

**DETERMINATION OF THERMAL TOLERANCE, DENSITY
AND DISTRIBUTION OF THE MANGROVE CRABS,
Perisesarma guttatum (SESARMIDAE) AND *Uca urvillei*
(OCYPODIDAE) AT GAZI-BAY, KENYA**

By

Kipyegon John Kochey (BSc. Fisheries (Hons))
Reg. NO. I56/CE/11951/2008
Department of Zoological Sciences

A thesis submitted in partial fulfilment of the requirements for the award of the degree of Master of Science in Aquatic Ecology in the School of Pure and Applied Sciences of Kenyatta University.

February 2013

Declaration

Declaration by the candidate

This thesis is my original work and has not been presented for a degree in any other university or any other award.

Kipyegon John Kochev (156/CE/11951/2008)

Signature: _____ Date: _____

Declaration by the Supervisors

We confirm that the work reported in this thesis was carried out by the candidate under our supervision

Prof. Penina Aloo Obudho
Karatina University College
Department of Aquaculture and Fisheries Management

Signature: _____ Date: _____

Dr. James Gitundu Kairo
Kenya Marine Fisheries and Research Institute, Mombasa

Signature: _____ Date: _____

Dedication

This work is dedicated to my beloved parents Lucas Bett Chepkochey and Consolata Kimoi and my son Roy Kibet Kochey.

Acknowledgements

My greatest appreciation and gratitude goes for the support and guidance by my Supervisors Professor Peninah Aloo-Obudho of Karatina university College and Dr. James Gitundu Kairo of Kenya Marine Fisheries and Research Institute (KMFRI). Dr. Kairo introduced me into the world of mangroves through an Earthwatch expedition where he is Co-Principal Investigator with Professor Mark Huxham and Professor Martin Skov and more importantly linked me to Professor Stefano Cannicci heading the project “Coastal Research Network on Environmental Changes–CREC” in which my MSc project was anchored. Many thanks also goes to Professor Cannicci’s Doctorate students Marco Fusi, Riccardo Simoni and Bruce Mostet for technical laboratory assistance.

I am highly indebted to Earthwatch Rufford grants for financial field support. My appreciation goes to KMFRI for laboratory facilities and staff assistance by Dr. Benard Kirui and Mr. Joseph Langat (PhD student) in data analysis skills and Hamisi Kirauni for field assistance. Finally, many thanks to my institution the National Museums of Kenya- Director General, Dr. Idle Omar Farah for allowing me to take time off to pursue my studies.

Table of Contents

Declaration	ii
Dedication.....	iii
Acknowledgements	iv
Table of Contents	v
List of tables	viii
List of figures.....	ix
List of plates	x
List of Abbreviations and Acronyms	xi
Abstract	xii
Chapter 1: Introduction	1
1.1 Background.....	1
1.2 Problem statement and justification	4
1.3 Research questions.....	5
1.4 Hypotheses.....	5
1.5 Objectives	6
1.5.1. General objective.....	6
1.5.2 Specific objectives	6
Chapter 2: Literature Review.....	7
2.1 Defination of mangroves	7
2.2 Importance of mangroves	8
2.3 Mangrove fauna.....	9

2.3.1 Mangrove crabs	10
(a) <i>Uca urvillei</i> (Family: Ocypodidae)	10
(b) <i>Perisesarma guttatum</i> (Family: Sesarmidae).....	12
2.3.2 Importance of mangrove crabs	14
2.4 Mangrove flora and climate change	17
2.5 Mangrove fauna and climate change	18
2.5.1 Effect of temperature changes on mangrove crabs.....	20
Chapter 3: Materials and Methods	29
3.1 Study Area	29
3.1.1 Location	29
3.1.2 Climate.....	30
3.1.3 Gazi-bay biodiversity	31
3.2 Sampling design.....	32
3.3 Data collection.....	33
3.3.1 Determination of density of <i>Perisesarma guttatum</i> and <i>Uca urvillei</i> crabs.....	33
3.3.2 Measurement of abiotic factors	35
3.3.3 Collection of crab specimens for laboratory experiments	36
3.3.4 Optimal thermal tolerance experiments for male adults of <i>Perisesarma</i> <i>guttatum</i> and <i>Uca urvillei</i>	37
3.4 Data analysis	42
Chapter 4: Results	44
4.1 Determination of thermal tolerance of adult males of <i>Perisesarma guttatum</i> and <i>Uca urvillei</i>	44

4.2 Crab density and distribution in mangroves	51
4.2.1 Environmental variables	53
4.2.2 Soil characteristics	59
4. 2. 3 Environmental variables and crab density	62
Chapter 5: Discussion.....	64
5.1 Determination of thermal tolerance of adult males of <i>Perisesarma guttatum</i> and <i>Uca urvillei</i>	64
5. 2 Determination of density and distribution of <i>Perisesarma guttatum</i> and <i>Uca</i> <i>urvillei</i> crabs	72
5.3 Conclusion and Recommendations.....	78
5. 3. 1 Conclusion	78
5. 3. 2 Recommendations	80
References.....	82

List of tables

Table 1. GLM ANOVA table for oxygen consumption rates verses temperature, species (Sp- <i>P. guttatum</i> and <i>U.urvillei</i>) and media	47
Table 2. GLM ANOVA Table of <i>Perisesarma guttatum</i> verses Temperature (T) and media.....	48
Table 3. GLM ANOVA Table of <i>Uca urvillei</i> verses Temperature (T) and media	48
Table 4. GLM ANOVA table of <i>Uca urvillei</i> density verses Zone, transect, season and interactions	52
Table 5. GLM ANOVA table of <i>Perisesarma guttatum</i> verses zone, transect, season and interactions	53
Table 6. Two-way-ANOVA of environmental factors verses zones and season.....	58
Table 7. Two-Way ANOVA table of environmental factors verses zones and transects	58
Table 8. Particle sizes (%) variation over month/seasons and mangrove zones.....	59
Table 9. Two-Way ANOVA of soil particle characteristics verses transects and zones	60
Table 10. Stepwise regression analysis (Backward) of the effects of dependent variable <i>Uca urvillei</i> density on the independent variables.....	62
Table 11. Stepwise regression analysis (Backward) results of the effects of dependent variable <i>P. guttatum</i> density on independent variables	63

List of figures

Figure 1. Map of the Kenyan coast showing the study area, Gazi-Bay. Adopted from Bosire <i>et al.</i> (2003). Sampling stations: 1. <i>Rhizophora mucronata</i> 2. <i>Ceriops tagal</i> 3. <i>Avicennia marina</i> zones	30
Figure 2. Laboratory crab experimental set-up to measure respiration rates	38
Figure 3. Relationship between temperature (mean \pm SE) and oxygen consumption rates of <i>P. guttatum</i> and <i>U. urvillei</i> crabs in air and water media.....	45
Figure 4. Relationship between temperature (mean \pm SE) and oxygen consumption rates of <i>P. guttatum</i> and <i>U. urvillei</i> crabs in water media.....	47
Figure 5. Mean density (\pm SE) of <i>P. guttatum</i> and <i>U. urvillei</i> in mangroves zones .	51
Figure 6. Mean (\pm SE) monthly salinity in different mangrove zones	54
Figure 7. Mean (\pm SE) monthly temperature in different mangrove zones	55
Figure 8. Mean (\pm SE) monthly pH in different mangrove zones	56
Figure 9. Mean (\pm SE) monthly Redox potential (eH) in different mangrove zones	57

List of plates

Plate 1. 1m ² quadrat (enclosed with a piece of rope round) used to sample crabs in <i>Cerriops tagal</i> zone.....	34
--	----

List of Abbreviations and Acronyms

ANOVA	Analysis Of Variance
DF	Degrees of freedom
EU	European Union
F	F-statistic
GLM	General Linear Model
GPS	Geographical Position System
Ha	Hactares
IPCC	Intergovenmental Pannel on Climate Change
KMFRI	Kenya Marine and Fisheries Research Institute
LT ₅₀	Lethal Temperaure at which 50% of animals experimented die
MPA	Marine Protected Areas
MS	Error Mean square
P	Probability associated with F statistic
<i>Pejus</i>	means getting worse or deleterious
Q ₁₀	Temperature coefficient and is the factor by which a rate increases over a 10°C interval and may be used to infer mechanistic insight about the physiological process under investigation
SS	Sum of squares
UNFCCC	United Nations Framework For Climate Change Conference

Abstract

Mangrove crabs are important in ecosystem functioning including; bioturbation of the soil resulting in soil particle size distribution, sediment aeration, reduction in sediment salinity and nutrient recycling and thus are fundamental for the viability of mangrove forests which are in turn important to the coastal communities' livelihoods. Mangroves are intertidal forested wetlands confined to the tropical and subtropical regions. They play important role as habitat for animals, provision of wood and non-wood products and a source of medicine to coastal people. The effects of climate change on ecosystems are real and thus the mangrove ecosystem are also threatened by this phenomenon. Therefore, the question that arises is what effects, if any, would increases in temperature have on those animals resident in the mangrove sediment. The aim of this study was to determine the thermal tolerance, density and distribution of the mangrove crabs *Perisesarma guttatum* and *Uca urvillei* at Gazi-Bay on the Kenyan coast. Field activities included collection of data on density and distribution of the two crab species and on environmental variables in the *Rhizophora mucronata*, *Ceriops tagal* and *Avicennia marina* monospecific stands. In the laboratory, the crabs were maintained at temperatures between 17-37°C and respiration rate measurements was performed in closed chamber systems after the crabs were acclimated for 8 hours at 27°C. The results indicate that the temperature ranges for *P. guttatum* and *U. urvillei* adult crabs were 27-31°C and 27-33°C respectively beyond which the crabs got stressed as indicated by increased metabolism. This suggest that *P. guttatum* is more sensitive to temperature variation than *U. urvillei* which has a wide thermal tolerance window. The highest average densities of *U. urvillei* and *P. guttatum* crabs recorded were $66.25 \pm 7.7/m^2$ and $11.75 \pm 4.1/m^2$ respectively in the *R. mucronata* zone. Very low densities of *U. urvillei* of $0.88 \pm 0.25/m^2$ were found in *C. tagal* and $0.47 \pm 0.28/m^2$ in *A. marina* zone while density of *P. guttatum* was 1.9 ± 1.8 in *A. marina* and was not significantly different between *C. tagal* and *R. mucronata* zones ($P > 0.05$). The densities of *U. urvillei* and *P. guttatum* were strongly related to temperature, fine sand and organic matter using stepwise regression analysis ($P < 0.05$). This study has increased the understanding of the physiological responses and possible distribution patterns of mangrove crab populations to expected impacts of climate change on these species.

Chapter 1: Introduction

1.1 Background

Mangroves support a distinctive fauna and flora; dominated by crabs and mollusks. Worldwide, there are 275 species of mangrove crabs with the highest diversity found in South East Asia with over 100 species of *Uca* recorded in Malaysia alone (Gillikin and Scubart, 2004) while 35 species occur in Kenyan mangroves (Cannicci *et al.*, 2009). The sesarmids and fiddler crabs (*Uca sp.*) reach densities of approximately 50 to 80 m⁻² and 40-300m⁻² respectively (McCraith *et al.*, 2003; Cannicci *et al.*, 2009). Mangrove crabs play important roles in mangrove ecosystem functioning including; bioturbation of the soil resulting in changes in soil surface topography, particle size distribution and increased degree of aeration, reduction in salinity and sediment sulfide concentration, nutrient recycling and as food sources (Gillikin *et al.*, 2001). Thus, their diversity and relative abundance are crucial for the viability of mangrove forests which in turn supports coastal community livelihoods.

The *Uca urvillei* (Family: Ocypodidae) and *Perisesarma guttatum* (Family: Sesarmidae) are intertidal semi-terrestrial crabs active at low tide. *U. urvillei* is detritivorous and dig burrows for shelter and refuge against environmental extremes. *P. guttatum* is mainly omnivorous and utilize other crabs' burrows and shade in mangroves to minimize thermal stress (Skov *et al.*, 2002). At Gazi-Bay, both *P. guttatum* and *U. urvillei* occur in the *Rhizophora mucronata* and *Avicennia*

marina zone (Cannicci *et al.*, 2009). Many aspects of the behavior, ecology and populational biology of these species are known (Cannicci *et al.*, 2009) but few studies have described densities of these crabs in *Cerriops tagal* pure stands (Dahdouh-Guebas *et al.*, 2002).

Mangroves and the associated fauna experience a suite of physical stresses, including fluctuations in temperature, salinity, hydrodynamic forces and aerial exposure (Valiela *et al.*, 2001). Globally, mangroves are threatened by overexploitation, degradation and transformation of habitat, diversion of fresh water flow and pollution effects (Macintosh and Ashton, 2002). Climate change now threaten mangroves through increases in temperature, sea level and salinity and low pH value, changes in precipitation and frequency of storms being located at the land-sea margins (Macintosh and Ashton, 2004). These changes in climate will in the near future affect abundance and distribution of aquatic fauna including crabs causing both local extinctions or relocation of populations (Perry *et al.*, 2008). Portner and Knust (2007) reported that in a climate context, thermal changes are the key drivers of ongoing ecosystem changes co-occurring with increasing hypoxia and carbon dioxide accumulation which affects systems of oxygen supply and demand in aquatic ectotherms. Portner (2010) observed that ecosystem changes evoked by anthropogenic impacts and global climate change have brought out the need for an understanding of mechanistic background underlying physiological responses of aquatic ectotherms to thermal stress.

Temperature determines distribution ranges and boundaries for marine and terrestrial species and evidence for this is mostly based on studies of thermal tolerance of adults and larval stages (Gaston, 2003; Sanford *et al.*, 2006).

Portner *et al.* (2000) proposed the concept of oxygen and capacity-limited thermal tolerance in aquatic ectotherms. The concept postulates that thermal limits of performance are set by the temperatures at which aerobic respiration fails to meet the energetic needs. This concept has successfully explained climate-induced effects of rising temperatures on species abundance in the field (Portner and Knust, 2007). Past studies on crabs supporting this concept are few and include; studies on spider crab, *Maja squinado* by Frederich and Pörtner (2000) who reported its optimum temperature range to be 8-17°C for aerobic performance. Other studies related to effect of temperature changes on oxygen consumption rates include those of Vernberg (1959b) on *Uca pugilator* and *Uca pugnax*. Weinstein (1998) reported a temperature range of 24-30°C for the ghost crab *Ocypode quadrata* where increasing temperature had little effect on their metabolism. However, Tewksbury *et al.* (2008) observed that data on the thermal relationships of crabs are incomplete. There is lack of documented studies on thermal tolerance of mangrove crabs, *P. guttatum* and *U. urvillei* in African mangroves which forms the basis of this study.

1.2 Problem statement and justification

Despite the importance of mangrove crabs in mangrove ecosystem functions, little is known on the effects of increasing temperature as a climate change indicator on mangrove crabs. Further, it is still unknown if there is a link between mangrove crab distribution and thermal determinants and tropical organisms are expected to be sensitive to elevated temperatures because they inhabit thermostable environments and are currently living very close to their optimal temperature (Tewksbury *et al.*, 2008). Meta-analyses of species distribution patterns have explained climate-driven effects which have emphasized discovery of large-scale patterns without necessarily understanding the mechanisms underlying the physiological processes and their response to abiotic stresses. In addition, studies on mangrove crab eco-physiology is patchy. The abundance of crabs in some mangrove zones such as the *Cerriops tagal* pure stands are yet to be fully documented.

Mangrove crabs are crucial for a series of important mangrove ecosystem functions including; bioturbation of soil resulting in changes in surface topography, increased sediment aeration and reduction in sediment salinity. Thus their diversity and relative abundance are fundamental for the viability of mangrove forests and sustainance of livelihoods. The effects of climate change on ecosystems is real (Kenendy *et al.*, 2002). Therefore, the question that arises is what effects, if any, would increases in temperature, salinity, sea level and low pH

value as a result of global warming have on those animals resident in the mangrove sediment like crabs. There is therefore need to address global warming effects on populations. The results from this study will allow an appraisal of possible differences in thermal tolerances of crab species that may help explain species distribution patterns within mangroves. Information on thermal tolerance range of organisms is important for their conservation. In the face of rapid depletion of world's aquatic resources accelerated by climate change, studies on population trends are critical for better understanding of community structure and ecological processes as well as the dynamics and resilience of mangrove ecosystems to changing environmental conditions so that a rational plan for conservation and management can be effectively instituted.

1.3 Research questions

This project was led by the following questions:

- i. What is the optimal thermal tolerance of male adults of *Perisesarma guttatum* and *Uca urvillei* crabs in air and water media?
- ii. What is the density of *P. guttatum* and *U. urvillei* crabs in the *Rhizophora mucronata*, *Ceriops tagal* and *Avicennia marina* zones at Gazi Bay?
- iii. How does the distribution of *P. guttatum* and *U. urvillei* crabs vary in the three mangrove zones in relation to environmental factors at Gazi-Bay?

1.4 Hypotheses

The study was guided by the following statistical hypotheses:

- i. Male adults of *P. guttatum* and *U. urvillei* crabs at Gazi-Bay have no

preferred optimal thermal range.

- ii. The density of *P. guttatum* and *U. urvillei* crabs is uniform in the *R. mucronata*, *C. tagal* and *marina* zones of Gazi- Bay.
- iii. The distribution of *P. guttatum* and *U. urvillei* in the *R. mucronata*, *C. tagal* and *A. marina* mangrove zones are not affected by environmental factors at Gazi-Bay.

1.5 Objectives

1.5.1. General objective

The overall objective of this study was to determine the thermal tolerance, density and distribution of the mangrove crabs, *P. guttatum* and *U. urvillei*.

1.5.2 Specific objectives

- i. To establish the optimal thermal tolerance of male adults of *P. guttatum* and *U. urvillei* crabs at Gazi-Bay.
- ii. To determine the density of *P. guttatum* and *U. urvillei* crabs within the *R. mucronata*, *C. tagal* and *A. marina* mangrove zones at Gazi-Bay.
- iii. To establish variation in distribution of *P. guttatum* and *U. urvillei* in relation to environmental factors in the *R. mucronata*, *C. tagal* and *A. marina* mangrove zones at Gazi-Bay.

Chapter 2: Literature Review

2.1 Definition of mangroves

Mangroves are woody plants that grow at the harsh interface between land and sea that are confined to tropical and subtropical regions along sheltered and shallow coastal water coastlines with large tidal excursions (Kathiresan and Bingham, 2001). Mangrove tree species zonation has been correlated with factors such as physiological adaptations to salinity and frequency of tidal inundation, tidal flow and geomorphology, nutrient availability, salinity of the soil, soil sulphide and redox levels, competition between species, tidal sorting of propagules, light availability to seedlings and predation of seedlings (Dahdouh-Guebas, 2001; Macintosh and Ashton, 2002; Dahdouh-Guebas *et al.*, 2007). Mangroves consisting of 73 known species are distributed circumtropically with an estimated global coverage of 152,000km² (Spalding *et al.*, 2010).

In Kenya, mangroves are found in creeks, bays and estuaries covering an estimated total area of 54,000 hectares along the Kenyan coastline stretching a distance of 640km (Kairo *et al.*, 2001). Most of the mangroves are mainly found in Lamu district (33,500 ha), Kwale district (8375 ha), Kilifi district (5570 ha), Tana River district (3045 ha) and Mombasa district (2490 ha)(Kairo *et al.*, 2001). There are ten species of mangroves found in Kenya; *Rhizophora mucronata*, *Avicennia marina*, *Ceriops tagal*, *Lumnitzera racemosa*, *Bruguiera gymnorrhiza*, *Sonneratia alba*, *Xylocarpus granatum*, *Xylocarpus moluccensis*, *Heritiera littoralis* and

Pemphis acidula (Richmond, 2010). *R. mucronata*, *C. tagal* and *A. marina* are the dominant species making 70% of the formation (Spalding *et al.*, 2010). Mangroves in Kenya display typical zonation pattern of the mangroves in Eastern Africa and the zonation is based on prominent trees and the seaward side is occupied by *Sonneratia-Rhizophora-giant Avicennia* community followed by *Rhizophora-Bruguiera-Ceriops* in the mid zone and dwarf *Avicennia-Lumnitzera-Xylocarpus* complex on the landward side (Kairo *et al.*, 2001).

2.2 Importance of mangroves

The mangrove forests are among the world's most productive ecosystems and provide many natural products and a wide range of ecological, environmental and socio-economical services while occupying only 0.12% of the world's total land area (Dodd and Ong, 2008). Mangroves are the economic foundations of many tropical coastal regions providing at least US\$1.6 billion per year in ecosystem services worldwide (Costanza *et al.*, 2008). Mangroves provide natural products such as timber (poles) for house building and firewood for cooking (Kokwaro, 1985). The ecological services provided by mangroves include; primary nursery areas for commercially important species of fish, crustaceans such as crabs and habitats for insects, acting as traps for particulate matter, storage and recycling of organic matter and nutrients as well as production of oxygen (Macintosh and Ashton, 2002). Mangroves provide shoreline protection against floods, hurricanes, erosion control and tsunamis (Dahdouh-Guebas *et al.*, 2005). Mangroves are

important carbon sinks and can sequester up to 25.5 million tonnes of carbon per year (Polidoro *et al.*, 2010). Mangroves provide biophysical support to other coastal ecosystems such as sea grasses and coral reefs. More recently, changes in mangroves have been proposed as a means to monitor change in coastal environments as indicators of global warming, climate change, storm effects, sea level change, pollution and sedimentation rates (UNEP, 2006).

2.3 Mangrove fauna

The mangrove forests support a high diversity of distinctive fauna of either marine or terrestrial origin with crucial functions within the ecosystem towards maintaining global biodiversity such as bioturbation of the soil, pollination, food sources, etc. many of which are vulnerable or threatened as a result of human activities in the coastal zone. The majority of mangrove fauna is composed of invertebrates with representatives from various animal phyla dominated by mollusks and crabs. The animal phyla represented include; arthropods such as crabs and insects, mollusks such as gastropods and bivalves, annelids, sipunculids, nemertean, platyhelminthes and sponges (Nagelkerken *et al.*, 2008). The vertebrates hosted include fish, birds, mammals, reptiles and amphibians. Determining the value of mangroves and other estuarine habitats for these animals requires knowledge of their life history, physiology and ecology as they interact across the dynamic mosaic of available habitats (Nagelkerken *et al.*, 2008).

2.3.1 Mangrove crabs

The brachyuran decapod crustaceans are the most abundant and ecologically important and well-studied group of invertebrates in the mangroves. Mangrove crab diversity is very high with an estimated 275 species from six families of brachyurans which include Ocypodidae, Sesarmidae, Grapsidae, Xanthidae, Portunidae, Geocarcinidae and Varunidae (Cannicci *et al.*, 2008). The family Ocypodidae comprises about a dozen genera but two genera, *Ocypode* and *Uca* are the only cosmopolitan genera in the family (Crane, 1975). Within the mangroves of East Africa, brachyuran crabs are the dominant taxa, both in terms of biomass and species richness. There are about 35 species of these crabs and four Anomuran hermit crabs occurring in Kenyan mangroves. There are six species of *Uca* and about 19 species of Sesarmides reported in East Africa (Richmond, 2010). Zonation of mangrove crabs are determined by many abiotic and biotic forces (Cannicci *et al.*, 2008).

(a) *Uca urvillei* (Family: Ocypodidae)

U. urvillei is a fiddler crab belonging to the family Ocypodidae and is among a hundred (100) species in the genus *Uca* often associated with mangrove forests (Gillikin and Schubart, 2004). *U. urvillei* is an intertidal crustacean that is well-suited for semi-terrestrial life and are deposit feeders ingesting organic matter from the exposed mud at low tide and retreat into burrows and remain inactive when the tide is in. Its distribution ranges from East coast of Africa from Gumbo, Somalia, to Cape Province, South Africa (mouth of Umtata River), Madagascar,

Karachi, Pakistan and western India (Lee, 2008). The *U. urvillei* is almost certainly the only *Deltuca* that reached Africa and reaches a maximum carapace width of 30mm and length of 17mm (Richmond, 2010). It lives characteristically in mangroves along streams well back from the shore, as do all the other members of its superspecies. In *U. urvillei*, however, its niche lies close to low-tide levels. In Natal and in Cape Province *U. urvillei* is exposed seasonally to chilly weather, although not to the extent of that tolerated, through hibernation, by its northern conspecific, *arcuata*, in Japan (Crane, 1975). The life history of all *Uca sp* including the *U. urvillei* has the following stages: the adult ovigerous female carries fertilized eggs on the ventral surface of her abdomen. Secondly, these developing eggs hatch into free swimming zoeae. There are five different zoeal stages and the fifth zoeal stage metamorphoses into a megalopa. Thirdly, the megalopae molt into young crabs which then invade the intertidal zone (Cannicci *et al.*, 1997).

Uca species is somewhat less well adapted to withstand desiccation. Fiddler crabs do not aerate the burrows by pumping water through it therefore the oxygen concentration remains low in burrows than in the surrounding mud and *Uca* can survive anoxic conditions for upto 40 hours by building up an oxygen debt (Hogarth, 1999). Many factors are known to affect the distribution of fiddler crab populations including substrate characteristics such as grain size composition, organic and moisture content, presence or absence of mangrove vegetation,

temperature and humidity, salinity, light intensity and duration, tidal wetting, interspecific and intraspecific competition (Kristensen, 2008; Cannicci *et al.*, 2008; 2009). Crane (1975) reported that no *Uca* species were found in very soft, deep mud of the seaward zone as this type of habitat is apparently unfavourable to all fiddler crab species.

(b) *Perisesarma guttatum* (Family: Sesarmidae)

P. guttatum belongs to the family Sesarmidae a group of semi-terrestrial crabs previously included in the family Grapsidae by many authors. Vanini and Valmori (1981) reported that *P. guttatum* is endemic to East Africa, occurring from Somalia down to the north coast of South Africa, in Madagascar and in the Red Sea. The genus *Sesarma* consists of more than 125 species inhabiting temperate and tropical regions of the world. At least 19 species have been recorded in Western Indian ocean region (Gillikin *et al.*, 2004). There are two species of *Perisesarma* in East African mangroves namely *P. guttatum* and *P. samawati* (Gillikin and Schubart 2004). *P. guttatum* has a maximum carapace width of 26mm and length 21mm (Richmond, 2010) and is found on the forest floor, utilizing other crabs burrows and natural crevices (Gillikin, 2000).

P. guttatum is completely omnivorous and its stomach contents are primarily leaves and to a lesser degree insects (Dahdouh-Guebas *et al.*, 1999). *P. guttatum* has five zoeal stages lasting from 22-25 days and one megalopa stage (Lago,

1993). *P. guttatum* is very common across entire mangrove forest in high densities preferring areas with very high organic sediment but avoids drier areas and they are often found in *Neosarmatium smithi* burrows (Gillikin, 2000). Skov *et al.* (2002) indicated that they occupy an area of about 16m² during in it's life. Maturity in males reached at a carapace width of about 9.35 mm and 15.3 mm for females (Flores *et al.*, 2002). *P. guttatum* has been confused with *P. Samawati* and therefore most literature dealing with *P. guttatum* most likely includes both species (Gillikin and Schubart, 2004). Sesarmines crabs have similar tolerance of low oxygen levels as the fiddler crabs although they have been found to indicate low tolerance of anoxia and high temperatures and evidence is in studies on sesarmines caught overnight in flooded pitfall traps in a hot Malaysian mangroves which were found dead (Hogarth, 1999). Most of the activities of sesarmines and fiddler crabs takes place in air where oxygen concentration of air is 20 per cent higher than in water even at saturation levels and have to offset this advantage since gills are not well adapted to air breathing. Further, gas exchange takes place across the gills primarily from residual water that is retained in the branchial chamber while these animals are exposed to air.

Chapman and Tolhurst (2004) indicated that faunal assemblages including fiddler and sesarmines crabs in mangroves vary considerably spatially which often confound the results. They vary in abundance and diversity at scales from centimeters to hundreds of meters in what appears to be similar habitats and thus

successful analysis of these relationships requires complex nested sampling designs involving many replicates needed to represent assemblages adequately at various spatio-temporal scales. Chapman and Tolhurst (2004) and Cannicci *et al.* (2009) reported that crab distribution patterns was influenced by environmental factors such as soil textural (percent sand, silt, clay and organic matter), Eh and pH and temperature properties. Middleburg *et al.* (1996) indicated that mangrove sediments have pH values that range from 3.5 to 8.3. This is due to the limited buffer capacity of these sediments and intense acidifying processes such as aerobic degradation of organic matter, oxidation of reduced components, ammonium uptake by roots and root respiration and could affect mangrove fauna. Ballerini *et al.* (2000) and Cannicci *et al.* (2000) reported no differential distribution in relation to mangrove tree species for sersarmid crabs within Mida Creek.

2.3.2 Importance of mangrove crabs

Mangrove crabs play a significant role in the functioning of the mangrove ecosystem including; bioturbation of soil hence are ecosystem engineers (Cannicci *et al.*, 2008) through their burrowing activities. These bioturbation activities affect the soil sediment chemistry, topography and biogeochemistry by modifying particle size distribution and increasing soil aeration in the anoxic mangrove soil through the burrows they make on the sediments which allow air to reach depths that would otherwise be very anoxic for organisms to survive; they affect redox conditions and decrease the sulfide concentration in the sediment by burrowing

(Kristensen, 2008). The crab burrows also provide an efficient mechanism for exchanging water between the anoxic substrate and the overlying tidal water in the process they help in salinity regulation in the sediments (Gillikin and Scubart, 2004). Kristensen (2008) indicated that the digging by crabs, in conjunction with other benthic fauna like nematodes, polychaetes and mudskippers can also have a profound effect on nutrient cycling and the physical and chemical environment of the mangal.

The mangrove crabs trap energy within the mangrove forest and thus contribute to secondary production and increase the amount of nutrients due to their burrowing activities (Cannicci *et al*, 2008). The removal of leaf litter by graspid crabs and taking them to their burrows from mangrove forest floor is important in mangrove litter turnover and nutrients cycling in the forest (Fratini and Vannini, 2002). Although sesarmids and ocypodids can consume up to 100% of the mangrove leaf litter, crabs' assimilation rate of the leaf litter is generally low (<50%), and about 60% of the dry mass of the material consumed is egested as faecal matter which is thus exploited by benthic invertebrate consumers in the coprophagus food chains (Cannicci *et al.*, 2008) hence enhancing the biodiversity and functioning of the mangroves. Burrowing crabs create microhabitat for other fauna (Gillikin *et al.*, 2001) for example the association of small burrowing fauna such as juvenile crabs, callianassids, polychaetes and gastropods within burrows of adult sesarmid crabs (Thongtham and Kristensen, 2003). Mangrove crabs are classified as *allogenic*

engineers in that they are able to change the environment by transforming living material from one state to another via mechanical and other actions (Kristensen, 2008). Their active incorporation of leaf-litter ensures the retention of mangrove productivity within the ecosystem (Kristensen *et al.*, 2008).

The sesarmids and Ocypodids have been shown to have the same role in terms of retention of forest products and organic matter processing and as ecosystem engineers, change particle size distribution and enhance soil aeration in New world mangroves (Cannicci *et al.*, 2008). Fiddler crabs feeding on the sediment surface and plant matter promotes nutrient recycling and they thus play a significant role in controlling algal mat growth in mangrove substrata and their bioengineering activities are fundamental for the growth of mangrove seedlings and eventually for mangrove regrowth (Kristensen, 2008). Cannicci *et al.* (2008) reported that the mangrove crab *Chiromantes spp.* and the sipuncula *Phascolosoma arcuatum* were found in the gut of fishes netted within the mangroves at high tide. This demonstrate that mangrove ecosystem support adjacent ecosystems such as the coral reefs and seagrass beds by offering breeding and feeding grounds and by sediment traps thus offering protection. The benthic invertebrates are a source of food for crab larvae which in turn are important food source for shallow-water fishes and juvenile fish that enter the mangroves at high tide a clear indication that crabs help near shore fisheries. Adult crabs are food for endangered bird species such as the crab plover, *Dromas ardeola* (Cannicci *et al.* (2008). Mangrove crabs

are keystone species as their removal alter ecosystem structure and function and it was found that removing crabs from an area caused significant increases in sulfides and ammonium concentrations, which in turn affects the productivity and reproductive output of the vegetation (Kristensen *et al.*, 2008). Herbivorous crabs are major seed predators in mangrove forests and thus play an important role in determining plant community structure through influencing the growth of mangrove seedlings by predation of propagules (Cannicci *et al.*, 2008). Mangrove trees and different crab species have evolved a mutual relationship with crabs where the crabs benefit from getting suitable habitat provided by the trees whereas the mangrove trees benefit from reduced competition between mangrove plants species through selective predation on seedlings (Bosire *et al.*, 2005b). Thus the mangrove crab presence, abundance and diversity are thus among the major drivers of tree recruitment in tropical coastal forest ecosystems and their conservation should be included in management plans of these forests.

2.4 Mangrove flora and climate change

In addition to local physical stresses and global anthropogenic threats such as overexploitation, degradation, transformation of habitat and pollution effects (Valiela *et al.*, 2001), climate change now threaten mangroves through increases in; sea level, temperature and salinity, low pH value, changes in precipitation patterns and frequency of storms being located at the land-sea margins (Macintosh and Ashton, 2004). This leads to their displacement further landward (Christensen

et al., 2007) in order to have optimal habitat conditions. Human encroachment at the landward boundary, however, may make this impossible and consequently, the width of mangrove systems would likely decrease as the sea-level rises. The mean global temperature and sea level have both risen and IPCC (2007) project increases of about 1-3.5°C and 9 to 88 cm respectively between the year 1990 and 2100 (Kennedy *et al.*, 2002) and land regions have warmed faster than the oceans. This will significantly affect mangroves and in the face of impending global climate change, the danger of biodiversity reduction is today a reality (Alongi and Carvalho, 2008).

2.5 Mangrove fauna and climate change

Climate change can be expected to alter temperature, salinity, pH, current, winds and tidal patterns. These changes will in effect affect the abundance and distribution of aquatic fauna and their larvae, species interactions such as predator prey relationship and timing of physiological events by changing the timing of reproduction as species struggle to adapt to changing environmental conditions (Kennedy *et al.*, 2002) causing both local extinction and relocation of populations following latitudinal thermal gradients (Perry *et al.*, 2008). Imevbore (2011) predicted that by 2085 between 25-42% of the African species' habitats are expected to be lost due to climate change alone. Most significant to the distribution of mangrove animals would be losses of exploitable habitats, should climatic change lead to the shrinking of the mangroves away from their present latitudinal

limits and as such any extension in mangrove range due to global warming, would create opportunities for range extensions by some mangrove animal species (UNEP, 1994). Parmesan (2006) reported that recent climatic changes have already caused shifts in species distributions and species have been found to be moving their ranges poleward in latitude and upward in elevation at rates that are consistent with recent temperature increases. For example, the planktonic larvae of decapod crustaceans have increased in abundance in the North Sea, especially since the mid-1980s, as sea surface temperature increased (Kirby *et al.* 2008).

Climate change involves environmental factors other than temperature such as the accumulation of anthropogenic carbon dioxide in the atmosphere and in the ocean leading to ocean acidification (Portner, 2010). Ecosystem changes evoked by anthropogenic impacts and global climate change have brought out the need for an understanding of mechanistic background underlying physiological responses of organisms to thermal stress. This will address questions of why species specialize on limited temperature ranges and how they deal with ambient oxygen deficiency and why they are sensitive to accumulating carbon dioxide. The pH of surface waters is predicted to decrease by a further 0.14–0.35 units by 2100 due to uptake of Carbon dioxide (Solomon *et al.*, 2007) and mangrove crabs are primary candidates to be strongly affected by such changes as ocean acidification may interfere with shell formation particularly if ocean pH falls below 7.5 (Kleypas *et al.*, 2006). The current and predicted changes of coastal systems due to global

warming depend on an increase of pore water salinity, caused by sea level rise and ocean acidification. Although changes in global climate may cause some increases in salinities, these changes would be chronic and may impact crab populations already living above their optimal salinity and therefore, further increase in water salinity could pose serious physiological problems (UNEP, 2006). The temperature rise resulting in extreme salinity regimes may adversely affect crab population (Jagtap, 2007). UNFCCC (2007) indicated that a 2°C rise in temperature will potentially severely increase rates of extinction for many habitats and species with estimates of up to 30 percent species extinctions. Higher temperatures may result to elimination of highly mobile species from part of its range since they can migrate to other more suitable environments depending on; number of adults available in the original habitat and their ability to produce young and to cross barriers, an adequate number of potential colonizers (larvae, migrating juveniles or adults) and their survival (Dijk *et al.*, 1999). Current evidence indicates temperature sensitivity to be highest at the organismal level (Pörtner, 2001) and thus understanding the physiological mechanisms that underlie how specific components of climate affect key life cycle stages will be important for predicting the ecological responses of many species to climate change.

2.5.1 Effect of temperature changes on mangrove crabs

Temperature is a major limiting factor for aquatic ectothermic organisms such as crabs that will tolerate fluctuations of the habitat temperature only within certain

limits (Kennedy *et al.*, 2002). Temperature extremes can be lethal to organisms and also influences physiological functions such as growth and metabolism, locomotion, reproduction, distribution patterns of organisms and their larval stages through changes in the rates of biochemical and physiological processes as it impairs enzymatic function and as such aquatic ectothermes are likely to be vulnerable to climate warming. For this reason, temperature-adaptive variation that establishes different thermal optimal and thermal limits among species is widespread (Hochachka and Somero, 2002). The ability of ectotherms to perform such physiological functions at different temperatures are explained by the thermal tolerance performance curves which index the direct effect of temperature on the organism fitness providing a physiological basis to explain clearly the fundamental component of the impact of global climate change (Deustch *et al.*, 2008).

Slight increases in temperature can cause appreciable impacts to many species including crabs and increase in water temperature tends to increase the metabolism of organisms moreover, warm waters have less capacity to hold oxygen, which is a primary reactant for metabolism. This imbalance of oxygen supply and demand will cause stress to the organisms (Kennedy *et al.*, 2002). Pörtner (2001) reported that temperature sensitivity is known to be highest at the organismal level through limited capacity of oxygen supply mechanisms to cover oxygen demand. Environmental temperature not only influences the total metabolic rate in aquatic ectotherms but can also significantly affect metabolic regulation causing transition

to anaerobiosis even in fully oxygenated waters (Pörtner *et al.*, 2001) due to limitation in capacity and ventilation processes. Hofmann and Somero (1996b) indicated that the body temperatures of intertidal organisms such as the crabs can fluctuate by 25°C or more in a matter of hours during aerial exposure at low tide. This would cause significant damage at the cellular and biochemical level where in turn antioxidative defence mechanisms and heat shock proteins were hypothesized to play a key role in stress protection especially under these conditions (Portner, 2002a). They experience combined exposure to temperature extremes, ambient hypoxia or even anoxia as well as transient carbon-dioxide accumulation in body fluids due to loss of gas exchange causing a narrowing of thermal windows and, possibly, lower performance optima through lower functional capacities and reduced systemic oxygen tensions in the long-term scales. These intertidal animals which spend a substantial amount of time exposed to air during low tides, sea water temperature does not adequately estimate body temperature during period of emersion and body temperature will be determined by thermal properties of the organism among other properties (Stillman and Somero, 2000).

To avoid thermal stress, common intertidal mangrove crabs like *Uca* species and sesarmids could probably adapt to expected increases in ambient temperature by making more frequent or extended burrow visits. Mangrove fiddler crabs are known to experience temperatures reaching 41°C on the exposed surface of a mangrove mudflat, but can retreat into their burrows where temperatures remain

constant at 28-30°C below 10 cm depth (Hogarth, 1999). Despite these behavioural mechanisms which serve to reduce the degree of thermal stress to which these ectotherms are exposed they may still experience a range of temperature which will have important physiological implications particularly in climate change scenarios. The upper lethal temperature for *Perisesarma guttatum* and *Uca urvillei* are not known but *Uca inversa* a related tropical species is just above 40°C (Eshky *et al.*, 1996). Portner (2001) indicated that the long term heat tolerance limits for all metazoans are found around 45-47°C and upper limit temperature of aquatic animals is between 35-40°C and many enzymes are inactive after 35-45°C and highly organized air breathers being more eurythermal, may approach that limit more closely than water breathers. However, the mechanisms limiting heat tolerance have not really been established in air breathers and oxygen limitation has not been investigated (Portner, 2001). Helmuth *et al.* (2005) reported that the intertidal habitats have very sharp temperature gradients and thermal tolerance is still governed by temperature variability, an organisms vulnerability to warming would depend on vertical position, latitude, daily time of exposure and interactions with predators and competitors.

Using Shelford law (1931) describing the changing performance of organisms within optimum, pejus and pessimum phases of the tolerance range with respect to environmental factors such as temperature, Portner *et al.* (2000) proposed a model of thermal tolerance based on oxygen limitation known as the concept of oxygen

and capacity-limited thermal tolerance in marine aquatic ectotherms which postulated that thermal limits of performance are set by the temperatures at which aerobic respiration fails to meet the energetic needs. The capacity of oxygen delivery matches full aerobic scope only within the thermal optimum and reflects functional capacity in ecosystem-level processes such as competition, foraging, immune response, growth and behaviour. Oxygen consumption rate and distribution by ventilation and circulation is generally regarded as a good index of aerobic metabolic activity and comprises energy demand for maintenance and include the element of aerobic scope that is crucial in setting the species thermal tolerance at the ecosystem level (Portner, 2001). Modlin and Froelich (1996) reported that within their optimal range of environmental conditions, most aerobic organisms can regulate and maintain constant rates of oxygen consumption which reflects energy metabolism and can be a sensitive indicator of the physiological health of an organism.

Thermal limitation set in at the transition from the optimum to *pejus* range characterised by the drop in aerobic scope and *peju's* temperature indicate the limitation of aerobic energy for activity, growth and reproduction and may therefore be closest to the temperature limits of the geographical distribution of a species. At temperatures outside thermal optimum range, only time-limited survival is supported by residual aerobic scope and towards critical temperatures associated with a drastic rise in oxygen demand, aerobic performance capacity

falls progressively and all functions except those essential for maintenance are reduced and then anaerobic metabolism occurs even in fully oxygenated waters. Beyond the critical temperatures it finally leads to oxidative and denaturation stress prompting molecular protection by heat shock proteins and antioxidative defence (Portner *et al.*, 2000). Portner (2010) indicated that at high temperatures ventilation and circulation fall below the level required to supply the mitochondria with sufficient oxygen to meet the energetic demands. The thermal tolerance limits in highly organised water breathers are set by limited oxygen supply to tissues and breathing air implies a reduction by one order of magnitude in the energy cost of ventilation at about 30 times higher levels of ambient oxygen (Portner, 2001) and this may have allowed air breathers to be more eurythermal than water breathers. Thus the reduction of aerobic scope sets the long-term limits of thermal tolerance in both air and water breathing ectotherms. Portner and Knust (2007) observed that warming beyond *pejus* thresholds leads to the onset of reduced growth performance and abundance of ectotherms such as fish in the field. The earliest limits of the thermal tolerance range with ecological effect are set by *pejus* temperatures and as such it is fundamental to understand the mechanisms that set *pejus* thresholds if we want to understand the effects of climate change on the biogeography and performance of individual species.

There is evidence that the concept of oxygen and capacity-limited thermal tolerance/temperature-dependent oxygen limitation are similar across animal

phyla; crustaceans and their larval stages, sipunculids, annelids, molluscs (bivalves, cephalopods) and fishes from various latitudes and many laboratory studies confirm the principles underlying this concept (Portner, 2001; Pörtner 2002a and b; Portner, 2010; Pörtner and Knust, 2007; Storch *et al.*, 2009). Early evidence came from studies in annelids and sipunculids which demonstrated a transition to anaerobic mitochondrial metabolism at both low and high critical temperatures of their thermal window (Zielinski and Pörtner, 1996; Sommer *et al.*, 1997). Studies on spider crab, *Maja squinado* (Frederich and Pörtner, 2000) indicated an optimum temperature range for maximum aerobic scope between 8-17°C where availability of aerobic energy is maximal for all physiological functions including growth and reproduction. Thermal limitation was set in at the transition from the optimum to pejus range characterized by the drop in aerobic scope and anaerobic mitochondrial metabolism not only occurs beyond low but also above high temperature extremes.

Pörtner and Knust (2007) reported that the negative effects of summer extreme temperatures on population dynamics of eelpout fish (*Zoarces viviparus*) in the German Wadden Sea were related to laboratory studies of the oxygen and capacity limitation of heat tolerance and experienced their upper thermal limits of functional capacity in the field exemplified in growth patterns observed as reduced field abundance coincides with reduced growth of laboratory maintained, temperature-acclimated individuals providing further support that the concept is

suitable to explain species responses in the field. Farrell *et al.* (2008) identified thermal limitation of Pacific salmon fish at the ecosystem level indicated that the warming river prevented adult spawners from reaching their upstream spawning grounds, because of thermal limitations to aerobic swimming capacity and they experienced their upper thermal limits of functional capacity in the field in muscular exercise. The long-term nature and irreversibility of the effect also suggest that this species experience their specific limits of warm acclimation capacity. Sommer *et al.* (1997) demonstrated that the lugworm, *Arenicola marina* that just like *Maja squinado*, that anaerobic mitochondrial metabolism not only occurring beyond low but also above high temperature extremes. Metzger *et al.* (2007) and Walther *et al.* (2009) indicated in cold temperate crustaceans like *Hyas araneus* or *Cancer pagurus* crab that the arterial hypoxaemia upon cold exposure is less expressed suggesting that kinetic reduction in functional capacity of the oxygen supply system can be overcome by cold acclimatization or cold adaptation.

Other studies related to oxygen consumption rates by crabs with effect of increasing temperature include those of Vernberg (1959b) indicated for *Uca pugilator* and *Uca pugnax* optimum temperature ranges of 12-17°C and 7-12°C respectively had little effect on their metabolism suggesting temperature of aerobic performance. Eshky *et al.* (1996) on study of *Uca inversa* and *Metopograpsus messor* at six test temperatures between 15 and 40°C indicated that temperature influenced their aerial respiration while Emmerson (1990) on studies of *Uca*

urvillei at five test temperatures between 15 and 30°C indicated also that temperature influenced their aerial respiration and summer acclimatized crabs consumed less oxygen than winter acclimatized crabs. Veeranan (1974) indicated that oxygen consumption rates in air by *Ocypode platytarsis* were lower than in water. Houlihan and Innes (1984) and Katsanevakis *et al.* (2007) on studies of *Pachygrapsus mamoratus*, Taylor and Leelapiyanart (2001) on *Cyclograpsus lavauxi* and *Heterozius Rotundifrons*, Roberts (1957b) on *Pachygrapsus crassipes*, Hawkins *et al.* (1982) on *Helice crassa* and Tashian (1956) on *Uca pugnax* reported that temperature influenced these crabs oxygen consumption rates and thus the concept is thus suitable to explain species responses in the field. Scholander *et al.* (1953) measured the rate of oxygen consumption at various temperatures of 38 species of tropical and arctic poikilotherms, including crustaceans, fishes and concluded that there was metabolic adaptation by aquatic arctic forms relative to tropical aquatic forms and that no evidence had been found to show that organisms are adapted to temperate fluctuation by being metabolically insensitive to temperature changes.

Chapter 3: Materials and Methods

3.1 Study Area

3.1.1 Location

The study site was Gazi-Bay situated in the south coast of Kenya about 55 km from Mombasa in Msambweni District. It lies between ($4^{\circ} 25'S$, $39^{\circ} 30'E$) (Figure 1). Mangroves of Gazi-Bay cover an estimated area of 615ha (Kairo *et al.*, 2008) with a maximum width of 3.3 km. The bay is sheltered from strong waves by the presence of the Chale peninsula to the east and a fringing coral reef to the south and is not continuously under direct influence of fresh water, because the two rivers Kidogoweni and Mkurumji draining into the bay are seasonal depending on the amount of rainfall inland. Groundwater seepage is also restricted to a few points (Kitheka, 1997).

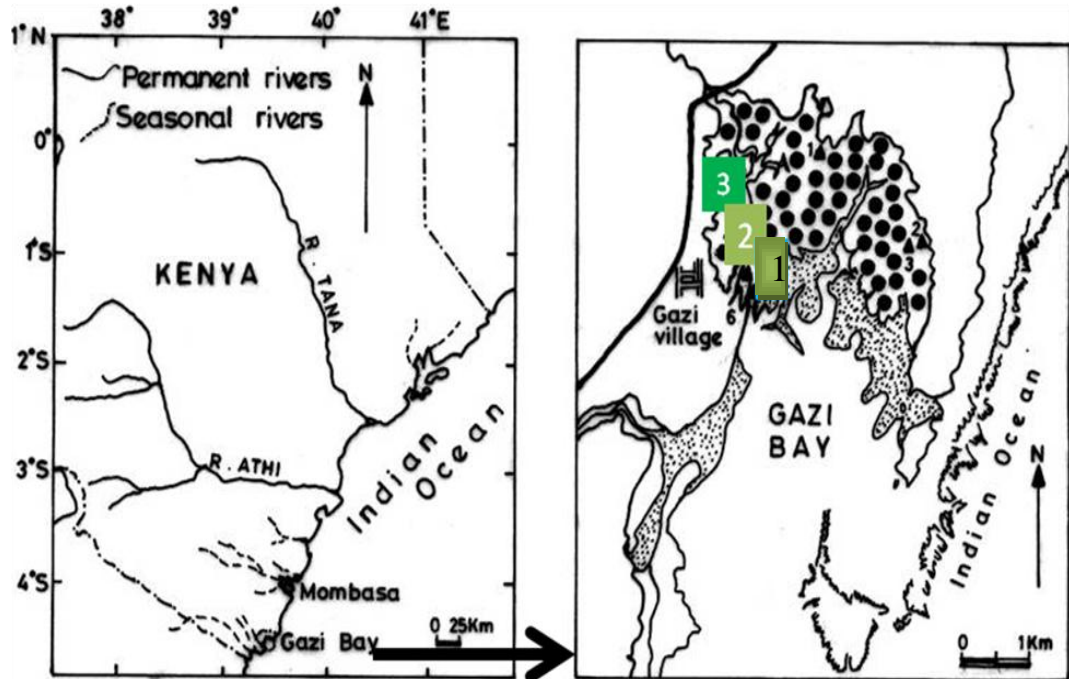


Figure 1. Map of the Kenyan coast showing the study area, Gazi-Bay. Adopted from Bosire *et al.* (2003). Sampling stations: 1. *Rhizophora mucronata* 2. *Ceriops tagal* 3. *Avicennia marina* zones

3.1.2 Climate

The climate in Gazi-Bay is typical of the Kenyan coast and is principally influenced by monsoon winds with two rainy seasons. The rains are heavier during the southeasterly monsoons and fall around April/August whereas the northeasterly Monsoon winds bring light rains around October/November (Bosire *et al.*, 2003). Total annual precipitation ranges from 1000-1600 mm at Gazi-Bay showing a bimodal pattern of distribution (Kairo, 2001). Average pore water salinity is 59 ppt with maximum salinity of over 70 ppt (Bosire *et al.*, 2006). It is normally hot and humid with an average annual air temperature of about 28°C

with little seasonal variation and temperature range between 24.8-39°C while relative humidity is about 95% due to close proximity to the sea (Bosire *et al.*, 2006). The seaward mangroves are inundated by tides twice a day with the highest tidal range of spring tide being about 4.0m (Bosire *et al.*, 2006).

3.1.3 Gazi-bay biodiversity

Ten species of mangroves represented at Gazi-bay include; *Avicennia marina* (Forsk.) Vierh., *Rhizophora mucronata* Lam., *Ceriops tagal* C. B. Rob., *Lumnitzera racemosa* Van Steenis, *Bruguiera gymnorrhiza* (L.) Lam., *Sonneratia alba* J. E. Smith, *Xylocarpus granatum* Koenig, *Xylocarpus moluccensis* (Lamk.) Roem, 1846 and *Heritiera littoralis* Dryand and *Pemphis acidula* Forst. *R. mucronata*, *C. tagal* and *A. marina* are the dominant species in Gazi-Bay (Spalding *et al.*, 2010). In Kenya, mangrove forests are facing increasing threats exacerbated by climate change leading to loss of biodiversity and 70% of the mangroves of Gazi-bay are degraded (Dahdouh-Guebas *et al.*, 2004) by several factors including effects of 1997/8 El-Niño rains that killed many mangroves. In order to enhance regeneration, trial mangrove plantations were initiated in degraded intertidal areas in 1991 (Kairo, 2001) and monospecific mangrove stands planted in denuded mudflats between 1994 and 2000 (Bosire *et al.*, 2004). There are more than 35 species of brachyurans belonging to six families and 4 anomurans associated within the Kenyan mangroves including Gazi-Bay (Cannicci *et al.*, 1997). The two species were chosen because: are abundant, ease of

collection, ease of maintenance under laboratory conditions and wide geographic distribution. Further the two species are strict residents of mangroves throughout their adult life and occupying different niches (Skov *et al.*, 2002) which could be easily exposed to effects of climate change. Richmond (2010) reported that mollusks found in Gazi-Bay mangroves include; *Terebralia palustris*, *Littoraria scabra*, *Cerithidea decollata*, *Peronia sp.*, *Isognomon ephippium*, *Isognomon isognomon* and *Crassostrea cucullata*. *Melampus sp* and *Terebralia palustris* (Linnaeus 1758) and shipworm *Dicyathifer sp.*

3.2 Sampling design

The project had both fieldwork and laboratory components. For crab density data, the sampling design adopted was stratified random sampling. The sampling stations here referred to as zones for density data collection were chosen based on type of vegetation along altitudinal gradient. Sampling was carried out in natural monospecific stands of *R. mucronata*, *C. tagal* and *A. marina*. Two transects approximately 100-500m apart perpendicular to the waterline were set randomly cutting across the three mangrove zones to ensure independence of samples. Four plots per zone of 10×10m² and at least 20m apart were randomly selected from a pool of eight plots for each of the three zones and their positions marked with a GPS. Thereafter, density surveys were carried out in these plots during the short rains months of October and November 2011 and repeated in the dry season months of December 2011 and January 2012. Each plot was divided into four

quarters and four 1-m² sub-quadrats were randomly selected for survey from each quarter making a total of 48 sub-quadrat samples per month. Stratified random sampling protocols were adapted during this study in order to minimise the effects of heterogeneous nature of the mangrove environment to the natural zonation of East African mangroves which has confounded efforts to quantify mangrove crab populations which are well known to vary even in a few centimetres (Chapman and Tolhurst, 2004; Cannicci *et al.*, 2009). Visual observation and burrow counts is known to provide at best crude estimates of population density, even where a single species is concerned unlike total excavation and extraction by sieving which is generally impractical as well as the destructive nature of the method and for logistical reasons (Macia *et al.*, 2001; Skov and Hartnoll, 2001).

3.3 Data collection

3.3.1 Determination of density of *Perisesarma guttatum* and *Uca urvillei* crabs

Sampling for the crab density was carried out across the intertidal area in the three mangrove zones during low tides of spring high tides using binoculars in the four 1-m² sub-quadrats per plot (Plate 1) five days during spring high tides of full moon to ensure maximum crab activities at all shore levels. For *U. urvillei*, density was estimated by a combination of visual and burrow counts which are both quick and non-invasive (Skov *et al.*, 2001; Cannicci *et al.*, 2009) due to complexity of mangrove habitat and behavior of these species. Visual counts of all the active crabs (species known to make burrows) on surface was done using binoculars

(8x40 magnification) when standing at a distance of about 3.5 metres from each quadrat and crabs were enumerated after observer remained motionless for 15 minutes in order to provide sufficient time for resumption of full activity. The highest count from at least two counts was taken and then the crab burrow openings were counted to avoid underestimation of crabs not active on the surface during visual counts (Hartnoll *et al.*, 2002). The density of *U. urvillei* was estimated by the burrow count data and calibrated with the species ratio (all species counted that make burrows observed within the quadrat) obtained from visual counting. For *P. guttatum* they were counted visually using binoculars throughout the 1-m² sub-quadrats. No burrow counts were used for *P. guttatum* because they do not make burrows (Skov *et al.*, 2002).

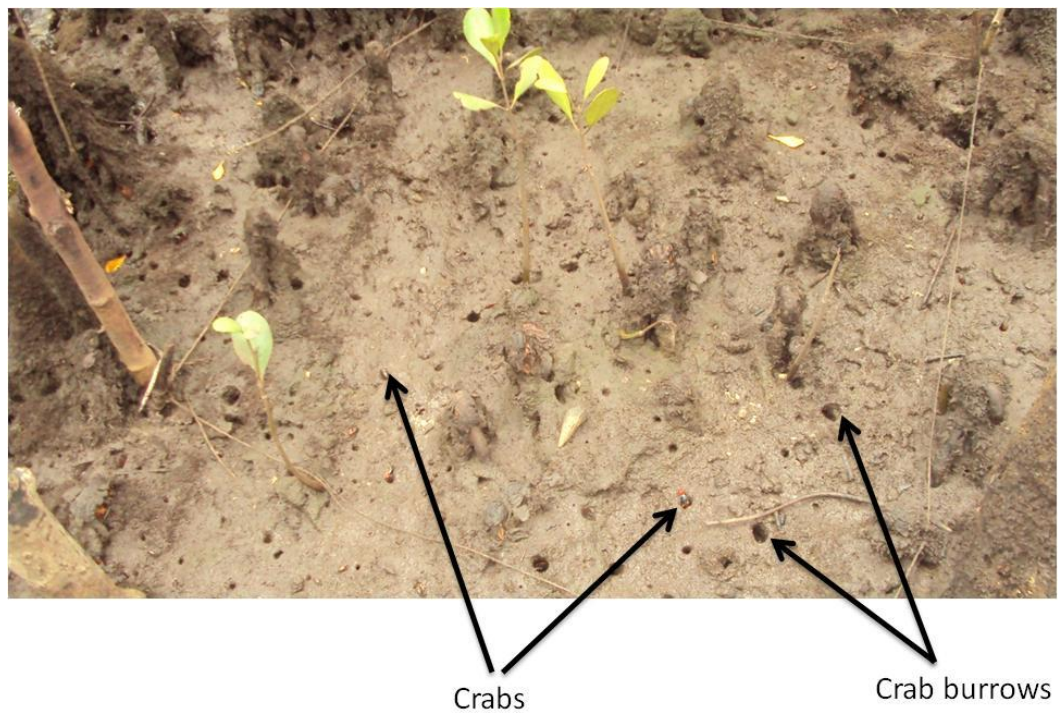


Plate 1. 1m² quadrat (enclosed with a piece of rope round) used to sample crabs in *Ceriops tagal* zone.

3.3.2 Measurement of abiotic factors

At each sampling station, data for the following parameters were collected to characterize the crab's habitat: Sediment temperature on the sub-surface was recorded using a digital probe thermometer, pore water salinity of sediment (determined from centrifuge-extracted interstitial water) measured using an optical refractometer (Atago brand), *in situ* data on Redox potential (Eh) and PH was measured using standard electrodes and a combination millivolt/pH meter. Redox potential (Eh) is a quantitative measure of reducing power which provides a diagnostic index of the degree of anaerobiosis or anoxia (Patrick and Delaune, 1977). Measurement of the pH was done with fresh samples of sediments to avoid oxidation of iron pyrites to sulphuric acid to avoid giving a much lower value of pH than normally occurs. Each of the above samples were taken at 10 cm and 40cm depths along the core.

Sediment characteristics sampled were; percent fine and coarse sand, silt and clay and organic matter of the sediment. In the sediment sampling, 4 cores of dimension 5cm deep by 2.5cm wide per plot per sub-quadrat in each zone were taken for granulometric analysis. Sediments were measured by placing a known weight of sediment of about 100-150 grames into an oven at 80°C for about 24 hours until constant dry weight was obtained for granulometric analysis. For granulometric analysis, about 25g for each dry sample from the oven were then weighed and transferred into pre-labeled beakers with 250ml water and 10ml of

aqueous sodium hexametaphosphate (NaPO₃)₆) and stirred for 10 minutes and left for a minimum of four hours. Thereafter, they were subjected to a series of sieves ranging from <63 to 500µm mesh sizes for wet-sieving to measure cumulative percent weights of soil particles sizes. The organic matter in the samples was obtained by ashing about 20g of the remaining dry sample from the oven to 450°C for four and half hours in the furnace and then cooling and weighing. The difference in weight gave an estimate of organic matter (Wartel *et al.*, 1995) as:

$$\% \text{ Organic matter} = \text{Initial weight(g)} - \text{Final weight(g)} \times 100\%$$

3.3.3 Collection of crab specimens for laboratory experiments

P. guttatum and *U. urvillei* specimens for thermal tolerance experiments were collected by hand capture during both day and night in selected mangrove sites at low tide. At least ten male adults per species per experiment were collected. They were kept and maintained in the laboratory for at least 24 hours (Vernberg, 1959b) at ambient temperatures of 27°C during the study period before the experiments. They were kept in plastic tanks with 5 cm mangrove soil sediment from their habitat area collected and were not fed. The health of the crabs was determined using the Righting Response Time method (Hogarth, 1999) and only those crabs that quickly righted themselves up were used.

3.3.4 Optimal thermal tolerance experiments for male adults of *Perisesarma guttatum* and *Uca urvillei*

Adults of *P. guttatum* and *U. urvillei* were maintained separately at different experimental temperatures (17-37°C) in temperature-controlled rooms. Respiration rate measurements were performed using a closed chamber system, consisting of five partially darkened respiration chambers (using aluminium foil to avoid visual stresses) and connected to single-channel, temperature compensated oxygen meters (Fibox 3-Presens de) as shown in Figure 2. The Fibox 3 was connected to a PC computer desktop that recorded all measurements. Each respiration chamber was put a single crab except the control without a crab and were submersed in a constant temperature recirculating water bath heated to the appropriate trial set-point temperature. The control chamber with no crab inside was used in order to correct for bacterial oxygen consumption.

The air and water experiments were performed separately for each species. The pipes aerating the chambers were sufficiently long enough to ensure that the air for air experiments or water for water experiments entering the chambers is similar to that of the surrounding water bath. For water experiments, within the crab chambers caution was taken to ensure no bubbles were introduced while putting the crab inside the chamber and sea water was always used that had been filtered to remove particulate matter (0.2µm filter). The water flow from each respirometer was controlled with a screw pinch clamp. The crab chambers were made of glass

with removable air tight lids and a screw fitting for the oxygen fibre optic cable and they had a capacity volume of 450ml.

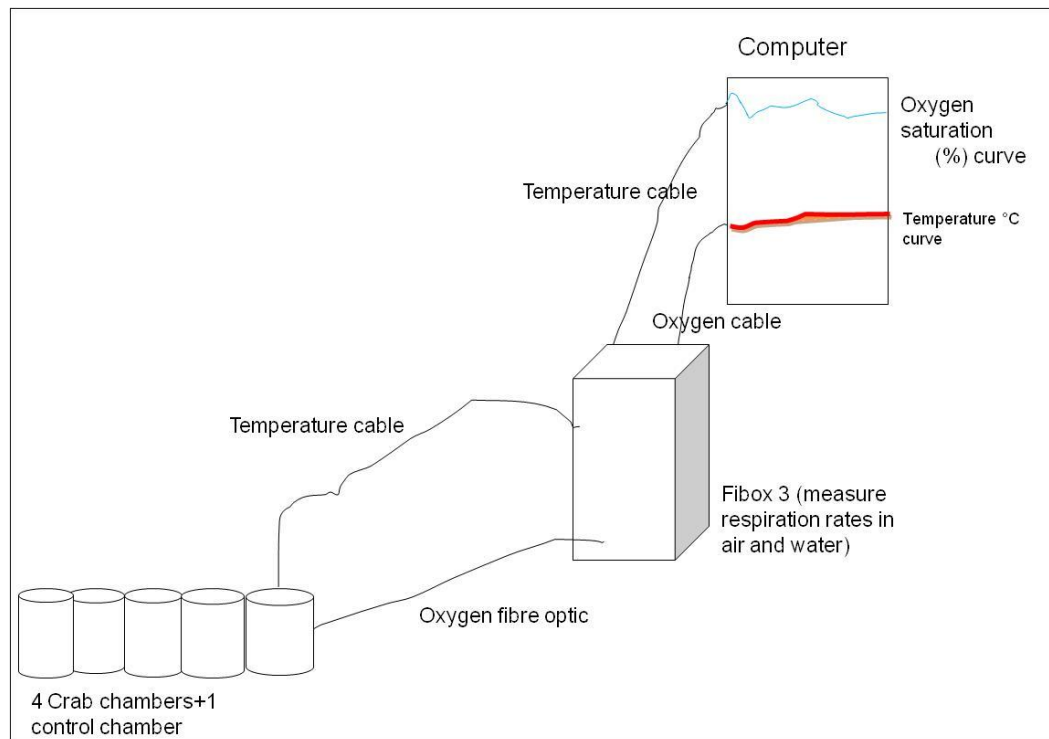


Figure 2. Laboratory crab experimental set-up to measure respiration rates

The experiments were divided into two parts; (a) increasing temperature from 27 to 37°C in air media per species separately and also increasing temperature from 27 to 37°C in water media per species separately (b) decreasing temperature from 27 to 17°C in water media only for each species separately. During each experiment, the crabs were acclimated for eight (8) hours in the respirometry chambers at 27°C the ambient temperature at Gazi Bay during the study period. The valves were then switched off using screw pinch valve/clamps to cut off

atmospheric oxygen for air experiments and external dissolved oxygen for water experiments as well as the control chambers to record oxygen consumption rate inside the chambers only. The respiration rate of each crab in the closed chamber was determined by measuring the decline in oxygen saturation (initial 100%) in the known volume of water and the air surrounding the crab in the chamber and was recorded each lasting 5 minutes making a total of 25 minutes for 5 chambers and used as their basal metabolism (Hervant *et al.*, 1998; Fredrick and Portner, 2000). At least two measurements/replicates of oxygen consumption rates per experiment were made for each crab respiration rates per temperature step to ensure a strong regression line of declining oxygen saturation.

Measurements of oxygen consumption rates were conducted every 20 minute between each of the two replicate measurements (one replicate here refers to one full measurement in 5 chambers per temperature step) at each experimental temperature per experiment. The declining rate of oxygen content/percent saturation (Y-axis) verses time (X-axis) was calculated as the slope of the regression line that fitted the oxygen consumption rates data verses time from the two pooled replicate measurements per temperature level which was automatically recorded by the computer. The oxygen content of the water was never allowed to fall below 80-90% saturation to avoid hypoxic stress during recording where for air experiments all measurements lasted for between 4 hours and for water experiments lasted upto 2 hours. In the case of air experiments, the

volume of the chambers was too great to allow feasible measurement of the consumption of 10-20% of the available oxygen so the volume was decreased by adding glass marbles to the chamber. The volume of glass marbles was recorded after the experiment and the new volume of the chamber was calculated. The crabs were used only once in each experiment and in water experiments water was not changed between replicate measurements. After the respiration rate at the acclimation temperature at 27°C was recorded, the valves were removed and the crab chambers reaerated again and the temperature was then increased gradually by 2°C interval for every 2 hours to the next experimental temperature while oxygen consumption rates was recorded till the maximum and minimum experimental temperature of 37°C and 17°C respectively.

At every experimental test temperature, the crabs were left to acclimate to the experimental temperature for a further 30 minutes and the experiment was then repeated at the new temperature and respiration rate was recorded. Each experiment lasted about 33 hours. 12 and 10 specimens or replicates of *P. guttatum* adult males were used in water and air respiration experiments respectively while for *U. urvillei* 15 and 12 specimens/replicates of males for water and air respiration experiments respectively were used and at least two measurements of temperature at each temperature level was performed. At the end of each experiment, the mass and volume of the crabs was recorded and subtracted from empty chamber to determine exact amount of respiratory medium of each crab per

experiment to get mean weight specific rates of oxygen consumption (μmol). All crabs were released 24 hours post experiment back to their area of collection (Eshky, 1999; Addo *et al.*, 2000 and Jimnezz and Bennet, 2005). Three incidences of mortalities of *P. guttatum* were reported during the experiments with two at 33°C and one at 37°C may be due to oxygen bubbles in the chambers. In, almost all instances in water experiments, therefore, measurements were made in 2°C increments over a total temperature range of 10°C above and below 27°C which for every species bracketed its preferred temperature. Assumption was made that the comparatively brief period of time spent at each measurement temperature (≤ 2 hours) provided for little or no temperature acclimation. Moreover, the considerable care taken to avoid disturbance during sampling or flushing of the respirometer probably prevented any cumulative stress effects during the course of the experiment.

Oxygen consumption rate recordings were carried out in constant darkness to try to eliminate the effects of diel changes in oxygen consumption rate. This follows studies with Warner (1977) and Brown *et al.* (1954) who observed that biological rhythms are relatively independent of temperature change and they reported that crabs did not show any diel rhythms of oxygen consumption rate over a temperature range at least 6-26°C in *Uca pugilator* which is most unusual with other biological processes. They noted that the amplitude of the diurnal rhythm neither increases nor decreases under constant laboratory conditions as was also

demonstrated in *Uca pugnax*. The decreasing temperature in water experiments was performed in order to understand the physiological responses/cold tolerance of these animals in cold water as these two crab species are naturally known to occur upto their southern latitudinal limit range in subtropical regions in the north coast of South Africa where they are exposed seasonally to chilly weather (Lee, 2008).

Only male crabs were used in this study following previous similar crab physiological studies which showed no differences in responses of either sex (Fredrick and Portner, 2000; Jimenez and Bennett, 2005) and thus was a representative model of these crab populations. Also thereproductive status of females varied among and between the two species with males being easy to collect unlike the berried females of *Uca urvillei* which spends more time in burrows. Further each experiment lasted for very long hours with each lasting 33 hours.

3.4 Data analysis

General Linear Model (GLM) ANOVA was used to test for the effect of increasing temperature (independent variable) on oxygen consumption rate (dependent variable) for each species while Tukey test was used to show which paired temperatures had significant effect on oxygen consumption rates. GLM was also used to test for the effect of temperature, species and media (independent variables) on oxygen consumption rates (dependent variable). GLM 3-factor

ANOVA with species (two levels), zones (3 levels), transects (2 levels), season (2 levels) as the factors and their interactions was used to test for significant effects of the factors on densities of the two species. Differences in environmental parameters between zones and season and also between zones and transects were tested using a two-way ANOVA with zones, season and transects as the factors. Relationship between crab density (dependent variable) and environmental parameters (independent variables) was carried out using Backward stepwise multiple regression analysis. Percentage data were arc-sine transformed prior to analysis. For the ANOVAs, the dependent variable crab density was square-root transformed prior to analysis to stabilize variance and ensure normality. All P-Values less than 0.05 ($P < 0.05$) were considered to be significantly different. All analysis were carried out using Minitab Version14 software.

Q_{10} is the factor by which an ectothermic physiological rate increases over a 10°C interval but also T_1 and T_2 do not need to be exactly 10 degrees apart in order to use this equation as shown in formula:

$Q_{10} = (\mathbf{R}_2/\mathbf{R}_1)^{10/(T_2-T_1)}$, where \mathbf{R}_2 = Final Respiration rate; \mathbf{R}_1 =Initial Respiration rate; T_2 =Temperature at \mathbf{R}_2 ; T_1 =Temperature at \mathbf{R}_1 (Jimenez and Bennett, 2005, www.physiologyweb.com).

Chapter 4: Results

4.1 Determination of thermal tolerance of adult males of *Perisesarma guttatum* and *Uca urvillei*

P. guttatum and *U. urvillei* displayed similar patterns of respiratory response to increasing temperature in both air and water media (Figure 3). The results show a general increase in oxygen consumption rate with increasing temperature in both media but not constantly at the range of temperatures tested. The graphs indicate two temperature levels, the low level where there was a discontinuous metabolic response despite increasing temperature generally and there was an almost apparent regulation of respiration rate. This temperature range was between 27-31°C for *P. guttatum* and 27-33°C for *U. urvillei*. The second level indicated by increasing oxygen consumption rates with increasing temperature was between 31-37°C for *P. guttatum* and 33-37°C for *U. urvillei* although there was a drop in oxygen consumption rates in *U. urvillei* at 33-35°C and then it rose again from 35-37°C. *P. guttatum* oxygen consumption rates nearly more than doubled that of *U. urvillei* at 37°C.

Oxygen consumption rate at initial temperature of 27°C was different for each species per media. At 27°C in water, *P. guttatum* and *U. urvillei* had 0.08 ± 0.04 and 0.06 ± 0.02 $\mu\text{mol/gmin}$ respectively while at 27°C in air, *P. guttatum* and *U. urvillei* had 0.14 ± 0.03 and 0.51 ± 0.02 $\mu\text{mol/gmin}$ respectively. At 37°C in water, oxygen consumption rates for *P. guttatum* and *U. urvillei* were 0.14 ± 0.02

$\mu\text{mol/gmin}$ and $0.09\pm 0.01 \mu\text{mol/gmin}$ respectively while at 37°C in air, $0.23\pm 0.11 \mu\text{mol/gmin}$ and $0.13\pm 0.04 \mu\text{mol/gmin}$ for *P. guttatum* and *U. urvillei* respectively.

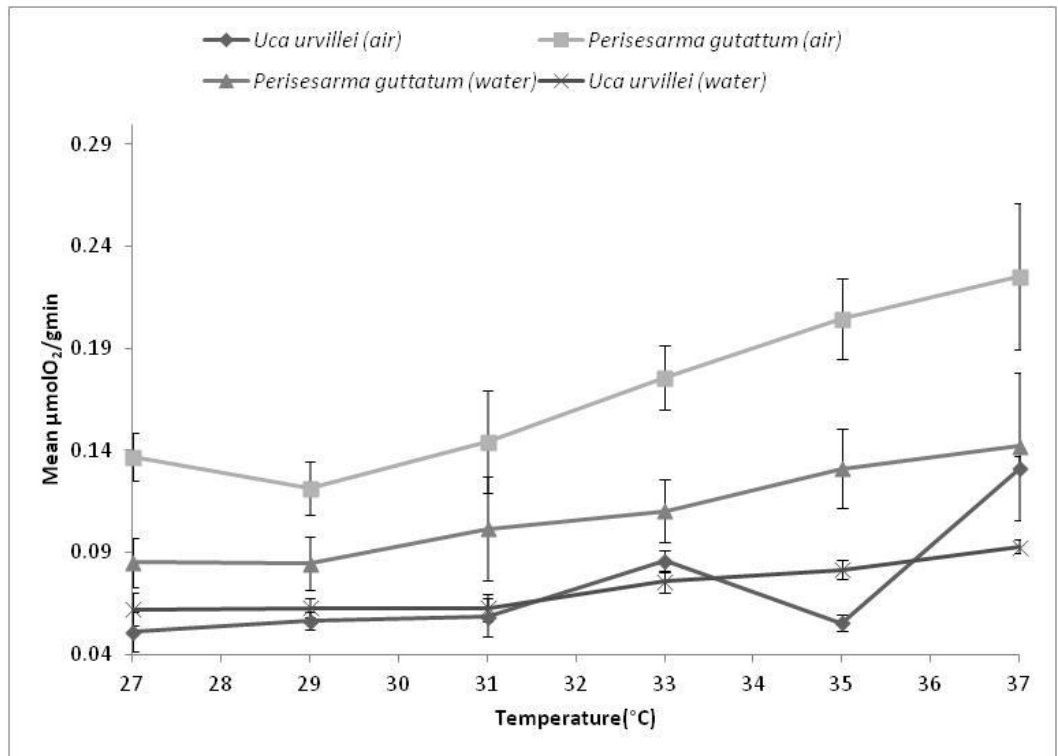


Figure 3. Relationship between temperature (mean±SE) and oxygen consumption rates of *P. guttatum* and *U. urvillei* crabs in air and water media.

Results in Figure 4 indicate oxygen consumption rates increased with increasing temperature in water media from 17-37°C in both species but not constantly at the range of temperatures tested. The graphs showed three major levels giving a staircase pattern; the lower temperature level 17-27°C and middle level 27-31°C for *P. guttatum* and 27-33°C for *U. urvillei* where there was an apparent regulation of respiration rate and lastly the high level temperature 31-37°C. In the low level

temperature, very low oxygen consumption rates with increase in temperature between 17-23°C was recorded indicating low metabolism for both species. Then oxygen consumption rate increased exponentially with temperature rise from 25-27°C. At the middle level, oxygen consumption rates did not increase with increasing temperature (oxygen consumption rate is temperature independent) where for *P. guttatum* this temperature range was 27-31°C while that of *U. urvillei* range was 27-33°C. The third level indicate an increase in oxygen consumption rates by both species with increasing temperature with *P. guttatum* rates nearly more than doubling that at 37°C.

The average rates of oxygen consumption of *P. guttatum* was $0.012 \pm 0.007 \mu\text{mol/gmin}$ half that for *U. urvillei* of $0.02 \pm 0.008 \mu\text{mol/gmin}$ at 17°C. On the hand oxygen consumption rates for *P. guttatum* and *U. urvillei* at 37°C were $0.14 \pm 0.02 \mu\text{mol/gmin}$ and $0.08 \pm 0.01 \mu\text{mol/gmin}$, respectively, which suggest that at low temperatures *U. urvillei* tend to have higher metabolic rates than *P. guttatum* while at high temperatures it is the opposite.

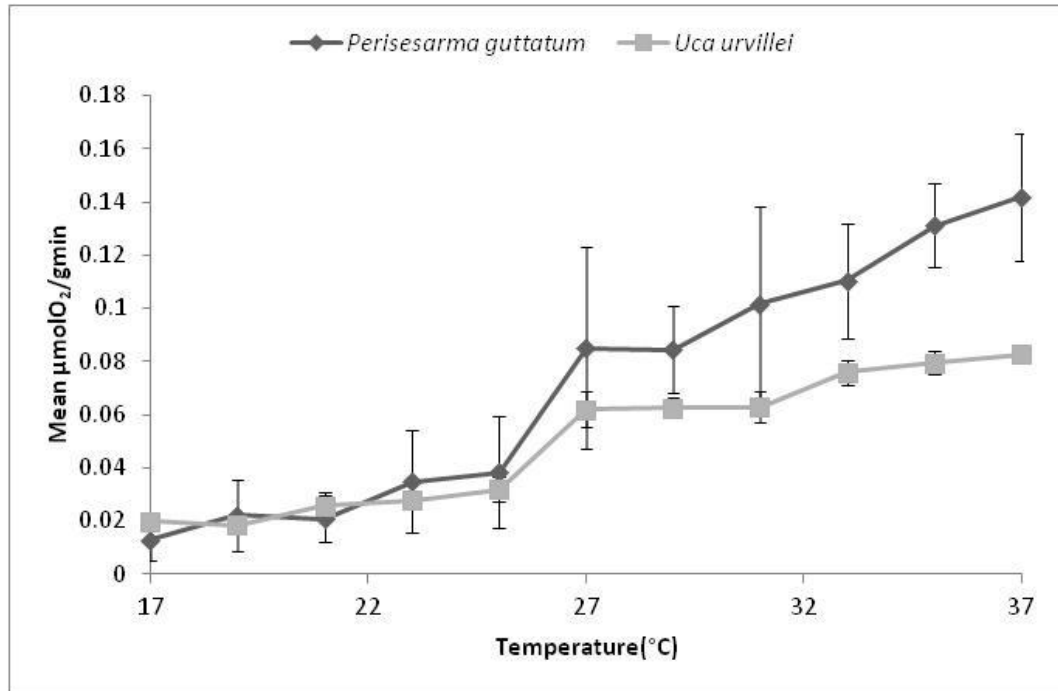


Figure 4. Relationship between temperature (mean \pm SE) and oxygen consumption rates of *P. guttatum* and *U. urvillei* crabs in water media.

Temperature variation showed significant effect on oxygen consumption rates ($F_{5,244}=15.95$, $P<0.05$) of *P. guttatum* and *U. urvillei* in both air and water media.

Oxygen consumption rates was significantly different between the two species ($F_{1,244}=155.39$, $P<0.05$) and also significantly different between air and water media ($F_{1,244}=27.64$, $P<0.05$) (Table 1).

Table 1. GLM ANOVA table for oxygen consumption rates verses temperature(T), species (Sp-*P. guttatum* and *U.urvillei*) and media

Source	DF	Seq SS	Adj SS	Adj MS	F	P
T	5	0.115618	0.126790	0.025358	15.95	0.000
Media	1	0.012297	0.043938	0.043938	27.64	0.000
Sp	1	0.247002	0.247002	0.247002	155.39	0.000
Error	244	0.387860	0.387860	0.001590		
Total	251	0.762776				

Temperature variation showed significant effect on oxygen consumption rates ($F_{5,125}=10.81$, $P<0.05$) in *P. guttatum* (Table 2) and in *U. urvillei* ($F_{5,134}=9.32$, $P<0.05$) (Table 3) in both air and water. There was a significant difference in oxygen consumption rates between air and water in *P. guttatum* ($F_{1,125}=61.35$, $P<0.05$) (Table 2) while there was no significant difference in oxygen consumption rates between air and water in *U. urvillei* ($F_{1,134}=0.12$, $P>0.05$) (Table 3). *P. guttatum* consumed higher oxygen consumption rates in air than in water throughout the tested temperatures while it is the opposite for *U. urvillei* with higher oxygen uptake in water than in air except between 33-35°C where there was a drop and then it rose again from 35-37°C (Figure 3).

Table 2. GLM ANOVA Table of *Perisesarma guttatum* verses Temperature (T) and media

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Temperaure	5	0.098564	0.096564	0.019313	10.81	0.000
Media	1	0.109636	0.109636	0.109636	61.35	0.000
Error	125	0.223396	0.223396	0.001787		
Total	131	0.431595				

Table 3. GLM ANOVA Table of *Uca urvillei* verses Temperature (T) and media

Source	DF	Seq SS	Adj SS	Adj MS	F	P
T	5	0.0413567	0.0413389	0.0082678	9.32	0.000
Media	1	0.0001090	0.0001090	0.0001090	0.12	0.726
Error	134	0.1188232	0.1188232	0.0008867		
Total	140	0.1602889				

For respiration rate of *P. guttatum* in air and water, temperature variation showed significant effect on oxygen consumption rates ($F_{5,125}=10.81$, $P<0.05$) (Table 2). Further analysis, by Tukey test, a low oxygen consumption rate which did not vary with increasing temperature was observed between the temperature range 27-31°C where temperature variation had no significant effect on oxygen consumption rates ($P>0.05$) in both air and water (Figure 3 and 4). Also by Tukey test, temperature variation showed significant effect on oxygen consumption rates between 33-37°C ($P<0.05$) and also between 17-27°C ($P<0.05$) (Figures 3 and 4).

For respiration rate of *U. urvillei* in air and water media, temperature variation had significant effect on oxygen consumption rates ($F_{5,134}=9.32$, $P<0.05$) (Table 3). Further analysis, by Tukey's test, the temperature range between 27-33°C did not show any significant effect on oxygen consumption rate ($P>0.05$) in both air and 4, water (Figures 3 and 4). Also by Tukey test, temperature variation showed significant effect on oxygen consumption rates between 33-37°C ($P<0.05$) and also between 17-27°C ($P<0.05$).

Q_{10} over the whole temperature range of 17-37°C for *P. guttatum* was 3.31 while for *U. urvillei* was 2.02. Aquatic oxygen consumption rates of *P. guttatum* and *U. urvillei* increased from 17-27°C with a Q_{10} value of 6.58 and 3.11 respectively thus clearly showing that Q_{10} of *P. guttatum* was higher than the later infact by double value. Over the temperature range 27-37°C in water media, the Q_{10} of

oxygen uptake was not similar for the two species with *P. guttatum* having 1.7 while that of *U. urvillei* was 1.3. Q_{10} for *P. guttatum* and *U. urvillei* in air over 27-37°C was 1.6 and 2.6 respectively which was the opposite for *Uca urvillei* to that recorded in water. Within the optimal temperature range for *P. guttatum* of 27-31°C, the Q_{10} was 1.5 while that for *U. urvillei* at optimum temperature range of 27-33°C Q_{10} was 1.4.

In summary, the optimum temperature range for *P. guttatum* was 27-31°C while that of *U. urvillei* was 27-33°C where temperature had no significant effect on oxygen consumption rates ($P>0.05$). The optimal thermal ranges of the two species are significantly different ($F_{3, 161}=4.02$, $P<0.05$) and thus the null hypothesis that the two species have no preferred optimal thermal range was rejected and the alternative hypothesis was accepted.

4.2 Crab density and distribution in mangroves

The results in Figure 5 indicate generally a high density of *Uca urvillei* than *Perisesarma guttatum* in the *Rhizophora mucronata* zone compared to that recorded in the *Avicennia marina* and *Ceriops tagal* zones. *P. guttatum* density was also highest in the *R. mucronata* zone followed closely by *C. tagal* zone and lowest in *A. marina* zone. The highest mean density (Number (No)/m²±SE) of *U. urvillei* and *P. guttatum* was 66.25±7.7 and 11.75±4.1, respectively, in the *R. mucronata* zone. *A. marina* zone recorded the lowest mean density (No/m²±SE) of the two species where that of *U. urvillei* was 0.18±0.7 and that of *P. guttatum* was 1.9±1.8. The density (No/m²±SE) of *U. urvillei* and *P. guttatum* in the *C. tagal* zone was 0.47±0.28 and 8.03±1.8 respectively.

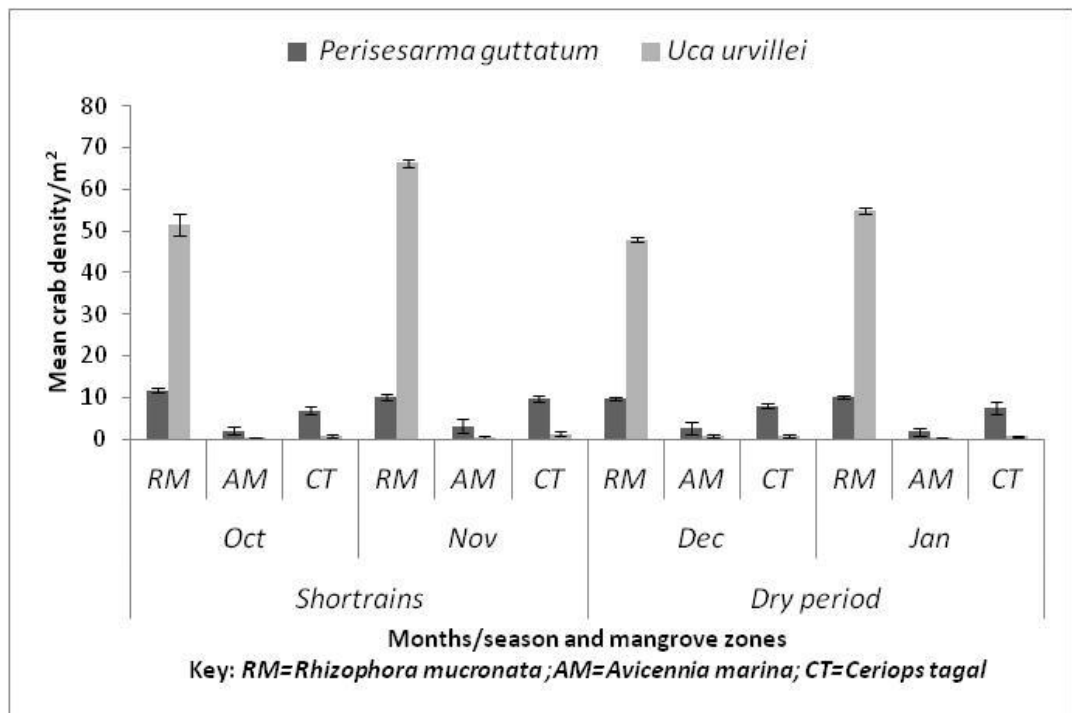


Figure 5. Mean density (±SE) of *P. guttatum* and *U. urvillei* in mangroves zones

There was a significant difference in the density of the two species between the three mangrove zones ($F_{2,47}=402.95$, $P<0.05$) for *U. urvillei* (Table 4) and ($F_{2,47}=65.04$, $P<0.05$) for *P. guttatum* (Table 5). Further analysis, using Tukey's test showed that *U. urvillei* density was significantly different between; *R. mucronata* and *A. marina* zones ($T=-28.75$, $P<0.05$), *R. mucronata* and *C. tagal* ($T=-27.66$, $P<0.05$) but was not significantly different between *A. marina* and *C. tagal* zones ($T=1.088$, $P>0.05$). For *P. guttatum*, there was significant difference in density between; *R. mucronata* and *A. marina* zone ($T=-9.996$, $P<0.05$), *C. tagal* and *A. marina* zones ($T=7.994$, $P<0.05$) but was not significantly different between *R. mucronata* and *C. tagal* zone ($T=-2.003$, $P>0.05$). The season, transects and neither interactions between zones, transects and seasons did not show any significant effect on density of these crabs ($P>0.05$) (Table 4 and 5, Figure 5).

Table 4. GLM ANOVA table of *Uca urvillei* density verses Zone, transect, season and interactions

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Zone	2	27170.3	27170.3	13585.2	402.95	0.000
Transect	1	1.6	1.6	1.6	0.05	0.829
Season	1	0.1	0.1	0.1	0.00	0.966
Transect*Season	1	6.9	6.9	6.9	0.21	0.653
Zone*Transect	2	71.4	71.4	35.7	1.06	0.358
Zone*Season	2	0.9	0.9	0.4	0.01	0.987
Zone*Transect*Season	2	17.7	17.7	8.9	0.26	0.771
Error	36	1213.7	1213.7	33.7		
Total	47	28482.6				

Table 5. GLM ANOVA table of *Perisesarma guttatum* verses zone, transect, season and interactions

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Zone	2	345.406	345.406	172.703	65.04	0.000
Transect	1	2.521	2.521	2.521	0.95	0.336
Season	1	1.880	1.880	1.880	0.71	0.406
Transect*Season	1	0.630	0.630	0.630	0.24	0.629
Zone*Transect	2	12.073	12.073	6.036	2.27	0.118
Zone*Season	2	0.448	0.448	0.224	0.08	0.919
Zone*Transect*Season	2	0.510	0.510	0.255	0.10	0.909
Error	36	95.594	95.594	2.655		
Total	47	459.063				

4.2.1 Environmental variables

The results revealed significant differences in environmental parameters and soil particle characteristics between the three mangrove zones ($P < 0.05$). The environmental factors did not show any significant variation with seasons and transects ($P > 0.05$) (Tables 6, 7 and 9).

Salinity

The highest porewater salinity recorded during the study period was 63‰ in the *A. marina* zone and the lowest was 21‰ in *R. mucronata*. The results in Figure 6 indicate mean porewater salinity in *A. marina* zone ranged from 42.25 to 51.75‰, for *R. mucronata* it ranged from 27.152 to 34.13‰ while for *C. tagal* it ranged from 34.53 to 44.75‰. There was a significant difference in salinity between the three mangrove zones ($F_{2,47} = 31.40$, $P < 0.05$) and but not between seasons ($F_{1,47} = 4.73$, $P > 0.05$) and neither interaction between season and zones ($F_{2,47} = 0.72$,

$P > 0.05$) (Table 6). There was no significant difference in salinity between transects ($F_{1,47} = 0.07$, $P > 0.05$) and neither interaction between transects and zones ($F_{2,47} = 0.29$, $P > 0.05$) (Table 7).

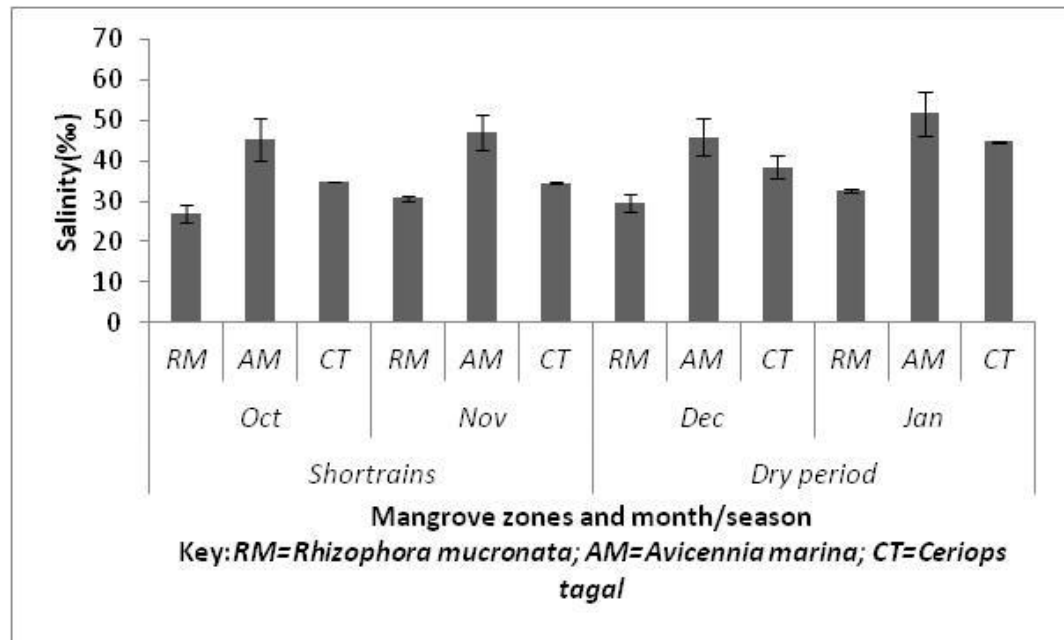


Figure 6. Mean (\pm SE) monthly salinity in mangrove zones

Temperature

The highest temperature recorded during the study period was 36.8°C in December in the *A. marina* zone while the lowest temperature recorded was 29.0°C in *R. mucronata* zone in November. In *R. mucronata* zone mean temperature ranged between 29.49-31.05°C, in the *A. marina* it ranged between 32.43-34.11°C while in *C. tagal* zones it ranged between 31.8-33.7°C (Figure 7). There was significant difference in temperature between the three mangrove zones ($F_{2,47} = 6.11$, $P < 0.05$)

and using Tukey test, temperature revealed significant difference between *R. mucronata* and *A. marina* zones ($T=2.548$, $P<0.05$) and between *R. mucronata* and *C. tagal* ($T=3.371$, $P<0.05$) while temperature was not significantly different between *A. marina* and *C. tagal* zones ($T=0.8225$, $P>0.05$). There was no significant difference in temperature between seasons ($F_{1,47}=0.72$, $P>0.05$) and neither interaction between season and zone ($F_{2,47}=1.21$, $P>0.05$) (Table 6). There was no significant effect of temperature on transects ($F_{1,47}=4.95$, $P>0.05$) and neither interaction between zone and transects ($F_{2,47}=1$, $P>0.05$) (Table 7).

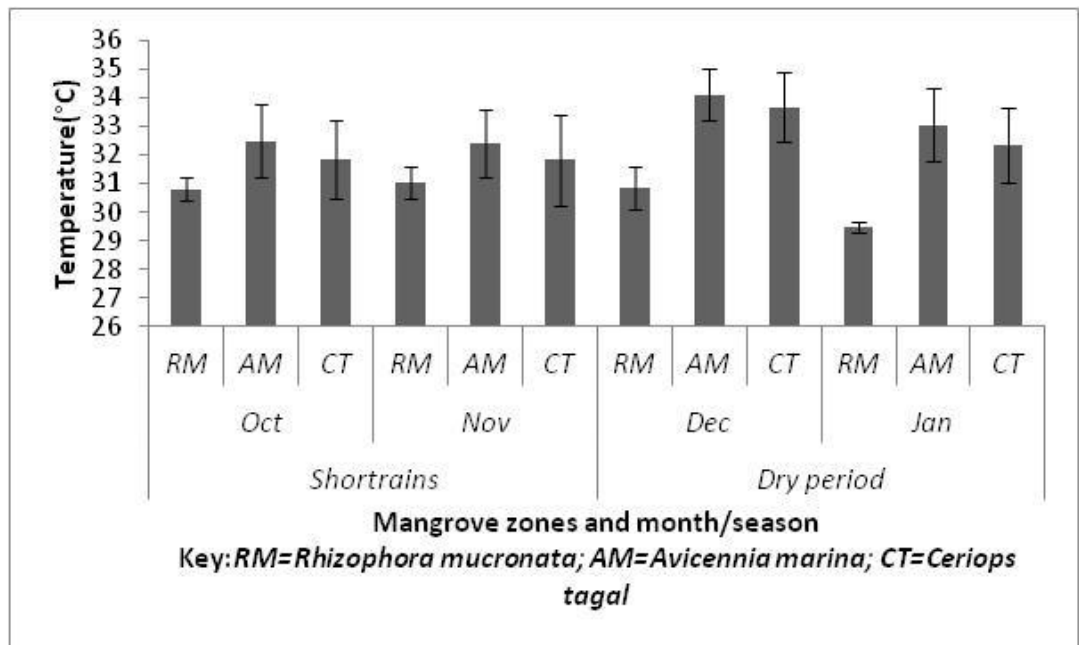


Figure 7. Mean (\pm SE) monthly temperature in different mangrove zones

PH

Mean PH value ranged between 5.6-6.67 in *R. mucronata* zone. In the *A. marina*, the pH ranged from 5.6-6.4 while in *C. tagal* it ranged from 6.0-6.3 (Figure 8).

There was no significant difference in pH between the three mangrove zones ($F_{2,47}=0.43$, $P>0.05$) nor interaction between season and zones ($F_{2,47}=0.32$, $P>0.05$) (Table 6). There was no significant difference in PH between zones and transects ($F_{1,47} =,0.24$ $P>0.05$) and neither interaction between zones and transects ($F_{2,47} =,0.30$, $P>0.05$)(Table7).

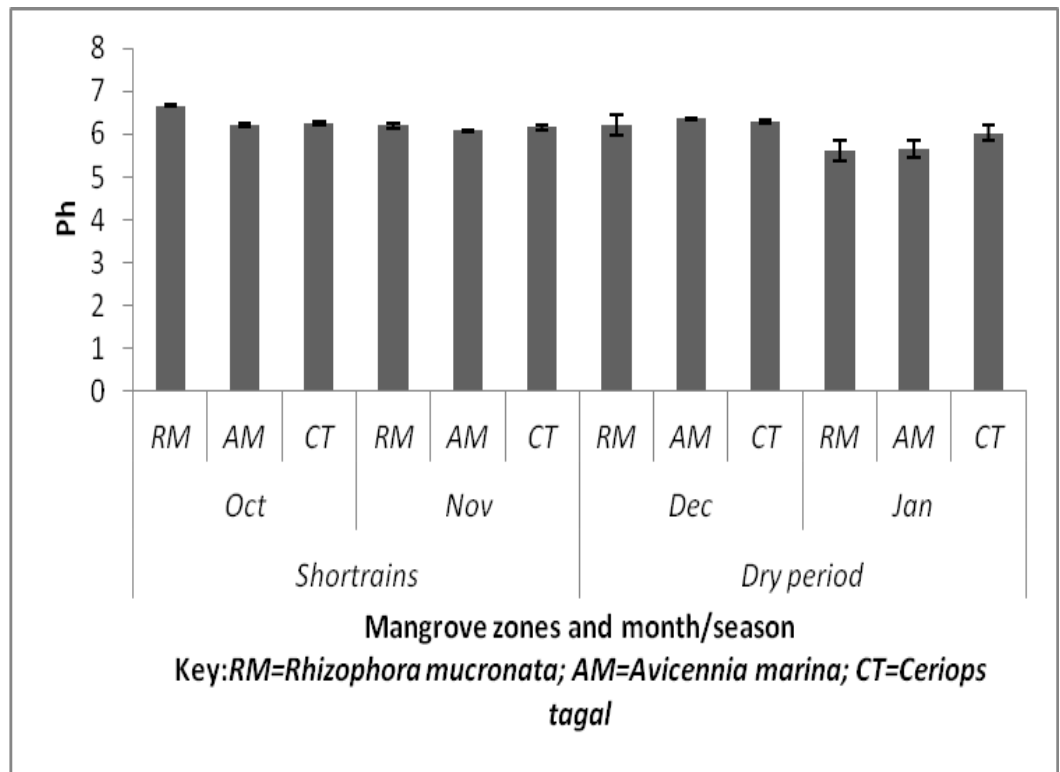


Figure 8. Mean (\pm SE) monthly pH in different mangrove zones

Redox potential (eH)

The highest redox potential recorded during the study period was 155.6 in *A. marina* and the lowest was -229.9 in *R. mucronata* zone. Redox potential in *R. mucronata* zone ranged between -186.68 and -113.38, in *A. marina* it ranged from

27.80 to 86.5 while in *C. tagal* zone it ranged between -146.0 to -74.81 (Figure 9). There was significant difference in Redox potential between the three mangrove zones ($F_{2,47}=28.3$, $P<0.05$) and Tukey test, revealed significant difference in redox between; *R. mucronata* and *A. marina* ($T=7.176$, $P<0.05$), *A. marina* and *C. tagal* ($T=-5.546$, $P<0.05$) while redox potential was not significantly different between *R. mucronata* and *C. tagal* zones ($T=1.630$, $P>0.05$). Redox potential did not show any significant difference between season ($F_{1,47}=4.01$, $P>0.05$) neither interaction between zone and seasons ($F_{2,47}=3.21$, $P>0.05$) (Table 6). There was no significant difference in Redox potential between transects ($F_{1,47}=1.78$, $P>0.05$) and neither interaction between transects and zones ($F_{2,47}=1.81$, $P>0.05$) (Table 7).

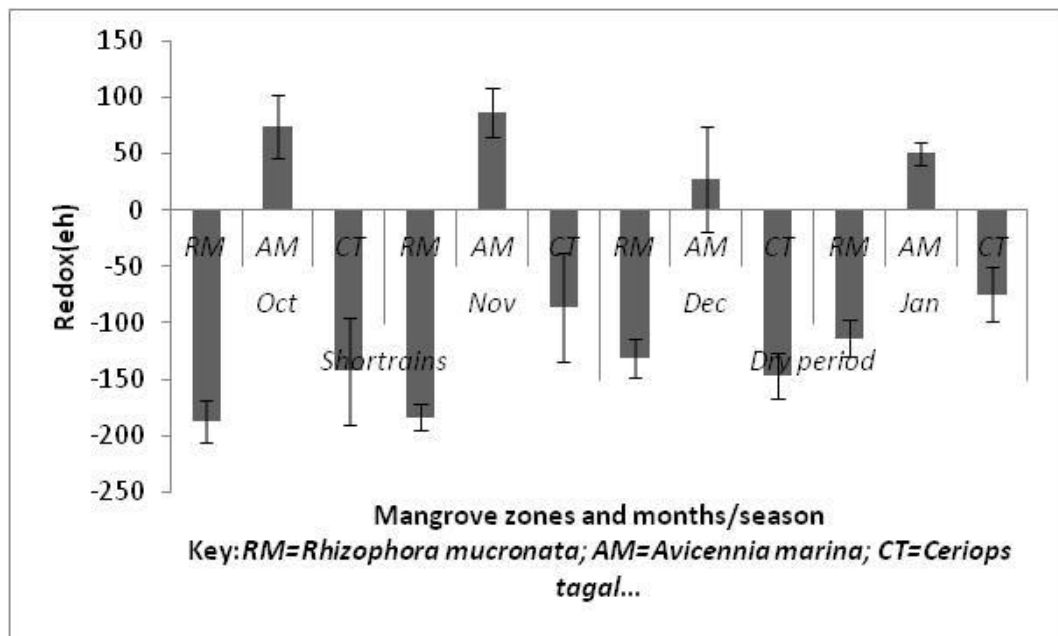


Figure 9. Mean (\pm SE) monthly Redox potential (eH) in different mangrove zones

Table 6. Two-way-ANOVA of environmental factors verses zones and season

Environmental						
Factor	Source	DF	SS	MS	F	P
Salinity	Season	1	185.06	185.06	4.73	0.053
	zone	2	2456.10	1228.05	31.40	0.000
	Zone*season	2	56.55	28.28	0.72	0.491
	Error	42	1642.69	39.11		
Temperature	season	1	3.276	3.2761	0.76	0.389
	zone	2	53.529	26.7645	6.18	0.004
	Zone*season	2	9.831	4.9157	1.14	0.331
	Error	42	181.868	4.3302		
PH	zone	2	0.10784	0.053920	0.48	0.620
	season	1	0.70333	0.703328	6.31	0.067
	Zone*season	2	0.49671	0.248355	2.23	0.120
	Error	42	4.68455	0.111537		
Redox potential	zone	2	2.71325	1.35663	28.30	0.000
	season	1	0.19203	0.19203	4.01	0.052
	Zone*season	2	0.30742	0.15371	3.21	0.051
	Error	42	2.01337	0.04794		

Table 7. Two-Way ANOVA table of environmental factors verses zones and transects

Parameter	Source	DF	SS	MS	F	P
Redox(Eh)	zone	2	2.71325	1.35663	25.58	0.000
	Transect	1	0.09435	0.09435	1.78	0.189
	zone*transect	2	0.19143	0.09571	1.81	0.177
	Error	42	2.22704	0.05302		
Salinity	zone	2	2456.10	1228.05	27.79	0.000
	Transect	1	2.88	2.88	0.07	0.800
	zone*transect	2	25.54	12.77	0.29	0.751
	Error	42	1855.89	44.19		
PH	zone	2	0.10784	0.053920	0.39	0.678
	Transect	1	0.03309	0.033091	0.24	0.626
	zone*transect	2	0.08375	0.041875	0.30	0.739
	Error	42	5.76774	0.137327		
Temperature	zone	2	53.529	26.7645	6.72	0.003
	Transect	1	19.712	19.7120	4.95	0.052
	zone*transect	2	7.944	3.9720	1.00	0.378
	Error	42	167.320	3.9838		

4.2.2 Soil characteristics

The *C. tagal*, *R. mucronata* and *A. marina* recorded the highest percent silt of $68.2 \pm 8.02\%$, $52.7 \pm 4.05\%$ and $31.3 \pm 18.8\%$ respectively (Table 8). There was significant differences in percent silt between the three zones ($F_{2,47}=125$, $P<0.05$) and Tukey test revealed significant differences between; *R. mucronata* and *A. marina*, *R. mucronata* and *C. tagal* and between *C. tagal* and *A. marina* zones ($P<0.05$). There was no significant difference in silt between transects ($F_{1,47}=0.01$, $P>0.05$) nor interaction between transects and zone ($F_{2,47}=0.01$ $P>0.05$) (Table 9).

Table 8. Particle sizes (%) variation over month/seasons and mangrove zones

Season	Month	Zone	Silt %	Fine sand (>63 μ m)%	Coarse sand (>500 μ m)%	Organic matter(%)
Short-rains	OCT	<i>RM</i>	52.7\pm4.05	36.3 \pm 4.1	10.95 \pm 4.5	22.7 \pm 2.6
		<i>AM</i>	20.1 \pm 8.15	63.2 \pm 14.7	16.7 \pm 6.6	12.3\pm8.1
		<i>CT</i>	68.2\pm8.02	24.8 \pm 5.8	6.9 \pm 2.3	14.6 \pm 10.7
	NOV	<i>RM</i>	34.6 \pm 10.7	52.8\pm6.7	12.6\pm7.4	24.2\pm2.4
		<i>AM</i>	23.8 \pm 4.6	56.9 \pm 4.2	19.3\pm7.0	10.9 \pm 5.3
		<i>CT</i>	54.27 \pm 5.1	37.3 \pm 12	8.4\pm0.6	13.8 \pm 10.2
Dry period	DEC	<i>RM</i>	51.2 \pm 20.9	39.4 \pm 15.6	9.3 \pm 6.7	24.1 \pm 0.9
		<i>AM</i>	31.3\pm18.8	53.9 \pm 17.8	14.8 \pm 9.1	9.7 \pm 5.7
		<i>CT</i>	60.3 \pm 15.4	32.9 \pm 12.8	6.8 \pm 2.7	14.7\pm11.4
	JAN	<i>RM</i>	42.4 \pm 25.2	51.1 \pm 1.3	6.5 \pm 23.9	23.6 \pm 1.6
		<i>AM</i>	13.1 \pm 3.3	73.6\pm7.5	13.4 \pm 10.2	11.8 \pm 6.4
		<i>CT</i>	48.8 \pm 17.4	43.6\pm2.4	7.6 \pm 15.0	12.6 \pm 9.1

Key: *RM*=*Rhizophora mucronata*; *AM*=*Avicennia marina*; *CT*=*Ceriops tagal*

Table 9. Two-Way ANOVA of soil particle characteristics verses transects and zones

Soil particle	Source	DF	SS	MS	F	P
Fine sand	Transect	1	0.04130	0.04130	0.72	0.399
	Zone	2	3.11883	1.55942	27.37	0.000
	Transect*zone 2	2	0.01748	0.00874	0.15	0.858
	Error	42	2.39327	0.05698		
Silt	Transect	1	158.0	158.0	1.08	0.305
	Zone	2	36678.4	18339.2	125.0	0.000
	Transect*zone 2	2	537.7	268.8	1.83	0.173
	Error	42	2.43050	0.057869		
Coarse sand	Transect	1	0.01029	0.01029	0.63	0.433
	Zone	2	2.32753	1.16376	71.00	0.000
	Transect*zone2	2	0.01718	0.00859	0.52	0.596
	Error	42	0.68846	0.01639		
Organic matter	Transect	1	249.43	249.427	62.53	0.0610
	Zone	2	1217.50	608.751	152.60	0.000
	Transect*zone 2	2	1202.29	601.144	150.70	0.000
	Error	42	0.017175	0.0004089		

A. marina zone generally had higher percent fine sand compared to the other two zones. *A. marina* recorded the highest value of 73.6% followed by *R. mucronata* at 52.8% while the highest value in *C. tagal* was 43.6% (Table 8). There was significant differences in percent fine sand between the three mangrove zones ($F_{2,47}=27.37$, $P<0.05$) and further analysis by Tukey test, fine sand showed significant differences between *R. mucronata* and *A. marina* zones ($T=2.552$, $P<0.05$), between *R. mucronata* and *C. tagal* zones ($T=3.372$, $P<0.05$) while there was no significant difference in fine sand between *C. tagal* and *A. marina* zones ($T=0.8198$, $P>0.05$). There was no significant difference in fine sand between transects ($F_{1,47}=0.72$, $P>0.5$) nor interaction between transect and zone ($F_{2,47}=0.15$, $P>0.05$)(Table 9).

The *A. marina* generally had the coarsest mean sediment or sand and recorded the highest value of $19.3 \pm 7.0\%$ followed by *R. mucronata* $12.6 \pm 7.4\%$ and finally *C. tagal* $8.4 \pm 0.6\%$ (Table 8). There was significant differences in percent coarse sand between the three mangrove zones ($F_{2,47}=71.00$, $P<0.05$). Further analysis by Tukey test coarse sand revealed significant difference between; *R. mucronata* and *A. marina* ($T=3.331$, $P<0.05$), *C. tagal* and *A. marina* zones ($T=-3.41$, $P<0.05$) while no significant difference was observed between *R. mucronata* and *C. tagal* zone ($T=-1.307$, $P>0.05$). There was no significant difference in coarse sand between transects ($F_{1,47}=0.63$, $P>0.05$) nor interaction between transects and zones ($F_{2,47}=0.52$, $P>0.05$) (Table 9).

The highest percent organic matter content was recorded in the *R. mucronata* zone of $24.2 \pm 2.4\%$ followed by *C. tagal* at $14.7 \pm 11.4\%$ and *A. marina* zone at $12.3 \pm 8.1\%$ (Table 8). The organic matter content revealed significant differences between the three mangrove zones ($F_{2,47}=152.60$, $P<0.05$) and also the interaction between zones and transects ($F_{2,47}=150.70$, $P<0.05$) but not between transects ($F_{1,47}=62.53$, $P>0.05$) (Table 9). Using Tukey test revealed significant differences in percent organic matter between; *R. mucronata* and *C. tagal* ($P<0.05$), *R. mucronata* and *A. marina* ($P<0.05$) but there was no significant difference in organic matter between *A. marina* and *C. tagal* zones ($P>0.05$).

4. 2. 3 Environmental variables and crab density

Table 10 indicate that temperature, salinity, silt, fine sand and organic matter had a significant effect on *U. urvillei* density ($P < 0.05$) and accounted for 69.82% of the variations in density. The lowest mean temperature, salinity and higher organic matter content, silt and fine sand were recorded in the *R. mucronata* zone which also recorded the highest densities of this species.

Table 10. Stepwise regression analysis (Backward) of the effects of dependent variable *Uca urvillei* density on the independent variables

Variable	Constant	T-Value	P-Value
Silt (<63 μm)	-27.4	-4.0	0.000
Fine sand (>63 μm)	-26	-4.13	0.000
Organic matter	0.155	-4.16	0.001
Temperature	-0.433	-3.66	0.001
Salinity	-0.086	-5.01	0.000

$S=0.442$, $R^2=69.82$, $R\text{-Sq}(\text{adj})=66.23$, Mallows $C\text{-p}=4.1$

$r^2=69.82\%$, $P < 0.05$

U. urvillei density (Y)=35.9(C)-27.4 Silt-26 Fine sand+0.155 Organic matter-0.433 Temperature-0.086Salinity

Table 11 indicate that temperature, fine sand and organic matter had a significant effect on *P. guttatum* density ($P < 0.05$) and accounted for 67.92% of the variations in density although silt could have a marginal effect on density of the species ($P > 0.074$).

Table 11. Stepwise regression analysis (Backward) results of the effects of dependent variable *P. guttatum* density on independent variables

Variable	Constant	T-Value	P-Value
Fine sand (>63 μm)	1.96	-2.05	0.047
Organic matter	4.3	3.80	0.000
Temperature	-0.074	-2.53	0.015

S=0.200, $R^2=67.92$, R-Sq(adj)=64.10, Mallows C-p=3.4
 $r^2=67.92\%$, $P < 0.05$

P. guttatum density (Y)=2.221(C)+1.96 Fine sand +4.3 Organic matter-0.074 Temperature

Chapter 5: Discussion

5.1 Determination of thermal tolerance of adult males of *Perisesarma guttatum* and *Uca urvillei*

The present investigation indicated that the metabolic rates of *P. guttatum* and *U. urvillei* increased over the temperature range 17-37°C indicating the animals were displaying standard metabolic rates since metabolism of ectothermes is temperature dependent (Bennett, 1988). However, within a certain temperature range of each species in both media oxygen consumption rate was more less independent of temperature and this suggests the optimum temperature range. This temperature range of no metabolic change with increasing temperature for *U. urvillei* was 27-33°C while that of *P. guttatum* was 27-31°C suggesting the later's thermal tolerance window is narrower thus indicating that the two species have different optimal thermal ranges. This clearly showed a difference in thermal sensitivity of the two species which agrees with the general observation by Angilleta *et al.* (2009) that no two organisms have exactly the same thermal restrictions.

These results are similar to those of Fredrick and Portner (2000) who determined the optimum temperature range for spider crab, *Maja squinado* to be between 8-17°C for maximum aerobic scope. Other similar studies by Teal (1959) for seven *Uca* species observed that oxygen consumption rates were relatively temperature-insensitive within a given optimum temperature range, for example *Uca minax* and

Uca pugilator consumed oxygen at the same rate between 11.1-15.9°C and 13.2-19.4°C respectively, and temperature had little effect on their metabolism. At certain points in the range it was observed a discontinuous metabolic response despite increasing temperature which in this case for *P. guttatum* corresponds to the temperature range 27-31°C with a Q_{10} of 1.5 while that for *U. urvillei* was at 27-33°C with a Q_{10} of 1.4. These Q_{10} values are closer to 1 which is thought to indicate thermal insensitivity. Relatively low Q_{10} values indicate wide thermal tolerance of the species (Katsanevakis *et al.*, 2007) and within the normal environmental temperature range, the Q_{10} values for oxygen consumption rates are consistently less than or equal to 2. Q_{10} over the whole temperature range of 17-37°C for *P. guttatum* was 3.31 while for *U. urvillei* was 2.02. This agrees with studies by Katsanevaskis *et al.* (2007) who reported that most crustaceans have a Q_{10} of between 2 and 3.

These studies have shown that, for both species, values of Q_{10} are lower in the temperature range normally experienced but increase at temperatures outside this range which indicate the temperature of stress and concurring with studies by Eshky *et al.* (1996). This reduction in the sensitivity of metabolic rate to changing temperature has been interpreted as a mechanism by which energy could be conserved despite the increase in environmental temperature. Newell (1969) reported that the metabolic rate in response to acute temperature change varies very little over a wide portion of physiological temperature range in intertidal

animals. The adaptive significance of this is that the standard rate of respiration of intertidal invertebrates is relatively independent of fluctuations in temperature and is not only lower but often has a low temperature coefficient. Some organisms may temporarily decrease metabolism below these levels or even enter ametabolic states in response to unfavorable environmental conditions. However, they are not fully functional organisms under these conditions and must return to normal metabolic levels to proceed with normal processes of life (Bennett, 1988). Thus, a comparatively stable oxygen consumption rate over that range of temperature fluctuation encountered on a daily basis is of significant value to these intertidal organisms. As a result, adaptation to intertidal life in these crabs entails high metabolic flexibility and efficient regulation of metabolism in a wide range of environmental temperatures. The difference in Q_{10} values for oxygen consumption rates between the two species *P. guttatum* and *U. urvillei* may reflect differences in the range of temperatures that they normally experience in the field. Although both species occur at the same location, differences in their life style in occupying different niches and behaviour may result in the two species experiencing somewhat different temperature regimes and is in agreement with studies by Eshky (1999).

The temperature ranges of 27-31°C and 27-33°C for *P. guttatum* and *U. urvillei* respectively infer the temperature window of maximum scope for aerobic activity suggesting the range of optimum performance supporting successful survival

where availability of aerobic energy is maximal for all physiological functions including growth and reproduction in the natural environment. This is also in agreement with studies by Weinstein (1998) on the ghost crab *Ocypode quadrata* who reported a temperature range of 24-30°C which did not display a significant change in resting metabolic rate suggesting the maximal rate for aerobic scope. However further studies on measurement of oxygen tension in crab haemolymph, heart rate and anaerobic products as well as LT₅₀ (Lethal Temperature at which 50% of animals experimented die) need to be done to validate optimum temperature range and establish critical temperature ranges.

The results suggest that *P. guttatum* is more sensitive to temperature variation than *U. urvillei* and above this optimal temperature ranges evidence of thermal stress is depicted by the high demand for oxygen indicated by increased oxygen consumption rates hence high metabolism at high temperatures. This could be interpreted to mean that at high temperatures, excessive oxygen demand causes insufficient oxygen levels in the body fluids to compensate for increased metabolic rates. But the higher oxygen demand is limited by oxygen availability as solubility of oxygen in warm water decreases with increasing temperature leading to stress in the crabs. Also, the limited capacity of the circulatory and ventilatory systems to keep pace with the increased oxygen demands of basal metabolism at higher temperatures causes a reduction in aerobic scope, allowing less energy to be devoted to, for example, feeding, growth and reproduction. Portner and Knust

(2007) suggested that a reduced aerobic scope is the key physiological mechanism that determine response of ectothermes to increased ocean temperature. In the decreasing temperature from 27 to 17°C for both animals, oxygen consumption rates decreased with decreasing temperatures. This could be interpreted to mean that at low temperatures even in fully aerated waters, there is limited capacity by the ventilatory and circulatory systems to match oxygen demand for basal metabolism. Also, the aerobic capacity of mitochondria may become limiting and could cause a reduction in aerobic scope where the animals could resort to anaerobic metabolism.

The rate of metabolism of both species in water and air displayed different patterns whereby the rate of oxygen consumption for *P. guttatum* was consistently lower in water compared to the rate in air while for *U. urvillei* the rate in water was higher than in air media. This observation in *P. guttatum* is in agreement with studies with Jimenez and Bennett (2005) on the fiddler crabs *U. vocans*, *U. tetragonon* and *U. crassipes* who reported similar patterns. They reported that the low aquatic oxygen uptake may be a characteristic common to semi-terrestrial crabs suggesting that aquatic oxygen uptake for these crabs may be insufficient to meet metabolic costs. This further suggest that *P. guttatum* use more energy in air than in water to meet metabolic costs and hence have to spend more time in air as compared to *U. urvillei* as evidenced by the more than twice the oxygen consumption rates by *P. guttatum* than *U. urvillei*. This could mean a better tolerance to temperature

change in air than in water by *P. guttatum* and is less dependent on anaerobic respiration and may not need to rapidly pay back oxygen debt. *U. urvillei* showed that oxygen uptake in air was lower with respect to water (except at temperatures 33-35°C) suggesting that *U. urvillei* is more sensitive in air than in water. This low oxygen uptake in air was interpreted to be the direct consequence of the lower metabolic cost of extracting oxygen from air than from water. This observation on *U. urvillei* agrees with studies by Eshky *et al.* (1990) on the ghost crabs, *Ocypode saratan*, Veerannan (1974) on *Ocypode platytarsis*, McMahon and Russell-Hunter (1977) on *Littorina littorea* snails and Cannicci *et al.* (2011) on bimodal respiration of crab embryos who reported similar respiratory patterns. On the other hand it contradicts studies by (Jimenez and Bennett, 2005) on related species *U. vocans* and *U. tetragon* which had low aquatic oxygen uptake than aerial uptake. This suggest that for *U. urvillei* water respiration is an active and expensive process, in terms of energy, to maintain normoxia.

Eshky *et al.* (1990) and Jimenez and Bennett (2005) reported that the difference in relative oxygen uptake in water and air by these semi-terrestrial crabs exhibiting a bimodal respiration is often used to ascertain how these organisms are adapted to the aquatic or terrestrial environment. Due to low dissolved oxygen tension crabs have adopted several methods to maintain a constant rate of oxygen uptake such as increasing the ventilation rate, increasing the percentage of extraction of oxygen and by opting to changing to air breathing (Eshky *et al.*, 1990). Skov *et al.* (2002)

noted that in their natural environmental conditions, *P. guttatum* is a free-roaming species found in shaded mangrove areas and not often in open areas and is active throughout the day and night at low tide to feed and utilize other crab burrows or crevices during high tide and only burrows when shelter such as root systems is unavailable for protection from temperature fluctuations and predators. On the hand, *U. urvillei* a known burrower and active during daytime only at low tide emerging from its burrow to feed and can be found in both exposed and shaded areas in the mangroves and this implies that it can withstand wide temperature variation. Thus *P. guttatum* spends more time in the air than *U. urvillei*.

Most activity of these crabs take place in air and oxygen concentration of air is 20% higher than in water (Hogarth, 1999) even at saturation levels. Because *P. guttatum* spends most of its time in air it is less dependent on anaerobic respiration and may not need to rapidly pay back oxygen debt. Portner (2002a) and Cannicci *et al.* (2011) reported that the leading advantage for evolving a terrestrial development is the thirty-fold abundance and 10,000 times higher diffusiveness of oxygen in air than in water. Therefore the opportunity to adopt aerial respiration could indeed reduce the problems described for marine species due to the limiting oxygen demand in water as it warms due to increased temperatures. The temperature tolerances of these *P. guttatum* and *U. urvillei* could reflect their distribution in the mangrove forests as the laboratory optimal temperature range of 27-33°C established does fall within the normal field environmental temperature

ranges of these animals observed. Therefore, small changes in temperature of a few degrees celsius from the current optimal limits suggest it could influence the physiological condition, developmental rate, growth rate and reproductive performance of these crabs all of which could affect the structure of the adult populations and consequently population sustainability. If environmental temperature rises beyond these optimal ranges, *P. guttatum* which is thermally sensitive than *U. urvillei* will be more vulnerable to thermal stress. This is because they live in constant shade and are not generally adapted to the high temperatures found in warmer open habitats and have few behavioral options available to evade rising temperatures. Consequently, any climate induced increase in operative temperature could cause declines in thermal performance and fitness.

When conditions change rapidly, resistance mechanisms are important, and oxygen limitation has been demonstrated in present study to be the mechanism dictating survival limits which is in agreement with Pery *et al.* (2008) under adaptational limitation. Although death may not be the immediate response, sublethal effects such as decrease in number of offspring may contribute to eventual decline or demise of species. Sanford *et al.* (2006) suggested factors that could limit northward expansion of fiddler crabs include availability of marsh habitats, transport of larvae by oceanographic currents and biological interactions.

5. 2 Determination of density and distribution of *Perisesarma guttatum* and *Uca urvillei* crabs

The current study recorded almost similar densities of these crabs to those recorded by Cannicci *et al.* (2009) although they compared only *Rhizophora mucronata* and *Avicennia marina* zones and excluded the *Ceriops tagal* zone. The results clearly show that the *U. urvillei* and *P. guttatum* reported high densities in the *R. mucronata* zone suggesting it is a preferred habitat hence a strong predictor for their densities as compared to the other two zones. However, densities of *P. guttatum* in the *R. mucronata* and *C. tagal* zone were comparable but very low densities were recorded in the *A. marina* zone. The results further indicated that the *P. guttatum* and *U. urvillei* were not evenly distributed within the three mangrove zones and varied widely with very low densities in the *A. marina* and *C. tagal* zones to very high densities in the *R. mucronata* zones. On the other hand, *P. guttatum* despite having much lower density compared to *U. urvillei* was found in all the three mangroves zones in shaded areas.

The very low densities of *U. urvillei* in the *A. marina* and *C. tagal* zone could be attributed to high temperatures, high salinities, high coarse sand particles and low organic matter content. These factors could also contribute to the trees being stunted which was observed during the study as the landward *A. marina* and *C. tagal* trees are stunted and have less dense canopy. Hypersalinity salinity has been shown to induce stunted growth of *A. marina* (Kathiresan and Bingham, 2001).

Salinity was highest in the landward *A. marina* zone and lowest in the lower shores of *R. mucronata*. The high salinity in the landward *A. marina* and *C. tagal* zone could be attributed to less dense shade canopy which is more open leading to high water evaporation due to high temperatures rates resulting in concentration of salts thus high soil salinity. There is also the restricted exchange between tidal water and interstitial water as these areas are rarely inundated except only during spring high tides. Mangrove vegetation is more luxuriant in lower salinities (Kathiresan and Bingham, 2001) which is true for *R. mucronata* compared to the other two mangrove species. This clearly indicated that *U. urvillei* is intolerant to higher salinities which is known to pose serious physiological problems.

There was no variation in pH between the three mangrove zones and Middelburg *et al.* (1996) reported similar results. Kathiresan and Bingham (2001) observed that mangroves achieve maximum root growth at an acidic pH of 6 indicating normal mangrove soil pH which is similar to what was recorded in this study. Acidic conditions can occur in mangrove sediments that are regularly flooded and mangroves are known to affect the acid-base balance of their sediments (Middelburg *et al.*, 1996) which could explain the similarity in pH in the three mangrove zones during this study at spring high tides. *U. urvillei* are the least advanced toward a terrestrial existence and are mostly confined to firmer mud substrates at lower tidal levels on less steep banks and flatter areas adjacent to channels in relatively shaded situations (Crane, 1975). Similar distribution patterns

were observed for this species in this study. Thus the presence of vegetation and its associated benefits is an important factor affecting the distribution of *U. urvillei* (Edney, 1962). The results of this study demonstrated a strong relationship between the density of *U. urvillei* and environmental variables such as temperature, salinity and soil characteristics such as organic matter, silt and fine sand. The factors overall explained more than $r^2=69\%$ of the variability in density of *U. urvillei* indicating that this study did not investigate all variables affecting their density distribution.

The high density of *U. urvillei* in the *R. mucronata* zone could be attributed to low sediment temperature and salinity as compared to the other two zones which recorded higher temperatures and salinities and consequently low densities as these factors are known to affect their physiological responses and behavior. This concur with past studies by Hartnoll *et al.* (2002); Ashton *et al.* (2003); Bosire *et al.* (2004) and Cannicci *et al.* (2009) who reported existence of a corelation between abundance and distribution of mangrove crabs with soil salinity, temperature and soil organic carbon. However, Ashton *et al.* (2003) indicated that environmental measurements should be treated with caution as they only give a general indication of conditions because they vary with the time of day and in relation to tidal inundation, seasons and weather. Sediment temperature within the mangrove forest during the study period varied from 29.01 to 36.8°C and was shown to be significantly different between the three mangrove zones which could

affect the density and distribution of the two crab species. However, there was no clear pattern on effect of temperature on density of these crabs over season. *U. urvillei* require fine grain size to sort their food hence percent silt and fine sand with a preference for the later becomes very important in their feeding habits and the suitability of this fine grain size for making permanent burrows thus it displayed a strong relation to the densities of these crabs. Substrate characteristics may play a very important role in influencing crab distribution and Seiple (1979) found that substrate preference appeared to regulate the distribution of sesarmid crabs in Atlantic coastal salt marshes. However, silt was also abundant in *C. tagal* zone which recorded very low densities of *U. urvillei* suggesting that silt may not be the only variable explaining their abundance but could be occurring in combination with the other factors. This agrees with Frith and Brunenmeister (1980) who observed the absence of *U. urvillei* from non-mangrove shores around Phuket Island even though suitable substrates were available to them.

Bosire *et al.* (2003) observed that organic matter content vary in relation to substrate type thus, the finer substrates silt and fine sand observed in *R. mucronata* and *C. tagal* zone contained more organic material than the coarser substrates of landward *A. marina* zone. The correlation of particle size with organic matter is appropriate for a deposit feeder with a sorting mechanism attuned to a certain particle grade (Cannicci *et al.*, 2009) and thus sediment quality with high organic matter content is more relevant to *U. urvillei*. Further, the high organic matter

content encourages growth of algae and diatoms which serves as the food for these detritivorous fiddler crabs. The presence of *P. guttatum* species in *C. tagal* pure zone in almost equal densities as in *R. mucronata* zone in the present study clearly indicates that this zone is an equally important preferred habitat for this species hence explaining their abundance patterns. This is in agreement with Dahdouh-Guebas and Koedam (2001) who found that the presence of mangrove trees and associated microhabitats accounted for the high abundance of grapsid crabs including the *P. guttatum*.

The stunted *C. tagal* and *A. marina* zone have less dense shade canopy hence more open and thus less leaf litter fall. This means less nutrient recycling hence low organic deposition and consequently leading to low soil organic matter content in these zones. *P. guttatum* density was significantly related to temperature, organic matter content and fine sand. Their low densities in *A. marina* zone could have been affected by the high temperature and the low organic matter content as these crabs are known to occupy shady areas to avoid thermal stress. *P. guttatum* like other *Perisesarma* spp supplement their diet with mangrove leaves in addition to sediment with high organic matter (Skov and Hartnoll, 2002) which was quite low in *A. marina* zone to sustain *P. guttatum* populations. *P. guttatum* is an omnivore although most of its diet through stomach content analysis (Hogarth, 1999) indicate it is mostly an herbivore and its ability to collect fallen leaves is very dependent on a prolonged exposure to air within the shaded mangrove areas

inundated by tides most of the time with high organic matter content. This suggest that since most of the landward shores of *A. marina* are rarely inundated except only during spring high tides coupled with higher temperatures due to less dense shade canopy could explain the observed low abundance patterns of this species in this zone. The high densities of *P. guttatum* in *C. tagal* and *R. mucronata* zone suggest it plays a big role in these mangrove zones. Bosire *et al.* (2003) reported that sesarmids including the *P. guttatum* assist in seedling predation in mangrove forests and determine mangrove plant community structure through influencing the growth of mangrove seedlings by selective predation of propagules thus reducing competition between mangrove plants species.

5.3 Conclusion and Recommendations

5.3.1 Conclusion

An important observation from these results is that the optimum temperature range established for *Perisesarma guttatum* and *Uca urvillei* crabs was 27-31°C and 27-33°C respectively. The results indicate that *P. guttatum* is more sensitive to temperature variation than *U. urvillei* and displayed a slightly narrower thermal tolerance window than *U. Urvillei* probably to minimize maintenance or energetic costs. Thus the null hypothesis that the two species have no preferred optimum thermal range was rejected and the alternative hypothesis accepted that the two species have a preferred optimal thermal range. Given the prevailing global warming trends as projected by the IPCC the results suggest that thermal extremes will affect the performance of the two species differently as indicated by the metabolic rates and the difference in thermal tolerance between the two species. Their community structure might change significantly as temperatures increases resulting to a reduced dissolved oxygen content in warm water. *P. guttatum* (Sesarmidae) will be more vulnerable to increase in temperature. This further suggest that the populations of *U. urvillei* are likely to persist at higher temperatures and may be more tolerant to climate change rise in temperature than *P.guttatum*.

This study showed that *U. urvillei* and *P. guttatum* were not evenly distributed in the three mangrove zones and very low densities of *U. urvillei* were recorded in

the *C. tagal* and *A. marina* zones while almost similar densities of *P. guttatum* were recorded in *C. tagal* as in *R. mucronata*. Thus the null hypothesis that the density of the two species is uniform within the three mangrove zones was rejected and the alternative hypothesis accepted.

Temperature, fine sand and organic matter strongly influenced the density and distribution of these crabs. Thus the null hypothesis that the distributions of the two species are not affected by environmental factors was rejected and the alternative hypothesis that the distributions of the two species are affected by environmental factors was accepted. The landward shores of *Avicennia marina* are rarely inundated except only during spring high tides and have higher temperatures and salinity and low organic matter content and could explain the observed low abundance patterns of these two species in this zone.

Temperature showed significant influence as supported by laboratory experiments. Information on thermal tolerance levels is important for the conservation of crabs in terms of ensuring the right community structure of mangrove trees. Monitoring of these animals will increase the knowledge and understanding on the structure, dynamics and resilience of mangrove ecosystems particularly in climate change scenarios.

5.3.2 Recommendations

- More studies on thermal tolerance of females of the two crab species should be done for comparison with male data. Additional data will be required for other crab species for purposes of predicting climate change effects.
- There is also need to study the effect of increasing salinity and low PH on mangrove crabs as they could be acting in a matrix causing more stresses to these animals to which little is known about them in particular to changing environmental conditions to mangrove ecosystems.
- More studies focussing on density and distribution of these crabs and others in other mangrove areas along the coast need to be done in future to augment these findings particularly in climate change scenario.
- There is need to create buffer zones in Marine Protected Areas (MPAs) containing mangroves as planned adaptation options to climate change so that incase of sea-level rise the mangroves and its fauna which assist in mangrove ecosystem functioning can migrate to have optimal habitat conditions which will assist in mitigating effects of climate change hence creating a more resilient ecosystem. This could be fast tracked through development of a national mangrove management plan in Kenya which is lacking which could address issues of human encouragement from the landward boundary which could make landward migration of mangroves impossible. Mangrove protection and conservation must consider impacts

of climate change for these efforts to be realized in the long-run.

- The government and other funding agencies should allocate more funds to climate change research to build local capacity in climate change science in mangrove ecosystems and other interconnected marine systems.

References

- Addo-Bediako, A.; Chown, S. L and Gaston, K. J. (2000). Thermal Tolerance, Climatic Variability And Latitude. Proceedings of Royal Society of London, Series B. *Biological Science* **267**:739–745.
- Alongi, D. M. and De Carvalho, N. (2008). The Effect Of Small-Scale Logging On Stand Characteristics And Soil Biogeochemistry In Mangrove Forests Of Timor Leste. *Forest Ecology And Management* **255**: 1359-1366.
- Angilletta, M. J. (2009). *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Ashton, E. C.; Hogarth, P. J. and Macintosh, D. J. (2003). A Comparison Of Brachyuran Crab Community Structure At Four Mangrove Locations Under Different Management Systems Along The Melaka Straits-Andaman Sea Coast Of Malaysia And Thailand. *Estuaries* **26**, 1461–1471.
- Ballerini, T.; Macia, A. and Cannicci, S. (2000). Zonation Of Mangrove Crabs At Inhaca Island (Mozambique): A New Hypothesis. In: *Abstract Volume of the Meeting on Mangrove Macrobenthos*, 7-11 September, Mombasa, Kenya: 9-10.
- Bennett, A. F. (1988): Structural And Functional Determinates Of Metabolic Rate. *American zoologist* **28**: 699-708.
- Bosire, J. O.; Dadouah-Quebas, F.; Kairo, J. G.; Cannicci, S. and Koedam, N. (2003). Spartial Variation In Macrobenthic Fauna Recolonization In A Tropical Mangrove Bay. *Biodiversity and conservation* **13**:1059-1074.
- Bosire, J. O.; Dahdouh-Guebas, F.; Kairo, J.G.; Cannicci, S. and Koedam, N. (2004). Spatial Variations In Macrobenthic Fauna Recolonisation In A Tropical Mangrove Bay. *Biodiversity and Conservation*. **13**, 1059–1074.
- Bosire, J. O.; Dahdouh-Guebas, F.; Kairo, J. G.; Kazungu, J. and Koedam, N. (2005b). Propagule Predation Regulates Natural Regeneration In A High-Density Reforested Mangrove Plantation. *Marine Ecological Progress Series* **299**:157–166.
- Bosire, J. O.; Dahdouh-Guebas, F.; Kairo, J. G.; Wartel, S.; Kazungu, J. and Koedam, N. (2006). Success Rates And Recruited Tree Species And Their Contribution To The Structural Development Of Reforested Mangrove Stands. *Marine Ecology Progress Series* **325**: 85-91.

Brown, F. A.; Bennett M. F. and Webb, H. M. (1954). Persistent Daily And Tidal Rhythms Of O₂-Consumption In Fiddler Crabs. *Journal of Cellular Comparative Physiology* **44**:477-506.

Cannicci, S.; Dahdouh-Guebas, F. and Montemagno, L. (1997). *Field Keys for Kenyan Mangrove Crabs*. Museo Zoologico "La Specola", Dipartimento di Biologia Animale e Genetica dell'Università Degli Studi di Firenze, Via Romana 17, I-50125 Firenze, Italia.

Cannicci, S.; Skov, M. W. and Vannini, M. (2000). The Influence Of Abiotic And Biotic Factors On The Distribution Of Mangrove Crabs At Mida Creek (Kenya): A Multivariate Approach. In: *Abstract Volume of the Meeting on Mangrove Macrobenthos*, 7-11 September, Mombasa, Kenya: 20-21.

Cannicci, S.; Damien B.; Fratini, S.; Thomas, J.; Joachim, O. and Dahdouh-Guebas, F. (2008). Faunal Impact On Vegetation Structure And Ecosystem Function In Mangrove Forests: A Review. *Aquatic Botany* **89** :186–200.

Cannicci, S.; Bartolini, F.; Dahdouh-Guebas, F.; Fratini, S.; Litulo, C.; Macia, A.; Mrabu, E. J.; Penha-Lopes, G. and Paula, J. (2009). Effects Of Urban Wastewater On Crab And Mollusc Assemblages In Equatorial And Subtropical Mangroves Of East Africa, *Estuarine, Coastal and Shelf Sciences* **84**: 305-317.

Cannicci, S.; Simoni, R. and Giomi, F. (2011). Role Of The Embryo In Crab Terrestrialisation: An Ontogenetic Approach. *Marine ecology progress series* Vol. **430**: 121–131.

Chapman, M. G. and Tolhurst, T. J. (2004). The Relationship Between Invertebrate Assemblages And Bio-Dependant Properties Of Sediment In Urbanized Temperate Mangrove Forests. *Journal of Experimental Marine Biology and Ecology* **304**, 51–73.

Christensen, J. H.; Hewitson, B.; Busuioc, A.; Chen, A.; Gao, X.; Held, I.; Jones, R.; Kolli, R. K.; Kwon, W.-T.; Laprise, R.; Magaña Rueda, V.; Mearns, L.; Mene´ndez, C.G.; Raˆısaˆnen, J.; Rinke, A.; Sarr, A. and Whetton, P. (2007), "Regional Climate Projections", in Solomon, S.; Qin, D.; Manning, M.; Chen, Z.; Marquis, M.; Averyt, K. B.; Tignor, M. and Miller, H.L. (Eds), *Climate Change 2007: The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, pp. 847-940

Costanza, R.; Perez-Maqueo, O.; Martinez, M. L.; Sutton, P.; Anderson, S. J. and Mulder, K. (2008). The Value Of Coastal Wetlands For Hurricane Protection. *Ambio* **37**:241–248

Crane, J. (1975). *Fiddler Crabs of the World: Ocypodidae: Genus Uca*. Princeton, NJ: Princeton University Press.

Dahdouh-Guebas F, Giuggioli M, Oluoch A, Vannini M, Cannicci S. (1999). Feeding Habits Of Non-Ocypodid Crabs From Two Mangrove Forests In Kenya. *Bulletin of Marine Scienc* **64**: 291–297.

Dahdouh-Guebas, F. and N. Koedam. (2001). Are The Northernmost Mangroves Of West Africa Viable? - A Case Study In Banc d'Arguin National Park, Mauritania. Pages 241–253 in D. Harper, R. Boar, M. Everard, and P. Hickley, eds. *Hydrobiologia 458: Science and the sustainable management of shallow tropical waters*. Kluwer Academic Publishers, Dordrecht.

Dahdouh-Guebas, F. (2001). Mangrove Vegetation Structure, Dynamics And Regeneration. PhD Thesis Vrije Universiteit Brussel, Belgium. 317 pp.

Dahdouh-Guebas, F.; Verneirt, M.; Cannicci, S.; Kairo, J. G.; Tack, J. F. and Koedam, N. (2002). An Exploratory Study On Grapsid Crab Zonation In Kenyan Mangroves. *Wetlands Ecology and Management* **10**: 179–187.

Dahdouh-Guebas, F.; VanPottelbergh, I.; Kairo, J. G.; Cannicci, S. and Koedam, N. (2004). Human-Impacted Mangroves In Gazi (Kenya): Predicting Future Vegetation Based On Retrospective Remote Sensing, Social Surveys, And Distribution Of Trees. *Marine Ecological Progress Series* **272**, 77–92.

Dahdouh-Guebas, F.; Hettiarachchi, S.; Lo Seen, D.; Batelaan, O.; Sooriyarachchi, S.; Jayatissa, L. P. and Koedam, N. (2005). Transitions In Ancient Inland Freshwater Resource Management In Sri Lanka Affect Biota And Human Populations In And Around Coastal Lagoons. *Current Biology* **15**: 579–586.

Dahdouh-Guebas, F.; Kairo, J. G.; De Bondt, R. and Koedam, N. (2007). Pneumatophore Height And Density In Relation To Microtopography In The Grey Mangrove *Avicennia marina*. - *Belgium Journal of Botany* **140**: 213-221.

Deutsch, C. A.; Tewksbury, J. J.; Huey, R. B.; Sheldon, K. S.; Ghalambor, C. K.; Haak, D. C. and Martin, P. R. (2008). Impacts Of Climate Warming On Terrestrial Ectotherms Across Latitude. *Proceedings of Natural Academy Sciences USA* **105**, 6668-6672.

Dijk Van, P. L. M.; Tesch, C., Hardewig, I. And Portner H. O. (1999). Physiological Disturbances At Critically High Temperatures: A Comparison Between Stenothermal Antarctic And Eurythermal Temperate Eelpouts (Zoarcidae). *The Journal of Experimental Biology* **202**, 3611–3621.

- Dodd, R. S. and Ong, J. E. (2008). Future Of Mangrove Ecosystems To 2025. In: Polunin NVC, ed. *Aquatic ecosystems: Trends and global prospects*. Cambridge: Foundation for Environmental Conservation, Cambridge University Press. pp 172–187.
- Edney, E. B. (1962). Some Aspects Of The Temperature Relations Of Fiddler Crabs (*Uca* spp.): In: S. W. Tromp (ed.), *Biometeorology*: 79-85 (Pergamon Press, Oxford, New York).
- Emmerson, W. D. (1990). The Effect Of Temperature And Season On The Aerial Oxygen Consumption of *Uca urvillei* (H. Milne Edwards) (Decapoda: Ocypodidae). *Journal of Thermal Biology* **15**:41–46.
- Eshky, A. A.; Al-Wassia, A. H., Atkinson, R. J. A. and Taylor A. C. (1990). Branchial Ventilation Of The Ghost Crab, *Ocypode saratan* (Forskål). *Marine Behavioural Physiology*, **16** (4): 237-248.
- Eshky, A. A.; Taylor, A. C. and Atkinson, R. J. A. (1996). The Effects Of Temperature On Aspects Of Respiratory Physiology Of The Semi-Terrestrial Crabs, *Uca inversa* (Hoffmann) and *Metopograpsus messor* (Forskål) from the Red Sea. *Comparative Biochemichal Physiology* **114A**:297–304.
- Eshky, A. A. (1999). Physiological Adaptation of the Amphibious Rock Crab *Grapsus tenuicrustatus* from the Red Sea. *Marine Science* **vol. 10**, pp. 109-124.
- Farrell, A. P.; Hinch, S. G.; Cooke, S. J.; Patterson, D. A.; Crossin, G. T.; Lapointe, M. and Mathes, M. T. (2008). Pacific Salmon In Hot Water: Applying Aerobic Scope Models And Biotelemetry To Predict The Success Of Spawning Migrations. *Physiological Biochemistry Zoologica* **81**, 697-708.
- Flores, A. A. V.; Saraiva, J. and Paula, J. (2002). Sexual Maturity, Reproductive Cycles, And Juvenile Recruitment Of *Perisesarma guttatum* (Brachyura, Sesarmidae) At Ponta Rasa Mangrove Swamp, Inhaca Island, Mozambique. *Journal of Crustacean Biology* **22(1)**: 143-156.
- Fratini, S. and Vannini M. (2002). Genetic Differentiation In The Mud Crab *Scylla Serrata* (Decapoda: Portunidae) within the Indian Ocean. *Journal of Experimental Marine Biology and Ecology* **272**:103–116.
- Frederich, M. and Pörtner, H. O. (2000). Oxygen Limitation Of Thermal Tolerance Defined By Cardiac And Ventilatory Performance In The Spider Crab *Maja squinado*. *American Journal of Physiology* **279**, R1531-R1538.
- Frith, D. W. and Brunenmeister, S. (1980). Ecological And Population Studies Of

Fiddler Crabs (Ocypodidae, Genus *Uca*) On A Mangrove Shore At Phuket Island, Western Peninsular Thailand. *Crustaceana* **39**: 157-183.

Gaston, K. J. (2003). *The Structure and Dynamics of Geographic Ranges*. New York: Oxford University Press.

Gillikin, D. P. (2000). Factors Controlling The Distribution Of Kenyan Brachyuran Mangrove Crabs: Salinity Tolerance And Ecophysiology Of Two Kenyan *Neosarmatium* Species. Unpublished MSc. Thesis, Vrije Universiteit Brussel, Belgium.

Gillikin, D. P.; De Grave, S. and Tack, J. F. (2001). The Occurrence Of The Semi-Terrestrial Shrimp *Merguia oligodon* (De Man, 1888) in *Neosarmatium smithi* (*H. Milne Edwards, 1853*) Burrows in Kenyan Mangroves. *Crustaceana* **74** (5), 505–508.

Gillikin, D. P. and Schubart, S. D. (2004). Ecology And Systematics Of Mangrove Crabs Of The Genus *Perisesarma* (Crustacea: Brachyura: Sesarmidae) From East Africa. *Zoological Journal of the Linnean Society*, 2004, **141**, 435–445.

Hawkins, A. J. S; Jones, M. B. and Marsden, I. D. (1982). Aerial And Aquatic Respiration In Two Mud Crabs, *Helice crassa* Dana (Grapsidae) and *Macrophthalmus hirtipes* (Jacquinot) (Ocypodidae), in relation to habitat. *Comparative Biochemichal Physiology* **73A**:341–347.

Hartnoll, R. G.; Cannicci, S.; Emmerson, W.D.; Fratini, S.; Macia, A.; Mgaya, Y.; Porri, F.; Ruwa, R. K.,; Shunula, J. P.; Skov, M. W. and Vannini, M. (2002). Geographic Trends In Mangrove Crab Abundance In East Africa. *Wetlands Ecological Management* **10**, 203–213.

Helmuth, B.; Carrington, E. and Kingsolver, J. G. (2005). Biophysics, Physiological Ecology, And Climate Change: Does Mechanism Matter? *Annual Review of Physiology* **67**, 177-201.

Hervant, F.; Mathieu, J. and Messana, G. (1998). Oxygen Consumption and Ventilation in Declining Oxygen Tension and Posthypoxic Recovery in Epigeal and Hypogean Crustaceans. *Journal of crustacean biology* **18**(4): 717-727.

Hochachka, P. W. and Somero, G. N. (2002). *Biochemical Adaptation: Mechanism And Process In Physiological Evolution*. Oxford University Press ,Oxford.

Hofmann, G. E. and G. N. Somero. (1996b). Protein Ubiquitination And Stress Protein Synthesis In *Mytilus trossulus* Occurs During Recovery From Tidal Emersion. *Molecular Marine Biological Biotechnology* **5**: 175-184.

Hogarth, P. J. (1999). *The Biology Of Mangroves*- Oxford University Press Inc.

Houlihan, D. F. and Innes, A. J. (1984). The Cost Of Walking In Crabs: Aerial And Aquatic Oxygen Consumption During Activity Of Two Species Of Intertidal Crab. *Comparative Biochemical Physiology*, **77A**:325–334.

Imevbore, A. M. A. (2011). Climate Change And Ecosystems Modification. In 2nd Joint International Conference organized by the University of Ilorin, Nigeria and University of Cape Coast, Ghana, at the University Auditorium, Ilorin, 1st – 5th May, 2011.

IPCC. (2007). Fourth Assessment Report. Intergovernmental Panel on Climate Change Secretariat. Geneva, Switzerland. <http://www.ipcc.ch/>.

Jagtap, G. T. (2007). Response And Adaptability Of Mangrove Habitats From Indian Subcontinent To Changing Climate. *Ambio*: 36(4); 2007; 328-334.

Jimenez, A. G. and Bennett, W. A. (2005). Respiratory Physiology Of Three Indo-Pacific Fiddler crabs: Metabolic Responses To Intertidal Zonation Patterns. *Crustaceana* **78 (8)**: 965-974.

Kairo, J. G. (2001). Ecology And Restoration Of Mangrove System In Kenya. Dissertation, Brussels

Kairo, J. G.; Dahdouh-Guebas, F.; Bosire, J.O. and Koedam, N. (2001). Restoration And Management Of Mangrove Systems - a lesson for and from the East African region. *South African Journal of Botany* **67**: 383-389.

Kairo, J. G.; Joseph, K .S. L.; Dahdouh-Guebas, F.; Bosire, J. and Karachi, M. (2008). Structural Development And Productivity Of Replanted Mangrove Plantations In Kenya. *Forest Ecology Management* **255**: 2670–2677.

Kathiresan, K. and Bingham, B. L. (2001). Biology Of Mangroves And Mangroves Ecosystems. *Advances in Marine Biology* **40** :383-389.

Katsanevakis, S.; Xanthopoulos, J.; Protopapas, G. and Verriopoulos, N. (2007). Oxygen Consumption Of The Semi-Terrestrial Crab, *Pachygrapsus marmoratus* In Relation To Body Mass And Temperature: An Information Theory Approach. *Marine Biology* **151**:343–352.

Kennedy, V. S.; Twilley, R. R.; Kleypas, J. A.; Cowan, J. H. and Hare, S. R. (2002). Coastal and Marine Ecosystems: Potential Effects on U.S. Resources and Global Climate Change. Pew Center on Global Climate Change.

Kirby R. R.; Beaugrand G. and Lindley J. A. (2008). Climate-Induced Effects On The Merozooplankton And The Benthic–Pelagic Ecology Of The North Sea. *Limnological Oceanography* **53**, 1805–1815.

Kitheka, J. U. (1997). Coastal Tidally-Driven Circulation And The Role Of Water Exchange In The Linkage Between Tropical Coastal Ecosystems. -*Estuarine, Coastal and Shelf Science* **45**: 177-187.

Kleypas, J. A.; Feely, R. A.; Fabry, V. J.; Langdon, C.; Sabine, C. L. and Robbins, L. L. (2006). Impacts of Ocean Acidification on Coral Reefs and Other Marine Calcifiers: A Guide for Future Research, Report Of A Workshop Held 18–20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the U.S. Geological Survey, 88 pp.

Kokwaro, J. O. (1985). The Distribution And Economic Importance Of The Mangrove Forests In Kenya. *Journal of East African Natural History Society*, **75**: 1–12.

Kristensen, K. (2008). Mangrove Crabs as Ecosystem Engineers; With Emphasis on sediment processes. *Journal of Sea Research* **59**, 30–43.

Kristensen, E.; Bouillon, S.; Dittmar, T. and Marchand, C. (2008). Organic Carbon Dynamics In Mangrove Ecosystems: A Review. *Aquatic Botany* **89**: 201–219.

Lago, R. P. (1993). Larval Development Of *Sesarma guttatum* (A. Milne Edwards (Decapoda: Brachyura: Grapsidae) Reared In The Laboratory, With Comments On Larval Generic And Familial Characters. *Journal of Crustacean Biology* **13(4)**: 645-762.

Lee, S.Y. (2008). Mangrove Macrobenthos: Assemblages, Services, And Linkages. *Journal of Sea Research* **59**: 16–29

Macia, A.; Quincardete, I. and Paula, J. (2001). A Comparison Of Alternative Methods For Estimating Population Density Of The Fiddler Crab *Uca annulipes* At Saco Mangrove, Inhaca Island (Mozambique). *Hydrobiologia* **449**:213–219.

Macintosh, D. J. and Ashton, E. C. (2002). A Review of Mangrove Biodiversity Conservation and Management. Centre for Tropical Ecosystems Research, University of Aarhus, Denmark (pdf file).

Macintosh, D. J. and Ashton, E. C. (2004). Principles For A Code Of Conduct For The Management And Sustainable Use Of Mangrove Ecosystems. Washington (DC): The World Bank.

McCraith, B. J.; Gardner, L. R.; Wethey, D. S. and Moore, W. S. (2003). The Effect Of Fiddler Crab Burrowing On Sediment Mixing And Radionuclide Profiles Along A Topographic Gradient In A Southeastern Salt Marsh. *Journal of Marine Resources* **61**, 359–390.

McMahon, R. F. and Russell-Hunter, D. W. (1977). Temperature Relations Of Aerial And Aquatic Respiration In Six Littoral Snails In Relation To Their Vertical. *Biological Bulletin*, **152**: 182-198.

Metzger, R.; Sartoris, F. J.; Langenbuch, M. and Pörtner, H. O. (2007). Influence Of Elevated CO₂ Concentrations On Thermal Tolerance Of The Edible Crab *Cancer Pagurus*. *Journal of Thermal Biology*, **32**, 144-151.

Middelburg, J. J., Nieuwenhuize, J. and Slim, F. J. Ohowa, B. (1996). Sediment Biogeochemistry In An East African Mangrove Forest (Gazi-Bay, Kenya). *Biogeochemistry*, **34**:133-155.

Modlin, F. R. and Froelich, A. J. (1997). Influence Of Temperature, Salinity, And Weight On The Oxygen Consumption Of A Laboratory Population Of *Americamysis Bahía* (MYSIDACEA). *Journal of Crustacean Biology*, **17(1)**: 21-26.

Nagelkerken, I.; Blaber, S. J. M.; Bouillon, S.; Green, P.; Haywood, M.; Kirton, L.G.; Meynecke, J.O.; Pawlik, J.; Penrose, H.M.; Sese Kumar, A. and Somerfield, P.J. (2008). The Habitat Function Of Mangroves For Terrestrial And Marine Fauna. *Aquatic Botany*. **89**, 155–185.

Newell, R. C. (1969). Effect of fluctuations in temperature on the metabolism of intertidal invertebrates. *American Zoology* **9**: 293-307.

Parmesan C. (2006). Ecological And Evolutionary Responses To Recent Climate Change. *Annual Review Of Ecology And Evolutionary Systematics* **37**: 637-669.

Patrick, W. H and Delaune, R. D. (1977). Chemical And Biological Redox Systems Affecting Nutrient Availability In The Coastal Wetlands. *Geoscience and Man*, **18**: 131-137.

Perry, A. L.; Low, P. J.; Ellis, J. R. and Reynolds, J. D. (2008). Climate Change and Distribution Shifts in Marine Fishes. *Science* **308**, 1912-1915.

Polidoro, B. A.; Carpenter, K. E.; Collins, L. N.; Duke, C.; Ellison, A. M.; Ellison, J. C.; Farnworth, E. J.; Fernando, E. S.; Kathiresan, K.; Koedam, N. E.; Livingstone, S. R.; Miyagi, T.; Moore, G. E.; Nam, V. N.; Ong, J. E.; Primavera, J. H.; Salmo, S. G.; Sanciangco, J. C.; Sukardjo, S.; Wang, Y. and Yong, Y. W., H.

(2010). *The loss of species: mangrove extinction risk and geographic areas of global concern*. Plos One 5: 310095.

Portner, H. O.; Dijk, P. L. M.; Hardewig, I. and Sommer, A. (2000). Levels Of Metabolic Cold Adaptation: Tradeoffs In Eurythermal And Stenothermal Ectotherms. In: *Davison W, Howard Williams C (eds) Antarctic ecosystems: Models for wider ecological understanding*. Caxton Press, Christchurch, New Zealand, pp 109–122.

Portner, H. O. (2001). Climate Change And Temperature-Dependent Biogeography: Oxygen Limitation Of Thermal Tolerance In Animals. *Naturwissenschaften* **88**, 137-146.

Portner, H. O.; Berdal, B.; Blust, R.; Brix, O.; Colosimo, A.; De Wachter, B.; Giuliani, A.; Johansen, T.; Fischer, T.; Knust, R. *et al.* (2001). Climate Induced Temperature Effects On Growth Performance, Fecundity And Recruitment In Marine Fish: Developing A Hypothesis For Cause And Effect Relationships In Atlantic Cod (*Gadus morhua*) And Common Eelpout (*Zoarces viviparus*). *Continental Shelf Research*. **21**, 1975-1997.

Portner, H. O. (2002a). Climate Variations And The Physiological Basis Of Temperature Dependent Biogeography: Systemic To Molecular Hierarchy Of Thermal Tolerance In Animals. *Comparative Biochemistry Physiology* **132A**, 739-761.

Portner, H. O. (2002b). Environmental And Functional Limits To Muscular Exercise And Body Size In Marine Invertebrate Athletes. *Comparative Biochemistry Physiology* **133A**, 303-321.

Portner, H. O. and Knust, R. (2007). Climate Change Affects Marine Fishes Through The Oxygen Limitation Of Thermal Tolerance. *Science* **315**, 95-97.

Portner, H. O. (2010). Oxygen And Capacity-Limitation Of Thermal Tolerance: A Matrix For Integrating climate-related stressor effects in marine ecosystems. *The Journal of Experimental Biology* **213**, 881-893.

Roberts, J. L. (1957b). Thermal Acclimation Of Metabolism In The Crab, *Pachygrapsus crassipes* Randall. II. *Mechanisms and the influence of season and latitude*. *Physiological Zoology* **30**:242–255.

Richmond, M. D. (ed). (2010). *A Field Guide To The Seashores Of Eastern Africa And The Western Indian Ocean Islands*. Sida/WIOMSA.464pp. ISBN 9987-8977-9-7.

Sanford, E.; Holzman, S. B.; Haney, R. A.; Rand, D. M. and Bertness, M. D. (2006). Larval Tolerance, Gene Flow, And The Northern Geographic Range Limit Of Fiddler Crabs. *Ecology*, **87**: 2882-2894.

Scholander, P. F.; Flagg, W.; Walters, V. and Irving, L. (1953). Climatic Adaptation In Arctic And Tropical Poikilotherms. *Physiological Zoology* **26**:67-92.

Seiple, W. H. (1979). Distribution, Habitat Preferences, And Breeding Periods In The Crustaceans *Sesarma cinereum* and *S. reticulatum* (Brachyura: Decapoda: Grapsidae). *Marine Biology* **52**:77-86.

Shelford, V. E. (1931). Some Concepts Of Bioecology. *Ecology* **123**: 455–467.

Skov, M. W. and Hartnoll, R. G. (2001). Comparative Suitability Of Binocular Observation, Burrow Counting And Excavation For The Quantification Of The Mangrove Fiddler Crab, *Uca annulipes* (H. Milne Edwards). *Hydrobiologia* **449**:201–212.

Skov, M. W. and Hartnoll, R. G. (2002). Paradoxical Selective Feeding On A Low-Nutrient Diet: Why Do Mangrove Crabs Eat Leaves? *Oecologia* **131**:1–7.

Skov, M. W.; Vannini, A. M.; Shunula, J. P.; Hartnoll, R. G. and Cannicci, S. (2002). Quantifying The Density Of Mangrove Crabs: Ocypodidae And Grapsidae. *Marine Biology* **141**: 725–732.

Solomon, S.; Qin, D. and Manning, M. M.; Chen, Z.; Marquis, M.; Averyt, K. B.; Tignor, M. and Miller, H. L. (Eds). (2007) Climate Change 2007: The Physical Science Basis. Contributions of Working Group I to the 4th Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, 996 pp.

Sommer, A., Klein, B. and Portner, H. O. (1997). Temperature Induced Anaerobiosis In Two Populations Of The Polychaete Worm *Arenicola marina*. *Journal of Comparative Physiology* **167B**, 25-35.

Spalding, M.; Kainuma and Collins, L. (2010). *World Atlas of Mangroves*. Earthsca. Publications.

Stillman, J. H. and G. N. Somero. (2000). A Comparative Analysis Of The Upper Thermal Tolerance Limits Of Eastern Pacific Porcelain Crabs, genus *Petrolisthes*: Influences Of Latitude, Vertical Zonation, Acclimation, And Phylogeny. *Physiological Biochemical Zoologica*, **73**:200–208.

Storch, D.; Santelices, P.; Barria, J.; Cabeza, K.; Pörtner, H. O. and Fernández, M.

(2009). Temperature Tolerance Of Zoea I From Two Different Populations Of The Kelp Crab *Taliepus dentatus*. *Journal of Experimental Biology* **212**, 1371-1376.

Tashian, R. E. (1956). Geographic Variation In The Respiratory Metabolism And Temperature Coefficient In Tropical And Temperate Forms Of The Fiddler Crab, *Uca pugnax*. *Zoologica* **41**: 39-47.

Taylor, H. H. and Leelapiyanart, N. (2001). Oxygen Uptake By Embryos And Oviparous Females Of Two Intertidal Crabs, *Heterozius rotundifrons* (Bellidae) and *Cyclograpsus lavauxi* (Grapsidae): Scaling And The Metabolic Costs Of Reproduction. *Journal of Experimental Biology* **204**:1083–1097.

Teal, J. M. (1959). Respiration Of Crabs In Georgia Salt Marshes And Its Relation To Their Ecology. *Physiological Zoology* **32** (1): 1-14.

Tewksbury, J. J.; Huey, R. B. and Deutsch, C. A. (2008). Putting The Heat On Tropical Animals. *Science*, **320**: 1296–1297.

Thongtham, N. and Kristensen, E. (2003). Physical And Chemical Characteristics Of Mangrove Crab (*Neopisesarma Versicolor*) Burrows In The Bangrong Mangrove Forest, Phuket, Thailand; With Emphasis On Behavioural Response To Changing Environmental Conditions. *Vie Milieu* **53**: 141–151.

UNEP. (1994). Assessment and Monitoring Of Climatic Change Impacts On Mangrove Ecosystems. UNEP Regional seas NO. 154.

UNEP. (2006). Marine And Coastal Ecosystems And Human Well-Being: A Synthesis Report Based On The Findings Of The Millennium Ecosystem Assessment. UNEP.

UNFCCC. (2007). Climate Change: Impacts, Vulnerabilities And Adaptation In Developing Countries.

Valiela I.; Bowen, J. L. and York J. K. (2001). Mangrove Forests: One Of The World's Threatened Major Tropical Environments. *Bioscience* **51**: 807-815.

Vannini, M. and Valmori, P. (1981). Researchers On The Coast Of Somalia. The Shore And The Dune Of Sar Uanle. 30. Grapsidae (Decapoda Brachyura). *Monitore Zoologico Italiano* **6**: 57–101.

Veeranan, K. M. (1974). Respiratory Metabolism Of Crabs From Marine And Estuarine Habitats: An Interspecific Comparison. *Marine Biology* **26**: 35-43.

Vernberg, F. J. (1959b). Studies On The Physiological Variation Between Tropical

And Temperate fiddler Crabs Of The Genus *Uca*. III. *The influence of temperature acclimation on oxygen consumption of whole organisms. Biological Bulletin* **117**, 582-593.

Walther, K.; Sartoris, F. J.; Bock, C. and Portner, H. O. (2009). Impact Of Anthropogenic Ocean Acidification On Thermal Tolerance Of The Spider Crab *Hyas araneus*. *Biogeochemical sciences* **6**, 2207-2215.

Warner, G. F. (1977). *The Biology of Crabs*. Van Nostrand Reinhold Company, New York, 202 p.

Wartel, S.; Barusseau, J. and Cornand, L. (1995). Improvement of Grain Size Analyzes Using the Automated Sedigraph 5100. *Studedocumenten van het K. B. I. N.*, 28 pp.

Weinstein, R. B. (1998). Effects Of Temperature And Water Loss On Terrestrial Locomotor Performance In Land Crabs: Integrating Laboratory And Field Studies. *American Zoologist*, **38**, 518–527.

[Http://www.physiologyweb.com/calculators/q10calculator.html](http://www.physiologyweb.com/calculators/q10calculator.html)

Zielinski, S. and Portner, H. O. (1996). Energy Metabolism and ATP Free-Energy Change Of The Intertidal Worm *Sipunculus nudus* below a critical temperature. *Journal of Comparative Physiology* **166B**, 492-500.