudi⁴, Narriman Jiddawi⁵, Muumin Hamad⁵, Max Troell⁶

¹Department of Marine Ecology, University of Gothenburg, Sweden

²Kenya Marine and Fisheries Research Institute (KMFRI), Mombasa, Kenya

³Department of Economics, University of Dar es Salaam, Tanzania

⁴Mafia Island Marine Park (MIMP), Tanzania

⁵Institute of Marine Sciences, Zanzibar, University of Dar es Salaam, Tanzania

⁶Beijer Institute, KVA and Stockholm Resilience Centre, Stockholm University, Sweden

Manuscript

Abstract

Small-scale farming of mud crabs (*Scylla serrata*) has been suggested as a possible source of alternative income for resource poor coastal communities in East Africa. These cultures depend on collection of seed and feed resources from the local mangrove ecosystems, and it is unclear if they would be ecologically sustainable if expanded to larger scales. In addition, it is unclear if the present culture methods constitute profitable activities. Here we assess the profitability of two culture methods: (1) farming large crabs in fixed cages (i.e. crab fattening) and (2) farming small juvenile crabs in ponds or pens (i.e. grow-out culture) in Kenya and Tanzania using cost-revenue analyses based on realistic growth rates of crabs, and on realistic inclusive costs (e.g. accounting for labor costs) and prices obtained through culture studies and market surveys in East Africa. In addition we also analyze the economy of scale of the culture systems, and assess how seed and feed resources may limit the maximum size of a sustainable aquaculture in coastal communities.

Market analyses showed that the common market size of crabs in East Africa (500-1000 g) was larger than in Southeast Asia (300 g), that prices for mud crabs were over 50% lower in Tanzania than in other East African countries, and that most of the profit in all countries appeared to go to middlemen and exporters. Cost-revenue analyses of crab-fattening cultures showed negative results in both countries even at large scales when the high cost of labor was included. Excluding the labor cost, the resulting profit was equivalent to only 6% and 45% of the average salary in coastal communities in Tanzania and Kenya, respectively, for the hours labored at the farm. Taking into account also the low survival and growth rates of crabs in this type of culture, the results suggest that crab fattening does not constitute a sustainable or profitable alternative livelihood for coastal communities in its present form.

Grow-out cultures of small juvenile mud crabs showed a better potential to develop into a profitable and sustainable activity. Cost-revenue analyses demonstrated a positive return of the investment if prices above \$US 3.4 per kg are obtained, which is achievable in Kenya and Mozambique, but difficult in Tanzania today. Analyses showed that it would be more profitable to farm smaller commercial crabs, and developing a market for 300 g crabs would be one way to increase the profitability of crab farming in East Africa. Increasing the size of the culture also increased the

profitability, however, the availability of small seed-crabs and local feed sources that are not used for human consumption limit the size of mud crab farms in a coastal community to approximately 500 commercial crabs that can be produced sustainably per year. Thus, the present constraints of sustainable sources of seed-crabs and feed will limit grow-out farming to a small-scale activity. Moreover, before crab farming can become a profitable alternative income to coastal communities in East Africa, survival rates in grow-out cultures need to be improved, and market conditions and profits to local crab farmers enhanced.

Key words: Sustainability, livelihoods, cost-revenue, grow-out farming, crab-fattening, pond

INTRODUCTION

The populations in coastal areas in East Africa have increased dramatically in the last decades, contributing to increased pressure and degradation of coastal resources. Examples are declining fish catches, deteriorating conditions of coral reefs and reduction of mangroves (Francis & Bryceson 2001, van der Elst et al. 2005). Various management responses are being undertaken to halt the deterioration of coastal resources, including restriction on fishing and extraction (e.g. MPAs), introduction of community based management practices and regulation of harvest practices. However, these measures, in combination with decreasing coastal resources, increase the need for additional livelihoods for the large number of impoverished people that directly depend on coastal resources for their survival. Due to unproductive soils for agriculture, coastal residents usually have few alternative livelihood options, and intensified competition for coastal resources increase conflicts between stakeholders within the increasingly crowded coastal zone (Hecht 2006). In the last decade, small-scale farming of mud crabs has been suggested as a viable alternative income for resource poor coastal communities in East Africa (ACDI/VOCA 2005, Shipton & Hecht 2007, Mirera 2009).

Mud crabs (*Scylla* spp.) are large portunid crabs that inhabit coastal mangrove habitats in the Indian Ocean. Four species of mud crabs are recognized (*S. serrata*, *S. paramamosain*, *S. tranquebarica* and *S. olivacea*), but only one species (*S. serrata*) is found in East Africa (Keenan et al. 1998). All mud crab species have good taste and generate high prices on domestic and international markets, and are fished by artisanal and commercial fishermen throughout the region. The unique ability of mud crabs to stay alive out of water for 4-5 days enables transport from remote coastal areas to national and international markets without the need of cooling (Keenan 2003).

Mud crabs survive and grow well in captivity and they have for the last 40 years been successfully farmed through-out Southeast Asia and Southern China. In Southeast Asia, there are two basic forms of mud crab aquaculture: 'fattening' of adult crabs with a low meat content, and 'grow-out' of juveniles to market size. Fattening is primarily conducted in ponds or small bamboo enclosures placed in the intertidal, where adult crabs with low meat content (and low market value) are fed for a short period (>1 month) to gain weight and higher market price. Generally, the fattening is completed prior to molting since mortality otherwise reduces production (Keenan 2003). Grow-out farming of crabs is usually carried out in intertidal ponds or pens (net-fence systems) with or without mangroves, where juvenile crabs (10-100 g) are farmed through several molts until they reach market size. High growth rates have been reported from Asia for all systems, with production of commercial-sized crabs (200-400 g) 3-6 months after stocking with seed crabs (Keenan 2003, Shelley and Lovatelli 2011).

Aquaculture of mud crabs in Asia consist of both small-scale farms and large industrial system of >100 hectares (Trino & Rodriguez 2002, Keenan 2003, Shelley and Lovatelli 2011). Because of an increasing demand for mud crabs, the aquaculture industry has expanded very rapidly in the last 10 years and In 2011 global production reached 158 000 tons (at value of US\$ 459 millions), with most of the production taking place in China (FAO 2013). For example, in Myanmar, the second largest crab producer, farming is performed in intensive mode with floating cages (up to a million cages in just one farm) where all seed crabs originate from wild caught. The rapid

expansion has been possible due to a increasing market for soft-shell crabs in Asia, ready access to feed fish and vast areas of mangroves providing a steady supply of juvenile crabs, although seed supply now seems to be decreasing (Nicolini 2013). The mud crab farms through-out Asia have historically been based on collection of wild seed crabs, but an unmet demand for mud crabs has led to over-exploitation of both adult and juvenile seed crabs, and decreasing stocks in many countries (Keenan 2003). Difficulties with obtaining wild caught juveniles for farming operations, plus concerns of further over-exploitation, have led to development of larval hatchery techniques, and today e.g. both Vietnam and China have industrial production of juvenile seed crabs for *S. serrata* and *S. paramamosain* (Shelley and Lovatelli 2011).

With the increasing industrial production of mud crabs based on seed crabs from hatcheries, feed is perceived as the next major bottleneck to mud crab aquaculture. Formulated diets to replace 'trash fish' are being developed but still the demand for low valued fish resources is high (Shelley and Lovatelli 2011).

Parallel with the development of industrial scale mud crab farming, the development of more extensive farming methods has also continued. In the Philippines and Malaysia, such technologies have been transferred to resource-poor fishing villages for adoption as sustainable alternative livelihoods. These are low investment small-scale grow-out farms in ponds or pens located within natural mangrove habitats and designed to maintain the integrity of the mangrove ecosystem. These farms show high survival and growth rates of crabs, with a high cost return (Wei Say & Ikhwanuddin 1999, Trino & Rodriguez 2002).

Aquaculture of mud crabs in East Africa.

East Africa has substantial populations of mud crabs (*S. serrata*) that are fished mainly by artisanal fishermen using traditional capture methods such as hook, sticks, traps, and seine nets (Muthiga 1986, Mirera et al. 2013). This fishery is minor in comparison to Southeast Asia, but the local demand for mud crabs is increasing, as well as experiencing an increasing demand from the Asian market (ASCI-VOCA 2005, Shipton & Hetch 2007, Mirera 2011). The fishery is unregulated and there are indications that some local crab populations in Tanzania have decreased significantly as a result of increased fishing effort (Francis & Bryceson 2001, Mahika et al. 2005, Mirera et al. 2013).

In contrast to Southeast Asia, there is little tradition of aquaculture in East Africa, and especially marine farming is still in its infancy (Bryceson 2002, Troell et al. 2011). Research on mud crab farming was initiated in Kenya in the late 1990s assessing the use of mangrove pens, but with limited success (Mwaluma 2002). Recent studies have assessed different methods for crab culture with the aim of involving local communities as a participatory management tool for mangrove forests (Mirera 2009, Mirera & Mtile 2009). These cultures are based on collection of wild seed crabs as, to our knowledge, no larval hatcheries of mud crabs exist in East Africa today.

In the last decades, developmental projects have been undertaken by various NGOs and research institutions in East Africa to develop small-scale crab farming in local communities, e.g. in Tanga, Rufiji, Kilwa, Mtwara and Mafia in Tanzania, and in the Mombasa, Kilifi, Kwale and Malindi area in Kenya (Shipton & Hetch 2007, Mirera 2011). These projects have all focused on a method referred to as 'crab-fattening' that use small (0.30 x 0.30 m) individual cages with lids, built of local material (usually mangrove sticks or bamboo), that are placed in the intertidal zone within the

mangroves, without cutting any trees. The cages are stocked with subadult crabs (one 150-300 g crab per cage) collected from the wild and farmed through several molts (many months) until they reach 500-1000 g. These 'extended' crab fattening farms are presented as an alternative source of income for the local communities where the crabs are sold as a cash crop to local hotels or middlemen for export markets (ACDI-VOCA 2005, Mahika et al. 2005, Shipton & Hecht 2007).

These initiatives are all in a more or less developmental stage, and only negligible quantities of mud crabs are today produced in Tanzania and Kenya (Shipton & Hecht 2007). Still, as interest is growing for this activity the development of mud crab farming may now be at a critical cross-road. A demand-driven rapid expansion of crab-fattening could result in overexploitation of seed-crabs with subsequent collapse of local mud crab stocks, and negative ecological and social impacts, similar to the situation in several Southeast Asian countries (Allan & Fielder 2004). A lack of fishery data and basic information of the ecology of small juvenile mud crabs in East Africa make it difficult to assess sustainable limits for a seed-crab fishery. Moreover, the present crab fattening in East Africa relies to a large extent on mangrove snails (*Terebralia palustris*) as a feed resources, which are also consumed by some segment of coastal communities, and there is a potential risk that an expansion of the aquaculture may have negative effects on human local food sources (Hamad 2012). There is therefore a need to assess if alternative feed-sources, not used for human consumption, could be used to support an expansion of mud crab aquaculture.

Importantly, farming crabs in cages for extended periods may not be the best aquaculture method for a sustainable development of mud crab farming in East Africa. Recent studies suggest that growth in these culture systems is low compared to natural growth of *S. serrata* in East Africa (Moksnes et al. **Paper II**), and that the mortality rates in the cultures may be higher than what the crabs experience in nature (Moksnes et al. **Paper I**). Moreover, it is also unclear if this farming system is sustainable from an economic perspective. A value-chain and profitability analysis of crab fattening in the Tanga region, Tanzania showed that farmers could not make a net-profit due to low prices, and suggested that the farms need to increase in size to increase profitability (ACDI-VOCA 2005). In contrast, profitability analyses of an experimental crab-fattening system in Kenya showed a high return of capital investment (Mirera et al. 2009). However, the cost of labor in maintaining crab fattening farms were not included in these analyses, and it is therefore not clear if this activity is rational from an economic perspective.

Grow-out aquaculture of mud crabs using small juvenile crabs (<10 g) in pond or pen systems may constitute an alternative culture method with a better chance to become sustainable in East Africa from both an ecological and economical context. Small-scale pond and pen systems in Southeast Asia show high survival and growth rates with high profitability (Trino & Rodriguez 2002). Recent field studies in East Africa demonstrate that small juvenile seed-crabs can be efficiently collected along mangrove fringes (Moksnes et al. **Paper I**), and studies of grow-out culture methods in pond and pen-systems in Kenya show high growth rates (Mirera & Moksnes **Paper IV**). However, it is not clear if this form of aquaculture could constitute a profitable activity since cost-revenue analyses are missing, and it is unclear how prices of mud crabs varies between different markets and countries in East Africa. It is also not clear if and how the profitability in crab-fattening and grow-out systems will increase with scale, and how seed-crabs and feed limits the maximum scale of a sustainable farm in a coastal community since analyses are lacking.

Here we assess the profitability of small-scale aquaculture of mud crabs in extended crab-fattening and grow-out systems in Kenya and Tanzania using cost-revenue analyses based on realistic growth rates of crabs, and on realistic costs (including labor costs) and prices in the two countries obtained through culture studies and market surveys in East Africa. Specific aims of the study was (1) to compare the profitability and identify the major costs in the two culture systems, (2) to assess how prices and profitability differ between markets and countries, (3) assess how the market size of the crab affect profitability in grow-out cultures, and (4) to assess the economy of scale in the two systems, and how seed and feed resources may limit the maximum size of a sustainable aquaculture in coastal communities.

MATERIAL AND METHODS

The present study was part of a larger research project financed by MASMA-WIOMSA to assess if small-scale aquaculture of mud crabs could be develop into a sustainable alternative livelihood for coastal communities in East Africa. Using a multidisciplinary approach, we carried out parallel field studies and surveys in Kenya and Tanzania to assess opportunities and constraints of this activity from both an ecological and economic context.

Markets and prices for mud crabs

To assess markets and price ranges available to mud crab farmers in East Africa, informal interview were carried out with crab fishermen, crab fattening farmers, middlemen, exporters, market salesmen and hotels in Mombasa and Malindi area in Kenya, in Dar es Salaam, Mafia and Zanzibar in Tanzania, and in Maputo in Mozambique. The prices were compared to earlier studies in East Africa and South East Asia obtained from the literature.

Cost-revenue analyses of grow-out farming and crab fattening in East Africa

To compare the cost and profit margins of grow-out and fattening cultures of mud crabs in Kenya and Tanzania, cost-revenue analyses were carried out. All cost estimates were based on data from experimental crab-fattening studies in Mtwapa Creek, north of Mombasa, Kenya 2005 (Mirera 2009) and from experimental grow-out pond studies in Mtwapa Creek (Mirera & Moksnes **Paper IV**) and on Mafia Island, Tanzania (H. Mahudi unpubl. data) in 2010-2011. We used realistic estimates of all costs, including the high initial construction costs of the pond, and cost of all labor (e.g., collection of seed crabs, daily feeding, repairs, guards to prevent theft of larger crabs, etc.) so that this activity could be compared to other established income generating activities. The labor times for construction and maintenance have been standardized between the two countries to make them comparable, whereas local cost for material were used. The material and labor costs were approximately 30% higher in Kenya than in Tanzania (see Appendix 1 for a detailed description and explanation of the different cost).

Because existing studies of mud crab culture in East Africa did not raise crabs to commercial size, we used a von Bertalanffy growth function of natural growth of *S. serrata* in East Africa

$$L_t = 310 * (1 - e^{-0.57 * (t - 0.019)})$$

where L_t is the size (carapace width) at time (t) since settlement (Moksnes et al. **Paper II**) to estimate the growth period to commercial size (500 g) for different sizes of seed crabs. In grow-out pond cultures, the growth rate is very similar to the modeled growth (99%; Mirera & Moksnes **Paper IV**), whereas in crab-fattening cultures the growth rate has been found to be substantially lower (on average 39% of the modeled growth; Moksnes et al. **Paper II**). To partly adjust for this difference, we used a growth rate in fattening cultures that was approximately 75% of the modeled growth, simulating an improvement of the present growing conditions with approximately 50%. The same growth-rates were used in both countries.

In both culture systems, the mortality rate was assumed to be 10% month⁻¹. This mortality rate is similar to what is obtained in mud crab cultures in Southeast Asia (Baliao et al. 1999, Trino et al 1999, Trino & Rodrigues 2002), but lower than what has yet been achieved in East Africa, where the mortality rate ranges from on average 20–60% month⁻¹ in different culture systems (Mwaluma 2002, Mirera 2009, Mirera & Mtile 2009, Mirera & Moksnes **Paper IV**). Thus, it is important to note that the cost-revenue analyses assumed a substantial improvement of survival rates in the cultures.

In the analysis, we compared the total cost to produce 450 commercially sized crabs (i.e. 500 g) with the two culture methods (growth-out culture in ponds and crab fattening in cages). The number of crabs was chosen to be larger than most existing small-scale operations in East Africa (to allow some economy of scale), but within sustainable levels of seed crabs and feed that could be obtained in a coastal community with access to mangrove ecosystems (see below).

For the grow-out culture, the estimates were based on farming 0.5 and 2.0 g small juvenile seed crabs, stocked at approximately 5 crabs m⁻² in 15x15 m earthen ponds, and farmed for 11.6 and 10.9 months, in Tanzania and Kenya, respectively. The difference in culture periods was due to smaller seed crabs dominating on Mafia Island (on average 15 mm CW) compared to Mtwapa Creek in Kenya (on average 24 mm CW; Moksnes et al. **Paper I**). Slightly higher stocking densities were used in Tanzania (5.2 crabs m⁻²) to compensate for the longer growth period. Crabs were harvested at 500 g at a density of 2 crabs m⁻². For the crab-fattening cultures, the estimates were based on 3 consecutive 3-month culture periods, growing 300 g seed crabs in cages with about 200 individual compartments (see Appendix 1 for detailed description of the culture methods).

The revenue of the cultures was estimated based on the prices obtainable for market sized mud crabs (>500 g) at local tourist hotels on Mafia Island and Dar es Salaam, Tanzania (2.5 \$US per kg) and the average hotel price in the Mombasa area, Kenya (5.4 \$US per kg; Table 1)

Effect of market size of crabs on costs in grow-out farms

A major difference between the Southeast Asian market, and the market in East Africa, in particular with Tanzania, is that smaller mud crabs (300 g) obtain good prices in the former market (Table 1). Because the intermolt period increases exponentially with the size of a mud crab (Moksnes et al. **Paper II**), and larger crabs need more feed than smaller crabs, the cost and the need for feed increase exponentially for each additional molt that the crab must pass through. Because the risk of theft is high mainly for commercial size crabs, the cost of preventing theft (e.g. night guard) take a larger proportion of the total culture cost the longer the

commercial sized crabs are kept in the farm. Thus, it may be more profitable to harvest and sell crabs smaller than the present market size in Tanzania (>500 g).

To assess how the cost may change with size of the crabs at harvest, we estimated the total number of seed crabs and the total amount of feed required (using a feeding-rate of 10% of the biomass of crabs per day), and the total cost of seed crabs, feed and theft prevention (employing a night guard one month before the crabs reach 300 g and thereafter) to produce 100 kg of mud crabs harvested at either 300, 500, 700 or 1000 g body weight, using the same methods as in the cost-revenue analyses (Appendix 1). In these analyses, we used seed crabs of 15 mm CW, an average mortality of 10% per month, and a 10x10 m pond for all size-classes, resulting in a stocking densities between 4 and 7 crabs m⁻² for the 4 size-classes (assuming no density-dependent mortality) to achieve the same total production of crabs.

Economy and sustainability of scale for grow-out pond farms

One possibly way to increase the profitability of crab cultures would be to increase the size of the culture system since the cost per produced crab may decrease with the scale of the operation (i.e. economy of scale). For example, if the size of a pond increases from 10x10 m to 20x20 m, the area of the pond (and available space for crabs) increases with 400%, whereas the circumference (and the cost of building a wall and fence) only increases with 200%, and the cost of transportation and distributing feed in the pond increase very little. However, for crab cultures based on collection of wild seed-crabs and local feed sources there are issues of sustainability if the farms are too large due to limitations of the local ecosystem (i.e. mangrove forest for placing the farm and for extraction of feed and seed resources). To assess these questions, we assess the economy of scale of a grow-out pond farm on Mafia Island in Tanzania, and how feed and seed resources limits the maximum size and the profitability of a sustainable farm. Mafia Island was chosen as an example since empiric data on seed and feed limitations are available (Nyqvist 2010, Hamad 2012).

The total amount of seed crabs and feed required, and the cost and revenue was estimated for grow-out pond farms ranging from 50 to 500 m² in size, using the same methods as in the cost-revenue analyses (Table 2, Appendix 1). The cost per crabs was assumed to decrease in larger ponds due to: (1) no increase in cost for tools and pipes for the pond construction, (2) no increase in labor costs of daily transportation of feed and feeding, and guarding the farm from theft, (3) only partial increase in the cost of building the fence around the pond and (4) in the labor cost in collecting and preparing of the feed (both costs were assumed to increase with area of the pond as the circumference increases with the area ($y = 4x^{0.5}$; where y is the circumference and x is the area). The labor cost of digging the pond and levies, and harvesting the crabs were assumed to increase proportionally with the area of the pond (i.e. no gains in scaling). We assessed two price-scenarios, \$US 2.5 and 5.0, representing the high end of prices offer by hotels at Mafia Island and in Dar es Salaam, respectively (Table 1).

Based on a field survey of alternative feed sources for mud crabs that were not used for human consumption on Mafia Island, it was estimated that approximately 20 kg of different feed sources (fish offal, maize bran and non-consumed dried anchovies remains) should be available per day in an average village on Mafia Island, assuming that a total of 10 kg of maize bran and unwanted dried anchovies could be collected from 5 households and 5 kiosks in the village, and that 10 kg fish offals could be collected at the village landing site for fisherman every day (Hamad 2012). These

resources were in this analysis assumed available for free but there could as well exist competing alternative usages. Based on an impact study of the collection of small juvenile mud crabs on Mafia Island, it was estimated that no more than 1200 small juvenile seed crabs could be fished from the same local area without negative effects on the local population (Nyqvist 2010).

No attempt was made to analyze the economy of scale of crab-fattening cultures because the cost-revenue analysis showed that the cost per crab decreased very little with the size of the culture system. This was due to the fact that the crabs were kept in individual cages that had to be constructed, repaired and open and closed at each feeding for each crab. Only the cost of theft protection and tools decreased with the size of the cage culture.

RESULTS

Markets and prices for mud crabs

In all markets, the best prices were obtained for live crabs, full of meat with both chelipeds (claws) intact. The market size and prices for mud crabs showed large variation both within and between countries and regions (Table 1). The commercial market size in Tanzania and Kenya (500-1000 g in most areas) are substantially higher than the general market size in Southeast Asia (150-400 g). Still, the price ranges per kg in Southeast Asia (US\$ 3.0-13.6 kg⁻¹), most of which were based on information >10 years old, was similar to the highest prices presently found in East Africa (i.e. in Kenya; Table 1), indicating higher profit margins in Southeast Asia. In Kenya, there are indications that market size have decreased in the last decade, as good prices were obtained also for 250-500 g crabs today. In contrast, the market size in Tanzania is still large (>500 g), and the prices (US\$ 0.8-7.0) are several times lower than in the other countries. A large variation was also found within the country. In northern Tanzania, in the Tanga region, the middlemen demanded large sizes (700-1000 g) and paid low prices (US\$ 0.8-1.4, ACIDI/VOCA 2005) whereas middlemen in southern Tanzania (Rufiji) accepted smaller crabs (500 g) at similar prices (Richmond et al. 2006). Hotels in Tanzania offered in general higher prices for crabs (US\$ 1.3-5.2) than did middlemen, and appeared to be more flexible in accepting also smaller crabs (300-500 g). In Kenya, the prices offered by middlemen and hotels were more similar (US\$ 2.9-6.5), and on average twice as high as in Tanzania. Highest prices in both Tanzania and Kenya were offered by exporters buying large, live crabs (700-1000 g) for the Asian market (Table 1). In Tanzania, there is also a small market for frozen crabs that are exported for the European market. This market accept smaller crabs (350-700 g), but the prices are lower (US\$ 3.0; Richmond et al. 2006).

In Maputo, Mozambique, mud crabs are an important ingredient in traditional dishes, and mainly sold on the local market, and the market size is smaller than in other East African countries (200-400 g) Still, the present prices on the local markets in Maputo are almost two times higher than in Tanzania (Table 2). In both Tanzania and Kenya, different sources gave very different information regarding size classes and prices for the same market section, indicating an unstructured and dynamic market.

Cost-revenue analyses of grow-out farming and crab fattening in East Africa

From a cost perspective, the two culture methods differ strongly in amount of initial investment, and the amount of labor needed during the growth period (Table 2). For ponds, a large initial investment is needed for the construction of the pond, including tools and labor, and the material costs are high, in particular for the net fence around the pond to prevent crabs from escaping. In the first year, the total cost for the construction of a 15 x 15 m pond is estimated to be \$US 998 in Tanzania and \$US 1051 in Kenya (not including the costs of supervision). The larger costs in Kenya was due to the approximately 30% higher prices of material and labor in Kenya. Since the pond with levees are expected to last for approximately 10 years (with minor yearly repairs), only the net fence needs to be replaced yearly the following 9 years. To estimate the total cost per 11-month growth cycle and harvest, the investment cost in the pond was split with the number of years that the construction, tools and material were expected to last. This resulted in a yearly investment cost of \$US 289 and \$US 360, and a total cost per harvest (including all cost) of \$US 773 and \$US 989 in Tanzania and Kenya, respectively, to grow 450 small juvenile seed crabs to commercial size (Table 2). The construction costs represented 36-37% of the total cost per harvest, whereas the costs of daily labor maintaining the culture (on average 2.4 h per day) constituted approximately 41-42% in both countries. Since theft of crabs appears to constitute a major problem, the cost of a night watch for the last 2.5 months of the culture period was included, constituting about 12% of the total cost. Seed crab collection represented 12% and 8% of the total cost in Kenya and Tanzania, respectively.

In contrast, the cost in crab fattening involves only a smaller initial investment to construct the cages (38 and 48 \$US in material and tools, and 79 and 104 \$US in labor in Tanzania and in Kenya, respectively), but a very high labor costs per growth cycle for maintenance. The total labor costs to maintain the crabs in 200 individual cages for three 3-month growth-cycles was 1464 and 1109 \$US in Kenya and Tanzania, respectively, representing approximately 69% of the total cost per harvest. On top of this, the need of guards during the whole production cycle to prevent theft of the easily accessible crabs constitute a major cost (441 and 339 \$US in Kenya and Tanzania) constituting approximately 21% of the total cost per harvest. In comparison, the total cost per 3-cycle harvest of crabs seeds and cage construction was small (4-6% in both countries). The high labor cost in crab fattening is a result of the time consuming labor of opening and closing the lid of individual cages each day to feed, and the high amount of labor to repair the cages (in total approximately 8 h per day).

The cost-revenue analyses showed that profit margins were low in both systems, particularly in crab fattening when using realistic costs of labor. Grow-out farming showed a 226 \$US profit in Kenya in this scenario, but a net loss in Tanzania. The difference between the countries was explained by the more than 2x higher prices paid for market sized crabs in Kenya compared to Tanzania, on average, which more than compensated for 30% higher labor and material costs in Kenya (Table 2). The break-even price to make a profit in Tanzania in this scenario was \$US 3.5 kg⁻¹, which is presently only obtained when selling directly to some hotels and restaurants in Dar es Salaam and Zanzibar (Table 1), a market presently handled by middlemen. If the high initial investment cost of constructing the pond was excluded through, for example, support by e.g. a NGO or government, grow-out farming would be profitable also in Tanzania. However, the economic activity may then not be

sustainable once the funding ends and the pond needs to be reconstructed. In contrast to grow-out farming, crab fattening at this scale (450 crabs per year) showed large net losses in both Kenya and in Tanzania, mainly due to high labor cost of daily maintenance, which by itself was higher than the revenue in both countries (Table 2).

Effect of market size of crabs on costs in pond grow-out farms

The results show that the culture time varied from 9.1 month to produce 300 g crabs to 11.6 and 16.4 months to produce a 500 g and 1000 g crab, respectively. The number of seed crabs needed to produce 100 kg crabs decreased from around 700 seeds for crabs harvest at 300 g, to around 400 seeds to produce 100 kg of 1000 g crabs (Fig. 1), i.e. the higher number of small crabs needed to produce 100 kg compared to large crabs outweighed the higher total mortality during the longer culture time to produce the larger crabs compared to small crabs, at the assessed mortality rate. In contrast, the total amount of feed needed for the whole culture period increased 2.6 times with the size of the harvested crabs, from 644 kg feed to produce 100 kg of 300 g crabs, to 1668 kg feed to produce the same biomass of 1000 g crabs. Because small seed crabs are relatively inexpensive to collect, whereas collection of the large amount of feed is costly, and because the cost of theft prevention was 3 times higher for the largest crabs, the total cost per harvest increased with over 100% with the size of the produced crabs, from \$US 473 for 300 g crabs, to \$US 996 to produce 100 kg of 1000 g crabs (Fig. 1).

Economy and sustainability of scale for grow-out farms

The results show that as the size of the pond increases from 50 to 500 m², the profit in the \$US 5 price-scenario increases rapidly from minus values at a pond size of 50 m², breaking even at a pond of 133 m² (11.5 x 11.5 m), and making a profit of almost \$US 1500 at a pond size of 500 m² (Fig. 2a). At the price-scenario of \$US 2.5, the increase in profit is much slower, and the farm is not breaking-even until the pond is 365 m², making a profit of \$US 213 at the 500 m² pond size (Fig. 2a). However, as the pond increases, the total number of seed crabs needed increases from 260 to over 2600 crabs, and the total amount of required feed increases from 463 to over 4630 kg (Fig. 2b).

For crab feed, the limiting factor was assumed to be the amount of feed needed per day during the last intermolt period (2.6 months) at the end of the growth period when the crabs are largest. Based on the maximum sustainable amount of feed sources that could be obtained per day from a village on Mafia (20 kg), a maximum of approximately 770 crabs with an average size around 270 g could be fed per village. This limits the maximum size of the pond to 300 m² (Fig. 2b), which in turn limits the maximum profit at a price \$US 5 per kg to approximately \$US 650 per harvest. However, at a price of \$US 2.5, the pond is too small to give any profit (Fig. 2a).

In addition, the availability of crab-seed limits the maximum pond size further. The maximum sustainable number of seed crabs that could be collected per month (1200 crabs) limits the maximum size of a pond to approximately 230 m² (15.2 x 15.2 m) that can raise a maximum of 460 market size crabs (assuming 10% mortality per month). This in turn limit the maximum profit of the \$US 5 price-scenario to approximately \$US 374 per harvest, and prevents the aquaculture from achieving a profit if the price is \$US 2.5 per kg. At this pond size, the break-even price is \$US 3.4 per kg.

DISCUSSION

Crab-fattening in cages

In the last decades, various NGOs in East Africa have tried to develop small-scale aquaculture of mud crabs as an alternative livelihood for coastal communities. The method promoted is based on collection of subadult mud crabs (80-110 mm CW) from the wild that are farmed in individual cage-system through several molts until they reach market size (Shipton & Hetch 2007, Mirera 2011). However, recent studies suggest that this culture method has several limitations, obtaining growth rates <40 % of natural growth of *S. serrata* in East Africa (Moksnes et al. **Paper II**). In addition, the high mortality rates in these cultures (on average 19% month⁻¹; Mirera 2009, Mirera & Mtile 2009) appear to be several times higher than natural mortality for this size-class of crabs (approximately 4% month⁻¹) suggesting that the aquaculture is in fact decreasing the local production of crabs (Moksnes et al. **Paper I**). The present study add to this critique by demonstrating that these cultures also provide low profit when taking into account the cost of labor.

Although we simulated much higher growth and survival rates than what is presently obtained in these cultures (75% of natural growth and 10% mortality month⁻¹, respectively) crab fattening resulted in net losses in both Tanzania and Kenya (equivalent to a loss of \$US 323 and 272 per 3-month growth cycle of 150 crabs, respectively). The low profit was mainly due to the high cost of labor for the daily maintenance, which is time consuming because each individual cage has to be open and closed at feeding, and the need of almost daily repair. Excluding this labor cost in the cost-revenue analysis, the resulting profit is equivalent to a salary of \$US 0.28 and \$US 0.03 per hour, approximately only 45% and 6% of the average salary in coastal communities in Kenya and Tanzania, respectively. Thus, the present crab-fattening aquaculture does not appear to constitute an attractive source of income for coastal communities, at least not for persons that have other alternatives. If more realistic growth and survival rates had been used in the analyses the profit and salaries of the culture would have been even lower.

The result showing low profit of mud crab fattening differ from analyses of an experimental crab-fattening system in Kenya, which showed a high return of capital investment (Mirera et al. 2009). However, in that analysis the cost of labor for daily maintenance was not included. The present result is consistent with cost-revenue analyses from the Tanga region that also showed a net loss (ACDI/VOCA 2005). In that study it was suggested that profit would increase for larger crab fattening farms. However, in the present example we assessed farms that were many times larger than the farms presently in use in East Africa (10-100 crabs per farm; ACDI/VOCA 2005; this study), and we found that profit increased very little with the size of the fattening operation.

Taken together, the low growth, survival, and profitability of mud crabs farmed through several molts in individual cages demonstrate that this culture method does not constitute a sustainable or profitable alternative livelihood in its present form. These issues need to be solved before cage farming could be promoted to coastal communities in East Africa. The low survival rates in the cages, despite the fact that the crabs are kept separate to prevent cannibalism, indicate that the intertidal cage environment where crabs only have access to water during high tides is a poor environment for completion of the molt processes. For aquacultures requiring molts,

culture systems that allow crabs permanent access to water, such as pond or pen system, appear to perform much better.

In Southeast Asia, mud crab fattening has been described as a profitable enterprise, but it differs in an important aspect from 'fattening' operation in East Africa, i.e. crabs are only fattened for a short period of time (<1 month; Table 1), and are sold prior to molt, to decrease mortality (Keenan 2003). Mud crab fattening in East Africa could possibly become profitable if farmers adopted the same strategy, and only fattened adult crabs with low meat content for a short period of time. Studies to investigate this possibility from both practical and economical perspectives are encouraged.

Grow-out culture in ponds and pens

Grow-out aquaculture of small juvenile mud crabs in ponds or pens show a better potential to develop into a sustainable and profitable livelihood in East Africa compared to present cage farming. Recent studies demonstrate that small juvenile mud crabs can be efficiently collected at low tides with minimal negative environmental impact, and that they show high growth rates in both pond and pen cultures. However, high mortality rates in the cultures and low market price and profitability are issues that need to be resolved for this farming to be profitable in East Africa.

Progress and challenges of grow-out culture methods in East Africa

Recent studies have identified mangrove fringes and back-flats as important habitats for small juvenile mud crabs in East Africa where high numbers of small seed crabs (up to 40 crabs person⁻¹ h⁻¹) can be collected at low tide by hand with no by-catch and minimal impact on the environment (Moksnes et al. **Paper I**). Recent studies also suggest that natural mortality of small juvenile mud crabs (<20 mm CW) in East Africa is very high (>50% month⁻¹), but decreases strongly with size indicating that small juvenile stages represent a bottleneck in the life-history of mud crabs where most crabs perish due to high predation mortality ((Moksnes et al. **Paper I**). This result suggest that negative impacts of a seed crab fishery on local populations would be minimized if small juvenile stages were used as seeds, and that the aquaculture could increase the local production of crabs if survival in the culture were higher than in nature. In South East Asia, small-scale, grow-out farms of *S. serrata* using small juvenile seed crabs (12-50 mm CW) in pond- or pens obtain mortality rates <10% month⁻¹ (Baliao et al. 1999, Trino et al 1999, Trino & Rodrigues 2002), suggesting that grow-out cultures based on collection on small juveniles crabs have the potential of increasing the local production of mud crabs and be more sustainable than cultures based on collection of large crabs.

Experimental pond and pen studies in East Africa using small juvenile seed crabs show high growth rates (93-112% of natural growth rates) when shelter is provided in the cultures (Mirera & Moksnes **Paper IV**). However, mortality rates during the first 2-3 months of culture in these studies have been very high (on average 41-58% month⁻¹), likely due to high rates of cannibalism (Mirera & Moksnes **Paper IV**), a problem that needs to be resolved before the culture could be profitable. Recent studies in East Africa demonstrate that juvenile cannibalism could be minimized by separating small and large juvenile seed crabs to keep the size-ratio below 50%, and by providing shelter to the juveniles in the cultures (Mirera and Moksnes 2013, Mirera & Moksnes **Paper IV**). Studies in Southeast Asia also indicate that cannibalism is lower at lower stocking densities (Trino et al 1999, Trino & Rodriguez,

2002). Further studies assessing how mortality can be decreased in East African grow-out cultures are needed.

Profitability and sustainability of grow-out cultures in East Africa

In the Philippines, small-scale, grow-out cultures of *S. serrata* in 200 m² pens integrated in mangrove forests was found to be profitable with a high return on capital investment (49-68%) also when including cost of labor (Trino & Rodriguez, 2002). In the present cost-revenue analysis of similarly sized grow-out pond cultures (225 m²) in East Africa, simulating survival rates presently obtained in Southeast Asia (90% month⁻¹), but using growth rates, cost and market prices presently obtained in East Africa showed much smaller profit margins. At this size of the culture, a positive return of the investment could only be obtained with prices above \$US 3.4 per kg of market sized crabs, which is achievable in Kenya and Mozambique, but difficult in Tanzania today. Market analyses showed that prices for mud crabs were over 50% lower in Tanzania than in other East African countries, and that most of the profit appears to go to middlemen and exporters (Table 1).

In Southeast Asia, the market size of mud crabs (>300 g) is smaller than the size in most markets in East Africa (>500-1000 g). Still, the prices for mud crabs available to farmers in South East Asia are much higher compared to East Africa (Table 1). Thus, there appear to be room to improve the prices given to crab farmers and fishermen in East Africa, in particular in Tanzania. Studies investigating ways to develop new markets and market-chains for crab farmers to improve the prices and the profitability of the culture in East Africa are needed.

The present study showed that farming 300 g crabs, would require 25% and 75% less time, 48% and 159% less feed, resulting in 36% and 111% lower total costs compared to farming the same total biomass of 500 g and 1000 g crabs, respectively. In addition to having lower costs, the shorter culture time of farming 300 g crabs would allow more harvests in the same amount of time, and decrease the risk for unpredictable events (e.g. heat chocks, storms, theft, diseases, etc.) that may ruin the crop and profit. Thus, farming 300 g crabs would be more sustainable from a feed perspective, less risky, and possibly also more profitable than farming larger crabs, if there was a market for this size class of crabs. In Kenya, a market for smaller crabs appear to be developing as both middlemen and hotels pay high prices (US\$ 2.9-4.7) for crabs as small as 250 g, although larger crabs still obtain a higher price, particularly for the export market (Table 1). In Tanzania, most middlemen and hotels still want crabs of 500 g or larger, but some hotel are starting to accept smaller crabs because of increasing demand. There are also reports that middlemen in the Rufiji area, and exporters in Dar es Salaam are starting to show interest in 300 g crabs, particularly for the market of frozen mud crabs destined for Europe, which obtain a relatively high price (US\$ 3.0; Richmond et al. 2006). In Tanzania, the break-even price for farming 300 g crabs of 225 m² pond would be \$US 2.2 per kg, and at price of \$US 3.0 per kg the farm would make net profit of \$US 180 per 9 month cycle (assuming 10% mortality month⁻¹). Promoting a market for 300 g mud crabs in East Africa could thus be one way to assist the development of a grow-out aquaculture in the region. However, since a larger number of seed crabs are needed to farm the same biomass of 300 g crabs compared to e.g., 500 g crabs (at 10% mortality month⁻¹), the availability of seed-crabs may limit the size of a sustainable pond, and therefore its profitability. Since *S. serrata* in East Africa becomes sexually mature around 300 g (Roberson &

Kruger 1994) care must also be taken not to promote a market for even smaller crabs, that may have negative effect on wild populations if fishermen start to exploit immature crabs before they had a chance to reproduce.

Another way to increase profitability would be to increase the size of the mud crab farm. The present study showed that the profit of a grow-out farm increased rapidly with the size of the pond, making a profit of almost \$US 1500 at a pond size of 500 m² in the \$US 5 price-scenario, and breaking-even at a pond size 365 m² in the \$US 2.5 price-scenario. However, both the availability of small-juvenile seed-crabs and sustainable crab feed limit the maximum size of grow-out aquacultures in a coastal community to approximately 460 and 770 market size crabs per 11-month growth cycle, respectively, which in turn limits the maximum profit to approximately \$US 374 per harvest at the \$US 5 price-scenario, and prevents the aquaculture from achieving a profit if the price is \$US 2.5 per kg.

The sustainable limit of 1200 seed crabs per village area (ca 5 km of mangrove shore line) is a rough estimate based mark-recapture studies on Mafia Island showing limited dispersal of juveniles (Björkvik 2011) and no detectable effects on the local juvenile populations by removing ca 330 small juveniles mud crabs (5-15 mm CW) from a 50 m area of the shore during 2 weeks of intensive sampling (Nyqvist 2011). Although more studies are needed to assess the sustainable levels of seed crab fisheries in different areas of East Africa, the experience from intensive sampling of small juvenile crabs during a two year period at multiple sites in Tanzania, Kenya and in Mozambique suggest that it would be very difficult to sample more than 1000 small juvenile mud crabs (<40 mm CW) within one month, from any mangrove area in East Africa due to the low densities of juveniles (Moksnes et al. **Paper IV**, Mirera *unpublished data*). Thus, natural availability of seed-crabs put strong limitations on the scale of mud crab cultures in East Africa.

In Southeast Asia, larval hatchery techniques have been developed for several species of mud crabs for production of juvenile seed crabs to industrial scale mud crabs farms (Shelley and Lovatelli 2011). Using seed crabs from hatcheries would clearly be more sustainable than collecting wild crabs, and could be a long-term solution to meet an increasing demand for seed-crabs in East Africa. However, larval hatcheries require advanced laboratories and are sensitive operations. For example, in Australia, despite considerable efforts, larval hatcheries methods for *S. serrata* has been slow to develop (Allan & Fielder 2004). It is therefore not realistic to expect high technology hatcheries to provide a dependent and low priced supply of seed-crabs to local farmers in East Africa within the nearest future. Also if they do, cost and transportation issues may prevent its use in remote resource poor coastal communities.

Even if hatchery produced seed-crabs become available in East Africa, the availability of sustainable crab feed also limits on the maximum size of grow-out farms in coastal communities. To find acceptable and sustainable sources of feed for aquacultures is critical in many developing countries where low valued fish resources constitute important protein sources for human consumption (Funge-Smith et al. 2005, Camber 2008, Beveridge et al. 2013). Most crab fattening farms in East Africa use mangrove snails (*T. palustris*) as a feed. However, these snails are also consumed by humans, and recent field studies on Mafia Island indicate that intense collection to feed small crab fattening farms can have negative effects on local snail populations (Hamad 2012). Thus, mud crab farms using mangrove snails as feed can if performed at large

scale compete with food for humans. In the present study, we assessed how the availability of alternative crab feed resources, which are not used for human consumption, could affect the scaling up of the farming operation. In a recent study, Hamad (2012) showed that fish offal, leftover maize bran and unwanted dried anchovies remains were not consumed by humans in villages on Mafia Islands, and that these alternative feed-resources, as well as mangrove snails, resulted in high growth rates in small juvenile mud crabs. On Mafia Island, it was estimated that approximately 20 kg of these feed sources should be available per day in an average sized village (Hamad 2012), which would limit the maximum size of grow-out culture to approximately 300 m² and 770 market size crabs (500 g) per village and year, and preventing a profit at the prices presently obtainable at the island. The size of the culture and the production could possibly increase by collecting mangrove snails as a complement. However, considering the large amount needed per day, it would be very time consuming and costly, affecting the profitability, and importantly, likely not sustainable.

On Mafia Island there is a fish processing plant that produces over 100 kg of byproducts per day that could possibly be used as feed, if made available to crab farmers (Hamad 2012). If the limitation of seed-crabs was solved, villages with access to such or similar resources could possibly increase the size of the total pond area and the production of mud crabs approximately 6 times. It is important to note that also a 1800 m² pond is still very small compared to the industrial grow-out farms for mud crabs in Southeast Asia and China that are often 10-100 times larger (Table 1). Even if all available byproducts on Mafia Island were used as feed there would not be enough feed resource on the island to support a commercial farm of that scale. A commercial-scale mud crab farm would therefore result in competition for food resources with humans, unless commercial feeds or feed resources were imported. In addition, large-scale industrial mud crab farms, would likely result in clearing of mangroves and destruction of coastal environment, similar to the cases with penaeid shrimp farms (Naylor et al. 2000).

In summary, grow-out aquaculture of mud crabs show potential to develop into a sustainable alternative source of income for coastal communities in East Africa. Wild seed-crabs and local sources of feeds are available for development of sustainable small-scale grow-out systems in pond- and pen-cultures. However, before this activity is recommended there is a need to refine the technology to solve problems with high mortality rates and improve markets and market-chains to increase crab farmers' profits. Decreasing market size to 300 g crabs may be one way to improve the profit margins. For expansion of these systems at large scales, interactions with local ecosystems need to be carefully evaluated and hatcheries and compounded feeds need to be developed.

Acknowledgement

We thank the Western Indian Ocean Marine Science Association (WIOMSA), Marine Science for Management (MASMA) for funding this research through a MASMA-grant to the project entitled '*Small-scale, community-based, grow-out aquacultures of mud crabs *S. serrata* as a sustainable livelihood in East Africa.*

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Table 1. Market sizes and prices for mud crabs in Southeast Asia and East Africa. All prices are in \$US based on exchange rates 2012-01-07. References: (1) Cholik 1999, (2) Wei Say 1999, (3) Trino et al. 1999, Trino & Rodrigues 2002 (4) Johnston & Keenan 1999, (5) Cann & Shelley 1999 (6) This study, (7) Mirera 2011, (8) ACIDI/VOCA 2005, (9) Richmond et al. 2006.

Country	Seed size (g)	Seed price US\$ kg ⁻¹	Market size (g)	Price/kg US\$	Buyer	Ref
Southeast Asia						
Indonesia	350		>400	3.1 ¹	-	1
Malaysia	100	1.2	150-300	3.0	Middlemen	2
Philippines	10		>300	8.9-9.5	Middlemen	3
Vietnam	25-100	2.0-4.0	>300	8.0-12.0	Middlemen	4
Australia		0.5-2.9	-	8.7-13.6	-	5
Kenya						
Mombasa			>500	4.7-6.5	Hotels	6
			250-500	2.9	Hotels	6
			>1000	15.0	Exporter	7
			>500	8.0	Exporter	6
Malindi			>500	4.1-5.2	Middlemen	6
			250-500	2.9-4.7	Middlemen	6
Tanzania						
Tanga	250	0.5	700-1000	0.8-1.4	Middlemen	8
Rufiji	-	-	500	1.0	Middlemen	9
Mafia Island	-	-	500	1.3-2.6	Hotels	6
Zanzibar	-	-	500	3.8 ²	Restuarant	6
Dar es Salaam	-	-	500	2.5-5.1	Hotels	6
Dar es Salaam	-	-	500	1.9-3.2	Exporter	9
Dar es Salaam	-	-	700-1000	2.6-7.0	Exporter	6, 8
Mozambique						
Maputo	-	-	200	2.0-3.7 ³	Market	6
			400	3.0-5.5 ³	Market	6

¹ Price in 1994

² Market food-stands selling cooked seafood products to tourist.

³ Prices paid by customers at fish market or to private vendors

Table 2. Cost-revenue of mud crab aquaculture in East Africa. Culture data and cost-revenue estimates assessing the total cost to produce 450 commercially sized crabs (i.e. 500 g) in grow-out pond aquaculture of mud crabs (15x15 m pond) and fattening of mud crabs in drive-in cages (200 compartments) in Tanzania and Kenya. To compare profit, 9 months growth-cycles in the pond systems are compared to 3 consecutive 3-month culture periods in cage fattening system. All costs estimates per harvest cycle of 450 commercial crabs, and are in \$US. See Appendix 1 for detailed explanation of costs.

	Grow-out pond		Crab fattening	
	Tanzania	Kenya	Tanzania	Kenya
A. Culture data				
Average seed-crab size (g)	0.5	2	300	300
No. seed-crabs	1170	1100	618	618
Stocking density	5.2	4.9	-	-
Culture duration (months)	9.2	8.6	3x3	3x3
Mortality per month	10%	10%	10%	10%
Mortality per harvest	62%	59%	27%	27%
Harvest density	2.0	2.0	-	-
Harvest (no. >500 g crabs)	450	450	450	450
B. Culture costs (\$US)				
1. Culture construction	289	360	84	111
Labour costs/harvest	140	169	59	78
Material/harvest	149	191	25	33
2. Crab-seed costs	65	102	71	121
3. Daily maintenance	325	405	1109	1464
Labour costs	316	391	1107	1461
Material	9	14	2	3
4. Security against theft	94	122	339	441
TOTAL COSTS	773	989	1607	2141
C. Culture revenue (\$US)				
Harvest (kg)	225	225	245	245
Price per kg	2.5	5.4	2.5	5.4
Revenue	563	1215	638	1324
D. Harvest profit (\$US)	-211	226	-970	-816

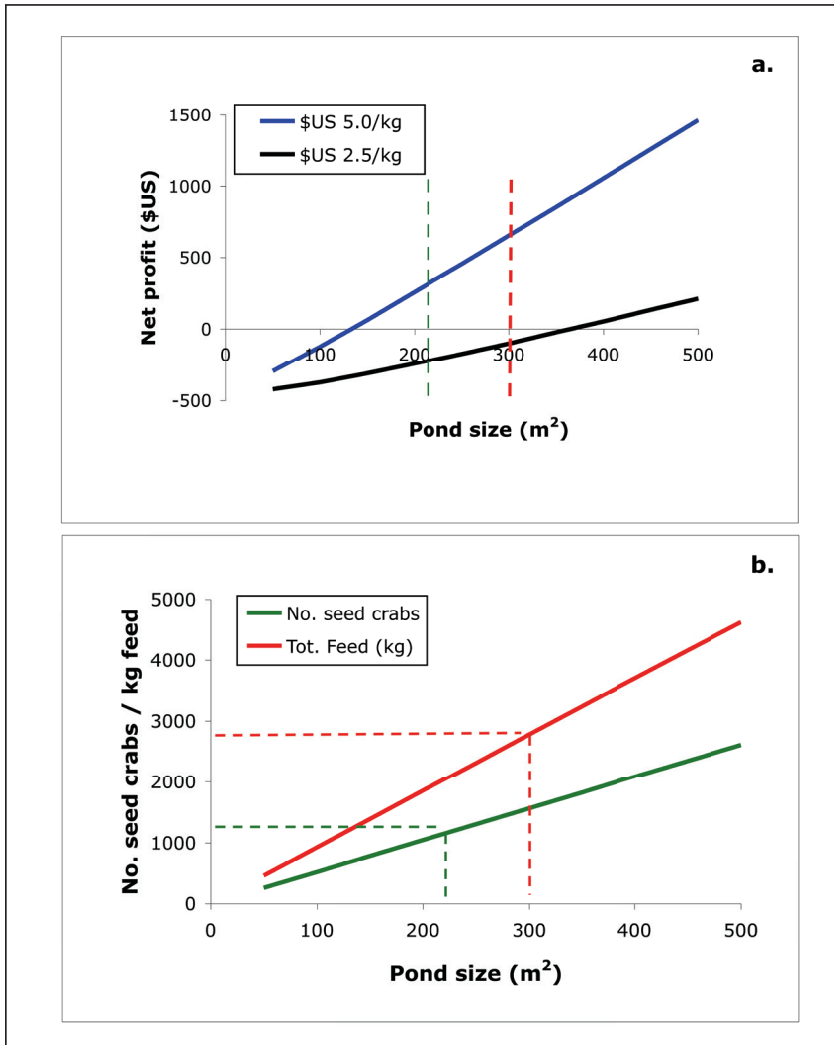


Fig. 1. *Grow-out pond culture of mud crabs.* Relationship between the size of aquaculture pond and (a) the profit of the aquaculture at two different price scenarios for 500 g crabs, and (b) the total number seed-crabs, and total amount of feed needed to produce two 500 g mud crabs m⁻². Dashed lines indicate the suggested maximum sustainable level of seed crabs and feed (green and red lines, respectively) that can be collected at an average village on Mafia Island.

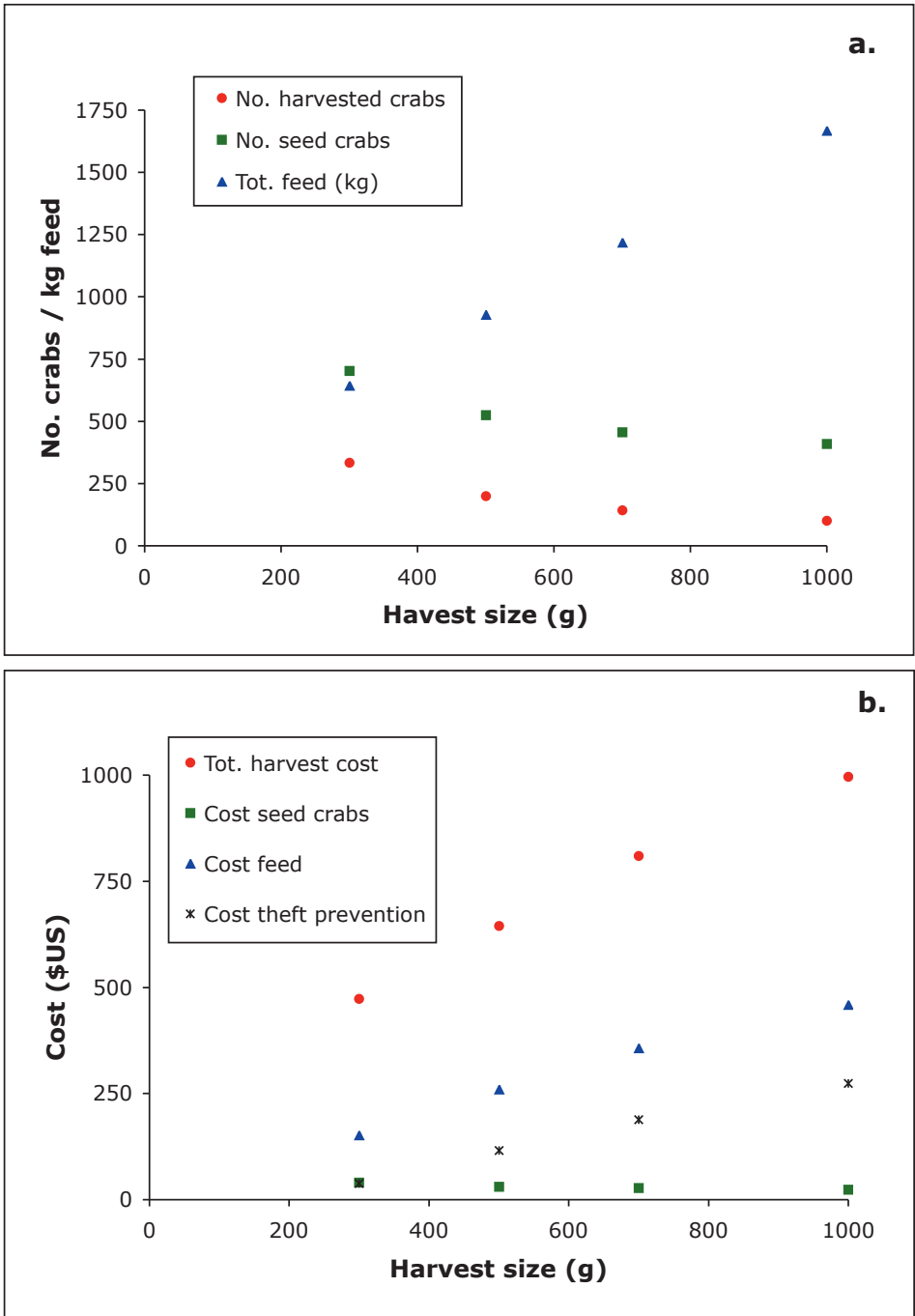


Fig. 2. *Grow-out pond culture of mud crabs.* Relationship between the size of mud crabs at harvest (300, 500, 700 and 1000 g) and (a) the total number harvested crabs, total number seed-crabs, and total amount of feed needed to produce 100 kg of mud crabs, and (b) the cost of seed crabs, feed, theft protection (night guard) and the total cost to produce 100 kg of mud crabs at different harvest size.

APPENDIX 1: COST-REVENUE ANALYSES

Explanation of costs used in the cost-benefit analyses

All cost estimates were based on data from experimental crab-fattening studies in Mtwapa Creek, Kenya 2005 (Mirera 2009) and from experimental grow-out pond cultures in Mtwapa Creek (Mirera & Moksnes **Paper IV**) and on Mafia Island, Tanzania (H. Mahudi unpubl. data) in 2010-2011. The labor times for construction and maintenance have been standardized between the two regions to make them comparable, whereas local cost for material were used. The costs used are based on constructing and maintaining a grow-out pond of 15 x 15 m size and for fattening cages of 150 compartments.

The total cost was separated into initial construction costs (labor and material) and running costs for each harvest cycle, i.e. labor and material costs associated with seed crabs, culture maintenance (e.g. including feed collection and feeding), security against theft, harvest and sale. To estimate a total cost per harvest, the initial cost of construction and material was divided with the life-expectancy of the material and construction. Conversions of currencies to US dollars were based on the exchange rate on Nov 15, 2011 (1 \$US = 1733 Tsh and 92 Ksh; www.oanda.com).

Labor costs for construction and farm maintenance were based on estimated daily salaries in coastal communities in Tanzania (5000 Tsh day⁻¹ = 2.9 \$US day⁻¹) and Kenya (350 Ksh day⁻¹ = 3.8 \$US day⁻¹). These were converted to monthly and hourly labor costs assuming a person working 6 h per day, 26 d per month. The costs of night guards were based on monthly salary of 65 000 Tsh (37 \$US) and 4500 Ksh (49 \$US) in Tanzania, and Kenya, respectively, working 8 h per day, 7 d per week. The labor costs are equivalent of approximately 30% higher labor costs in Kenya.

Prices for market size crabs (>500 g) were set at the higher end of the prices obtainable at local tourist hotels on Mafia Island, Tanzania (2.5 \$US per kg) and Mombasa, Kenya (5.4 \$US per kg)

1. Grow-out culture in ponds

Pond construction. Initial labor costs of pond constructions consisted of manual digging of the pond, building a mud levy around the pond and installing water pipes (10 persons working for a total of 10 days to build a 15 x 15 m pond). A pond was expected to last for 10 years. Yearly labor costs consisted of building a net-fence around the pond (3 persons working 2 days), and yearly maintenance and repair of the pond (10 persons working for a total of 2 days).

Material costs consisted of an initial investment in tools for the construction (17 and 22 \$US in Tanzania and Kenya, respectively), PVC-water pipes (17 and 22 \$US), mangrove poles, mosquito, plastic lining and other material for the net fence (90 and 104 \$US), and lime to kill fauna in the pond before the start of each growth cycle (4 and 3 \$US). Life expectancy was assumed to be 3-10 years for tools, 10 years PVC-pipes and 1 year for the fence material.

Seed crabs. Cost of seed crabs were based on the average number of seed crabs collected per hour during monthly sampling on Mafia Island, Tanzania (13 crabs h⁻¹), and in Mtwapa Creek, Kenya (7 crabs h⁻¹) during the higher recruitment season (April to October in Mafia; Moksnes et al. **Paper I**). On Mafia Island, where collection can

only be carried out at night (Moksnes et al. **Paper I**) a cost of flashlight and batteries was added (9 \$US per growth cycle).

Growth rates and culture duration. Growth rates in ponds were based on model estimates of natural growth rates (Moksnes et al. **Paper II**), which are similar to growth rates found in grow-out pond cultures in Kenya (Mirera & Moksnes **Paper IV**). The same growth rate was used in both countries and the crabs were farmed until they reached approximately 500 g (market size). The total durations of the cultures were estimated to 9.2 and 8.6 months in Tanzania and Kenya, respectively; the difference due to smaller seed crabs in Tanzania (on average 15 mm CW) compared to Kenya (on average 24 mm CW).

Crab densities and mortality rates. In the pond cultures, seed-crabs (10-30 mm CW) were stocked at approximately 5 crabs m^{-2} . With an estimated mortality rate of 10% $month^{-1}$ (equivalent of approximately 60% during the whole growth cycle), the density of the crabs at harvest was 2 crabs m^{-2} . This mortality rate is similar to what is obtained in growth-out pond cultures in Southeast Asia (Table 1), but lower than what has yet been achieved in East Africa (Mirera & Moksnes **Paper IV**). Slightly higher stocking densities were used in Tanzania to compensate for the longer culture times.

Culture maintenance and harvesting. The average daily labor costs for a 15 x 15 m pond consisted of collecting and preparing feed (1 persons 1 h) and walking to the pond and feeding (1 persons 1 h). Thus, no costs of buying feed is included in the estimate, only the labor cost of collecting e.g. *Terrebralia* snails around the pond in the mangrove forest, fish offals from local fish markets, etc. The feed preparation is minor for the first 4-6 month when the total biomass of crabs are small, and more than 1 h per day the last month when the crabs are large. Harvesting was assumed to be carried out with drop-traps once a week for the last 4 weeks of the harvest cycle, to fish out the fast growing larger crabs and selling them on the local market (1 person 3 h per week), and to drain the pond and harvest all remaining crabs at the end of the harvest cycle (2 persons 4 h).

Security against theft. The crabs were assumed to be valuable enough to warrant guards against theft once they reached 300 g (the smallest market size), whereby guards were needed for the last molt (approximately 2.5 months). Theft was assumed to only be a high risk at night because of the presence of people in mangrove and persons working at the pond during the day. The labor cost of guards was therefore based on 1 person working 7 nights (8 h/night) per week for 3 months.

2. Crab-fattening in drive-in cages.

Cage construction for crab fattening. Initial labor costs for the constructions of crab fattening cages consisted of building the cages out of mangrove sticks (2 persons working for a total of 20 h to build a cages with 50 individual compartments). Material costs consisted of an initial investment in tools for the construction (6 and 8 \$US in Tanzania and Kenya, respectively), and mangrove sticks, plastic string, etc as material for constructing the cages (32 and 40 \$US). Life expectancy was assumed to be 4-8 years for tools, and 4 growing cycles for the cage material.

Seed crabs. Cost of seed crabs were based on purchasing 250-300 g crabs from local fishermen for 0.12 \$US in Tanzania (ASDI/VOCA 2005) and 0.20 \$US per individual in Kenya (Mirera 2009).

Growth rates and culture duration. In the fattening cages, it was assumed that the average 300 g seed crab would molt and gain meat content to reach 545 g in 3 months, equivalent to a growth rate of 2.7 g per day. This growth rate is lower than the modeled natural growth rate of a 300 g crab that molt within 2.5 months (equivalent to a growth rate of 3.3 g d⁻¹), but still higher than the average growth measured in experimental drive-in cage system in Kenya for 250-300 g crabs (i.e. 1.0-1.3 g d⁻¹; Mirera 2009, Mirera & Mitele 2009), and may be an overestimate of the growth rates obtainable in fattening cages.

Crab densities and mortality rates. In the cage cultures, the crabs are kept in individual cages, approximately 30 x 30 cm. The mortality rate was assumed to be 10% month⁻¹ (the same as in the pond-study), which is lower than measured loss rates in experimental culture systems (i.e 19-22% mortality month⁻¹; Mirera 2009, Mirera & Mitele 2009).

Culture maintenance and harvesting. The average daily labor costs for a 50 compartment cage farm consisted of collecting and preparing feed (1 persons 2 h) and walking to the pond and feeding (1 persons 1 h), and weekly repair of the cages (1 person 3 d per week). Harvesting was carried out once a week for the last 4 weeks of the harvest cycle, harvesting the fast growing crabs and selling them on the local market (1 person 3 h per week).

Security against theft. The costs of guards was assumed to be the same as for the pond culture (1 person working 7 nights per week), but for the whole culture period (3 months).

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